

Effect of El Niño on the diet of a specialist seabird, *Sula nebouxii*, in the warm eastern tropical Pacific

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ABSTRACT: Reductions in the availability of energetically valuable prey associated with the El Niño Southern Oscillation (ENSO) may force seabirds to switch to low-energy prey or smaller prey, with consequent effects on their fitness. Impacts of ENSO on seabird diet have been documented in several regions but remain unexplored in the warm eastern tropical Pacific. Analysis of 5 yr of data on the blue-footed booby *Sula nebouxii*, a seabird specialized on small pelagic fish, revealed that both sexes switch diet and capture fewer types of prey when warm El Niño conditions prevail during the breeding season. Moreover, ENSO-related alternations in the relative abundances of anchovies and herrings, the main prey of these boobies and important commercial fishes in the region, were associated with boobies feeding on more and larger anchovies and fewer and smaller herrings during warm El Niño events, and vice versa during cold La Niña episodes. Females consumed herrings more frequently than males across the 5 yr and consistently fed on larger anchovies and herrings than males, with these differences likely due to this booby's reversed sexual size-dimorphism. We conclude that diet composition and prey size of boobies may be sensitive to variation in relative availabilities of different prey species associated with the ENSO, making these birds robust indicators of environmental fluctuations in the warm eastern tropical Pacific. Inter-annual variations in the availability of herrings, probably the most energetically valuable prey for these boobies, may explain the large ENSO-related variations in booby reproduction documented previously.

KEY WORDS: El Niño Southern Oscillation · Seabird diet · Eastern tropical Pacific · Fish abundance · Anchovies · Herrings · Sardine fisheries

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INTRODUCTION

Several studies have documented changes in the survival and reproduction of seabirds associated with major oceanographic fluctuations such as the North Atlantic Oscillation (NAO; e.g. Wanless et al. 2005, Frederiksen et al. 2007b) and El Niño–Southern Oscillation (ENSO; e.g. Devney et al. 2009, Oro et al. 2010). These associations have been attributed to fine-scale variations in sea-surface temperature that force shifts in the abundance of prey through a bot-

tom-up process (Barber & Chavez 1983) or affect the behaviour or physiology of prey and their distribution in the water column (Peck et al. 2004). Oceanographic anomalies may influence the demography of seabirds, not only through changes in prey availability, but also through changes in the physical scenario in which foraging, breeding and offspring development occur (Clark et al. 1990), suggesting that effects of climate on seabird populations may involve multiple variables (Abraham & Sydeman 2004, Thayer & Sydeman 2007).

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Changes in food availability and abundance, and their effect on foraging success, food intake and provisioning of offspring, are the most studied mechanisms by which ocean climate affects seabird demographic processes, particularly reproduction (e.g. Smithers et al. 2003, Abraham & Sydeman 2004, Frederiksen et al. 2007b). However, in addition to food availability and abundance, food quality could be a critical factor influencing the demography and dynamics of seabird populations (Wanless et al. 2005, Jodice et al. 2006). For example, intra- and inter-seasonal variation in diet composition explains variation in breeding phenology, survival and growth of chicks and reproductive success in many seabird species (e.g. Barbraud & Chastel 1999, Österblom et al. 2001, Sorensen et al. 2009). Dietary changes and their consequent effects on fitness may be due to reductions in the availability of preferred and high energy prey: oceanographic anomalies may force seabirds to switch to low energy prey or smaller prey (Davoren & Montevecchi 2003, Österblom et al. 2008). Dietary changes have been viewed as a mechanism enabling seabirds to cope with fluctuations in food availability and abundance (Furness 1996), and the efficiency of this buffering may depend on particular foraging methods of seabird species (e.g. Baird 1990). Importantly, the relationships between food availability and seabirds' foraging and demographic parameters may be evident only under extreme prey scarcity (Cairns 1987).

Furthermore, changes in diet composition and other foraging parameters (e.g. foraging success, chick provisioning) in breeding seabirds can reflect the abundance of particular prey items and shifts in the marine trophic webs that occur at different spatial and temporal scales (Montevecchi & Myers 1995, Sydeman et al. 2001). Such sensitivity to variations in the marine environment has led researchers to advocate using seabirds as indicators of marine resources (Bunce 2004, Einoder 2009) and major climatic and oceanographic fluctuations (Montevecchi 2007, Thayer & Sydeman 2007; but see Grémillet & Charmantier 2010).

