

ECOLOGY

Warm oceanographic anomalies and fishing pressure drive seabird nesting north

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Parallel studies of nesting colonies in Mexico and the United States show that Elegant Terns (*Thalasseus elegans*) have expanded from the Gulf of California Midriff Island Region into Southern California, but the expansion fluctuates from year to year. A strong inverse relationship between nesting pairs in three Southern California nesting areas [San Diego saltworks, Bolsa Chica Ecological Reserve, and Los Angeles Harbor (1991 to 2014)] and Isla Rasa in the Midriff (1980 to 2014) shows that terns migrate northward when confronting warm oceanographic anomalies (>1.0°C), which may decrease fish availability and hamper nesting success. Migration pulses are triggered by sea surface temperature anomalies localized in the Midriff and, secondarily, by reductions in the sardine population as a result of intensive fishing. This behavior is new; before year 2000, the terns stayed in the Midriff even when oceanographic conditions were adverse. Our results show that terns are responding dynamically to rapidly changing oceanographic conditions and fish availability by migrating 600 km northwest in search of more productive waters.

INTRODUCTION

Large-scale climatic and oceanographic anomalies such as El Niño events affect marine organisms chiefly through variations in marine productivity that influence the whole food web (1–5), affecting ecosystem dynamics and regional economies (6–9). Warm oceanographic anomalies drive the thermocline down and decrease the intensity of upwelling, causing reduction of both marine productivity and fish availability for seabirds, inducing their breeding failure (4, 5, 10–13). Consequences are particularly noticeable in island seabird colonies such as Isla Rasa in the Gulf of California's Midriff region (3). Rasa, a protected area, has been regarded for decades as the nesting site of more than 95% of the world population of Elegant Terns (*Thalasseus elegans*) (14, 15). Most studies have assumed a strong fidelity of nesting seabirds to this colony, even during anomalous seasons when there was not enough fish to feed their chicks (3, 16).

History of Elegant Tern nesting distribution

Despite their apparently constant nesting in Isla Rasa during the second half of the 20th century, the range and distribution of nesting Elegant Terns have substantially varied during the last 150 years. Federico Craveri, who visited the Midriff Islands in 1856 and spent 5 days in Rasa during the typical peak period nesting for terns (23–28 April), did not mention in his detailed diary the presence of terns in Rasa (17, 18). Thayer (19) reported terns nesting in Cerralvo in April 1910, some 600 km south of Rasa. Bent (20) described the terns' breeding range as restricted to the islands of San Pedro Mártir and Cerralvo, both south of Rasa. Mailliard (21) reported finding only three Elegant Tern nests on Isla Rasa on 21 April 1921 while finding, in contrast, more than 3000 nesting birds 5 days later on a flat portion of Isla San Jorge, the Gulf's northernmost rocky island. He attributed the low numbers of terns in Rasa to "eggs from the mainland who gathered the eggs to sell for food." Bancroft (22) reported the presence of nest-

ing Elegant Terns on sandy islands near the mouth of Scammon's Lagoon and on Isla San Roque off the southern coast of the Vizcaíno Peninsula, both sites on the Pacific side of Baja California, but also reported nesting terns on San Jorge and on Rasa in the Gulf (23). It was not until the publication of L. W. Walker's account of extraordinary aggregations of nesting seabirds in Rasa (24) that the scientific community acknowledged that almost the entire world population of Elegant Terns congregated on Rasa for nesting.

Black rats (*Rattus rattus*) and house mice (*Mus musculus*) apparently were introduced to Isla Rasa during guano mining operations in the late 19th century. These animals depredated the eggs and small chicks of seabirds during the nesting season. Guano mining ended in the early 20th century, but commercial egg harvesting started shortly thereafter. At its peak, some 500,000 eggs were extracted from Isla Rasa by local fishermen (25). Egg harvesting was declared illegal in the 1960s and ended in the early 1980s, but rodents remained a problem until 1993, when a program to eradicate them from the colony was successfully carried out by the late J. Ramírez in collaboration with E.V. (26). By early 1995, complete eradication of rats and mice had been achieved, and the population of seabirds on the island started to recover rapidly with new colonies of Elegant Terns being observed in the neighboring Isla Cardonosa in 2004 and again in 2008, with about 1000 and 15,000 nests in each season, respectively. However, these colonies did not last long, possibly as a result of the competition for food from the large colony in Rasa, because food depletion tends to develop in the vicinity of large seabird colonies (27–31).

