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# Population Dynamics of Hawaiian Seabird Colonies Vulnerable to Sea-Level Rise

JEFF S. HATFIELD,* MICHELLE H. REYNOLDS,† NATHANIEL E. SEAVY,‡§ AND CRYSTAL M. KRAUSE†

*U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708, U.S.A., email jhatfield@usgs.gov
†U.S. Geological Survey, Pacific Island Ecosystems Research Center, Kilauea Field Station, Hawaii National Park, HI 96718, U.S.A.
‡Hawaii Cooperative Studies Unit, University of Hawaii at Hilo, Pacific Aquaculture and Coastal Resources Center, Hawaii National Park, HI 96718, U.S.A.
§PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954, U.S.A.

**Abstract:** *Globally, seabirds are vulnerable to anthropogenic threats both at sea and on land. Seabirds typically nest colonially and show strong fidelity to natal colonies, and such colonies on low-lying islands may be threatened by sea-level rise. We used French Frigate Shoals, the largest atoll in the Hawaiian Archipelago, as a case study to explore the population dynamics of seabird colonies and the potential effects sea-level rise may have on these rookeries. We compiled historic observations, a 30-year time series of seabird population abundance, lidar-derived elevations, and aerial imagery of all the islands of French Frigate Shoals. To estimate the population dynamics of 8 species of breeding seabirds on Tern Island from 1980 to 2009, we used a Gompertz model with a Bayesian approach to infer population growth rates, density dependence, process variation, and observation error. All species increased in abundance, in a pattern that provided evidence of density dependence. Great Frigatebirds (*Fregata minor*), Masked Boobies (*Sula dactylatra*), Red-tailed Tropicbirds (*Phaethon rubricauda*), Spectacled Terns (*Onychoprion lunatus*), and White Terns (*Gygis alba*) are likely at carrying capacity. Density dependence may exacerbate the effects of sea-level rise on seabirds because populations near carrying capacity on an island will be more negatively affected than populations with room for growth. We projected 12% of French Frigate Shoals will be inundated if sea level rises 1 m and 28% if sea level rises 2 m. Spectacled Terns and shrub-nesting species are especially vulnerable to sea-level rise, but seawalls and habitat restoration may mitigate the effects of sea-level rise. Losses of seabird nesting habitat may be substantial in the Hawaiian Islands by 2100 if sea levels rise 2 m. Restoration of higher-elevation seabird colonies represent a more enduring conservation solution for Pacific seabirds.*

**Keywords:** carrying capacity, climate change, French Frigate Shoals, Gompertz model, process variation, viable population monitoring

Dinámica Poblacional de Colonias de Aves Marinas Vulnerables al Incremento del Nivel del Mar en Hawaii

**Resumen:** *Globalmente, las aves marinas son vulnerables a amenazas antropogénicas tanto en el mar como en tierra. Las aves marinas típicamente anidan en colonias y muestran alta fidelidad a las colonias natales, y tales colonias en islas de baja elevación pueden ser amenazadas por el incremento del nivel del mar. Utilizamos French Frigate Shoals, el mayor atolón en el Archipiélago Hawaiano, como un estudio de caso para explorar la dinámica poblacional de colonias de aves marinas y los efectos potenciales que puede tener el incremento del nivel del mar sobre estas colonias. Compilamos observaciones históricas, una serie de tiempo de 30 años de la abundancia de poblaciones de aves marinas, elevaciones e imágenes aéreas de todas las islas de French Frigate Shoals. Para estimar la dinámica poblacional de 8 especies de aves marinas que se reprodujeron en la Isla Tern de 1980 a 2009, utilizamos un modelo Gompertz con un método Bayesiano*

