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Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation

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ABSTRACT

We hypothesized that change in the annual population size of guano-producing seabirds (cormorant, *Phalacrocorax bougainvillii*; booby, *Sula variegata*; pelican, *Pelecanus thagus*) is a response to changes in primary and secondary production of the Peruvian upwelling system. We tested this hypothesis by modeling nitrate input through upwelling to the upper layers of the ocean off Peru between 6° and 14°S using data on wind stress and sea surface temperature. The model predicted the amount of carbon fixed by primary production each year from 1925 to 2000, which was then apportioned to the Peruvian anchovy (*Engraulis ringens*) biomass and ultimately to the seabird population and the anchovy fishery, the largest single-species fishery on Earth. The model predicted a marked increase in primary production as a consequence of increasing wind stress. It overestimated the anchovy biomass after the collapse of the fishery in 1972, but closely predicted the growth of seabird populations from 1925 to the mid-1960s, and their decline thereafter, explaining about 94% of the variation in seabird numbers from 1925 to 2000. The model indicates the seabirds consumed 14.4% of the available anchovies and, thus, that seabirds consumed 2.3% of the new production, before the development of the anchovy fishery, and only 2.2% of the available anchovies and 0.3% of the new production after the development of the fishery. The model results clarify the roles that environmental and anthropogenic factors may have had in regulating the guano-producing seabird populations. It indicates that the growth of

seabird populations from 1925 to 1955 was likely a response to increased productivity of the Peruvian upwelling system and that the subsequent drastic decline in seabird abundance was likely due to competition for food with the fishery, which caught ~85% of the anchovies, which otherwise would have been available for the seabirds. This model also shows that an increase in oceanic primary production promotes reproductive success and population growth in higher trophic level organisms.

Key words: anchovy, carbon flux, fishery, Peru, seabirds, upwelling

INTRODUCTION

Eastern boundary current systems of the world's oceans are among the most productive marine environments, supporting rich and diverse communities (Cushing, 1971; Hill, 1998; Carr, 2002). The Peruvian current and adjacent waters off the west coast of South America contain such an ecosystem (Ryther *et al.*, 1971). Upwelling of inorganic nutrients (e.g. N, P, and Si) to the surface water in this tropical setting results in exceptional, yet highly variable, levels of primary production which, in turn, may be related to the abundance of fish and top marine predators (Ryther, 1969; Cushing, 1971; Carr, 2002). Seabirds have proved to be sensitive to changes in prey abundance in many systems worldwide (Cairns, 1987; Montevecchi, 1993; Furness, 1997).

The guanay cormorant (*Phalacrocorax bougainvillii*), Peruvian booby (*Sula variegata*), and Peruvian pelican (*Pelecanus thagus*) are the most abundant seabirds in the Peruvian current region (Murphy, 1936; Jahncke, 1998). They inhabit the west coast of South America, within the cool upwelling zone from Isla Lobos de Tierra (06°8'S) off northern Peru to Isla Mocha (38°30'S) off southern Chile (Murphy, 1936). These birds were of great economic importance for the large guano deposits they produced (Tovar *et al.*, 1987). More than 23 millions tons of guano were estimated to exist in 1847 on an unstated number of islands (Murphy, 1936). Ten million tons of guano was harvested during the following 20 yr (Coker, 1920).

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Guano was extracted initially for gunpowder production and later for fertilizer (Muck and Pauly, 1987).

These seabirds feed primarily on Peruvian anchovies (*Engraulis ringens*), the most abundant pelagic fish of the Peruvian upwelling system (Jahncke and Goya, 1998 and references therein; Table 1). Peruvian anchovies are restricted to the cold waters from 4°30'S off Peru to 42°30'S off Chile (Pauly and Tsukayama, 1987). The largest concentrations of anchovy occur along the northern and central coast of Peru, downstream of the strongest upwelling area (Pauly and Tsukayama, 1987). Anchovy consumption by seabirds is high in these areas and low to the south (Jahncke and Goya, 1997, 1998). The proportion of anchovy found in the diet of cormorants and boobies is strongly correlated with anchovy biomass (Jahncke and Goya, 1998).

Several factors have affected the population dynamics of the guano-producing seabirds of Peru during the last two centuries. Birds were decimated in the 1800s by the unregulated harvest of guano, which was loosened by use of dynamite (Tovar *et al.*, 1987), and young birds were captured to feed the workers, leaving few birds and little guano on the colonies by the early 1900s (Duffy, 1994). New management regulations allowed seabirds to recover from about 4 million birds in the 1910s to 8–10 million in the 1930s (Jordán and Fuentes, 1966; Duffy, 1994). The creation of 'artificial islands' (i.e. fenced headlands), which offered protection from predators, allowed seabirds to rebound to 16–20 million birds in the 1950s (Duffy,

1983a, 1994). There is no estimate of seabird abundance prior to guano exploitation.

An industrial fishery for the Peruvian anchovy was established during the 1950s and grew to be the largest single-species fishery on Earth, landing over 12 million metric tons (MT) in 1970 (Paulik, 1971; Duffy, 1994; Niquen *et al.*, 2000). Birds and fish coexisted until the 1965 El Niño that caused a major seabird population crash from which they have not recovered (Duffy, 1994). Heavy fishing pressure in the late 1960s and early 1970s, combined with the strong 1972 El Niño, led to the collapse of the Peruvian anchovy population (Brainard and McLain, 1987). Peruvian Pacific sardine (*Sardinops sagax*) landings rose after the anchovy crash, yet were always small compared with peak landings of anchovy (Schwartzlose *et al.*, 1999). The maximal annual landings of sardine in Peru (3.5 million MT, 1988) was less than one-third of that for anchovy. After 1983, anchovy stocks recovered (Brainard and McLain, 1987), reaching a population level comparable with that observed prior to the 1972 collapse (Gutiérrez, 2000). However, seabirds have not recovered to levels observed prior to the fishery.

We hypothesized that change in the summed populations of guano-producing seabirds off Peru is a response to changes in primary and secondary production in the Peruvian upwelling. The guano-producing seabirds of Peru are the species that depend most on Peruvian anchovies for food and are the most conspicuous competitors of the anchovy fishery (Muck and Pauly, 1987). Therefore, we predicted that seabird numbers should be positively related to anchovy pro-

Table 1. Relative importance of anchovy and sardine in the diets of guanay cormorants and Peruvian boobies.

Years	Guanay cormorant (%)		Peruvian booby (%)		References
	Anchovy	Sardine	Anchovy	Sardine	
1920–40s	~100	–	~100	–	Murphy (1925*, 1936†), Vogt (1942)‡
1950s	90–96	–	80	–	Jordán (1959, 1961, 1967)
1960s	5–70	0	70	0	Galarza (1968)§
1970s	5–100	0	–	–	Tovar and Galarza (1984)¶
1980s	88	<0.1	67–87	6–12	Tovar <i>et al.</i> (1988); Guillén (1993)**
1990s	49–81	<0.1	79–93	2–8	Goya (2000)††

*The anchovies are the principal food of the guano birds.

†The only food I noticed in the (booby) stomachs was the native anchovy.

‡These (cormorants) depend entirely on anchovies.

