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RESEARCH ARTICLE

Are seabirds' life history traits maladaptive under present oceanographic variability? The case of Heermann's Gull (*Larus heermanni*)

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ABSTRACT

Ocean warming events are becoming more frequent, with potential consequences for birds that use marine resources. We analyzed the annual population growth of Heermann's Gulls (*Larus heermanni*) through matrix-based demographic models under normal and high sea surface temperature (SST) conditions. Under stable, normal conditions, predicted population growth was ~4%, with survival of fledglings and juveniles contributing to population growth. Under high SST conditions, predicted population growth dropped to -15% and adult survival became the key factor determining species fitness. Simulations showed a declining growth rate as the frequency of warm SST anomalies increased. Heermann's Gulls can resist oceanographic anomalies of up to 1 event every 5 yr without seriously compromising their population growth rate or their individual fitness, but populations may decline rapidly if the frequency of warm-phase anomalies continues to increase, as it has done during the last decade.

Keywords: demographic predictions, El Niño, Gulf of California, Heermann's Gull, *Larus heermanni*, life history parameters, variable environments, warm ocean anomalies

¿Son mal-adaptativos los parámetros de historia de vida de las aves marinas bajo las condiciones actuales de variabilidad oceanográfica? El caso de la gaviota ploma *Larus heermanni* (Charadriiformes: Laridae)

RESUMEN

No se conocen los efectos de largo plazo sobre la fauna silvestre que resultarán del aumento en la frecuencia de eventos de incremento en la temperatura del océano. Analizamos el crecimiento poblacional anual de *Larus heermanni* por medio de modelos demográficos matriciales bajo condiciones normales y de temperatura superficial del mar (TSM) alta. Bajo condiciones normales estables se predice un crecimiento poblacional anual de cerca del 4% y sobrevivencia de volantes y juveniles contribuye de forma crítica al crecimiento poblacional. Bajo condiciones de TSM alta se predice un crecimiento poblacional anual de aproximadamente -15% y la sobrevivencia de los adultos se transforma en el factor clave para la adecuación de la especie. Las simulaciones mostraron una tasa de crecimiento descendente conforme la frecuencia de anomalías oceanográficas positivas se incrementa. *Larus heermanni* puede resistir anomalías oceanográficas positivas de hasta un evento cada cinco años sin comprometer de manera grave su crecimiento poblacional o adecuación individual, pero su tamaño poblacional puede descender rápidamente si la frecuencia de anomalías positivas continúa incrementándose de la forma en que lo ha hecho esta última década.

Palabras clave: ambientes variables, anomalías oceanográficas positivas, El Niño, gaviota ploma, Golfo de California, *Larus heermanni*, parámetros de historia de vida, predicciones demográficas

INTRODUCTION

Marine productivity of eastern boundary current marine systems is extremely high. These ecosystems support huge populations of forage fishes, which, in turn, feed large populations of larger fish, seabirds, marine mammals, and some large invertebrates. The dynamics of these marine ecosystems are significantly affected by climatic variability, especially by high sea surface temperature (SST) anomalies (Ainley et al. 1988, Sydeman et al. 2006,

Cubaynes et al. 2011). The frequency of local high SST anomalies has increased in recent years in these ecosystems, such as the system in the North Pacific Ocean and its encompassing marine basins (Freeland and Whitney 2014, Humphries et al. 2015). Since June of 2014, positive SST anomalies have prevailed in most of the North Pacific (Freeland and Whitney 2014, Ludescher et al. 2014, Yuan and Yamagata 2014) and the Gulf of California (Velarde et al. 2015b), even before the official onset of the 2015–2016 El Niño.

Seabird breeding success, particularly in these upwelling ecosystems, has long been identified as a robust indicator of climatic and ecosystem conditions (Ainley et al. 1995, Lyver et al. 1999, Sydeman et al. 2006, Humphries 2014, Humphries et al. 2015). Seabirds are long-lived homeotherms (Austad and Fischer 1991, Anderson and Apanius 2003) and adults exhibit high survival rates, although mortality at young ages is high. Small species such as the Common Tern (*Sterna hirundo*; body mass of ~120 g) may live as long as 26 yr, and pelagic seabirds such as albatrosses may live for 60–100 yr (Buckland 1982, Sagar et al. 2000, Nisbet 2001). Seabirds exhibit not only extraordinary longevity but also some of the lowest fecundities among birds (Lack 1968, Holmes and Austad 1995, Nisbet 2001), due to their relatively small clutch sizes and deferred sexual maturity (Croxall and Rothery 1991). Seabirds that nest in areas within upwelling marine systems may skip breeding in years of low food availability during unfavorable environmental fluctuations (Fisher 1976, Ollason and Dunet 1988, Wooller et al. 1989, Ainley and Boekelheide 1990, Chastel et al. 1993, 1995, Fowler 1995). Environmental stochasticity in marine environments is commonly driven by positive SST anomalies that reduce upwelling and thus decrease the abundance of small pelagic fishes or make them unavailable to seabirds by increasing the depth of the thermocline. Warm SST events may affect seabirds several times over their reproductive life, during which obtaining food can make the difference between breeding successfully or not breeding at all (Velarde et al. 2004, Vieyra et al. 2009).

In the Midriff Islands region of the Gulf of California, past large-scale El Niño events (also called El Niño–Southern Oscillation [ENSO] events) during the springs of 1983, 1988, 1992, and 1998 triggered declines in the availability of forage fishes, leading to massive nesting collapses for the seabirds that depend on these fish (Velarde and Ezcurra 2002, Velarde et al. 2004). In 2003, a mild El Niño season, a severe nesting crash was recorded for seabirds nesting on Isla Rasa in the Midriff Islands (Velarde et al. 2015b). Similar collapses followed in 2009, 2010, 2014, 2015, and 2016. Three of these unsuccessful seasons (2009, 2014, and 2015) corresponded to non-El Niño years, but the SST anomaly in the Midriff Islands region was significantly higher than on the west side of the Baja California Peninsula. During these periods of warm SST anomalies, seabirds abandoned Isla Rasa without nesting. The frequency of local SST anomalies has increased in the Gulf of California during the past decade, raising the question as to how frequently these warm SST anomalies can occur before seabird populations enter into a serious demographic decline. In this study, we established a demographic model to analyze population growth of the Heermann's Gull (*Larus heermanni*) under anomalously warm and normal nesting seasons on Isla Rasa in

the Midriff Islands region of the Gulf of California, where >95% of the world's population nests. Breeding seasons with anomalously warm SST are those that show an increase in temperature of at least 2°C above the historical record of the last 50 yr (Velarde et al. 2015b).