Long-term associations between major climatic drivers (i.e. NAO and ENSO), food availability, foraging and fitness of seabirds have been extensively explored in temperate waters of the Atlantic (Frederiksen et al. 2007b, Montevecchi 2007, Wanless et al. 2007) and Pacific Oceans (Sydeman et al. 2001, Piatt et al. 2007b, Black et al. 2010), as well as in Antarctic waters (Bunce 2004, Jenouvrier et al. 2005, Le Bohec et al. 2008). Similar associations have been documented in the subtropical regions of Benguela

(Crawford & Shelton 1978, Crawford 2007) and the Gulf of California (Velarde et al. 2004). In the tropics, similar studies have been carried out in the warm western Pacific (e.g. Ramos et al. 2002, Devney et al. 2009) and the western Indian Ocean (e.g. Monticelli et al. 2007). In the warm eastern tropical Pacific, 2 long-term studies showed that ENSO influences seabird survival and reproduction (Oro et al. 2010, Ancona et al. 2011), but associations with foraging parameters of seabirds in this region remain virtually unexplored (but see Velarde et al. 2004 for the temperate Gulf of California).

Investigating associations between ENSO and foraging parameters of seabirds in the eastern tropical Pacific may expand our understanding about how major climatic drivers affect the marine environment and prey populations (many of them commercially exploited; Piatt et al. 2007a and references therein) in highly variable tropical oceans. The warm eastern tropical Pacific is a transitional zone where the temperate Equatorial Current mixes with the cold nutrient-rich waters of the California Current and the warm waters from the southern Gulf of California, making this a dynamic and highly productive zone where short El Niño events may occur (Aguirre 2002). In this region, warming of surface waters related to ENSO affects upwelling dynamics mostly in winter, with consequent effects on local phytoplankton communities and the upper trophic levels (Wilkinson et al. 2006).

We asked how ENSO conditions in the current year influence diet of the blue-footed booby *Sula nebouxii*, a locally foraging seabird that breeds on islands in the warm eastern tropical Pacific (Nelson 2005) and whose survival and reproduction are highly affected by El Niño events (Anderson 1989, Oro et al. 2010, Ancona et al. 2011). Using stomach contents collected over 5 seasons (1981 to 1985), we tested whether male and female breeders (1) switch diet or (2) capture fewer types of prey when the Southern Oscillation Index (SOI) is negative, signifying El Niño conditions in the Pacific Ocean. After finding that Engraulidae (i.e. anchovies) and Clupeidae (sardines and herrings) were the fish families most consumed by these boobies over the years, we asked whether (3) the relative abundance of these families in the diet or (4) the size of specimens of these families captured vary with the SOI. Engraulids and clupeids support the sardine fishery off Mexico's southern Pacific coast, our study region, and their relative abundances are thought to alternate in association with ENSO, anchovies predominating in commercial catches during warm El Niño episodes and

herrings during cold La Niña events (Jacob-Cervantes et al. 2005, Vallarta-Zárate 2010). Hence, we expected a similar alternation in the blue-footed booby's diet, with anchovies predominating when the SOI is negative and sardines and herrings predominating when the SOI is positive.

MATERIALS AND METHODS

Study species

Fieldwork was carried out in the blue-footed booby *Sula nebouxii* colony on Isla Isabel, a small tropical island 28 km off the northwest coast of Mexico, at the southern boundary of the Gulf of California (21° 52' N, 105° 54' W). Blue-footed boobies are socially monogamous seabirds (Osorio-Beristain & Drummond 1998) that breed on islands in the tropical Pacific (Nelson 2005). Males and females feed on small pelagic fishes such as anchovies, sardines and herrings (Anderson 1989, Zavalaga et al. 2008, Castillo-Guerrero & Mellink 2010, present study), which they catch by plunge-diving (Nelson 2005) in dispersed areas within a radius of up to 30 km around their breeding colonies at the Galápagos Archipelago (Anderson & Ricklefs 1987), off Peru (Zavalaga et al. 2008) and in the Gulf of California (Weimerskirch et al. 2009). Females, which are larger and heavier than males (Torres & Drummond 1999), dive deeper (Zavalaga et al. 2007), make longer foraging trips, forage farther from the colony, fly greater distances and forage over larger areas than males (Weimerskirch et al. 2009; but see Zavalaga et al. 2007).

Blue-footed boobies lay 1 to 3 eggs on the ground and fledge 0 to 3 chicks after 41 to 49 d of incubation and >3 mo of biparental feeding of the brood (Guerra & Drummond 1995). On Isla Isabel, reproduction starts between December and February, but laying and hatching of eggs extend until early June, and the last fledglings reach independence at the end of July (Peña 2009). Delays in the onset of breeding, as well as partial and occasional total breeding failures, in the Isla Isabel colony are associated with El Niño, apparently because warm surface waters deplete local productivity and prey availability for booby breeders (Ancona et al. 2011).

Stomach contents and dietary parameters

Between 1981 and 1985, we obtained data during the first 5 yr (only) of a long-term study of reproduc-

tion. Every 2 to 6 d between March and July of each year, observers checked all nests in a 15 000 m² study area. When their nests were approached, some adults (usually incubating or brooding) regurgitated prey onto the ground, all of which were fish. Each sample of regurgitated prey was individually fixed in 10% formalin and preserved in 70% alcohol a few weeks later. Each fish was measured with callipers (standard length \pm 0.1 cm) and identified to species, genus, or family level, using the keys and catalogs of Jordan & Evermann (1898), Hildebrand (1946), Walls (1975), Castro-Aguirre (1978), Thomson et al. (1979), Randall (1983) and Nelson (1984).