§Samples for both bird species collected during and after El Niño 1965/66.

¶Guanay cormorant samples collected during and after El Niño 1976/77.

**Peruvian booby samples collected before and during El Niño 1986/87.

††Samples for both birds collected at several locations, including areas outside (i.e. south) of the modeling area where anchovy consumption is consistently low. Does not include samples from El Niño 1997/98.

duction when competition for prey with the fishery was taken into account. Fish production is determined by primary production and the ecological efficiency with which this production is converted into zooplankton and fish biomass (Gulland, 1971). Therefore, we further predicted that anchovy biomass should be proportional to primary production when the appropriate transfer efficiencies were considered.

Primary production is highly variable in space and time (Steele, 1978), and long time series of primary production are not available for the Peruvian upwelling area (Chavez *et al.*, 1989). The high productivity of this area is the result of coastal upwelling, which is an oceanic response to the SE trade winds, which cause offshore Ekman transport (coastal advection), elevating the thermocline and bringing relatively cold, nutrient-rich water to the euphotic zone where nutrients can be used by phytoplankton (Barber *et al.*, 1985). The Peruvian upwelling is intense due to persistent alongshore winds and its proximity to the equator (Mann and Lazier, 1996).

We investigated the relative importance of wind-driven input of nutrients and the removal of Peruvian anchovies by the fishery to the population dynamics of guano-producing seabirds. We modeled nitrate upwelled to the upper layers of the ocean off Peru be-

tween 6° and 14°S (Fig. 1) using data for wind stress and sea surface temperature (SST). The model predicts, from 1925 to 2000, the amount of carbon fixed annually by primary production, and apportions this carbon to anchovy biomass and ultimately the seabirds. We consider two scenarios: before and after the development of the industrial fishery for anchovies, which limits prey availability for the birds. In this paper, we show how wind and fishing have worked together to determine the rise and fall of the populations of guano-producing seabirds of Peru.

MATERIALS AND METHODS

Wind stress and SST

We used data series on wind stress and SST from the Comprehensive Ocean-Atmosphere Data Set (COADS) (Woodruff *et al.*, 1998; <http://ferret.pmel.noaa.gov/nvods/servlets/dataset>), available as monthly means for 1854–1993 [COADS monthly time series (1854–1993)] and as individual observations for 1950–97 (COADS 2-degree Standard). We obtained data for the six 2-degree boxes shown in Fig. 1. On the coast of Peru, upwelling is continuous throughout the year (Wooster, 1970). We calculated annual mean values of meridional wind pseudo-stress and SST for years with at least eight months of data and estimated missing values for single years by interpolation from the annual mean series for each box. For overlapping years, we used the monthly means already calculated in the COADS monthly time series (1854–1993).

COADS meridional wind pseudo-stress ($\text{m}^2 \text{s}^{-2}$) is the product of wind speed (m s^{-1}) and the meridional component of wind velocity (m s^{-1}) (Tables 2 and 3). We transformed the meridional wind pseudo-stress into wind stress (N m^{-2} ; Table 3, eqn 1) by multiplying it by the density of air (1.22 kg m^{-3}) and the drag coefficient of the water (0.0013, dimensionless). This drag coefficient is standard in climatological studies of upwelling regions (e.g. Bakun, 1987).

We assumed that the scarcity of offshore, relative to coastal, temperature records caused early data to be relatively 'colder' than more recent data. We used the SST series from Chicama (7°S, 79°W) to assess if there was a trend in SST between 1925 and 2000. Chicama is a coastal town in the north of Peru (Fig. 1) for which monthly SST data have been recorded. This series, from 1925 to 1998, is publicly available at the Joint Institute for the Study of the Atmosphere and Ocean (University of Washington, Seattle, WA; http://tao.atmos.washington.edu/data_sets/chicama_sst/). We updated this series to 2000 using publicly available data from the

Figure 1. Map of the Peruvian coast showing the location of the six 2-degree boxes for which wind pseudo-stress and sea surface temperature data were obtained from the Comprehensive Ocean-Atmosphere Data Set (see text for details). Filled circles represent the location of colonies of guano-producing seabirds within this region (modified from Tovar *et al.*, 1987).

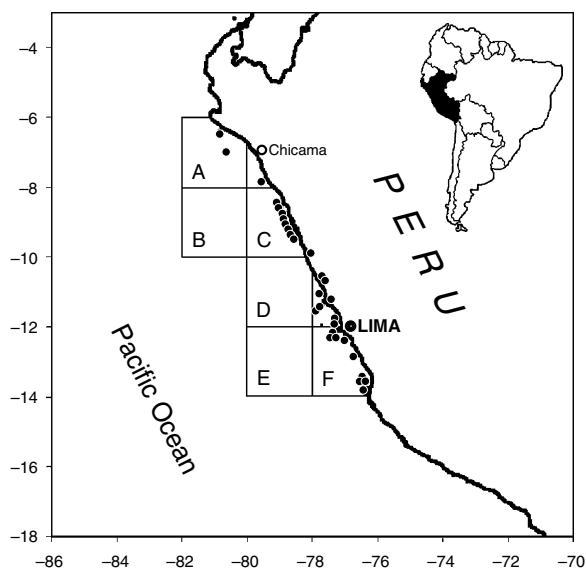


Table 2. Variables, parameters and constants used in the model.

Symbol	Variables, parameters and constants	Value	Units
A	Assimilation efficiency	0.650	
a_a	Alongshore wind stress linear function intercept	0.005	N m^{-2}
a_b	Bird linear function intercept	137 620	birds
B_a	Anchovy biomass		MT
b_a	Alongshore to meridional wind stress ratio	1.015	
b_b	Annual estimate of bird production relative to the annual estimate of anchovy consumed by the birds	8.760	birds yr MT^{-1}
C_D	Drag coefficient of the water	0.0013	
C_1	Conversion from μM to grams	0.000012	$\text{g } \mu\text{M}^{-1}$
C_2	Conversion from grams into MT	0.000001	MT g^{-1}
F	Fishing mortality	0.850	yr^{-1}
f	Coriolis force		s^{-1}
σ_{air}	Density of air	1.220	kg m^{-3}
K_a	Anchovy net growth efficiency	0.300	
K_z	Zooplankton net growth efficiency	0.800	
k	Growth of the anchovy fishery	0.322	yr^{-1}
M	Ekman transport		$\text{kg m}^{-1} \text{s}^{-1}$
M_d	Daily Ekman transport between 6° and 14°S		kg day^{-1}
m	Length of the coast	1 035 627	m
N	Nitrate concentration		$\mu\text{M L}^{-1}$
N_b	Number of guano-producing seabirds		birds
N_d	Daily nitrate upwelled between 6° and 14°S		$\mu\text{M day}^{-1}$
P_{af}	Anchovy production considering potential removals by the fishery		MT yr^{-1}
P_c	Daily production consumed by all anchovies		g day^{-1}
P_d	Daily estimate of new primary production		g day^{-1}
P_r	Daily <i>per capita</i> production required by one anchovy		$\text{g day}^{-1} \text{fish}^{-1}$
R_a	Anchovy ingestion efficiency	0.616	
R_b	Seabird ingestion efficiency	0.144	
R_r	Redfield ratio (1 N to 6.8 C)		$\mu\text{M day}^{-1}$
R_z	Zooplankton ingestion efficiency ($R_z = 1 - 0.15 - R_a$)	0.234	
s	Duration of a day	86 400	s day^{-1}
T	Annual mean sea surface temperature derived from COADS (after subtracting 3.8°C)		$^\circ\text{C}$
t	Inflection point in the growth of the anchovy fishery	1963	
τ_a	Annual mean alongshore wind stress derived from COADS		N m^{-2}
τ_m	Annual mean meridional wind stress derived from COADS		N m^{-2}
v_m	Annual mean meridional wind pseudo-stress from COADS		$\text{m}^2 \text{s}^{-2}$
W	Anchovy mean weight		g fish^{-1}
y	Year		yr