Using a long-term dataset for nesting Heermann's Gulls, our objectives were to (1) examine the survival and fecundity rates of Heermann's Gulls on their breeding grounds on Isla Rasa under different environmental conditions (anomalously warm and normal nesting seasons), (2) establish, with these 2 parameters, a demographic model to analyze population growth rates under these 2 contrasting conditions, and (3) simulate population growth rates at different frequencies of warm SST events to test the frequency of warm-phase anomalies that may induce a demographic decline. The hypotheses behind our study were (1) that the long life cycle of Heermann's Gulls would allow them to withstand a certain frequency of reproductive failures during their lifetime and to recover during normal years when marine productivity and the amount of small pelagic fish are both high, and (2) that an increased frequency of warm-phase anomalies in the Gulf of California could lead to a demographic collapse and, eventually, the extinction of the species.

METHODS

Study Site

Isla Rasa (28.82°N, 112.98°W; Figure 1A) is located in the midst of an extremely productive marine area where large numbers of many seabird species breed on different islands (Velarde and Anderson 1994, Velarde et al. 2005). Under normal conditions, wind and tidal currents create a strong upwelling that maintains very high marine productivity (Álvarez-Borrego 1983, Álvarez-Borrego and Lara-Lara 1991), which supports large populations of sardines and other small pelagic fishes on which nesting seabirds feed. With a surface area of <1 km², Isla Rasa is one of the smallest islands in the Midriff Islands region (Figure 1A). Its markedly flat topography, with a maximum elevation of 33 m, stands in contrast to the more pronounced topographic relief of other islands in the area (Bourillón et al. 1988, Velarde G 1989). The climate is hot and arid (García 1964), and vegetation is sparse and dominated by xeric growth forms (Velarde et al. 2015a). The island has 2 main substrate types: rocky hills with some vegetation, and, in between them, valleys formed by deep guano deposits which are mostly devoid of vegetation (see Velarde et al. 2015a for a detailed description).

The main breeding seabird species on Isla Rasa are the Heermann's Gull (Figure 1B), with a relatively constant nesting population of ~260,000 individuals since our censuses began in 1980, and the Elegant Tern (*Thalasseus elegans*), with fluctuating numbers and a maximum of

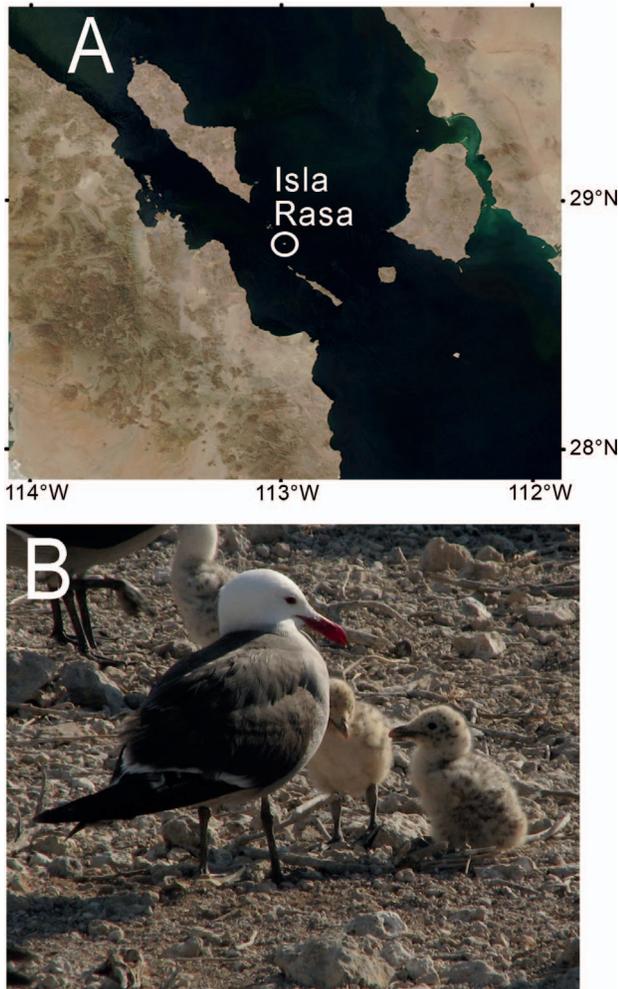


FIGURE 1. (A) Isla Rasa, in the Gulf of California's Midriff Archipelago. Image credit: NASA Goddard Space Flight Center Rapid Response LANCE-MODIS image, April 14, 2010 (<https://lance.modaps.eosdis.nasa.gov>). (B) Heermann's Gull adult with chicks.

~300,000 individuals recorded in 2012 (Velarde et al. 2015b), both of which nest between late March and early July (Velarde 1999). The Royal Tern (*Thalasseus maximus*) also breeds here and has a nesting population that fluctuates between 10,000 and 17,000 individuals (Velarde G 1989, Velarde and Anderson 1994, Velarde et al. 2005). Seabird nesting density is very high (9 nests per m² for Royal Tern, 15 nests per m² for Elegant Tern, and up to 110 nests per 100 m² for Heermann's Gull in some valleys of the island; Velarde 1999). Introduced black rats (*Rattus rattus*) and house mice (*Mus musculus*) used to prey upon chicks, mainly in the rocky areas of the island, until 1995, when a successful eradication campaign increased the breeding success of seabirds (Velarde et al. 2007). The island presently lacks terrestrial predators. Nesting seabirds also suffered severe decimation of their populations

in the mid-20th century due to egg collection by local fishers (Bahre and Bourillón 2002). Populations increased after 1964, when Isla Rasa was declared a protected area by the Mexican government (DOF 1964) and egg poaching stopped.

Study Population

More than 99% of the world's Heermann's Gull population breeds in the Gulf of California, with ~95% concentrated on Isla Rasa (Anderson 1983). Most of the population exhibits postreproductive dispersal to the Pacific coast of North and Central America, ranging from southern Canada to Panama (Bent 1921, Burger and Gochfeld 1996, Islam 2002).