Individual fishes within a regurgitation are not independent, so we analysed frequencies of regurgitations containing each type of prey. Only 15 of 312 regurgitations contained >1 prey taxon, and these regurgitations were included in the analysis representing only the most abundant type of prey they contained. We used family level prey classification because this allowed the greatest scope for meaningful comparisons, given our generally small sample sizes at the species level. The size of the prey consumed by each bird was represented by the mean standard length of the items it regurgitated (the distance between the mouth and the tip of the caudal peduncle). Size of clupeids in 1983 could not be computed because none were consumed by males, and those consumed by females were incomplete specimens.

ENSO conditions

For the 5 yr study period, we obtained monthly average SOI values from the NOAA Climate Prediction Center (www.cpc.ncep.noaa.gov/data/indices/soi). Sea-surface temperature, a more local index of the strength of ENSO (Doney 2006), could not be used because no data were available for the first year of the present study.

Data analyses

We computed the annual proportions of regurgitations containing each of the 4 most numerous fish families identified in the samples and the proportions of regurgitations containing unidentified fish families, which we lumped as 'others'. Then we calculated the Levins' index of niche breadth to quantify the annual diversity of fish families recorded in the regurgitations of male and female

boobies, an estimation of the level of dietary specialization (Krebs 1999). Annual Levins' index of niche breadth (B) was computed as the reciprocal of the sum of the squared proportions (p) of regurgitations containing each fish family (j) using the formula $B = 1/\sum(p_j^2)$. We calculated this index separately for each sex and standardized it as $B - 1/n - 1$, where n is the total number of fish families found in all regurgitations (Krebs 1999).

We computed annual average values of the SOI during the period from December to May, including 3 winter months and 3 spring months, the seasons when ENSO affects ocean productivity in the study region (Wilkinson et al. 2006).

We built a linear model to examine the association between the average SOI in December to May and boobies' sex (independent variables) and the annual standardized niche breadth (dependent variable). After finding that engraulids and clupeids were the families most consumed over the years, we built models to examine associations with additional dependent variables: annual proportions of regurgitations containing each family and the average standard length of items in each family. To examine the association between number of fishes regurgitated and the SOI and sex, we used a generalized linear model with a quasi-Poisson error distribution and a log-link function to account for over-dispersion (recommended by Crawley 2007).

Models initially included the average SOI in December to May, sex and the interaction SOI \times sex as fixed effect terms and were simplified by sequentially dropping non-significant effect terms. We used deletion tests to compare the simplified minimal adequate model with the model including a non-significant term or with the model excluding a significant term, to assess the statistical significance ($p < 0.05$) of the increase in variance and/or deviance for each model (Crawley 2005). Analyses were carried out using R (R Development Core Team 2006) Version 2.12.1.

RESULTS

Diet composition

Over the 5 reproductive seasons, we recovered 907 prey from 312 regurgitations of 98 male *Sula nebouxii* (1981 and 1984, $n = 23$; 1982 and 1983, $n = 13$; 1985, $n = 26$) and 214 females (1981, $n = 55$; 1982, $n = 31$; 1983, $n = 37$; 1984, $n = 39$; 1985, $n = 52$). All prey were fish belonging to 4 orders, 10 families and

8 genera. Engraulids (60.9% of all fish, 37.8% of all regurgitations) and clupeids (27.1% of fish, 39.7% of regurgitations) were represented most numerously by the Pacific anchoveta *Cetengraulis mysticetus* and the Pacific thread herring *Ophistonema libertate*, respectively (Table 1, Fig. 1).

The standardized niche breadth was positively correlated with the SOI in December to May, but unrelated to boobies' sex (Table 2), and the interaction between the SOI and sex was not significant ($F_{1,8} = 0.51$, $p = 0.50$). The more positive the values of the SOI (i.e. non-El Niño conditions), the more diversified were the diets of male and female boobies (Fig. 2).

More positive values of the SOI were also associated with lower proportions of regurgitations containing engraulid prey, namely anchovies (Table 2, Fig. 3a), and neither sex (Table 2) nor the interaction between the SOI and sex influenced this proportion ($F_{1,8} = 0.48$, $p = 0.51$). Only 14% of regurgitations contained anchovies in 1985, a markedly non-El Niño year, compared to 78% in 1983, a year with an extreme El Niño event (Schreiber 2002).