Variable name	Equations	Equation no.
Annual mean meridional wind stress	$\tau_m = v_m \times \sigma_{\text{air}} \times C_D$	(1)
Ekman transport	$M = -\tau_a/f$	(2)
Annual mean alongshore wind stress	$\tau_a = a_a + b_a(\tau_m)$	(3)
Daily Ekman transport between 6° and 14°S	$M_d = M \times s \times m$	(4)
Nitrate concentration (from Chavez <i>et al.</i> , 1996)	$N = 13.73 - 2.04(T - 19.25) + 0.103(T - 19.25)^2$	(5)
Daily nitrate upwelled between 6° and 14°S	$N_d = M_d \times N$	(6)
Daily estimate of new primary production	$P_d = N_d \times R_r \times C_1$	(7)
Daily production consumed by all anchovies	$P_c = R_a(P_d)A K_a + R_a[R_z(P_d)AK_z]A K_a$	(8)
Anchovy biomass	$B_a = (P_c/P_r) \times W \times C_2$	(9)
Anchovy production considering potential removals by the fishery	$P_{af} = B_a\{1 - [F/(1 + e^{-k(y-t)})]\}$	(10)
Number of guano-producing seabirds	$N_b = a_b + b_b(R_b \times P_{af})$	(11)

Table 3. Equations used in the model. Model parameters are defined in Table 2.

Instituto del Mar del Peru (IMARPE, Apartado 22, Callao, Peru; <http://www.imarpe.gob.pe/imarpe/info-semanales.php>).

We calculated the mean meridional wind stress and SST between 6° and 14°S by averaging the annual mean values from the four coastal 2-degree boxes (A, C, D and F in Fig. 1) for which complete series were available. We removed the linear trend, assumed to be an artifact of sampling, from the time series of mean SST by first subtracting linear regression estimates of SST and then adding back the initial mean value of the series to these residuals. The resulting meridional wind stress and SST data series were not cross-correlated ($r = 0.187$, $n = 76$, $P > 0.05$).

Nutrient input through upwelling

Ekman transport provides an acceptable description of ocean surface transport directly driven by surface wind stress (Bakun, 1987). Offshore Ekman transport at a given latitude is the product of the equatorward, alongshore wind stress and the reciprocal of the local Coriolis parameter (Table 3, eqn 2; Bakun, 1987). The alongshore wind stress for the Peruvian coast was determined from the component of the wind blowing parallel to 332° from true north (Bakun, 1987). An alongshore wind stress series from 1953 to 1986 was previously derived by Bakun and Mendelsohn (1989) from empirical data (wind velocity) in maritime reports for a similar area (Bakun, 1987). The mean, northward wind stress series we derived from COADS, on average, underestimates by 12% the alongshore

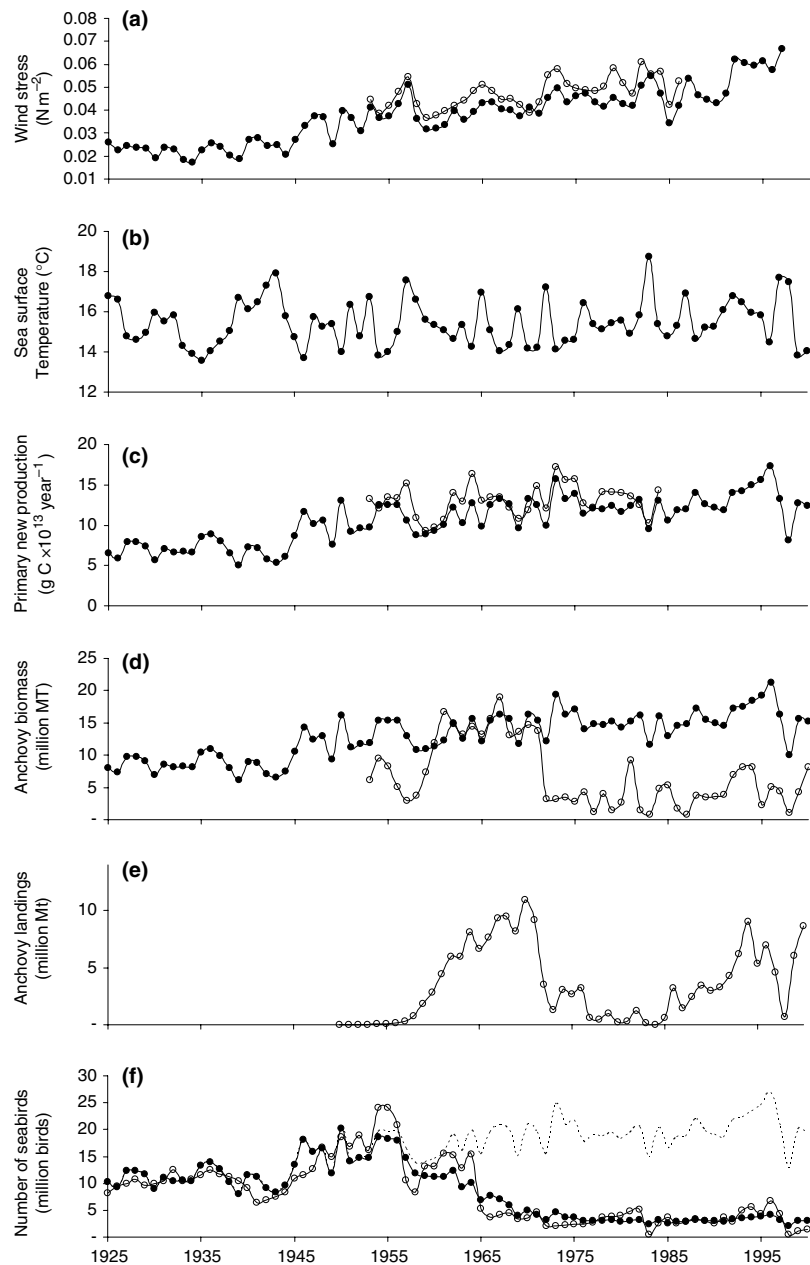
wind stress of Bakun (1987) in the modeled area (Fig. 2a).