Mellink (32) found that during the two strong El Niño events of the 1990s (1992 and 1998), nesting Elegant Terns were found on the muddy plains of Isla Montague, in the delta of the Colorado River, where they had not been previously seen. Mellink argued that the presence of Elegant Terns in the Upper Gulf reflects the impoverished conditions in the Gulf's Midriff during El Niño events rather than the existence of especially attractive conditions in the Colorado River estuary, where nutrient suspension is driven by tidal mixing rather than by deep-water upwelling but where the resulting turbidity makes it difficult for plunging seabirds to fish.

The northward expansion of nesting Elegant Terns, specifically driven by unfavorable anomalies in the Midriff, has also reached the coasts of California. Gallup and Bailey (33) discovered 31 pairs of Elegant

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Terns nesting in the saltworks of San Diego Bay in May 1959, a place where they had not been previously known to nest. The colony maintained steady numbers of a few hundred through the 1980s (33, 34) but started growing rapidly after 1993, reaching more than 22,275 in 2014. Additional nesting attempts adjacent to San Diego Bay included two nests at Zuñiga Point in 1998 (35), one nest at Chula Vista Wildlife Reserve in 2004, and five nests in 2014. New nesting colonies continued to appear northward with the establishment of a colony at Bolsa Chica Ecological Reserve in Huntington Beach, Orange County, in 1987 (36) and a second one at the tip of Pier 400 Container Terminal in Los Angeles Harbor in 1998 (37), reaching a regional total of more than 50,000 nests in 2014. In these areas, the stability and growth of the tern colonies was likely due to the protection granted by their protected area status, as has happened with other tern species in other areas in California (38), and also to a reliable availability of small pelagic fish.

Elegant Terns feed on small pelagic fish and are sensitive indicators of sardine (*Sardinops sagax*) availability to other seabirds and of fishery catches, accurately reflecting ecosystem conditions in the Midriff (5, 16, 39) and also in the Pacific coast of Southern California (34, 40). Here, we examine the expansion of nesting Elegant Terns from the Midriff into Southern California and analyze its relationship to (i) the success of conservation measures in the tern's nesting grounds, (ii) shifting ocean conditions and frequent pulses of high sea surface temperatures (SSTs) in the Gulf of California's Midriff region, and (iii) the industrial fishery of Pacific sardines in the Gulf of California.

RESULTS

Population growth and variation

The number of nesting pairs on Isla Rasa during normal, non-anomalously warm years increased from 15,038 in 1980 to more than 100,000 in 2013 (Fig. 1A). Between 1980 and 1994, the number of nests grew at a mean annual rate of 0.046 (SE ± 0.009 ; $r^2 = 0.69$; $F_{2,10} = 11.3$, $P = 0.003$), increasing after 1995 (when introduced rodents were eradicated) to 0.077 (SE ± 0.007 ; $r^2 = 0.46$; $F_{2,12} = 10.93$, $P = 0.006$), a significantly higher growth rate ($t = 3.94$; $P = 0.0004$). The variance around the trend also increased ($F_{12,10} = 29.9$; $P < 0.0001$), in part because of the increased difference in nesting pairs between normal and anomalously warm years: whereas before 1995, a warm SST event produced nesting declines of 35 to 50%, after 1995, high SSTs in the Midriff brought collapses of almost 100%.