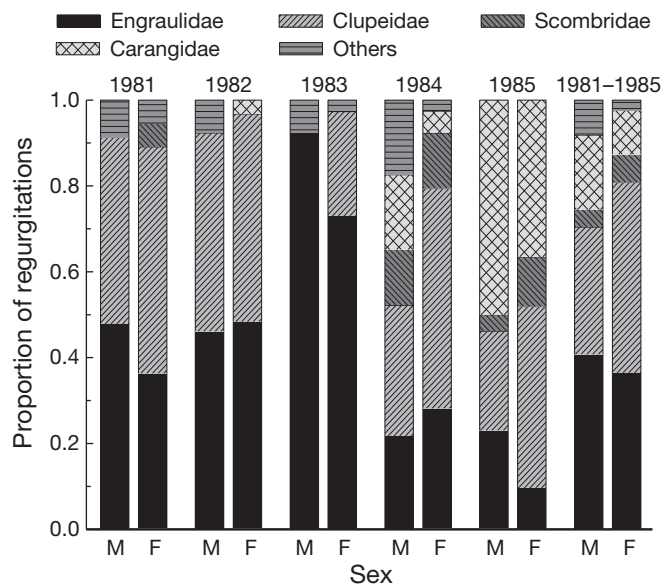
The proportion of regurgitations containing clupeid fishes, such as sardines and herrings, was strongly associated with the SOI and sex (Table 2). The interaction SOI \times sex was not significant ($F_{2,7} = 0.39$, $p = 0.55$). Positive SOI values were associated with greater consumption of sardines and herrings, and more so in females than in males across the 5 yr (Fig. 3b). During the strong El Niño event of 1983, clupeids were absent from males' regurgitations and were found in only 24% of females' regurgitations; whereas in the non-El Niño conditions of 1985, clupeid consumption rose to 23% in males and 42% in females.

Size of main prey fish

Females consumed 9.4% larger engraulids than males, both sexes taking bigger items as SOI values declined (Table 2, Fig. 4) and responding similarly to the SOI (SOI \times sex: $F_{2,131} = 1.76$, $p = 0.19$). Further, females consumed 13.4% larger clupeids than males, and both sexes consumed bigger items as SOI values increased (Table 2, Fig. 5), and this effect of the SOI did not differ between the sexes ($F_{2,88} = 0.22$, $p = 0.64$). Each additional unit of atmospheric pressure differential (hPa) across the Pacific Ocean meant a decrease of 0.6 cm in the length of engraulids and an increase of 3.0 cm in the length of clupeids taken by boobies.

Table 1. *Sula neboxii*. Fish regurgitated by male and female boobies over 5 reproductive seasons (1981 to 1985). Frequencies calculated from a total of 907 fishes and 312 regurgitations containing them. All values shown as percentages (parentheses)

	Females		Males		Overall totals	
	Regurgitations	Fishes	Regurgitations	Fishes	Regurgitations	Fishes
Clupeidae	95 (30.5)	200 (22.0)	29 (9.3)	46 (5.1)	124 (39.7)	246 (27.1)
<i>Opisthonema libertate</i>	50 (16.0)	60 (6.6)	13 (4.2)	14 (1.5)	63 (20.2)	74 (8.2)
<i>Opisthonema medirastre</i>	1 (0.3)	1 (0.1)	0	0	1 (0.3)	1 (0.1)
<i>Opisthonema</i> sp.	29 (9.4)	82 (9.0)	10 (3.2)	17 (1.9)	39 (12.5)	99 (10.9)
Genus unknown	15 (4.8)	57 (6.3)	6 (1.9)	15 (1.7)	21 (6.7)	72 (7.9)
Engraulidae	78 (25.0)	352 (38.8)	40 (12.8)	200 (22.1)	118 (37.8)	552 (60.9)
<i>Cetengraulis mysticetus</i>	54 (17.3)	138 (15.2)	26 (8.3)	60 (6.6)	80 (25.6)	198 (21.8)
<i>Cetengraulis</i> sp.	8 (2.6)	112 (12.3)	4 (1.3)	37 (4.1)	12 (3.9)	149 (16.4)
Genus unknown	16 (5.1)	102 (11.3)	10 (3.2)	103 (11.4)	26 (8.3)	205 (22.6)
Scombridae	14 (4.5)	21 (2.3)	4 (1.3)	5 (0.5)	18 (5.8)	26 (2.9)
<i>Scomber japonicus</i>	7 (2.3)	7 (0.8)	2 (0.6)	2 (0.2)	9 (2.9)	9 (1.0)
<i>Scomber</i> sp.	4 (1.3)	6 (0.6)	0	0	4 (1.3)	6 (0.7)
<i>Auxis</i> sp.	1 (0.3)	1 (0.1)	0	0	1 (0.3)	1 (0.1)
Genus unknown	2 (0.6)	7 (0.8)	2 (0.6)	3 (0.3)	4 (1.3)	10 (1.1)
Carangidae	23 (7.4)	37 (4.1)	17 (5.5)	30 (3.3)	40 (12.8)	67 (7.4)
<i>Decapterus hypodus</i>	10 (3.2)	10 (1.1)	9 (2.9)	11 (1.2)	19 (6.1)	21 (2.3)
<i>Decapterus</i> sp.	11 (3.6)	20 (2.2)	7 (2.2)	13 (1.4)	18 (5.8)	33 (3.6)
<i>Selar crumenophthalmus</i>	0	0	1 (0.3)	1 (0.1)	1 (0.3)	1 (0.1)
Genus unknown	2 (0.6)	7 (0.8)	0	5 (0.6)	2 (0.6)	12 (1.3)
Stromatidae	0	0	3 (1.0)	6 (0.7)	3 (1.0)	6 (0.7)
<i>Prepilus simillimus</i>	0	0	2 (0.6)	5 (0.6)	2 (0.6)	5 (0.6)
Genus unknown	0	0	1 (0.3)	1 (0.1)	1 (0.3)	1 (0.1)
Sphyraenidae	0	0	1 (0.3)	1 (0.1)	1 (0.3)	1 (0.1)
<i>Sphyraena</i> sp.	0	0	1 (0.3)	1 (0.1)	1 (0.3)	1 (0.1)
Sciaenidae	0	0	2 (0.6)	2 (0.2)	2 (0.6)	2 (0.2)
Albulidae	1 (0.3)	1 (0.1)	0	0	1 (0.3)	1 (0.1)
Hemiramphidae	1 (0.3)	1 (0.1)	0	0	1 (0.3)	1 (0.1)
Belanidae	1 (0.3)	2 (0.2)	0	0	1 (0.3)	2 (0.2)
Unidentified	1 (0.3)	1 (0.1)	2 (0.6)	2 (0.2)	3 (1.0)	3 (0.3)