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*para inferir las tasas de crecimiento poblacional, la densodependencia, la variación del proceso y el error de observación. Todas las especies incrementaron en abundancia, en un patrón que proporcionó evidencia de la densodependencia. Es probable que* Fregata minor, Sula dactylatra, Phaeton rubricauda, Onychoprion lunatus *y* Gygis alba *se encuentren en capacidad de carga. La densodependencia puede exacerbar los efectos del incremento del nivel del mar sobre aves marinas porque las poblaciones cercanas a la capacidad de carga en una isla serán más afectadas que poblaciones con espacio para crecer. Proyectamos que 12% de French Frigate Shoals se inundará si el nivel del mar incrementa 1 m y 28% si el nivel del mar incrementa 2 m.* Onychoprion lunatus *y especies que anidan en arbustos son especialmente vulnerables al incremento del nivel de mar, pero diques y la restauración de hábitat pueden mitigar los efectos del incremento del nivel del mar. Las pérdidas de hábitat para la anidación de aves marinas puede ser sustancial en las Islas Hawaianas en 2100 si el nivel del mar incrementa 2 m. La restauración de colonias de aves marinas en sitios más elevados representa una solución más perdurable para la conservación de aves marinas del Pacífico.*

**Palabras Clave:** cambio climático, capacidad de carga, French Frigate Shoals, modelo Gompertz, monitoreo de población viable, variación del proceso

## Introduction

Seabird populations are influenced globally by mortality from fisheries bycatch (de la Mare & Kerry 1994), ingestion of plastic (Spear et al. 1995), harvesting of eggs and adults (Moller 2006), and introduced predators (Moors & Atkinson 1984; Burger & Gochfeld 1994). Breeding colonies on low-lying islands may also be threatened by sea-level rise (Baker et al. 2006; Woodroffe 2008; Marcelja 2010). To protect seabirds from these threats, there is an increasing emphasis on understanding seabird population dynamics (Nettleship et al. 1994; Wilcox & Donlan 2007). Long-term monitoring of breeding colonies can provide information on the status of populations and the effectiveness of management actions. Time-series data can be used to describe seabird population trends and provide insights into density dependence, carrying capacity, anthropogenic disturbance, habitat changes, and year-to-year variability (Lewis et al. 2001; Micol & Jouventin 2001; Kokko et al. 2004).

The Hawaiian Islands exemplify many of the challenges of managing seabirds. Most seabirds were extirpated from the main Hawaiian Islands 800 years ago (Olson & James 1982). In the late 19th century, seabird adults, nestlings, and eggs were harvested extensively for human consumption, and feathers were exported for the fashion industry (Spennemann 1998). United States federal legislation ended seabird and seabird egg harvesting in the Northwestern Hawaiian Islands in 1909, but then introduced species (e.g., rabbits [*Oryctolagus cuniculus*], mice [*Mus musculus*]) damaged the vegetation on many islands (Ely & Clapp 1973). Moreover, World War II military activities had large effects on many Pacific islands and their seabird populations (Fisher & Baldwin 1946). In recent decades, there has been increasing emphasis on conservation of seabirds, including increased protection for the largest rookery of migratory seabirds in the Pacific islands with the designation of Papahānaumokuākea Marine National Monument in 2006 (Presidential Proclamation 2007). Today, these small islands provide nesting habitat for over 14 million seabirds and are protected under the U.S. Migratory Bird Treaty Act (Fefer et al. 1984).

However, long-term conservation of seabird colonies in the Northwestern Hawaiian Islands is complicated by climate change. Recent projections that include thermal expansion of ocean water and melting of polar ice sheets estimate sea level may rise 1–2 m by the end of the 21st century (Fletcher 2009; Vermeer & Rahmstorf 2009; Rahmstorf 2010). Sea-level rise could decrease the amount of nesting habitat available for seabirds, especially in the Northwestern Hawaiian Islands, where many low-lying coral atoll islets have maximum elevations of <3 m. Nesting seabirds on low-lying islands may also be affected by severe storms that create wash-over events that can destroy nesting habitat (Richardson et al. 2009) and wash-away eggs, chicks, fledglings, and adults (Spendelow et al. 2002; USFWS 2005, 2011). Because an increase in the frequency and severity of extreme weather events is one of the projected consequences of climate change (IPCC 2007), this may exacerbate the effect of rising sea level on seabird population dynamics. The interaction between climate change and at-sea threats to seabirds, in combination with the inherent difficulties of studying seabird populations at sea, underscores the value of understanding population dynamics at breeding colonies in the context of sea-level rise. The long-term monitoring of seabird abundance on Tern Island provides a wealth of information that can be used to gain understanding of issues associated with the disturbance and recovery of seabird colonies on low-lying Pacific islands.