Since 1991, when systematic recording of nesting pairs began, the California population (which, for the purpose of this work, includes all birds nesting in the three areas of San Diego, Bolsa Chica, and Los Angeles Harbor described above) has been increasing during normal (that is, non-anomalously warm) years at a mean annual rate of 0.139 (SE ± 0.05 ; $r^2 = 0.58$; $F_{2,14} = 7.0$, $P = 0.013$; see Fig. 1B). From year 2000 onward, whenever there has been a nesting failure (that is, when the terns either did not lay eggs or abandoned the nesting colony before incubation was completed) in the Midriff, nest numbers in the coastal California colonies have peaked, particularly in San Diego (2003, 2009, 2010, and 2014; Fig. 1, C and D), yielding a negative correlation between

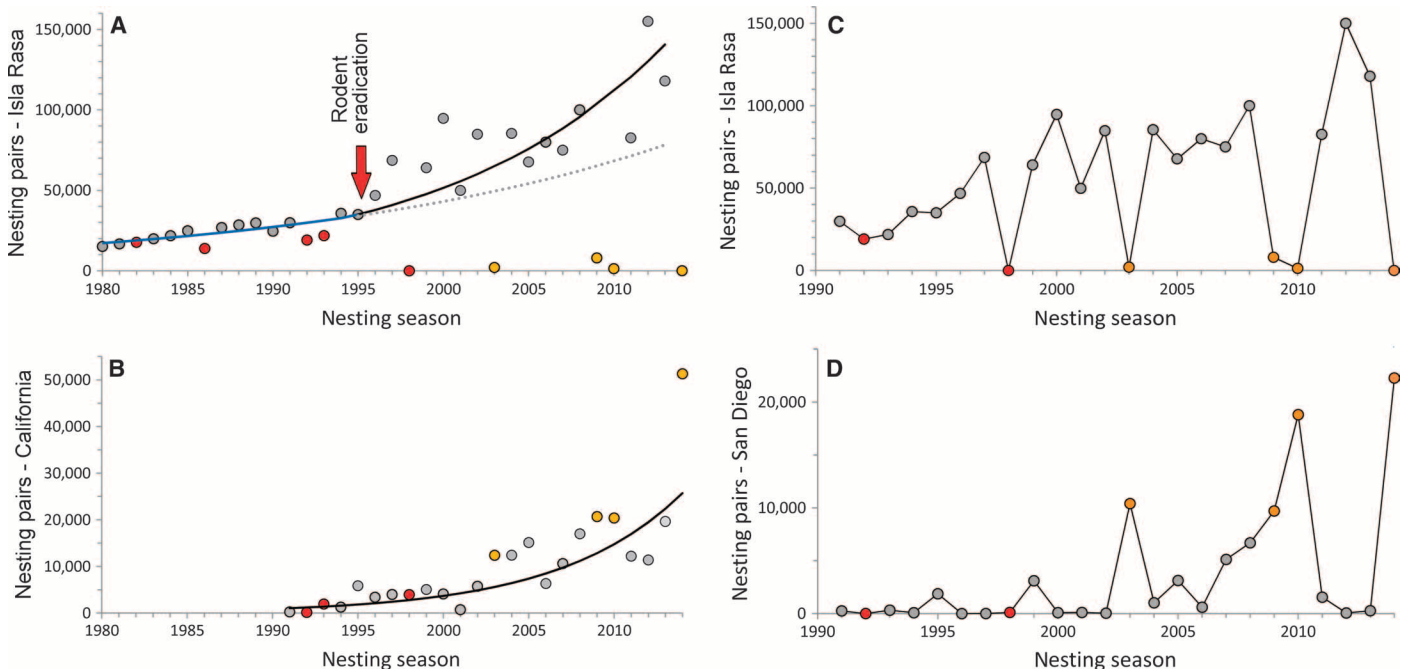


Fig. 1. Elegant Tern population data. Population growth rates: (A) Growth rate of nesting pairs on Isla Rasa between 1980 and 2014. Before rodent eradication in 1995, mean annual growth rate in the Midriff was 0.046, increasing after to 0.077. The dotted line projects the pre-1995 trend to highlight the difference with the post-1995 real values. (B) The growth rate of nesting pairs after 1991 in all three California colonies taken together was 0.14. In both models, only the data points from normal years (gray symbols) were taken into account to fit the equations. Relationship between Isla Rasa and San Diego Bay: (C and D) Elegant Tern colony size (nesting pairs) in Isla Rasa (C) compared against colony size in San Diego Bay (D). In all plots, yellow points indicate years in which nesting collapsed in the Midriff, and red dots indicate strong El Niño years in the Pacific Ocean.