Incubation and chick rearing take place in an environment with wide temperature fluctuations, little or no shade, and lack of fresh water. Chicks that stray into neighboring territories in the dense breeding colonies are attacked by neighbors (Velarde G 1989, Velarde 1999). Morphological and behavioral characteristics seem to be adapted to survival in these conditions (Bartholomew and Dawson 1979, Bennett and Dawson 1979, Rahn and Dawson 1979). Breeding adults regurgitate food and water, since chicks spend 6–7 weeks in their natal territory before having access to seawater (E. Velarde personal observation).

Heermann's Gulls feed mostly on small pelagic fishes. Pacific sardine (*Sardinops sagax*) availability and parental age have been found to be the 2 most important predictors of breeding success in these gulls (Velarde and Ezcurra 2002, Velarde et al. 2004, Vieyra et al. 2009). The experience that Heermann's Gulls acquire with age in capturing fish, coping with harsh environments, defending a small territory within dense nesting areas, and protecting their eggs and chicks against predators affects their breeding performance (Vieyra et al. 2009). The warm-phase SST anomalies that periodically affect the area limit food availability for this and other seabird species, and hence influence their breeding success. These anomalies may also intensify the degree to which some facultative predators, such as the Yellow-footed Gull (*Larus livens*), prey on Heermann's Gull chicks, further decreasing gull breeding success (Velarde 1992).

Data Collection

This study is based on information collected between 1989 and 2015 from band recoveries and from recaptures and resightings of banded nesting adults. A total of 28,700 Heermann's Gull fledglings were banded between 1984 and 1993; 18,700 were banded in the 6 valleys where the demography data was later gathered. Banding was not carried out in 1988 and 1992, 2 yr in which breeding success was extremely low and banding operations would have caused disturbance to the few surviving fledglings.

Banding was initially done using U.S. Fish and Wildlife Service (USFWS) aluminum bands. Later, when banded nesting adults were recaptured in the nesting colony, these bands were exchanged for Incoloy (stainless steel) USFWS bands. A total of 2,707 resightings were collected from 953 individuals (many individuals were resighted in different years).

From these banded individuals, we derived 2 sets of data. The first, and more important, dataset originated from our in situ recaptures and resightings of live nesting individuals in the breeding colony of Isla Rasa. Searches were carried out on the island during the early part of the nesting season (first 2 weeks of egg laying and incubation) in every year, and recaptures or band reading were carried out during the third and fourth week of incubation and until the first chicks started hatching, when all banding and monitoring activities were stopped in order to avoid disturbance to the nesting colony. Frightened chicks tend to run off their territories, often suffering the attacks of neighbors that defend their own territories and running the risk of dying from exposure to extreme temperatures, starvation, dehydration, or injuries (Heerman's Gulls were never observed to eat chicks of their own species). The second dataset originated from USFWS band recovery reports, corresponding to bands or dead banded individuals that were reported from within the known distribution of the species, from southern Canada to Colombia, with some out-of-distribution reports as well.

Estimation of Age-specific Survival Rates

To estimate survival rates, we used a Burnham model for dead recoveries and live recaptures (Burnham 1993), which was run in program MARK, with a sine link function and the second derivative of the Hessian matrix (the "2ndPart" option in MARK) to estimate parameter errors (Cooch and White 2017). Different models were tried with combinations of different assumptions around survival and recapture rates. For each parameter, we tested 4 assumptions: (1) the parameter is constant through time; (2) the parameter changes with time, from one season to the next; (3) the parameter changes only during El Niño (ENSO) years; and (4) the value of the parameter is driven by the age of the cohort. We searched for the best estimates of the parameters using a stepwise procedure. We first searched for the best estimation of survival using each of the 4 assumptions—constant survival (ϕ_{constant}), year-driven survival (ϕ_{year}), El Niño-driven survival (ϕ_{ENSO}), and age-driven survival (ϕ_{age})—while modeling recapture probabilities (p) as time-dependent. We then improved the model by testing the same assumptions for recapture probabilities: constant (p_{constant}), season-driven (p_{year}), El Niño-driven (p_{ENSO}), and age-driven (p_{age}). Model significance was tested using Akaike's information criterion and the χ^2 deviance of the model fit. The bias

potentially introduced into our demographic estimates by the presence of transients (nesting individuals that leave the study area after first capture), which may negatively bias estimation of survival (Oro et al. 2004), was considered negligible because Isla Rasa is the main nesting site for the species.

After being banded as fledglings, birds were not sighted or captured in the monitored valleys before 4 yr of age, the age at which they normally become reproductive. The survivorship values for these first 4 yr were estimated in program MARK using the Burnham model mostly by using band recovery data from dead birds (a detailed record of the numbers of recovered bands is given in Appendix Table 2).

Estimation of Age-specific Fecundity of Reproductive Adults

Fecundity was estimated for each age class from the number of fledglings produced in each nest for a total of 2,707 nests belonging to banded, known-age individuals. These data were obtained from 1989 to 2015, excluding years in which either nests were not monitored (1993, 1994) or no nests were established (1998, 2003, 2014, and 2015), giving an average of 129 nests studied each year for the years when the colony was established on Isla Rasa. Only banded, known-age, adult Heermann's Gulls were monitored. Because chicks are raised by 2 parents, per capita fecundities were calculated as nesting success divided by 2. Fecundities were classified into age classes, and compared among years using generalized linear models (GLM) in R (R Core Team 2017). Because there were marked differences in age-specific fecundities between normal years and those with high SST anomalies, but no significant differences within normal years, we constructed 2 different age-specific fecundity vectors, one for normal years and one for years with high SST anomalies (Appendix Figures 7 and 8), as explained below.

Construction of the Demographic Matrix and Matrix Projections

The age-specific survival and fecundity values obtained from our sampling procedures were smoothed using moving averages for survival values and GLM regression for fecundities, and the resulting vectors of fitted values were organized into 2 demographic projection matrices for 27 age classes, from age 1 yr to age 27 yr, using PopTools (Hood 2010; Figure 2). The first matrix contained the transition values for normal, nonanomalous years, and the second held the values for years with anomalously warm SST. Survival rates did not differ between normal and warm years and, for this reason, the same survival values were used in both matrices (Appendix Figures 7 and 8). For age-specific fecundities, we used predictions from the GLM regression for both normal and ENSO years. A

TABLE 1. Model selection results for different assumptions regarding survivorship and the probability of detection of Heermann's Gulls on Isla Rasa in the Gulf of California's Midriff Archipelago, 1989–2015. Parameters were modeled as constant, time-driven, ENSO-driven, or age-driven. In all cases, recovery (r) and fidelity (f) probabilities were incorporated into the model as time-driven, as no other assumption improved the model's fit to the data. The survivorship and detection probabilities from the best model (ϕ_{age} , p_{age}) were incorporated into Markovian simulations of Heermann's Gull populations in years of normal and anomalously warm sea surface temperatures. AIC is Akaike's information criterion, and ΔAIC is the difference in AIC value from the top model; w_i is the Akaike weight, an indication of support for the model from the data.