Number of prey fish

The effect of the SOI on the number of prey regurgitated depended on the sex of the booby (GLM—SOI: $\beta = -0.092 \pm 0.036$, deviance_{3,308} = 7.44, $p = 0.11$; sex: $\beta = 0.16 \pm 0.13$, deviance_{3,308} = 0.60, $p = 0.65$; SOI \times sex: $\beta = 0.15 \pm 0.08$, deviance_{3,308} = 11.70, $p = 0.04$). The more positive the SOI values in December to May, the fewer fishes regurgitated by females and the more fishes regurgitated by males (Fig. 6); females regurgitated 50% fewer fishes than males in

Fig. 1. *Sula neboxii*. Proportions of fish families in prey of male (M) and female (F) boobies at Isla Isabel over 5 reproductive seasons (1981, $n = 23, 55$; 1982, $n = 13, 31$; 1983, $n = 13, 37$; 1984, $n = 23, 39$ and 1985, $n = 26, 52$ male and female regurgitations, respectively)

Table 2. *Sula nebouxii*. Linear models examining the relationship between dietary parameters of Isla Isabel blue-footed boobies over 5 yr and the Southern Oscillation Index (SOI) from December to May and sex. **Bold:** explanatory variables (either SOI, sex, or both) that were retained in each minimal adequate model

Dietary parameter	SOI December–May			Sex			R ²
	Slope ± SE	F	p	Slope ± SE	F	p	
Standardized niche breadth	0.077 ± 0.033	5.40	0.049	–	0.26	0.63	0.33
Proportion of samples with Engraulidae	–0.11 ± 0.023	24.99	0.001	–	0.74	0.42	0.73
Proportion of samples with Clupeidae	0.061 ± 0.018	11.87	0.011	–0.15 ± 0.064	5.70	0.048	0.63
Mean length of engraulid prey	–0.58 ± 0.083	49.78	<0.001	–1.06 ± 0.36	8.75	0.004	0.31
Mean length of clupeid prey	3.00 ± 0.48	39.02	<0.001	–1.99 ± 0.61	10.73	0.001	0.34

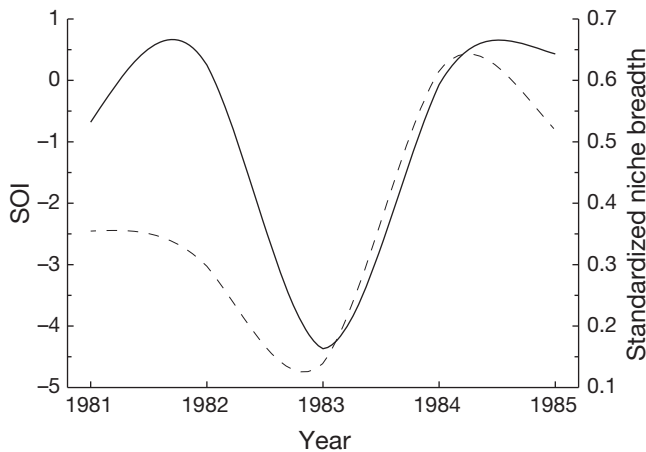


Fig. 2. *Sula nebouxii*. Mean Southern Oscillation Index (SOI) in December to May (solid line) and standardized niche breadth (dashed line) of male and female blue-footed boobies on Isla Isabel over 5 breeding seasons. Negative SOI values indicate El Niño conditions, and large values of niche breadth indicate high dietary diversification

the non–El Niño conditions of 1985 and 57% more fishes than males during the strong El Niño event of 1983.