Rasa and San Diego ($r = -0.78, P = 0.001$; fig. S1). Although historically, nesting terns stayed on Rasa during anomalously warm years when the availability of pelagic fish was low, after year 2000 whenever the SST became anomalously warm (over 1.0°C), the birds have left in search of alternative nesting sites.

The effect of oceanographic conditions

This migratory pattern is related to warm SST anomalies in the Midriff Region during spring (Fig. 2B). Five years with high SSTs were observed in the Midriff Region since 1995 (Fig. 2B and fig. S2). The first one, 1998,

was a strong El Niño year with strong impacts throughout the eastern Pacific (Fig. 2F); the other four—2003, 2009, 2010, and 2014—were periods in which the SST anomaly was high in the Midriff (1.1° to 1.9°C) but lower along the Pacific (0.2° to 0.8°C ; Fig. 2 and fig. S2). Although these four periods were not part of strong El Niño events in the larger Pacific Ocean, they all involved abandonment of nesting colonies in Rasa before completion of the incubation or no colony establishment at all, and with the exception of 2009, they were all seasons in which the thermal anomaly between February and April was higher in the Midriff Region than in the Pacific. The effect of localized warm SST anomalies in the

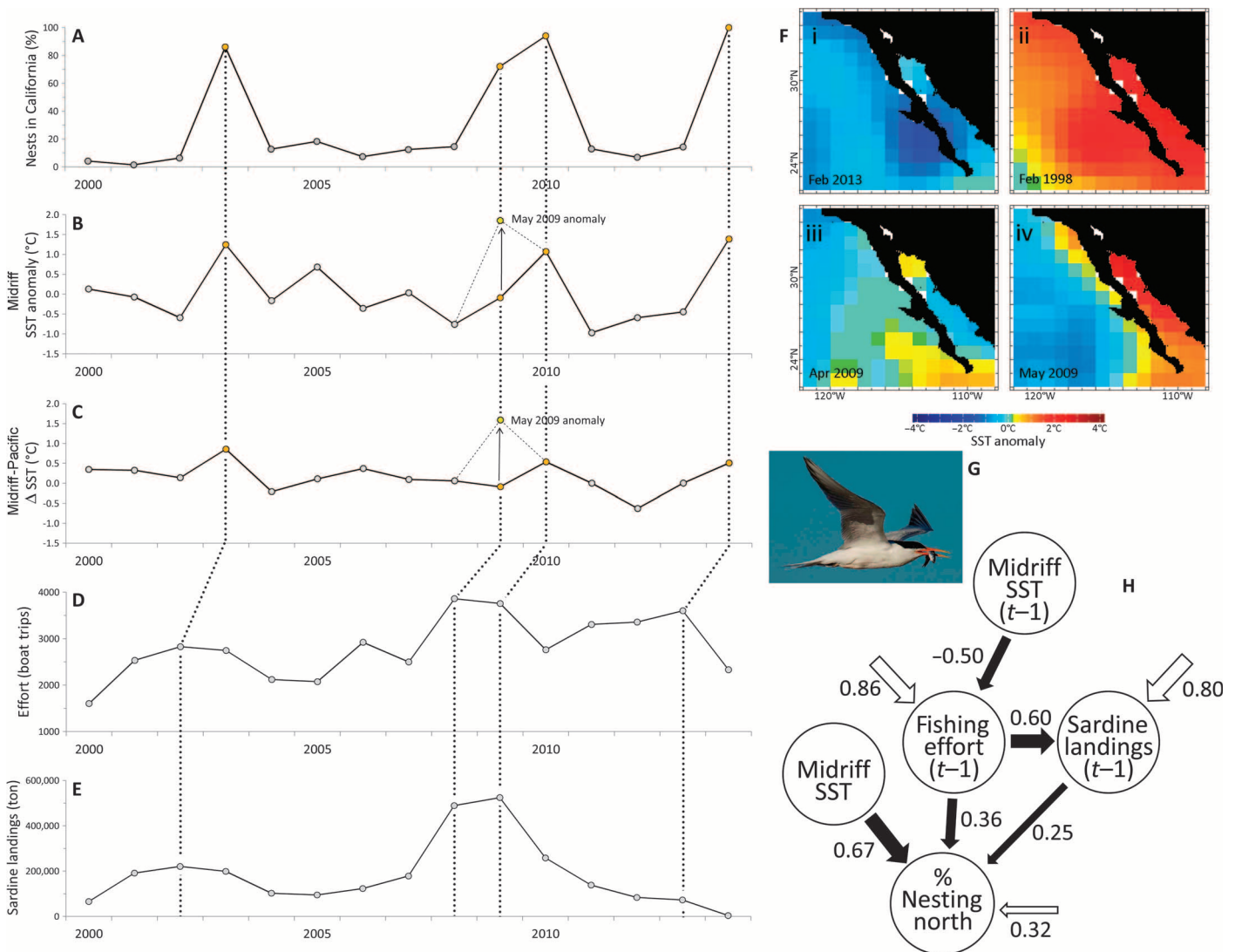


Fig. 2. Time series correlations between oceanographic variables, fisheries, and Elegant Tern nesting populations. (A) Proportions of Elegant Tern nests established in California in relation to total nests counted. (B) Midriff winter-spring SST anomaly. (C) SST difference between the Pacific and Midriff. (D) Fishing effort by the Sonora fleet. (E) Total sardine landings. (F) SST anomalies in the Gulf of California and the Pacific. Top images depict the