Model	ΔAIC	Parameters	Deviance	w_i
$\phi_{\text{age}}, p_{\text{age}}$	0.00 ^a	107	11,164.77	1.00
$\phi_{\text{age}}, p_{\text{year}}$	359.83	111	11,516.54	0.00
$\phi_{\text{age}}, p_{\text{ENSO}}$	7,128.20	85	18,337.23	0.00
$\phi_{\text{age}}, p_{\text{constant}}$	7,139.96	84	18,351.00	0.00
$\phi_{\text{year}}, p_{\text{year}}$	19,682.90	92	30,877.85	0.00
$\phi_{\text{ENSO}}, p_{\text{year}}$	25,399.52	86	36,576.55	0.00
$\phi_{\text{constant}}, p_{\text{year}}$	26,476.69	85	37,685.73	0.00
$\phi_{\text{constant}}, p_{\text{constant}}$	33,305.18	59	44,566.45	0.00

^a The AIC of the top model = 31,264.09.

detailed explanation of the matrix generation methods is given in the Appendix.

For each matrix, we calculated the eigenvalue (λ , the population growth rate under a stable age distribution; Caswell 2006), the left and right eigenvectors (reproductive values and stable age structure), and the elasticity values of the matrix parameters. The standard error of the λ values was calculated through numerical randomization (see Alvarez-Buylla and Slatkin 1993). We used a gamma distribution (which has a zero-bounded probability density function and will thus always generate positive randomized values around the expected mean and standard error) for randomized fecundity values, and a logit distribution (constrained between 0 and 1) for randomized survivorship values. We ran 1,000 randomized simulations for both normal and high-SST years.

Finally, by multiplying the normal and the warm SST matrices and analyzing the eigenvalues of the resulting product, we obtained predicted population growth rates under different scenarios of episodic warm-SST recurrence: One warm SST event every other year, one event followed by 2 normal years, one followed by 3 normal years, and so on. With these results, we analyzed the maximum frequency of warm SST events that the population could withstand without suffering a serious demographic decline.

Estimation of the Nesting Population

The nesting population of Heermann's Gull on Isla Rasa was estimated in 14 yr between 1980 and 2016. Estimates were based on nesting density and surface area covered by the nesting gulls. Nesting density varied according to substrate type. Nest density was much lower in the rocky areas of the island than in the valleys due to the fact that gulls can establish many more nests in a flat area devoid of

rocks or vegetation. In both areas, density was estimated by counting the number of nests in ten 10×10 m quadrats established in several areas of the island. To estimate the total number of nests established on the island, nest counts were done during the peak of the laying period (~ 2 weeks after the first eggs were laid) in the 10 quadrats per substrate, and the mean number of nests for each substrate was multiplied by the surface of the island covered by gull territories in that type of substrate. Estimates were rounded up to the nearest 100. Estimates for 3 of these 14 yr have already been published (Velarde 1999, Velarde and Anderson 1994, Velarde et al. 2005).

RESULTS

The best-fitting MARK model had cohort age as the best predictor of survival rates and recapture probabilities (Table 1). Models using the ENSO signal as a predictor gave consistently higher AIC and deviance values, indicating poorer model fit. The MARK-estimated survival rates of reproductive adults and juveniles >1 yr of age were relatively constant up to 16 yr of age, mostly oscillating between 0.9 and 1.0. After that age, survivorship started declining to values of ~ 0.5 (Figure 3C); the low sample size for older birds, however, makes the trend less certain in older age classes. Survivorship of fledglings, or first-year juveniles (<1 yr old), was lower ($\sim 0.40 \pm 0.16$), indicating that most prereproductive mortality occurs during the first year of age. Indeed, most (61%) of the bands recovered from dead individuals came from first-year birds (Appendix Table 2). The only important explanatory factor of survival rate was the age of the nesting bird, as survival rates tended to decrease after 16 yr of age; neither the cohort nor the SST anomaly showed any significant relationship with survival rate.

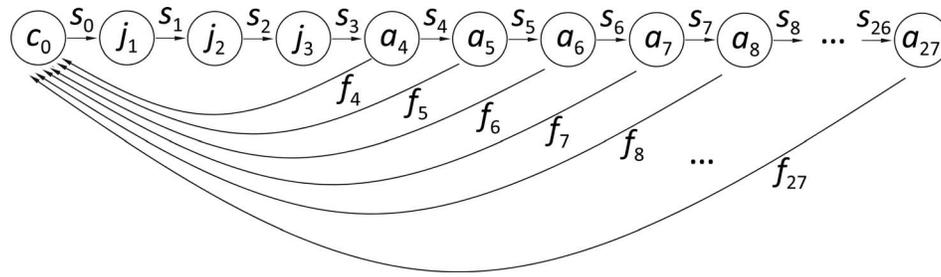


FIGURE 2. Markovian transition diagram for the Heermann's Gull population on Isla Rasa in the Gulf of California's Midriff Archipelago. The circles indicate age-class groups: fledgling chicks (c), nonbreeding juveniles (j), and reproductive adults (a). The arrows indicate Markovian transition values for fecundity (f) and survivorship (s). For all variables, the subscripts indicate the age class (e.g., f_{10} is the fecundity of 10-yr-old birds; j_3 is the number of juveniles in age class 3 (3-yr-olds); s_0 indicates the probability of survival from age class 0 to age class 1).

In sharp contrast to survival rates, there was a negative relationship between fecundity of nesting gulls and SST anomalies in the Midriff Islands (Figure 3A): In normal years, average nesting success of Heermann's Gulls was $\sim 1.10 \pm 0.06$ (SE) fledglings per nest, but during warm SST years it collapsed to less than a tenth of the normal value (0.09 ± 0.05 [SE] fledglings per nest). A multiple regression analysis showed that the fishing effort of the small pelagic fishing fleet operating in the area during the previous season also explained a significant part of the residual variance (partial $r^2 = 0.09$, $P < 0.02$). During normal years, age-specific nesting success increased between ages 4 and 12 yr from 0.7 to 1.3, and then declined gradually, leveling off at ~ 1.0 in older individuals (Figure 3B).