We assume that the time series of alongshore wind stress of Bakun (1987) is the most accurate for our purpose of estimating upwelling. Thus, we adjusted our COADS-derived time series of wind stress with a linear function of the alongshore wind stress on meridional wind stress (Table 3, eqn 3; $a_a = 0.005$, $b_a = 1.015$, $n = 34$, $r^2 = 0.74$, $P < 0.001$). We used the resultant time series for mean annual wind stress with the Coriolis parameter at 10°S ($2.53 \times 10^{-5} \text{ s}^{-1}$) to estimate the offshore Ekman transport ($\text{kg m}^{-1} \text{ s}^{-1}$) (Table 3, eqn 2). We then extrapolated these values to obtain daily estimates for the entire coast between 6° and 14°S, a total of 1036 km (Table 3, eqn 4, Fig. 1). We used the Coriolis parameter at 10°S because it corresponds to the mean value for the entire modeled area.

The water flowing offshore as Ekman transport is replaced by cold, nutrient-rich water upwelled close to shore. There is a consistent negative correlation between ocean temperature and the concentration of nitrate, phosphate and silicate (Chavez *et al.*, 1996). We used the quadratic model in Chavez *et al.*, (1996) corresponding to the region located between 5°–10°S and 75°–110°W (Table 3, eqn 5) to predict nitrate concentration from SST in our area (Table 3, eqn 6). This model predicts an average (± 1 SD) concentration of $13.7 \pm 2.4 \mu\text{M}$ of nitrate in the water upwelled during 1925–2000.

The nutricline is close to the surface along the eastern boundary of the Pacific basin (Barber and

Figure 2. Time series of alongshore wind stress (N m^{-2}), sea surface temperature ($^{\circ}\text{C}$), new primary production for the modeling region ($\text{g C yr}^{-1} \times 10^{13}$), anchovy biomass (million MT), and number of seabirds (millions of birds) off the coast of Peru between 6° and 14°S . The alongshore wind stress from COADS (a, filled circles) is compared with previously derived estimates from empirical data in maritime report files for a similar area (a, open circles, Bakun and Mendelsohn, 1989). The sea surface temperature values (b, filled circles) are derived from COADS, detrended and less than 3.8°C (see text for explanation). The new potential primary production estimated by the model (c, filled circles) is compared with previously obtained estimates using a different proxy for nitrogen (c, open circles, Chavez *et al.*, 1989). The anchovy biomass estimated by the model (d, filled circles) is compared with IMARPE's estimates obtained using virtual population analyses and acoustic surveys (d, open circles). Anchovy landings (e, open circles) are shown to illustrate the rapid growth of the fishery. The number of seabirds estimated by the model before accounting for the effect of the industrial fishery for anchovies which limits prey availability for the birds (f, dotted line) and after accounting for the effect of the anchovy fishery (f, filled circles) are compared with IMARPE's estimates of seabird abundance (f, open circles).



Chavez, 1986) and nitrate concentration in the upwelled water is about $25 \mu\text{M}$ (Chavez and Barber, 1987). The temperature of the water upwelled off Peru varies between 14 and 17°C , except during intense El Niño and La Niña years (Morón, 2000). Thus, we assumed the 'mean' long-term temperature of the upwelling water was 15.5°C . The average temperature of the water in the mean annual COADS SST series, which is centered offshore, is 19.3°C and does not appropriately represent the temperature of the upwelled water, thus leading to an underestimate of its nitrate concentration. We corrected for this bias by

subtracting 3.8°C (i.e. $19.3 - 3.8^{\circ}\text{C}$) from the initial mean value of the series (Fig. 2b). This corrected time series of mean annual SST (Fig. 2b), when used with the quadratic model (Table 3, eqn 6), provides an average (± 1 SD) concentration of $23.2 \pm 3.1 \mu\text{M}$ of nitrate in the upwelled water over the 76 yr. Variability of the original time series of temperature is preserved in the time series of upwelled nitrate.

Primary production

We use the Redfield ratio to convert the total amount of nitrogen upwelled daily into organic carbon

(Table 3, eqn 7). The total amount of nitrogen upwelled daily is given by the concentration of nitrogen in the upwelled water (μM) times the total volume of water upwelled along the coast (kg day^{-1}). We converted from nitrogen (atoms) to carbon (atoms) using a Redfield ratio of 1 N to 6.8 C (Chavez and Barber, 1985) and further converted these values into grams of carbon (g C day^{-1}) to estimate the potential new primary production (*sensu* Dugdale and Goering, 1967). We used a linear regression through the origin to compare our estimates of new primary production with those previously obtained by Chavez *et al.* (1989), who used a different proxy for nitrate and a shorter time series.

Anchovy biomass

We estimated the number of anchovies that could forage on the available new primary production and transformed these values into anchovy biomass. Observations with drifting and moored sediment traps made under highly productive upwelling plumes off Peru indicate that 10–20% of the surface primary production is rapidly transported to the bottom (Staresinic, 1980). Thus, we assumed that 15% of new primary production is not grazed and sinks to the bottom and apportioned the remaining 85% to support secondary production, including zooplankton and fish.

Adult Peruvian anchovies weigh 20.4 g on average and consume about 3.5% of their weight in food each day (Pauly *et al.*, 1989). Anchovies feed on phytoplankton and zooplankton, switching from filter to particulate feeding depending on environmental conditions (Rojas de Mendiola, 1989). Phytoplankton represents more than 90%, by number, of the prey items consumed by anchovies off the north-central coast of Peru (Rojas de Mendiola, 1989). However, individual zooplankters, such as copepods and euphausiids are larger and comprise from 40 to 60% of the diet in terms of mass (Alamo, 1989). We thus assume that anchovies consume equal masses of phytoplankton and zooplankton and that both food types have a net carbon content of 10% by wet weight (Vinogradov, 1953).

The efficiency with which phytoplankton mass is transferred to anchovies depends on the assimilation, net growth, and ingestion efficiencies (Table 3, eqn 8). The assimilation efficiency is the proportion of ingested food that is digested and assimilated through the gut wall by an animal (Begon *et al.*, 1996). It varies between 0.5 and 0.8 in herbivores (Lalli and Parsons, 1997). We assumed anchovies have an assimilation efficiency of 0.65 (Nonacs *et al.*, 1998) and that this efficiency also applies to the zooplankton. The net growth efficiency is the proportion of assim-

ilated food that is incorporated in new tissue (Begon *et al.*, 1996). It ranges between 0.3 and 0.8 for fish and zooplankton (Lalli and Parsons, 1997), with vertebrates, in general, having lower efficiencies than invertebrates (Begon *et al.*, 1996). Thus, we assumed anchovies and zooplankton have net growth efficiencies of 0.35 and 0.8 respectively. The ingestion efficiency is the proportion of production of one trophic level ingested by the next higher trophic level (Begon *et al.*, 1996). We estimated the ingestion efficiency using a linear regression through the origin between estimates from IMARPE and the model of anchovy abundance (Table 3, eqn 9) from 1959 to 1971, aiming for an ingestion efficiency that provides the closest overall estimate of anchovy abundance (i.e. slope = 1). We assumed anchovy was the dominant fish in the system between 1959 and 1971. The model does not account for shifts in species dominance between anchovy and sardine. We consider the predicted series of anchovy biomass as an index of the overall abundance of the dominant forage fish in the Peruvian upwelling system, including anchovy and sardine.