general winter-spring conditions during normal and El Niño cycles: (i) February 2013, a highly productive year with cool surface temperatures; (ii) February 1998, the most intense El Niño of the last decades. Lower images show the formation of a local anomaly during a non-El Niño year: (iii) April 2009, an apparently normal year, transitioned in (iv) May 2009 into a high SST condition in the Gulf of California that forced most of the nesting terns to abandon the area. (G) Elegant Tern carrying a Northern Anchovy to feed its chick (photo by P. Robles-Gil). (H) Network of significant path relationships between variables: Numerical values with black arrows indicate path coefficients; white arrows indicate the lumped influence of unidentified extraneous variables. Variables identified with label “ $t - 1$ ” have a 1-year-lag influence on the decision by nesting terns to migrate away from the Midriff.

Midriff was particularly evident during the spring of 2009. In this year, the anomaly was relatively low in the Midriff from February to April, and birds started to nest; however, in late April, surface temperatures in the Midriff rapidly increased (Fig. 2F), resulting in the abandonment of the tern nesting colonies at Rasa in May in coincidence with a notable increase in the size of the California nesting colonies, located in areas adjacent to the Southern California Bight, where waters that year were much cooler. The nest numbers on Rasa after year 2000 show a significant negative correlation with both Midriff SST values and the SST difference between the Midriff and the Pacific ($r = -0.68$, $P = 0.003$; and $r = -0.53$, $P = 0.02$), but no significant correlation with the Southern Oscillation Index (SOI) that measures the intensity of large-scale ENSO anomalies.