The eigenvalues of the demographic transition matrices (λ) were 1.04 ± 0.01 (SE) for normal years and 0.87 ± 0.02 for years of warm SST anomalies, and they differed significantly according to a one-tailed normal deviate test ($z = 2.6$, $P = 0.01$). That is, the matrix model predicted 4% annual population growth during normal years, and a rapid population decline (-15%) under sustained anomalously warm conditions. Under both normal and high SST conditions, elasticity values for survival were much higher than those for fecundity (Figure 4A), suggesting that, in a species as long-lived as the Heermann's Gull, annual survival contributes more than fecundity to population growth.

The values of λ under different frequencies of recurrence of warm SST anomalies (Figure 4B) showed a gradual but nonlinear decline of the predicted combined growth rate as the frequency increased. The model predicted that with one warm anomaly every 4 yr or greater, values of λ would remain above unity, but that λ would start to decrease drastically with shorter recurrence periods.

Finally, during the period between 1980 and 2016 when Heermann's Gull nest counts were performed on Isla Rasa in 14 different breeding seasons, there were 7 warm SST

years when gulls did not establish a nesting colony or nested in markedly lower numbers than in normal years: 1998, 2003, 2009, 2010, 2014, 2015, and 2016. During the El Niño season of 1992, gulls started laying eggs late but laid eggs in normal numbers; however, chick survival was extremely low. In the remainder of the years in which nest counts were performed, which were years with no oceanographic anomalies, counts showed a stable Heermann's Gull population that fluctuated between 130,000 and 145,000 nests and showed no time-series trend (Figure 4C).

DISCUSSION

During warm SST events, Heermann's Gull mortality did not increase significantly, suggesting that the demographic strategy of these gulls is to prioritize survival during years of low food abundance and maximize reproductive effort during periods when food is abundant. Their fecundity followed a pattern similar to that of other seabird species, increasing from first breeding to ~ 12 yr of age, and then remaining relatively constant during a long period of adulthood (Mills 1973, Ryder 1975, Charlesworth and León 1976, Pugsek 1983, Pugsek and Diem 1983, 1990, Pyle et al. 1991, Sydeman et al. 1991).

In congruence with the observed demographic patterns of survival and fecundity, our analysis showed that population growth was more sensitive to variations in survivorship than in fecundity (Figure 4A). The elasticity analysis showed that the contribution of survival to demographic growth during the early life stages was higher in normal years than when warm SST conditions prevailed. In birds older than 6–8 yr the opposite prevailed: During anomalously warm periods, population growth was more sensitive to variations in adult survivorship than during normal years. In summary, in iteroparous, long-lived birds, survival plays a more critical role in population growth than annual reproduction. The capacity to survive breeding collapses during anomalous years,

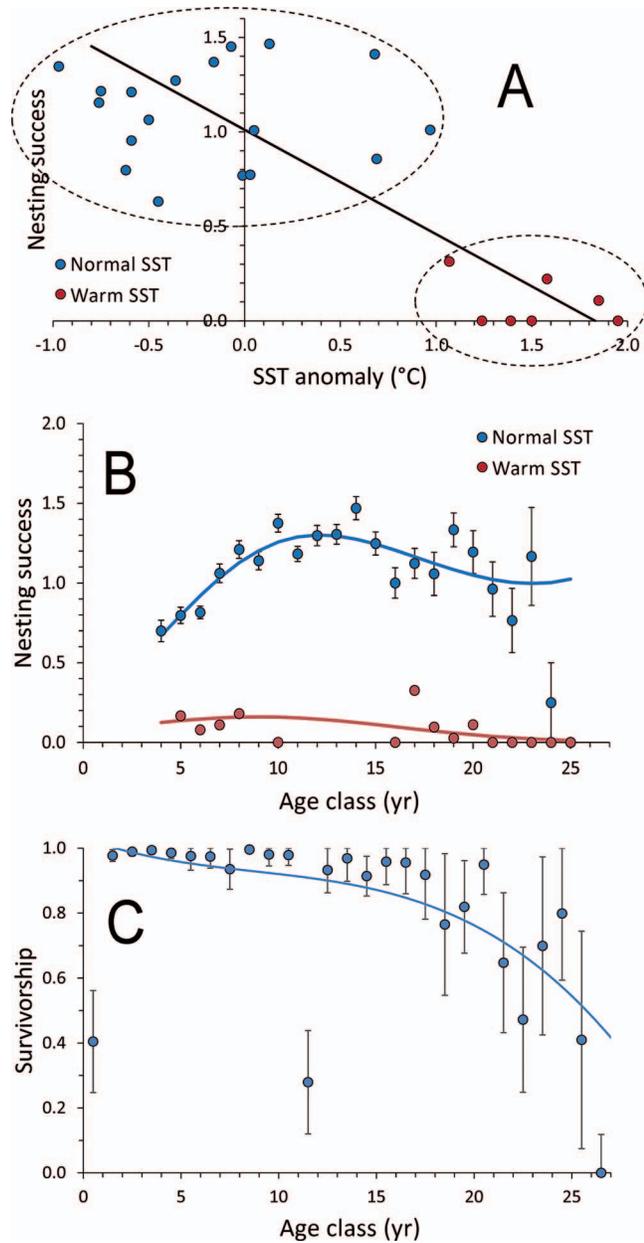


FIGURE 3. (A) There is a significant inverse relationship ($r^2 = 0.56$, $P < 0.001$) between the sea surface temperature (SST) anomaly and nesting success (measured as the number of fledglings per nest) of Heermann's Gulls on Isla Rasa, 1989–2015 (blue points show normal years and red points show anomalously warm years). (B) The SST-induced nesting collapse occurred in all age classes (blue points show normal years and red points show anomalously warm years). (C) In contrast, survivorship of reproductive birds did not change significantly from normal to warm nesting seasons, maintaining a similar overall trend. In (B) and (C), the regression lines were fitted by polynomial regression and are intended to highlight the trends in fecundity and survivorship throughout the life of a cohort.