Virtual population analysis estimates of the monthly biomass of Peruvian anchovy off Peru between 6° and 14°S are available from January 1953 to December 1981 (Pauly *et al.*, 1987); we calculated annual mean values for these years. Acoustic estimates of anchovy biomass from 1984 to 2000, for the same area, were taken from Gutiérrez (2000); we calculated mean values when more than one annual biomass estimate (i.e. from more than one assessment cruise) was available. We used annual biomass estimates of anchovy 6 months old and older to fill the gap of information from 1982 to 1983 (Csirke *et al.*, 1996).

Seabird population

We estimated the total anchovy biomass required to support the seabirds in any given year by multiplying the annual population of guano-producing seabirds by their required prey, assuming these birds prey exclusively on anchovies. The annual population of guano-producing seabirds from 1925 to 1952 was estimated from guano production (Jordán and Fuentes, 1966), while population estimates thereafter were derived from maps showing the areas occupied by breeding and non-breeding birds at islands and headlands and estimates of densities of these birds (Tovar *et al.*, 1987). Annual population estimates for each of the three guano-producing species from 1953 to 1997 are available in the literature (Jahncke, 1998; Crawford and Jahncke, 1999). Population estimates from 1998 to 2000 were obtained from IMARPE (E. Goya, IMARPE, Apartado 22 Callao, Peru; unpubl. data).

Prey requirements were determined by assuming prey consumption rates are proportional to the body mass of the birds. Guanay cormorants and Peruvian boobies weigh on average 1.8 and 1.3 kg, respectively, and consume about 17.5% of their weight in food (Muck and Pauly, 1987) each day. Peruvian pelicans weigh an average of 6 kg and consume about 10% of their weight in food daily (Muck and Pauly, 1987). Guano-producing seabirds of the northern and central coast of Peru forage mainly on Peruvian anchovies (Table 1; Jahncke and Goya, 1997, 1998), supporting our assumption that anchovies represent the prey of birds in our modeled area.

To determine the total anchovy biomass required to support the seabirds in any given year, we used regression analysis to transform the number of birds to biomass of anchovy consumed (Table 3, eqn 11; $a_b = 137\ 620$ birds, $b_b = 8.764$ birds yr MT^{-1} , $n = 48$). We applied this function to our model estimates of potential anchovy biomass from 1925 to 2000, times a factor that represents the seabird ingestion efficiency. We estimated the ingestion efficiency using a linear regression through the origin, between IMARPE and the model estimates of seabird abundance (Table 3, eqn 11; P_{af} estimated setting removals by the fishery to zero), aiming for an ingestion efficiency that provides the closest overall estimate of anchovy abundance (i.e. slope = 1).

This model thus far does not account for the effect of the fishery, which limits the prey available to the birds, and thus it overestimates bird numbers after 1960. Hence, we added a new term to the model that represents the proportion of anchovy removed by the fishery. This proportion has a logistic shape over time, changing from zero, before the fishery, to an asymptotic value during the fishery. The asymptote represents the maximal fishing mortality (F , yr^{-1}) determined mathematically using a nonlinear regression (Systat Software Inc., Richmond, CA, USA, v. 9.01) (Table 3, eqn 10; $F = 0.85$ yr^{-1} ; $k = 0.322$ yr^{-1} ;

$t = 1963$). Data for the catch of Peruvian anchovies in the northern and central coast of Peru, obtained from IMARPE (M. Bouchon, IMARPE, Apartado 22 Callao, Peru; pers. comm.), were used as an index of the rapid development of the fishery.

We used linear regression to measure how much of the variance in the seabird population was explained by the model. We employed a linear regression through the origin (Sokal and Rohlf, 1998) of the observed and predicted (modeled) seabird population. Spectral analysis (Chatfield, 1996) was used to identify dominant frequencies in the time series of seabird abundance observed by IMARPE and estimated by the model. Spectral analysis was conducted using a Fast Fourier Transform algorithm (MATLAB). Power (arbitrary units) was plotted as a function of period (yr cycle^{-1}). We used a Pearson correlation to compare these two power spectra.

Sensitivity analysis

Linear regressions through the origin were used to compare estimates by IMARPE and our model while varying the ingestion efficiency, first for anchovy biomass (1959–71) and then for seabird abundance (1925–2000). Changes in the regression slope were recorded and used to measure the effect of varying the ingestion efficiency on the anchovy biomass and seabird abundance estimates, respectively. We performed these analyses assuming that IMARPE's estimates of anchovy and seabird abundance are a function of the physical characteristics of the atmosphere and ocean used in the model.

RESULTS

Physical variables

The meridional wind stress and the SST series derived from COADS increased during 1925–2000. The meridional wind stress presented significant positive trends in all six 2-degree boxes (Table 4), as did SST

Table 4. Trends in the annual mean meridional wind stress of the six 2-degree boxes for which COADS data were obtained. We report the slope (\pm SE) of the regressions and associated ANOVA statistics.

2-degree boxes	Symbol (Fig. 1)	Environments	n (yr)	Slope ($\times 10^{-5}$ $\text{N m}^{-2} \text{yr}^{-1}$)	SE ($\times 10^{-5}$)	F -ratio	P -value
7°S, 81°W	A	Coastal to oceanic	69	+20.4	2.1	95.1	<0.001
9°S, 81°W	B	Oceanic only	69	+29.1	2.7	115.4	<0.001
9°S, 79°W	C	Coastal to oceanic	66	+28.4	2.3	150.2	<0.001
11°S, 79°W	D	Coastal to oceanic	73	+33.5	2.2	235.8	<0.001
13°S, 79°W	E	Oceanic only	57	+35.9	4.7	57.4	<0.001
13°S, 77°W	F	Coastal to oceanic	73	+45.2	3.6	161.5	<0.001

Table 5. Trends in the annual mean sea surface temperature of the six 2-degree boxes for which COADS data were obtained. Trends for Chicama, a coastal town in Peru, are also included for comparison. We report the slope (\pm SE) of the regressions and associated ANOVA statistics.

2-degree boxes	Symbol (Fig. 1)	Environments	n (yr)	Slope ($^{\circ}\text{C yr}^{-1}$)	SE	F-ratio	P-value
7°S, 81°W	A	Coastal to oceanic	69	+0.020	0.007	9.230	0.003
7°S, 79°W		Coastal only*	76	-0.000	0.007	0.001	0.970
9°S, 81°W	B	Oceanic only	66	+0.009	0.007	1.623	0.207
9°S, 79°W	C	Coastal to oceanic	66	+0.028	0.007	16.796	<0.001
11°S, 79°W	D	Coastal to oceanic	73	+0.030	0.006	23.672	<0.001
13°S, 79°W	E	Oceanic only	57	+0.009	0.006	2.291	0.136
13°S, 77°W	F	Coastal to oceanic	73	+0.019	0.006	11.362	0.001

*Local data series from Chicama.

in the four boxes where nearshore and offshore data were averaged (Table 5). SST had no significant trends in the two boxes where only offshore data were included (B, E; Table 5). The SST series from Chicama did not show a significant trend, indicating that the trend in COADS-derived SST was the result of more offshore records becoming available in recent years. No local time series of wind stress is available for us to perform an analysis analogous to that for SST. However, the fact that the wind stress for the offshore-nearshore boxes as well as the offshore-only boxes present significant and similar positive trends leads us to conclude that these trends in wind stress do not represent sampling artifacts.