The impact of fisheries

To test the effect of fishing added to that of local SST anomalies, we analyzed the proportion of total nests recorded in the California colonies from year 2000 onward against both Midriff SST and sardine fishery data (total landings and fishing effort in boat trips). The proportion of the total (Rasa + California) Elegant Tern pairs nesting in the California colonies in the years when the SST anomaly in the Midriff area exceeded 1°C (years 2003, 2009, 2010, and 2014) was always above 70%, whereas for the rest of the nesting seasons, the proportion of the total nests established in the California colonies has never exceeded 20% (time series correlation $r = 0.78$, $P = 0.0003$; Fig. 2, A and B), but also in coincidence with one-season-lagged fishing effort. That is, all seasons in which the birds abandoned Rasa were preceded by seasons of high fishing effort (more than 3600 boat trips for 2008, 2009, and 2013, and 2827 boat trips for 2002, about 1.5 times the 45-year average for the fishery of 2413 trips by the commercial fleet; $r = 0.66$, $P = 0.004$; Fig. 2D). Similarly, the proportion of pairs nesting in California was correlated with the total sardine landings of the previous year ($r = 0.56$, $P = 0.016$; Fig. 2E). In turn, fishing effort was negatively correlated with the SST anomaly during the same fishing season ($r = -0.50$, $P = 0.03$), showing that the fleet tends to increase fishing effort when upwelling is strong. A path analysis identified significant functional pathways between variables (Fig. 2H), revealing that warm SST anomalies are the main factor determining the proportion of tern population nesting away from the Midriff (path coefficient $\phi = 0.67$, $P < 0.0001$), but that fishing effort and total landings during the previous year also play a significant role ($\phi = 0.36$, $P = 0.006$, and $\phi = 0.25$, $P = 0.03$, respectively).

DISCUSSION

Range extension and population growth

The rapid growth observed in the Isla Rasa nesting tern population during years when the SST anomaly has been low ($<1.0^{\circ}\text{C}$) is associated with its protected status, the continued presence of researchers since 1980 (which deters egg poachers), and rodent eradication in 1995 (26) eliminating egg and chick predation. As colonies grow, seabirds become less successful in reproduction because of food depletion close to the nesting grounds (27–29). Increasing competition for food, especially for sardines (one of the tern's preferred food items), may have contributed to the birds searching for alternate sites along the California coast: the 1991 to 1993 period, when the first massive sardine fishery collapse occurred in the Midriff (7, 41), coincided with a reduction of sardine in the Elegant Tern diet (5) and with a period of fast increase of

Elegant Tern nests in California (250 to 5870, a 23-fold increase in 3 years that may only be achieved through immigration). In the last decades (1991 to 2014), growth rate in the total nest number of the three California colonies has averaged 13.9%, a value never observed in the wild for seabirds (42) and that almost doubles that of the Midriff (7.7%), indicating that migratory spillover is playing a central role in the northward extension of nesting colonies.

The effect of local SST anomalies

Furthermore, there has been a marked regime shift in the pattern of the anomalies and in the way Elegant Terns react to anomalies in the Midriff. Before year 2000, all warm anomalies observed in the Midriff Region followed by nesting failures of Elegant Terns in Isla Rasa (when terns did not establish nests at all, abandoned the colonies before hatching of the chicks, or had massive chick mortality) were part of large-scale El Niño events (for example, 1992 and 1998), and indices such as SOI were accurate predictors of nesting success (fig. S2A). After year 2000, the numbers of successfully nesting terns in Rasa became uncoupled from large-scale El Niño indices, and local SST anomalies became the most accurate predictors of nesting success (table S3). Simultaneously, more than 70% of the total Elegant Tern nesting population started to be observed in the three California colonies, but especially in the San Diego colony (Fig. 1D), during years in which the SST anomaly in the Midriff was above 1.0°C . By contrast, in years in which the anomaly in the Midriff was low ($<1.0^{\circ}\text{C}$), less than 20% of the total nesting population was observed in the three California colonies.

The impact of fishing effort

Fishing effort and total sardine landings during the previous season also play a significant role in determining the proportion of terns nesting in the California colonies. Terns respond to fish availability; the extraction of a great proportion of the reproductive sardine population driven by high fishing efforts may have an impact on availability for seabirds during the following season. Although there is no sardine stock estimation for the Gulf, some authors (43) have shown that sardine harvest rates are unsustainably high and recommend lower catch limits to avoid repeated fishery collapses. From data collected for a dietary study (16), we estimate that the amount of fish consumed per day by all the nesting birds in Rasa is ca. 100 tons, around 56% of the average catch of one fishing vessel (mean holding capacity, 180 tons) (41). Furthermore, nesting seabirds are present in the region for only 4 months each year (ca. 120 days), whereas the fleet fishes for 11 months. Thus, the fish extracted in a year by seabirds nesting on Rasa is equivalent to about 67 units of fishing effort, whereas during the 2012/2013 season, the fleet totaled 3600 units of effort, 54 times more than the amount harvested by seabirds nesting on Isla Rasa. These numbers show that the depletion of sardines due to high fishing efforts by the fleet can have a disproportionate impact on the availability of small pelagic fish for other ecosystem components.