Seabird conservation in the Northwestern Hawaiian Islands and on other atolls and coral islets in the Pacific will require an understanding of how and where seabird populations are expected to decline as a result of sea-level rise and if management actions can be taken to slow seabird colony losses. Quantifying the negative effects of sea-level rise on breeding seabirds requires an understanding of how topography and spatial patterns of seawater inundation and vegetation change will in-

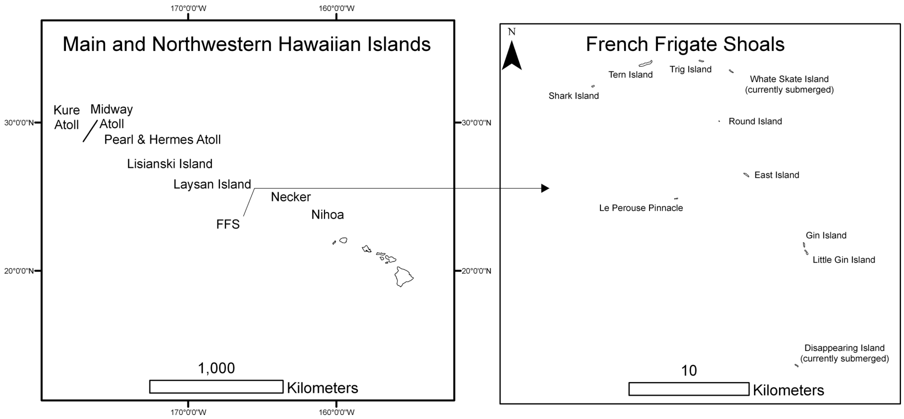


*Figure 1. French Frigate Shoals (FFS) of the Northwestern Hawaiian Islands (23°45'N, 166°17'W).*

teract to constrain seabird breeding on small low lying islands. We acquired new topographic data and used sea-level rise projections, information on historical changes in seabird nesting habitat, and data from long-term monitoring of seabird abundance to explore seabird colony vulnerability to sea-level rise at French Frigate Shoals. We used these data to quantify historical changes in the spatial extent and distribution of seabird habitat on the atoll and to provide scenarios of how sea-level rise and habitat restoration could change the distribution of seabird habitat in the future. We used data from long-term monitoring to estimate population growth rates, carrying capacities, and the strength of density dependence for 8 seabird species on Tern Island to test the assumption that seabirds respond to habitat management. Finally, we used our results to highlight management options that may help protect Hawaiian seabirds as sea levels rise.

## Methods

### Study Area

French Frigate Shoals (23°45'N, 166°17'W) is part of the U.S. Fish and Wildlife Service (USFWS) Hawaiian Islands National Wildlife Refuge and Papahānaumokuākea Marine National Monument, and it is the largest atoll in the Hawaiian archipelago. French Frigate Shoals is currently composed of 8 low islands (Shark, Tern, Trig, East, Round, Gin, Little Gin, and Disappearing; 22.5 total ha) and La Perouse rock pinnacle (Fig. 1). Eighteen species of seabirds nest at French Frigate Shoals, including more than 196,000 breeding pairs, and there are no terrestrial mammalian predators on the atoll (USFWS 2005).