Primary production

The annual mean potential new primary production ($\text{g C}\cdot\text{yr}^{-1}$) off the coast of Peru shows a marked increase between 1925 and 2000 (Fig. 2c). This increase is a consequence of the increasing wind stress observed in the modeled area. The alongshore wind stress we derived from COADS data suggests that wind stress doubled over 1925–2000, from 0.03 N m^{-2} in the 1930s to 0.06 N m^{-2} in the 1990s, causing new primary production to increase from 7.0×10^{13} to $13.4 \times 10^{13} \text{ g C}\cdot\text{yr}^{-1}$ over this period. The mean potential new primary production for the study area (± 1 SD) estimated by the model was $11(\pm 3) \times 10^{13} \text{ g C}\cdot\text{yr}^{-1}$ ($n = 76$ yr), ranging between $5 \times 10^{13} \text{ g C}\cdot\text{yr}^{-1}$ in 1939 and $17 \times 10^{13} \text{ g C}\cdot\text{yr}^{-1}$ in 1996. Our model yielded estimates of new primary production which were, on average, 11.5% lower than those estimated for 1953 to 1984 from total primary production and an f -ratio (new/total primary production) of 0.75 (Chavez *et al.*, 1989). Our time series explained 98% of the temporal variation present in their series ($n = 32$, $r^2 = 0.98$, $P < 0.001$).

Anchovy biomass

The annual mean of the potential anchovy biomass estimated by the model also shows a marked increase between 1925 and 2000 (Fig. 2d). The model suggests that anchovy biomass should have increased from 8.6 million MT in the 1930s to 16.5 million MT in the 1990s due to the increase in primary production. The mean anchovy biomass (± 1 SD) estimated by the model was 12.9 ± 3.5 million MT ($n = 76$ yr), ranging between 6.2 million MT in 1939 and 21.3 million MT in 1996. The model closely predicts anchovy abundance during the 1960s, years when anchovy was the dominant prey in the system, but largely overestimates anchovy abundance later in the series, when changes in pelagic species occurred and the Peruvian Pacific sardine became more abundant.

Seabird population

The annual mean number of guano-producing seabirds estimated by the model shows the same increasing trend between 1925 and 2000 (Fig. 2f) described previously for primary production and anchovy biomass. This is expected under the assumption that the seabird population was solely limited by prey production. The model indicates that the number of seabirds should have increased from 11 million birds in the 1930s to 21 million birds in the 1990s as a consequence of the increase in their primary prey, the anchovy. The mean seabird abundance (± 1 SD) estimated by the model was 16.5 ± 4.4 million birds, ranging between 8 million birds in 1939 and 27 million birds in 1996. The large initial increase in seabird numbers is consistent with measured abundance, which shows an increase in the number of seabirds from about 10 million birds in 1925 to about 25 million birds in 1955. The model closely predicts seabird

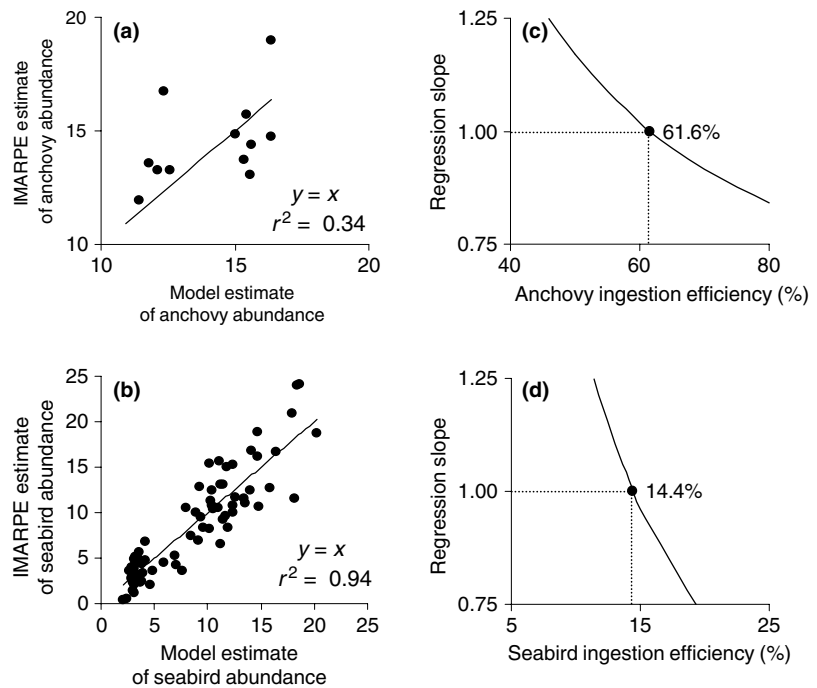


Figure 3. Scatter plots showing IMARPE's estimates of anchovy (million MT) and seabird abundance (millions of birds) as a function of the model estimates of anchovy (a) and seabird (b) abundance respectively. Also shown are changes in the regression slope of the scatter plots due to changes in the ingestion efficiency values assumed by the model for anchovy (c) and seabirds (d). Points indicated are the values for ingestion efficiencies used in the main model runs.

numbers from 1925 to 1960, years when anchovies were the dominant pelagic fish in the Peruvian upwelling system and the main prey consumed by the birds (Murphy, 1936; Jordán, 1961), and prior to and during the growth of the anchovy fishery, but the model overestimates seabird numbers thereafter.

Fisheries effects on seabird populations

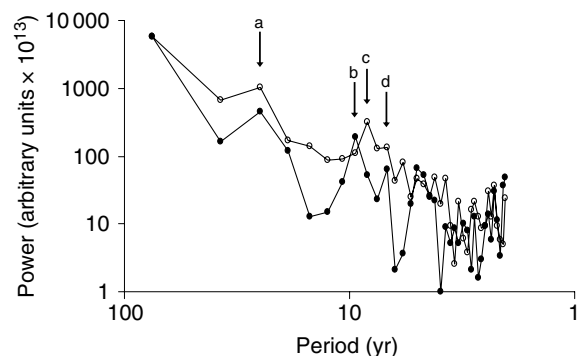
The anchovy fishery developed rapidly from 1950 to 1960. The model indicates that, after 1960, the seabird population was limited by prey availability, due especially to the competition by the fishery for anchovies. The annual mean number of guano-producing seabirds estimated by the model, after removing the biomass of anchovy taken by the fishery, shows a trend similar to the observed number of seabirds: a large increase from 1925 to 1955 and a dramatic decrease from 1955 to 2000 (Fig. 2f). The model shows the number of seabirds increased from 11 million birds in the 1930s to 15.7 million birds in the 1950s and decreased to 3.3 million birds in the 1990s. The mean seabird abundance (± 1 SD) estimated by the model after including the fishery was 8.4 ± 5 million birds, ranging from 2 million birds in 1998 to 20 million birds in 1950.