DISCUSSION

Our findings indicate that in the warm eastern tropical Pacific, ENSO may drive inter-annual variation in diet composition, prey size and the number of prey consumed by the blue-footed booby *Sula nebouxii*, an apical predator specialized in plunge-diving for small pelagic fish. Similar associations between ENSO and seabird dietary parameters have been documented in the Antarctic and temperate waters of the Pacific and Atlantic Oceans, as well as in the warm waters of the tropical western Pacific and the western Indian Ocean (references in 'Introduction').

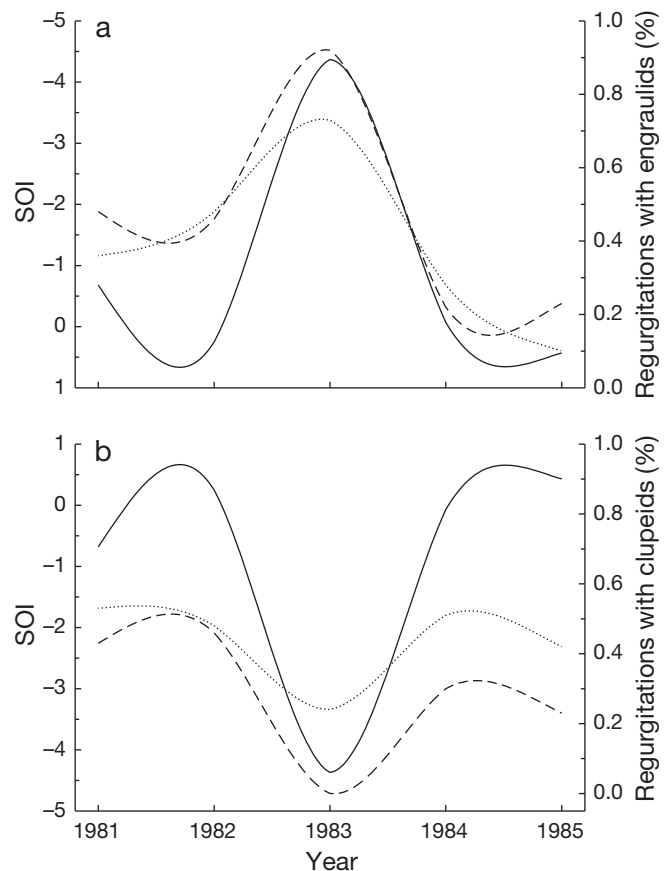


Fig. 3. *Sula nebouxii*. Mean Southern Oscillation Index (SOI) in December to May (solid line) and proportion of regurgitations of male (dashed line) and female (dotted line) boobies containing (a) engraulids (anchovies) and (b) clupeids (sardines and herrings). Panel a uses a descending scale for SOI (large negative values indicate El Niño conditions) and an ascending scale for the proportion of samples containing engraulids to better show the strength of their negative association

The diet of Isla Isabel boobies apparently reflects changes in the abundances of pelagic fishes in the waters surrounding the colony. Diet was less diverse when SOI was negative in the breeding season, indi-

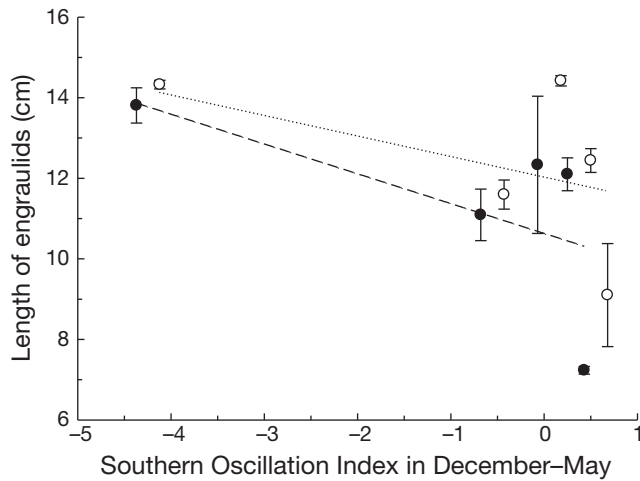


Fig. 4. *Sula neboxii*. Southern Oscillation Index in December to May and mean standard length (\pm SE) of engraulid fishes regurgitated by 43 male (dashed line, ●) and 91 female (dotted line, ○) boobies over 5 yr. To simplify visualization, we show females' values slightly displaced