In 1925 French Frigate Shoals was comprised of 15 islands, 4 with well-established vegetation (Wetmore 1925). Relative to its 1932 shoreline (Fig. 2), Tern Island was expanded by the U.S. military during World War II

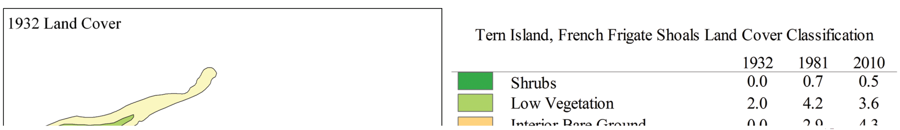


*Figure 2. Land cover in 1932, 1981, and 2010; changes in land cover (ha) 1981–2010; and land cover if runway were removed and seabird nesting habitat restored on Tern Island, French Frigate Shoals.*

for use as a landing strip (Amerson 1971). Despite the engineering that increased island size and doubled the area of potential nesting habitat, human activity was a major limiting factor to breeding seabird populations at French Frigate Shoals. During World War II, 127 people and several dogs resided on Tern Island. Seabird nests on the runway were destroyed on a daily basis, and only 3 of 12 species that bred on Tern Island before 1940 persisted after 1969 (Amerson 1971). After World War II, Tern Island had a U.S. Coast Guard Long Range Navigation station and a Pacific Missile Range tracking installation, and weekly flights occurred until 1979, at which time management of the island was transferred to the USFWS and it became part of the Hawaiian Islands National Wildlife Refuge. Currently, the number of personnel on the island ranges from 4 to 17, and the runway is maintained, although its use is limited to emergency evacuations (P. Hartzell, personal communication).

### Geospatial Analyses of Land Cover, Nesting Habitat, and Sea-Level Rise

We used historical accounts and aerial photography to quantify land cover on Tern Island in 1932, 1942, 1981, and 2010, and aerial photographs to quantify land cover on East Island in 1981 and 2010. For 1981 and 2010, we classified areas on aerial photographs into 7 land-cover classes: tree or shrub, low vegetation, bare ground, beach, runway, human structures, and seawalls. For our analyses, *beach* was land subjected to normal wave inundation at high tide. Beach is not typically seabird-nesting habitat. *Bare ground* was sandy or rocky areas beyond the typical wave reach. We classified nesting habitat into 7 land-cover classes on the basis of species-specific nesting behavior: tree or shrub (Black Noddy [*Anous minutus*], Great Frigatebird [*Fregata minor*], Red-footed Booby [*Sula sula*], Red-tailed Tropicbird [*Phaethon rubricauda*], and White Tern [*Gygis alba*]); bare ground close to beach (Spectacled Tern [*Onychoprion lunatus*]); low vegetation and bare ground (Brown Noddy [*Anous stolidus*] and Masked Booby [*Sula dactylatra*]).

We collected aerial light detection and ranging (LiDAR) data in July 2010 to develop digital elevation models for French Frigate Shoals (ILMF 2010; U.S. Geological Survey, unpublished data). We also acquired satellite digital elevation models (PhotoSat 2010; Mitchell & MacNabb 2010). We evaluated the amount of land area that would be lost under 4 scenarios of sea-level rise. High-resolution bathymetric data for French Frigate Shoals are currently unavailable, and more complex models of dynamic wave run-up inundation were beyond the scope of this paper. We used ArcGIS 10 (ESRI 2011) and digital elevation models to simulate a 0.5-, 1.0-, 1.5-, and 2.0-m rise in sea level. To estimate potential inundation extent for a specific scenario, we identified all locations with elevations below that projected sea level and our model flooded areas connected to the ocean (Li et al. 2009; NOAA 2009). In our scenarios, we assumed little change in the Greenland and Antarctic ice sheets. Although we assumed our scenarios would occur over the next century, the actual timing of these events is unknown.