We used a regression to measure how much of the variance in the observed numbers of seabirds was explained by the model (Fig. 3b). Our model, based solely on the physical characteristics of the atmosphere and ocean that determine productivity and the

competitive effect of the fishery that limits prey availability, explained about 94% of the variation in seabird numbers observed from 1925 to 2000.

We used spectral analysis to identify the important frequencies of the time series of bird abundance (Fig. 4). The power spectra of the bird abundance predicted by the model and observed by IMARPE were significantly correlated ($r_{\text{pearson}} = 0.909$, $n = 37$, $P < 0.01$). The strongest peaks in the power spectra of the model time series occurred at 25, 9.4, and 6.8 yr,

Figure 4. Average power spectra from the univariate spectral analysis of the model estimates of seabird abundance after considering the negative effect of the anchovy fishery on prey availability (filled circles), and IMARPE's estimates of seabird abundance (open circles). Arrows indicate dominant peaks at 25 (a), 9.4 (b), 8.3 (c) and 6.8 yr (d).



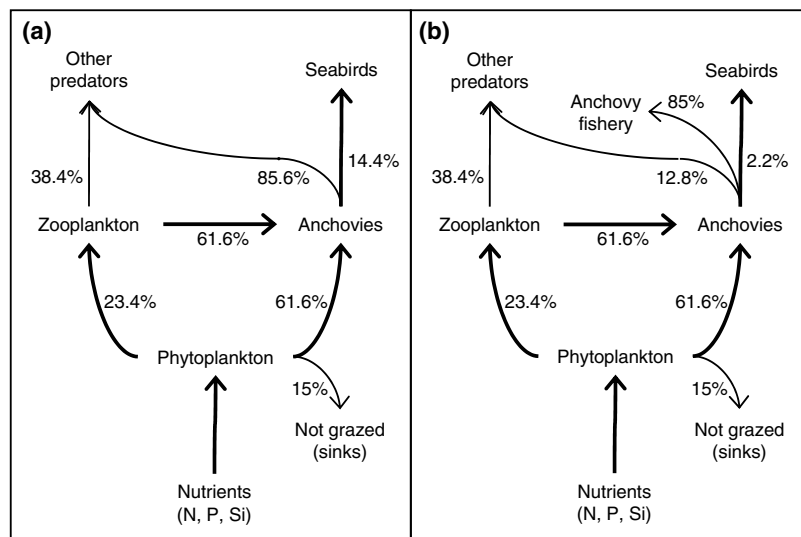


Figure 5. Schematic representation of the food web in the Peruvian upwelling system without (a) and with (b) the industrial fishery for anchovies included in the model. The numbers correspond to the proportion of productivity available at one trophic level consumed by the next trophic level at any given time.

while the strongest peaks in the power spectra of the time series of seabird abundance from IMARPE observations occurred at 25, 8.3, and 6.8 yr.

Trends in carbon flux

Figure 5 shows a schematic representation of our model of the carbon transfer through a simplified food web in the Peruvian upwelling system with and without the industrial fishery for anchovies. The model required anchovies to consume 61.6% of the available phytoplankton and zooplankton to produce the series shown in Fig. 2d. The assumptions we made about ingestion, assimilation and net growth efficiencies for anchovies and zooplankton represent a 28% transfer of new production from the primary producers to the anchovies. This value is high but comparable with an efficiency of 25% previously reported for upwelling ecosystems (Pauly and Christensen, 1995). The model required seabirds to consume 14.4% of the available anchovies to produce the series shown in Fig. 2f, and suggests seabirds indirectly consumed 2.3% of the new production before the development of the anchovy fishery, and only 0.3% of the new production during this fishery. Our 14.4% efficiency assumed for the seabirds is similar to Furness' (1982) estimates that seabirds consumed 17% of the anchovy stock between 1961 and 1965 in the Peruvian upwelling system.

Sensitivity analysis

There was a direct relationship between ingestion efficiency and abundance estimates. Low ingestion efficiencies led to low model estimates of anchovy biomass and seabird abundance, resulting in regression slopes higher than unity between IMARPE's and the

model estimates, respectively, for these two variables. Conversely, high ingestion efficiencies led to high model estimates of anchovy biomass and seabird abundance, resulting in regression slopes lower than unity. The ingestion efficiency value of 61.6% used for anchovies corresponded to a slope of one for the regression between anchovy biomass estimated by IMARPE and the model and provided the best overall estimates of anchovy abundance between 1959 and 1971 (Fig. 3a,c). The ingestion efficiency value of 14.4% for seabirds corresponded to a regression slope of one between estimates of seabird abundance by IMARPE and the model and resulted in the best estimates of seabird abundance from 1925 to 2000 (Fig. 3b,d).

DISCUSSION

The model indicates that primary production off the coast of Peru increased from 1925 to 2000 in response to increased wind stress observed in the modeled area. Wind stress increased in the 1950–80s in upwelling areas off California, Peru, the Iberian Peninsula and Morocco (Bakun, 1990). The increase in wind stress has been hypothesized to cause an increase in primary production (Bakun, 1990). The trend of increasing wind stress reversed after 1975 off California and persisted off Peru. Our model is consistent with Bakun's (1990) hypothesis and with the hypothesis that an increase in the wind stress that forces upwelling off Peru causes an increase in primary production by increasing the rate of nitrate input to the system. No conceptual differences exist between Bakun (1973) upwelling index and the steps followed in this model

to estimate offshore Ekman transport. However, our model goes further and uses nitrate in upwelled water to predict primary production, anchovy biomass and seabird abundance.

An increase in wind stress potentially means an increase in turbulent mixing, which may have negative effects on the anchovy and therefore on the seabirds. Reproductive success of pelagic fish in upwelling regions depends on the winds being neither so weak that there is insufficient upwelling, nor so strong that turbulent mixing of the water column disperses fine-scale aggregations of prey essential for the survival of larval fish (Cury and Roy, 1989). To date, there has been little demonstration that increased primary production actually promotes reproductive success and population growth at higher trophic levels (Bakun, 1990; Micheli, 1999).

Our results indicate that anchovy biomass increased in response to the increase of primary production off north-central Peru between 1925 and 2000. There are no comparable data for primary production and anchovy biomass over this time period; all available data start with the advent of the fishery. The seabirds considered here are probably the species that depend most on the Peruvian anchovies as a food source (Muck and Pauly, 1987), and thus may be used as a proxy for changes in the anchovy biomass prior to the industrial fishery for anchovies. Seabird abundance shows a marked, increasing trend from 1908, reaching a maximal value in 1955 (Jahncke, 1998; Crawford and Jahncke, 1999). This increasing trend in the number of seabirds suggests a positive effect of wind stress on their main prey, the Peruvian anchovy, and its food. The model predicts the growth of the seabird populations and their prey, and may be one of the few examples showing how an increase in primary production affects the population dynamics of top marine predators.