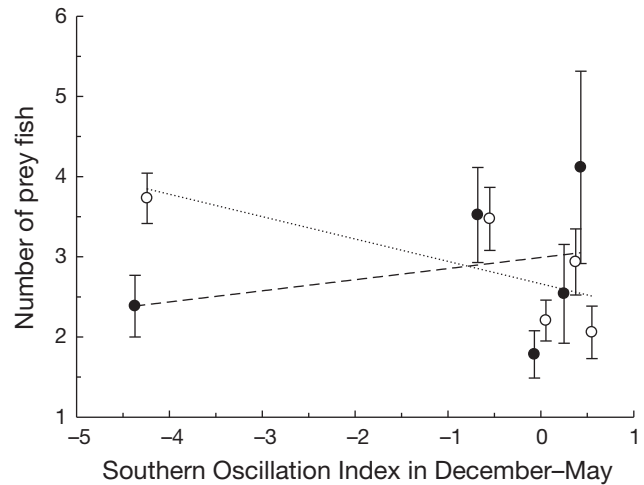


Fig. 6. *Sula neboxii*. Southern Oscillation Index in December to May and mean (\pm SE) number of fishes regurgitated by male (dashed line, ●) and female (dotted line, ○) boobies during 5 yr

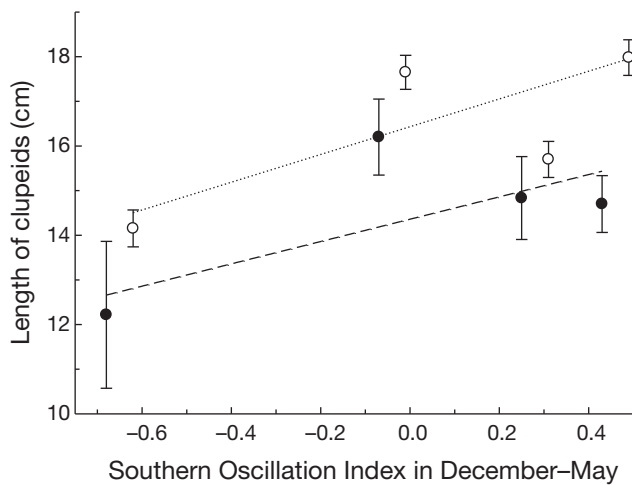


Fig. 5. *Sula neboxii*. Southern Oscillation Index in December to May and mean standard length (\pm SE) of clupeid fishes regurgitated by 16 male (dashed line, ●) and 75 female (dotted line, ○) boobies over 4 yr (data on clupeid lengths were not available in 1983). To simplify visualization, we show females' values slightly displaced

cating that prey options are reduced during El Niño events, probably because warm water conditions and reductions in ocean productivity have similar negative impacts on diverse fish populations. Reductions in dietary diversity related to El Niño have also been observed in a dietary generalist, the Peruvian petrel *Pelecanoides garronii*, in the temperate south-eastern Pacific (García-Godos & Goya 2006); hence, decrements in prey options associated with El Niño can affect both specialist and generalist seabirds. Moreover, the proportions of regurgitations contain-

ing anchovies and herrings, the prey most consumed by these boobies over the years, reflect alternations in dominance between these fishes that are driven by ENSO-related fluctuations in sea-surface temperature (Vallarta-Zárate 2010). Anchovies are more abundant than herrings in commercial catches during warm El Niño episodes and vice versa during cold La Niña events (Vallarta-Zárate 2010), and the presence of these fishes in booby regurgitations matches this pattern in relation to ENSO. Boobies apparently track and feed on more abundant or energetically valuable prey such as anchovies and herrings (Sidwell 1981, Becker et al. 2007) according to their fluctuating relative abundances, and incorporate other less preferred or less abundant fishes (e.g. jacks, family Carangidae and mackerels, family Scombridae) into their diet when they become available in more productive years; this pattern is commonly observed in pelagic seabirds (Ainley et al. 1996, Litzow et al. 2002, Wanless et al. 2005; but see Zavalaga et al. 2007).

Fluctuations in the relative local abundance of anchovies and herrings may be due to differences in their temperature preferences (Lluch-Belda et al. 1992b) and migratory capacities (Bakun & Broad 2003). During warm El Niño events, when anchovies proliferate in the region of our study, herrings migrate northward to the colder waters of the Gulf of California (where they become more abundant in commercial catches) in order to complete their maturation and reproduction (Lluch-Belda et al. 1986, Cisneros-Mata et al. 2000), whereas during cold La Niña events, herrings dominate and anchovy stocks de-

cline (Jacob-Cervantes et al. 2005, Vallarta-Zárate 2010). Herrings, similar to many other clupeids, are able to migrate large distances, whereas anchovies tend to range around a fixed geographic center and migrate less than their clupeid counterparts (Lluch-Belda et al. 1992a, Bakun & Broad 2003). Thus, reductions in the abundance of herrings around Isla Isabel during El Niño events could be partially explained by their northerly migration, whereas reductions in the abundance of anchovies during cold La Niña conditions are possibly associated to reductions in recruitment. The causes of alternations between engraulid and clupeid fishes are imperfectly understood (Bakun & Broad 2003) and are currently under scrutiny in the study region (Jacob-Cervantes 2010) and in other productive regions such as the Japanese, California, Humboldt and the Benguela Current systems (reviews by Lluch-Belda et al. 1992a, Bakun & Broad 2003).