CONCLUSIONS

In conclusion, three factors seem to be playing a role in the range changes of nesting Elegant Terns. (i) The success of conservation measures in the tern's nesting grounds both in Mexico and California has allowed an increased population growth of the species, and the exponential increase in the Isla Rasa colony in particular seems to be pushing

reproductive pairs onto new nesting grounds in California. (ii) Superimposed on this systematic and continuous expansion, there is a pulse-like variation in local SST conditions in the Midriff, which seems to drive nesting pairs to emigrate toward California when surface seawater in the Midriff is too warm, the thermocline is too deep, and fish availability is poor. (iii) The decision by seabirds to abandon their traditional nesting grounds in the Midriff is compounded by the fishing effort during the previous season, which further increases the proportion of Elegant Terns migrating away from the Gulf of California.

Besides an overall growth of nesting Elegant Terns in Isla Rasa and southern California colonies as a result of successful conservation efforts, since year 2000 whenever Elegant Terns have confronted poor oceanographic conditions, indicated by high SST ($>1.0^{\circ}\text{C}$) anomalies in the Midriff, breeding pairs have abandoned Rasa, a behavior that is further augmented by high sardine fishing effort and landings in the Midriff. This oscillatory migration dynamics between distant nesting sites suggests that Elegant Terns can make fast decisions and dynamically adapt to rapid changes in the global environment. The adequate maintenance of a healthy fish community in both the Gulf of California and the Pacific is an important priority that will help support healthy seabird communities, as well as healthy marine ecosystems in general and sustainable fisheries.

METHODS

Estimating colony size

Elegant Tern nesting colony size in Isla Rasa was estimated using three different methods in different years. Each year, at least one method was used, but when possible, two methods were applied for the estimation of the number of established nests. During 1986, all three methods were used, and the resulting colony size estimates proved to be quite similar and showed no significant differences (44). This study also showed that the nesting density of Elegant Terns on these flat areas is, on average, 15 nests/ m^2 . The methods used were (1) ground estimate of existing nests, (2) estimate of colony size through aerial photography, and (3) post-nesting ground measurements of colony size. Both methods 1 and 2 are accomplished with the aid of landmarks forming a grid established on the nesting areas during 1986, before the arrival of nesting birds. This grid was established by the placement of marks on the ground. The marks consisted of rocks placed every 10 m, forming a grid covering the surface of the two valleys where Elegant Terns nest in Isla Rasa: Valle de los Gallitos and Valle de la Gran Estación Central (45). Each square of the grid is 10×10 m, covering an area of 100 m^2 .

In method 1, an approximate measurement of colony size and shape is obtained through the on-site observation of the tern colonies during the early nesting season, at the time when nest establishment has ended and colonies are not growing anymore. With the estimation of the number of squares and square fractions covered by the colony, an estimate of the area covered by the colony is made (in square meters) and the surface is multiplied times 15 to estimate nest number. Method 2 is similar to method 1, but the shape and size of the colonies are estimated from aerial photos instead of on-site observation. Finally, method 3 is based on the fact that these terns defecate by standing up from their nesting position, so that a crust of guano is accumulated around the nest and forms a rim around each nest, with the final result that the outlined nests, together, clearly demarcate the area of the nesting colony. After the nesting birds and their chicks have abandoned the nesting grounds,

the area occupied by the nesting colony can easily be mapped and measured, and its surface area estimated.