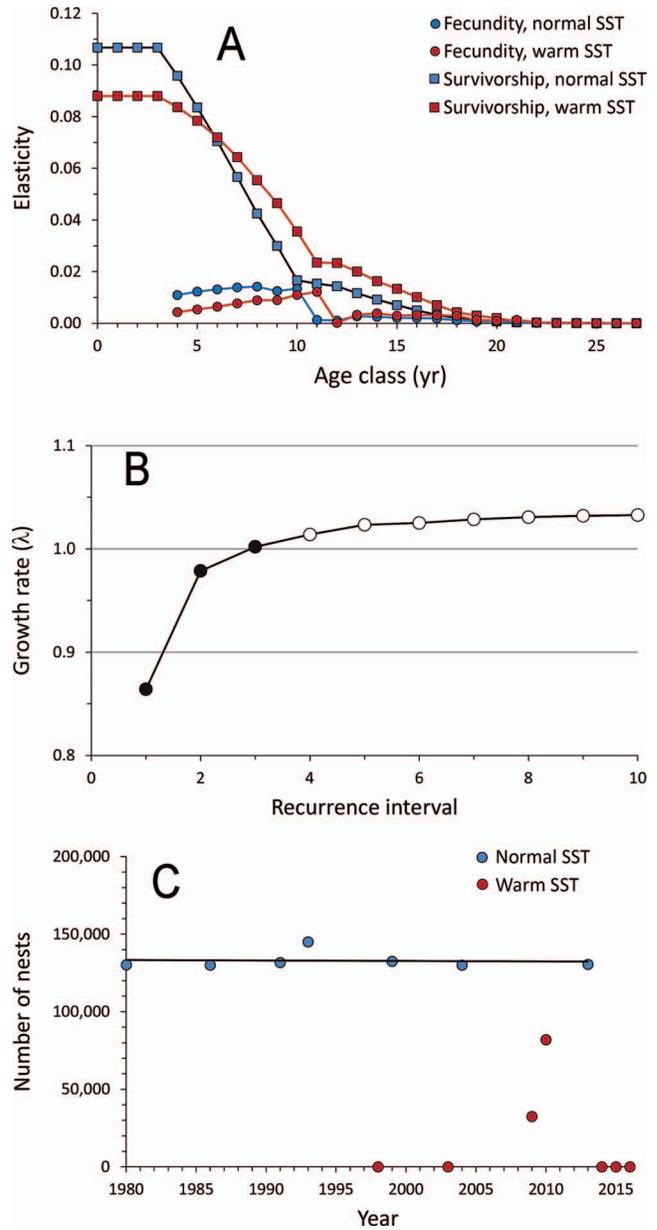


FIGURE 4. (A) Elasticity values of age-specific demographic parameters of Heermann's Gull on Isla Rasa, 1989–2015 (circles: fecundity, squares: survivorship; blue dots: years with normal sea surface temperatures (SST), red dots: years with anomalously warm SST). (B) Long-term Heermann's Gull population growth rates for different recurrence intervals of warm SST anomalies (1 = one anomaly every year, 2 = one anomaly every 2 yr, etc.). Filled circles indicate a declining population, and unfilled circles indicate an increasing population. (C) Population of nesting Heermann's Gulls on Isla Rasa, 1980–2016 (blue dots: normal years, red dots: warm SST seasons). The number of nesting pairs in normal years has remained constant.

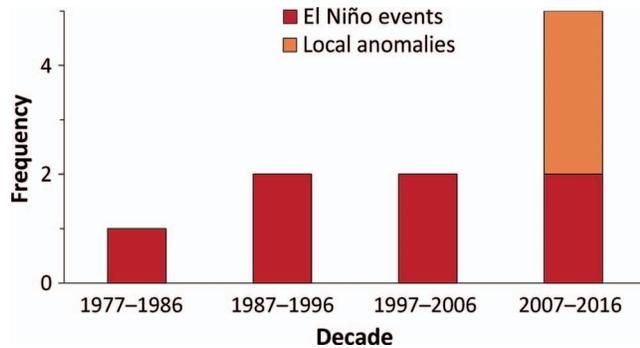


FIGURE 5. Number of warm sea surface temperature (SST) anomalies in the Gulf of California during the past 4 decades. El Niño events were identified from the IRI/LDEO Climate Data Library (ENSO Monitoring, Monthly Standardized Sea Surface Temperature Anomaly; <http://iridl.ldeo.columbia.edu>), while the local anomalies were calculated from the pixel-level digital data from the same repository. Details on the procedures to determine the occurrence of a local warm anomaly in the Gulf of California from digital satellite data are given by Velarde et al. (2015b).

permitting reproduction later, appears to be a major selective factor in the evolution of longevity in these, and likely other, seabirds.

For our matrix analysis, we assumed that breeding in the Heermann Gull starts at 4 yr of age. This threshold is the result of our own observations. On the one hand, we never observed birds younger than 4 yr old nesting, so we can safely assume that individuals stay in their prereproductive phase until they reach at least 4 yr of age. Additionally, most (>50%) banded birds were first resighted nesting at age 4 yr, and many of the individuals that were not first resighted at that age could have been missed during their first nesting season. Thus, although we cannot entirely discard the possibility that some birds may start nesting later than 4 yr of age, our conclusions are qualitatively robust because this potential source of bias in the estimation of fecundity in young adults would affect nesting during both ENSO and non-ENSO years, and thus the comparative conclusions of our study still hold.

The values of λ found in our study for different simulated frequencies of warm SST anomalies indicated that the Heermann's Gull, like other species, is resilient to environmental variation (Fisher 1976, Ollason and Dunet 1988, Wooller et al. 1989, Ainley and Boekelheide 1990, Chastel et al. 1993, 1995). This supports our first hypothesis that the long life cycle of Heermann's Gulls allows them to withstand a certain frequency of reproductive failure during their lifetime and to recover during years when marine productivity is high. Furthermore, there is strong evidence showing that the oceans of the world have been subject to wide fluctuations in their physical oceanography during the last centuries and possibly also