Fluctuating relative abundance of anchovies and herrings was also confirmed by the size of specimens observed in booby regurgitations. Isla Isabel boobies fed on larger anchovies and smaller herrings when the SOI was negative, and on smaller anchovies and larger herrings when the SOI was positive, suggesting that anchovies and herrings develop optimally in different oceanographic conditions. However, only partial evidence is available for this hypothesis. El Niño conditions elicit a reduction in the number and body condition of herrings that attain sexual maturity (Vallarta-Zárate 2010), but whether anchovies develop better than herrings during these same conditions is unclear. On another note, the smallest anchovies and herrings preyed upon by Isla Isabel boobies were smaller than those recorded in commercial catches, even smaller than specimens caught in early stages of maturation, whereas the largest fishes in booby regurgitations matched mature fishes in commercial catches in size (see Jacob-Cervantes et al. 2001, Jacob-Cervantes 2010). This result suggests that boobies feed on diverse life stages of anchovies and herrings, although consumption of juveniles (rather than adults in poor body condition) still needs to be confirmed.

While dietary diversity and the proportion of samples containing anchovies did not differ between the sexes, females consumed herrings more frequently than males did across the 5 yr and consistently fed on larger herrings and anchovies than males did. These differences are likely due to body size: females are 5 to 10% larger and 30 to 32% heavier than males (Torres & Drummond 1999). Females may reach higher flight speeds and forage farther and over

larger areas than males (Weimerskirch et al. 2009), and these abilities may allow them to encounter migratory herrings more often than males. Heavier bodies may also allow females to dive deeper than males (Ropert-Coudert et al. 2004, Zavalaga et al. 2007), increasing their chance of reaching the larger anchovies and herrings found at greater depth (Petitgas et al. 2004, Didrikas 2005). Besides these consistent differences associated with sexual size-dimorphism, occasional sexual differences may emerge in periods of low and high food availability (Castillo-Guerrero & Mellink 2010). At Isla Isabel, females captured more fishes than males during warm El Niño events, but fewer fishes than males during cold La Niña episodes, probably implying that each sex is more efficient than the other under different oceanographic conditions. Such differential flexibility, if complementary, could reduce variance in offspring provisioning in highly variable environments (Ishikawa & Watanuki 2002, Castillo-Guerrero & Mellink 2010), a mechanism analogous to the variability among cells or species within a functional group in their responsiveness to a specific stimulus that enhances resilience of biological systems to environmental changes (Elmqvist et al. 2003). Superior flexibility of either sex is not implied, and, indeed, the sexes do not differ in their annual survival (Oro et al. 2010).

Changes in dietary parameters of blue-footed boobies appear to indicate changes in oceanographic conditions associated to ENSO and may inform on the status of populations of anchovies and herrings, 2 commercially important fishes in the region. Seabird foraging parameters have been proven to be good indicators of fish stocks and major climatic and oceanographic fluctuations in many other regions (references in 'Introduction'), and our data suggest that dietary parameters of blue-footed boobies could be similarly useful in the warm eastern tropical Pacific. As in other seabirds, the reliability of these boobies as indicators of marine resources may depend on such factors as the spatial and temporal scales of environmental fluctuations and changes in fish stocks (reviewed in Piatt et al. 2007a, Einoder 2009), as well as on the diversity of the boobies' responses to these fluctuations and changes (Grémillet & Charmantier 2010). Differential responses of the sexes could be particularly relevant (Weimerskirch et al. 2009, Castillo-Guerrero & Mellink 2010), and sex-specific dietary data could be required.

Inter-annual variations in diet, including prey taxa and sizes, could mediate the negative impacts of El Niño on breeding participation, chick growth and

breeding effort and success at Isla Isabel (Ancona et al. 2011). Although herrings and anchovies have similar protein contents (Ariyawansa 2000) and the energetic value of both increases with body size and mass (Hartman & Brandt 1995, Tirelli et al. 2006), herrings have a greater caloric value than anchovies (roughly 5700 versus 4900 cal g⁻¹ dry weight; Sidwell 1981, Gunderson & Dygert 1988, Becker et al. 2007) and many other fish species (Browne et al. 2011). During warm episodes, the boobies consume fewer and smaller herrings and more and larger anchovies, implying a decline in nutrition. Elsewhere, El Niño effects on seabird reproduction have been linked to reduction in the availability of high-energy prey fish (e.g. Baird 1990, Österblom et al. 2008 and references therein) or reduction in the energy content of high-energy prey whose availability was not necessarily affected (Wanless et al. 2005, Jodice et al. 2006, Sorensen et al. 2009). However, El Niño also affects regional weather patterns, which can influence seabird reproduction by altering foraging, breeding and developmental environments (Schreiber 2002), so further study will be required to unravel the mechanisms of booby breeding failures.

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