For Tern Island, we combined projections of inundation with 2 land-cover response models: a dynamic vegetation-response model and a static response land-cover model. In the dynamic vegetation-response model land cover shifted upslope via replanting or natural succession. The dynamic response model allowed shifts in vegetation and assumed vegetation propagates toward higher elevations as sea level rises (LaFever et al. 2007). The static response land-cover model predicted sea-level rise will outpace the ability of vegetation to shift upslope. We modified the dynamic vegetation-response model for Tern Island to incorporate protection of the beach by a seawall. In addition, at Tern Island, we estimated the potential for the interior runway to be converted to nesting habitat by calculating the proportion of the island composed of each land-cover class (tree or shrub, low vegetation, and bare ground). We assumed that equal proportions of these land-cover types occurred on the runway area.

For Spectacled Tern and Brown Noddy, we used current spatial-distribution maps (U.S. Fish and Wildlife Service, unpublished data) to model changes in colony habitat with sea-level rise. For all other species, we estimated changes in habitat with land-cover analyses and calculated nesting area lost to sea-level rise. This allowed us to predict decreases in carrying capacity ($K$) or abundance for each species, assuming the relation between the proportion of nesting habitat lost and $K$ or abundance of each species is linear.

### Seabird Population Responses to Changes in Nesting Habitat

In our analyses of the vulnerability of nesting seabirds to inundation of nesting habitat from sea-level rise, we assumed seabirds are limited by the amount of nesting habitat and if new habitat is created, populations recruit into it. To test the assumption that seabird populations respond to changes in area of nesting habitat, we reviewed the published literature on historical changes in seabird abundance on French Frigate Shoals and used long-term monitoring data of nesting seabirds on Tern Island to quantify population dynamics.

We analyzed abundance data collected over 30 years (1980–2009) for 8 species of breeding seabirds on Tern Island: Black Noddy, Brown Noddy, Great Frigatebird, Masked Booby, Red-footed Booby, Red-tailed Tropicbird, Spectacled Tern, and White Tern. Personnel of the U.S. Fish and Wildlife Service conducted island-wide mean incubation counts of nesting seabirds. In mean incubation counts abundance of nests with eggs are counted at intervals that correspond to the mean incubation period of that species. This method has been widely applied to monitoring of seabirds on Pacific islands (Megyesi & Griffin 1996; Citta et al. 2007; Seavy & Reynolds 2009). Because most eggs hatch by the subsequent visit, it is unlikely that the same nest is counted more than once. However, if pairs breed more than once in a single season or renest after failure, then the sum of nests counted during all visits in a season overestimates the number of breeding individuals. Therefore, we used the maximum mean incubation count during a breeding season as a conservative measure of the total number of breeding pairs (Megyesi & Griffin 1996; Seavy & Reynolds 2009). We refer to all counts used in our models as observed abundance and recognize that they provide an index of the total breeding population.

Describing population dynamics is complicated by the effects of process variation and observation error (Shenk et al. 1998). Process variation represents true fluctuations in population size that result from environmental stochasticity. As a result of process variation, carrying capacity is increasingly described as a stationary probability distribution rather than a point equilibrium (Dennis & Constantino 1988; Dennis et al. 2006). Observation error represents fluctuations in the observed (not true) population size that can be attributed to sampling inaccuracies. Attributing all variability to process variation or observation error can result in incorrect estimates of population parameters (Staples et al. 2004, 2005; Freckleton et al. 2006).

We used a state–space approach to investigate the temporal dynamics of breeding seabird counts. We modeled density-dependent growth with the Gompertz equation:

$$X_t = a + cX_{t-1} + E_t, \tag{1}$$

where $X_t$ is the natural logarithm of the true population size ($N_t$) at time $t$, $a$ is the rate of population growth (in the absence of density dependence), $c$ is the strength of density dependence, and $E_t$ is process variation generated by environmental stochasticity, which is assumed to be distributed as $\mathcal{N}(0, \sigma^2)$ (where $\mathcal{N}$ denotes a normal distribution and $\sigma$ is process variation). The case where $c = 1$ is the density independent model, whereas $c < 1$ implies density dependence (smaller values of $c$ imply greater density dependence) (Staples et al. 2004, 2005; Dennis et al. 2006; Seavy et al. 2009). We incorporated observation error by assuming