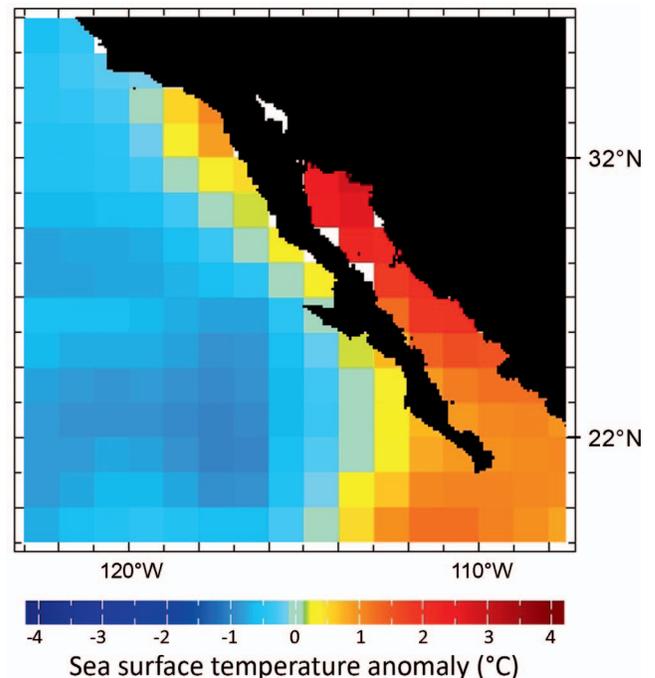


FIGURE 6. In some years, local sea surface temperature (SST) anomalies weaken regional productivity, inducing massive seabird nesting collapses. The image shows mean temperature anomalies in the Gulf of California and Mexico's Pacific Ocean in the month of May, 2009, when a nesting collapse occurred in the Heermann's Gull colony on Isla Rasa in the Midriff Islands. Note that while the Gulf of California is 3–4°C warmer than the seasonal long-term average, Pacific Ocean waters are at the average temperature. Image credit: IRI/LDEO Climate Data Library, ENSO Monitoring, Monthly Standardized Sea Surface Temperature Anomaly (<http://iridl.ldeo.columbia.edu>).

during past geological periods, particularly in the upwelling regions (Biondi et al. 2001, Cheshire et al. 2005). Indeed, available data on the Southern Oscillation Index show that during the last 139 yr alone (1878–2016) there have been 6 nesting seasons with strong, and 9 with mild, El Niño conditions, that is, 1 El Niño season every 10 or 11 yr, on average. Our model suggests that the gulls could have survived and even increased their population numbers with that frequency of recurrence of nesting collapses. However, during the past several decades, warm SST anomalies seem to have become more frequent. During the last decade (2007–2016), there were 5 catastrophically warm SST seasons in the Gulf of California, 3 of them of local nature and unrelated to global El Niño events (Figures 5 and 6). To our knowledge, Heermann's Gulls have not adopted alternative nesting sites to cope with these unfavorable seasons.

Coastal upwelling, characteristic of eastern boundary current systems, fuels high marine productivity and thus a large quantity of forage fishes, which in turn feeds large

populations of different species up the food chain, including larger fish, seabirds, marine mammals, and some large invertebrates. Oceanographic models forecasting future oceanographic conditions in these high-upwelling systems predict intensification of the winds and thus of the upwelling along these productive coasts (e.g., Bakun 1990, Sydeman et al. 2014). This could lead to higher nutrient input and primary productivity. However, it has also been shown that wind intensification may lead to disruption of trophic interactions or may not result in productivity increases across higher trophic levels (Sydeman et al. 2014), so the effects of future climate change on marine upwelling ecosystems are still unclear.

To cope with recurring collapses in food resources, seabirds breeding in upwelling regions have adapted their life histories to survive catastrophic environmental pulses and successfully raise offspring in productive years. Accordingly, the extraordinary longevity of seabirds seems to be an evolutionary response to fluctuating environmental conditions in coastal upwelling marine ecosystems. Further, because of their inherent demographic resilience, seabirds such as the Heermann's Gull have been particularly adept at coping with the frequent El Niño and other SST warming events of recent decades. As our demographic simulation indicated, Heermann's Gulls have been able to withstand the oceanographic anomalies of the last century without seriously compromising their population growth. However, our model also showed that their population growth will decline rapidly if warm SST events that induce low marine productivity in the Midriff Islands region maintain the high frequency that they have had in the last decade, or if these events increase in frequency, which may occur in the future. These results support our second hypothesis that increased frequency of warm-phase anomalies in the Gulf of California could lead to a demographic collapse and, eventually, the extinction of the species. Longevity and iteroparous reproduction have allowed these seabirds to maintain their fitness in an unpredictable and strongly pulsating environment, but this resiliency has a limit. If the frequency of local SST anomalies in the Gulf of California continues to increase, warm sea surface temperatures and low marine productivity could drive a catastrophic population decline, and even threaten the entire species with eventual extinction.

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APPENDIX

Theoretical Basis of the Matrix Model

Given the population structure of Heermann's Gulls, which reproduce annually and in which each age class is 1 yr apart, we can define a Leslie matrix L that contains all of the age-specific fecundities in the first row and all of the age-specific survivorships in the first subdiagonal, such that:

$$L = \begin{matrix} & \begin{matrix} 0 & 0 & 0 & 0 & f_4 & f_5 & f_6 & \dots & f_{23} & f_{24} & f_{25} & f_{27} \end{matrix} \\ \begin{matrix} s_0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ \vdots \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{matrix} & \begin{matrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ s_1 & 0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ \vdots & \vdots \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \dots & s_{24} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 & s_{25} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & s_{26} & 0 \end{matrix} \end{matrix}$$

The subdiagonal element s_i describes the probability of an individual of age i surviving to age class $i + 1$, while the first-row value f_j contains the mean fecundities of all individuals in age class j . In our case, because nesting success was obtained from a postbreeding census, the assumption was made that an annual birth pulse occurred, i.e. all births for the year happened within a short period of time. We conducted our census of the gull population immediately after the birth pulse (hence the name "postbreeding census"), thus the age of newborn individuals incorporated into the population was 0. Because the matrix model calculates population numbers from the population age distribution in the previous year, fecundities are calculated as the product of nesting success (g_i , the mean number of fledglings that individuals in age class i will produce) multiplied by the probability of survival of parents from the last breeding season to the current one (s_{i-1}). For example, the number of fledglings produced by 4-yr-old parents is obtained from the number of 3-yr-old birds that were alive in the previous year (n_3) multiplied by the probability that the 3-yr-olds survive to reach 4 yr of age (s_3), and then multiplied by the nesting success of 4-yr-old birds (g_4). It follows that, in a postbreeding census, fecundities are obtained by multiplying nesting success by the survival probability of the previous cohort ($f_i = g_i \times s_{i-1}$).