Elegant Tern colony size at the San Diego saltworks was estimated from the maximum nest counts of each subcolony or nest cluster. Counts were conducted every 2 to 4 weeks by linearly moving along the 3- to 5-m-wide levees and tallying the number of nests and chicks by clutch size. After hatching of most chicks in each subcolony, counts were conducted through spotting scope or binoculars from adjacent levees to avoid exposing chicks to predation or causing panic among the crèches. Elegant Tern colony size at Bolsa Chica has been determined by C. Collins by estimating nest numbers from total counts of clusters of about 500 or fewer nests and obtaining subsamples of larger clusters (getting the count of one or more subsamples and then multiplying by the total estimated area). These counts were made with eggs or chicks in the nests. In 2011, after the nests were vacated, M. Horn and students estimated nest numbers by laying out meter tapes to encompass each of the clusters and then counting all the nests in the smaller clusters or subsamples of the larger clusters, and then multiplying by the calculated total area. In 2012 and 2013, the Bolsa Chica nesting colony was not visited, and estimates were obtained from counts of roving chicks performed by K. O'Reilly, because of the small numbers. Elegant Tern nest numbers have been estimated in most years by C. Collins, using the same method that he used at Bolsa Chica. However, in 2012 and 2013, M. Horn and students used the same meter tape method as they had used at Bolsa Chica in 2011. All seabird census data are summarized in table S1.

Modeling population growth

Population growth was fitted using a simple exponential growth function of the type $n_t = n_0 e^{rt}$, where n_t is the number of nests estimated at year t , r is the population mean annual growth rate, and n_0 is a constant estimating the population size at $t = 0$. Both parameters (the growth rate r and the initial population size n_0) were estimated by log-linear regression. The fit of the function was tested using a simple analysis of variance (ANOVA) decomposition of the residuals.

Oceanographic conditions

SST data were obtained from National Oceanic and Atmospheric Administration's Climate Program and Columbia University's International Research Institute for Climate and Society "ENSO Monitor" Web site (<http://iridl.ldeo.columbia.edu/SOURCES/Indices/ensomonitor.html>). We downloaded SST mean monthly anomaly values in degrees Celsius (46) for all months between January 1990 and July 2014 for two areas: (i) the first area is located in the Gulf of California Midriff and occupies a 1° latitude \times 1° longitude cartographic cell ranging from 29°N to 30°N and 113°W to 114°W , and (ii) the second area is located in the Pacific coast off Baja California and occupies a 1° latitude \times 1° longitude cartographic cell ranging from 29°N to 30°N and from 115°W to 116°W . Both cells are at the same latitude, only separated by the peninsula of Baja California, and occupy a similar oceanic area of $10,746 \text{ km}^2$. For both cells, and for all years, we averaged the SST anomaly from January to April, describing the local oceanographic conditions before the arrival of the nesting terns (January to early March) and during the initiation of the nesting process (late March to April). Similarly, we calculated the winter-spring values of the SOI for the whole Pacific Ocean by averaging the monthly values of the SOI index between January and April. SOI values were downloaded from Australia's Bureau of Meteorology (www.bom.gov.au/climate/current/soihtm1.shtml). All oceanographic

data are presented in table S3. Fishery data were downloaded from Mexico's National Institute of Fisheries' Pacific sardine database (<http://sardinagolfodecalifornia.org/>) (21). The information is summarized in table S2.

Statistical analyses

To quantify the relative importance of SST anomalies compared to fishery variables for nesting terns deciding to migrate away from the Midriff, we first performed a simple time series analysis with lagged correlograms, calculating the correlation between the proportion of terns nesting away from the Midriff against both oceanographic and fishery data. After identifying the most significant correlations, we performed a path analysis (47) using (i) winter-spring SST conditions in the Midriff during the season in which the birds nest, as well as (ii) fishing effort and (iii) total sardine landings during the previous season ($t - 1$), as predictors of the proportion of seabirds migrating away from the Midriff. Path coefficients were estimated from the standardized multiple regression coefficients of the model and show only the direct effect of each independent variable on the dependent variable (proportion nesting away from the Midriff) in the path model, removing indirect effects.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/1/5/e1400210/DC1>

Fig. S1. Demographic spillover from Isla Rasa into San Diego Bay.

Fig. S2. Local oceanographic anomalies in the Gulf of California.

Table S1. Elegant Tern demography data.

Table S2. Fisheries data.

Table S3. Oceanographic data.

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