The power spectra for the time series of observed and modeled bird abundances were consistent with one another (Fig. 4). A peak in variance at 6.8 yr is consistent with the known frequency of occurrence of El Niño. The dominant variance of the spectral analysis of El Niño-Southern Oscillation (ENSO) indices occurs at low-frequency periods ranging from 3 to 7 yr (Barnett, 1991; Trenberth and Hoar, 1996). The peaks in variance at ~9 and 25 yr are less evident, and may be associated with solar cycles and/or coupled atmosphere-ocean dynamics (Mendelssohn and Schwing, 2002 and references therein). Consistency between the structure of the spectra of the observed and modeled seabird abundance data indicates that the model contains dynamics representative of nature. It is

also noteworthy that the model-derived spectrum shows greater variation, especially at higher frequency (shorter periods), than the spectrum based on the observed bird abundances. This is consistent with the short-term variation in the environment being mitigated at higher trophic levels.

The anchovy biomass estimates from our model closely predicted anchovy abundance during the 1950s and 1960s, when anchovy was the dominant small, pelagic fish in the system, but overestimated anchovy abundance later, when changes in the total abundance and relative composition of pelagic species occurred. Heavy fishing pressure in the late 1960s and early 1970s, combined with the strong El Niño of 1972, caused a collapse of the anchovy population (Brainard and McLain, 1987). The moderate 1976–77 El Niño and the warm conditions thereafter, especially during the 1982–83 El Niño (Brainard and McLain, 1987), resulted in a very low anchovy biomass (Schwartzlose *et al.*, 1999) and a higher sardine biomass (Csirke *et al.*, 1996). However, the reversal to cooler conditions that has occurred since the 1980s (Brainard and McLain, 1987) has been associated with the recovery of the anchovy stock in the 1990s. The recent catch of anchovy off Peru is similar to that recorded before the 1972 El Niño (Ñiquen *et al.*, 2000).

Before its collapse in the 1972 El Niño, the Peruvian anchovy was by far the largest and most productive single fishery stock on record, reaching a peak annual production of more than 12 million MT in the 1970s and by itself accounting for approximately one-sixth of the world's total fishery production during 1963–72 (Bakun, 1996). After the collapse of the anchovy stocks, the sardine became the most abundant pelagic fish in the Peruvian upwelling area (Csirke *et al.*, 1996). The combined Ecuadorian, Peruvian and Chilean landings of sardine reached the largest annual total (6.5 million MT in 1985) ever recorded for any sardine population (Bakun, 1996). Fluctuations in the abundance of anchovies and sardines have occurred in different places around the world (Lluch-Belda *et al.*, 1989, 1992; Crawford and Jahncke, 1999; Schwartzlose *et al.*, 1999). Many recent fluctuations have been in phase, indicating that the populations of these two types of fish may have been influenced by climate factors operating at a global scale (Kawasaki, 1983; Crawford and Jahncke, 1999). Our model fish production is for anchovy and sardine combined and does not distinguish between these two types.

The model suggests that the growth of populations of guano-producing seabirds from 1925 to 1955 was likely a response to increasing productivity of the

Peruvian upwelling system and not necessarily a result of seabird colony management. The Peruvian upwelling bears the full brunt of the ENSO and so is uniquely subject to environmental rearrangements, which are both intermittent and drastic (Bakun, 1996). These recurrent disruptions may be advantageous to the rapidly responding population of anchovies and sardines, whose life cycles are short compared with other fish living in the same habitat and feeding at relatively higher trophic levels but slower to respond (Bakun, 1996). Peruvian seabirds have high potential fecundity relative to most seabirds and have likely been selected to be able to take advantage of periods of high prey abundance thus compensating for breeding failure and elevated adult mortality during years of low prey abundance (Weimerskirch, 2001). The closure of the headlands, which offered seabirds protection from their predators, came from observations of attempts by birds to nest on unprotected headlands during the 1940s (Schweigger, 1964). These nesting attempts indicate a growing population in need of more nesting space. The model predicts seabird abundance increasing almost exponentially during the 1940s as a consequence of the carrying capacity of the system increasing due to natural causes, i.e. increased wind.

The decrease in numbers of guano-producing seabirds that occurred since the mid-1960s appears to be due to depletion of their food by the fishery, which grew to catch about 85% of the prey otherwise available to the seabirds. The Peruvian guano-producing seabirds are the most conspicuous competitors for the anchovy fishery (Muck and Pauly, 1987) with their forage being anchovy of the same size classes as captured by the fishery (Jahncke and Zileri, 1998). Duffy (1983b) found that the fishery explained 72% of the variation in the annual seabird productivity; the more anchovies that were taken by the fishery, the fewer offspring produced by the birds (Duffy, 1983b). Seabird populations crashed during the 1957–58 El Niño, partly recovered afterwards, crashed again in the 1965 El Niño, and have not recovered fully. Subsequent to the 1965 El Niño, a new equilibrium level in the size of the seabird populations was established that was much lower than the one prior to the fishery. The model explains the drastic decline of the number of seabirds during the 1960s to be a consequence of a fishery that lowered prey availability, thereby setting a new equilibrium level with fewer seabirds.

Seabird populations were likely limited by the fishery during the 1990s, as they were in the 1960s and early 1970s. However, during the late 1970s and 80s, the model predicted increased primary production that

should have resulted in a larger fish biomass than indicated by stock assessments (Pauly *et al.*, 1987; Gutiérrez, 2000). We do not know why the anchovy stocks did not rebound during what we believe was a period of elevated primary production. However, such decadal-scale variation is characteristic of stocks of small, pelagic fish worldwide (Schwartzlose *et al.*, 1999). Landings of anchovy in the late 1970s and the combined landings of anchovy and sardine during the 1980s were low compared with those from the 1960s (early), 70s and 90s (M. Bouchon, IMARPE, Apartado 22 Callao, Peru; unpubl. data). It is likely that the collapse of the anchovy in the early 1970s freed some of the primary production that would otherwise have been consumed by anchovies. Some of this carbon was used by sardines, which became more abundant during the 1980s (Csirke *et al.*, 1996). The remaining production could have resulted in an increased accumulation of carbon in the sediments, or may have been used by secondary producers that were consumed by predatory fish. No significant differences in carbon deposition rates were found before and after 1971 (Henrichs and Farrington, 1984). There are no estimates of biomass of predatory fish landed prior to the 1980s with which we could assess changes in their abundance.

Murphy (1925) described the extraordinary number of seabirds off Peru during the first half of the 20th century. The latter half of that century saw the decline in seabird numbers from about 20 million birds (1950–65) to about 5 million birds (1965–2000) (Fig. 2f). Today, many of the bird islands of Peru are largely devoid of seabirds. These long-term changes, if indeed due to fishing, are of a magnitude experienced by terrestrial bird assemblages due to loss of habitat, such as woodlands in China (Menzies, 1994). Such changes also reflect a basic change to the marine ecosystem due to fishing, on a scale comparable with loss of habitat due to trawling (Thrush *et al.*, 1998) and changes in species composition due to human removals (Jackson *et al.*, 2001; Myers and Worm, 2003). Fortunately, the dominant species, including the small pelagic fish and seabirds, of the Peruvian upwelling ecosystem are adapted to a fluctuating environment, due to natural causes such as El Niño. They thus appear able to endure change associated with fishing. However, it is unknown how these species would respond to long-term change in the climate and ocean.

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