If we have a vector n_t describing the state of the population at time t , it is clear that if we multiply the matrix L by the population vector at time t we will get the population vector next year n_{t+1} :

$$n_{t+1} = L \times n_t.$$

If the population has a stable age-class distribution w , in which the proportion of individuals in each age class is maintained through time, then it follows that $\lambda w = L \times w$. Thus, the stable age-class distribution of our population (w) is the eigenvector of the fecundity and survivorship matrix L , and the eigenvalue λ is the intrinsic growth rate. It can also be shown (e.g., Caswell 2010) that the left eigenvector v of the matrix L reveals the reproductive value for each age class in our population. Reproductive values summarize the contribution to reproduction (i.e. the reproductive "worth") of individuals of different age classes in terms of the future offspring that they are likely to contribute to the next generation, adjusted for the growth rate of the population. Contribution to reproduction depends on the amount of future reproduction, the probability of surviving to realize it, and the time required for offspring to be produced. In matrix terms, the left eigenvector is calculated as $v' L = \lambda \times v'$, which can also be written as $\lambda v = L' \times v$ (the symbol $'$ indicates the transposed form of the matrix).

The sensitivity matrix S , of the same dimensions as matrix L , contains in each cell an estimate of how much the population growth rate changes if that matrix element changes, that is $s_{ij} = \partial \lambda / \partial l_{ij}$. It can also be shown (Caswell 1978, 2006) that S can be calculated from the left and right eigenvectors, so that $S = v w' / v' w$, where $v w'$ is the matrix product of both vectors and $v' w$ is the scalar product. Comparing sensitivities among different demographic parameters can be misleading, however, because demographic variables are measured in different units: Survival rates are probabilities and can only take values between 0 and 1, whereas fecundities have no such restrictions. Therefore, the sensitivity of λ to changes in survival rates is difficult to compare with the sensitivity to changes in fecundity rates. Elasticities are proportional sensitivities, scaled by the value of the parameter, so that they can be compared among all life history variables. As described by Caswell (2010), the elasticity of a matrix element e_{ij} is the product of the sensitivity of a matrix element (s_{ij}) and the matrix element itself (l_{ij}), divided by λ ($e_{ij} = (s_{ij} \times l_{ij}) / \lambda$). In matrix terms, the elasticity matrix E is calculated as $E = L \cdot S / \lambda$, where the symbol " \cdot " denotes the Hadamard product, or element-to-element product, of the 2 matrices.

Construction of the Demographic Matrix and Matrix Projections

The age-specific survival and fecundity values obtained from our sampling procedures were smoothed using moving averages for survival values and log-linear regression for fecundities, and the resulting vectors of fitted values were organized into 2 demographic projection matrices for 27 age classes, from age 1 yr to age 27 yr. The first matrix contained the transition values for normal,

0.00	0.00	0.00	0.00	0.33	0.39	0.45	0.51	0.55	0.55	0.62	0.06	0.18	0.57	0.56	0.54	0.57	0.55	0.41	0.31	0.41	0.27	0.13	0.16	0.34	0.15	0.00	0.00
0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.49	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.87	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00

APPENDIX FIGURE 7. Leslie matrix with fecundities and survivorship values for Heermann’s Gulls for normal, non-ENSO years. Age-specific fecundities are in the first row and age-specific survivorship values are in the first subdiagonal.

nonanomalous years, and the second matrix contained the values for years with anomalously warm sea surface temperatures (SSTs). Survival rates did not differ between normal and warm years and, for this reason, the same survival values were used in both matrices. Age-specific

fecundities during El Niño years were ca. one-fifth of normal values in 1992, and were zero in 1998, jointly averaging around one-tenth of the normal fecundity values, and their standard errors were about half that of normal years. Based on this result, in cases in which we did

APPENDIX TABLE 2. Numbers of bands recovered from dead Heermann’s Gulls along the Pacific coast, classified by the age and cohort of the banded birds. These numbers were used in conjunction with live recapture data to estimate survivorship values in program MARK using the Burnham method for mixed dead recovery–live recapture data. Most of the recovered bands came from the U.S. and Canada, and almost none were recovered from Mexico, Central America, and South America, a fact that may highlight a spatial bias in the recovery process.

Age (yr)	Cohort									Total
	1984	1985	1986	1987	1989	1990	1991	1993		
0	16	30	41	15	27	28	6	2		165
1	5	6	4	3	6	0	11	2		37
2	4	3	1	4	2	0	1	1		16
3	2	4	3	1	1	0	3	1		15
4	3	2	1	0	0	1	5	4		16
5	1	2	0	0	0	3	3	0		9
6	0	0	0	0	1	0	4	1		6
7	0	0	0	0	0	0	2	0		2
8	0	0	0	0	0	0	0	0		0
9	0	0	0	0	0	0	0	0		0
10	0	0	0	1	0	0	0	0		1
11	2	0	2	1	0	0	0	0		5
Total	33	47	52	25	37	32	35	11		272

0.00	0.00	0.00	0.00	0.06	0.07	0.07	0.08	0.08	0.07	0.08	0.08	0.00	0.06	0.06	0.04	0.04	0.04	0.03	0.02	0.01	0.02	0.01	0.00	0.00	0.01	0.00	0.00
0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.49	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.87	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01

APPENDIX FIGURE 8. Leslie matrix with fecundities and survivorship values for Heermann’s Gulls for years with anomalously warm sea surface temperatures (SST), or ENSO years. Age-specific fecundities are in the first row and age-specific survivorship values are in the first subdiagonal.

not have age-class-specific fecundities for average ENSO or high SST years, we used the values of normal years divided by 10, and we used as standard errors those of the normal years divided by 2.

For each matrix, we calculated the eigenvalue (λ , the population growth rate under a stable age distribution; Caswell 2006), the left and right eigenvectors (reproductive values and stable age structure), and the elasticity values of the matrix parameters. The standard errors of the λ values were calculated through numerical randomization (see Alvarez-Buylla and Slatkin 1993). We used a gamma distribution (which has a zero-bounded probability density function and will thus always generate positive randomized values around the expected mean and standard error) for

randomized fecundity values, and a logit distribution (constrained between 0 and 1) for randomized survivorship values. We ran 1,000 randomized simulations for both normal and high SST years.

Finally, by multiplying the normal and the warm SST matrices and analyzing the eigenvalues of the resulting product, we obtained predicted population growth rates under different scenarios of episodic warm SST recurrence: One warm SST event every other year, one followed by 2 normal years, one followed by 3 normal years, and so on. With these results, we analyzed the maximum frequency of warm SST events that the population could withstand without suffering a serious demographic decline.