$$Y_t = X_t + F_t, \tag{2}$$

where $F_t \sim \mathcal{N}$ (0, $\tau^2$) ($\tau$ is the observation error, or sampling error, generated because the true number of individuals in the population cannot be counted exactly). We used the program WinBUGS (version 1.4.3) (Lunn et al. 2000) for Bayesian analyses (Link & Barker 2010), which circumvents the need for asymptotic results used by Dennis et al. (2006). We assumed vague uniform priors for $\sigma^2$, $\tau^2$, and the first observed abundance of each species, a vague normal prior for $a$, and a uniform (–2, 3) prior for $c$. We described the posterior distributions for $\sigma$, $\tau$, $a$, and $c$ by their means, standard deviations, medians, and credible intervals. We calculated $K$ and SD with Eqs. (47)–(51) in Dennis et al. (2006). More details of our Bayesian analyses are in Seavy et al. (2009).

## Results

### Geospatial Analyses of Land Cover, Habitat Change, and Sea-Level Rise

After the runway was built on Tern Island in 1942, 46% of the island's 15.5 ha was runway. By 2010, encroachment of vegetation decreased the runway area to 27% (Fig. 2). Since 1942, shoreline erosion has decreased the island's area by 2.0 ha (Fig. 2). Buildings, often used by nesting

**Table 1. Elevation and land area (above mean high water [MHW]) for islands of French Frigate Shoals, Hawaii, derived from lidar digital elevation models (DEM) and PhotoSat DEM, under 4 scenarios of sea-level rise, each associated with a particular percentage of lost land area.**

| *Model and island* | *Mean (SD)* | *Max* | *Total area MHW(ha)* | *Loss of land (%)* | | | |
|---|---|---|---|---|---|---|---|
| | | | | *0.5 m* | *1.0 m* | *1.5 m* | *2.0 m* |
| Lidar DEM 2010[a] | | | | | | | |
| Shark | 1.2 (0.3) | 1.9 | 0.3 | 0.0 | 33.3 | 100 | 100 |
| Tern | 2.3 (0.5) | 3.4 | 13.8 | 0.0 | 0.7 | 0.7 | 1.4 |
| Gin | 1.6 (0.5) | 2.9 | 1.7 | 17.6 | 52.9 | 82.4 | 100 |
| Disappearing | 0.6 (0.6) | 2.3 | 0.4 | 50.0 | 75.0 | 100 | 100 |
| PhotoSat DEM 2011[b] | | | | | | | |
| Trig | 0.5 (0.8) | 2.5 | 1.4 | 7.1 | 21.4 | 42.9 | 78.6 |
| East | 2.3 (0.5) | 3.1 | 2.8 | 0.1 | 3.1 | 3.3 | 3.6 |
| Little Gin | 1.0 (0.4) | 1.8 | 1.7 | 11.8 | 35.3 | 94.1 | 100 |
| Round | 1.0 (0.6) | 2.0 | 0.1 | 0.0 | 100 | 100 | 100 |

[a] *Accuracy assessment: root mean-square error 0.17 m.*
[b] *Accuracy assessment: root mean-square error 0.15 m.*

Red-tailed Tropicbirds, Black Noddies, and White Terns, covered <3% of Tern Island's area in 2010, and shrubs covered almost 4% of the island (Fig. 2). If the runway were to be decommissioned, 0.20 ha (39%) of shrubs, 1.53 ha (42%) of low vegetation, and 1.82 ha (43%) of interior bare ground could be used as nesting habitat (Fig. 2).

Tern Island had a mean elevation of 2.29 m (SD 0.5), a median elevation of 2.44 m, and an elevation range of 0–3.37 m. Little variation in elevation existed across Tern Island in part because of seawall fortification. The other islets of French Frigate Shoals are not protected by seawalls. With the exception of La Perouse

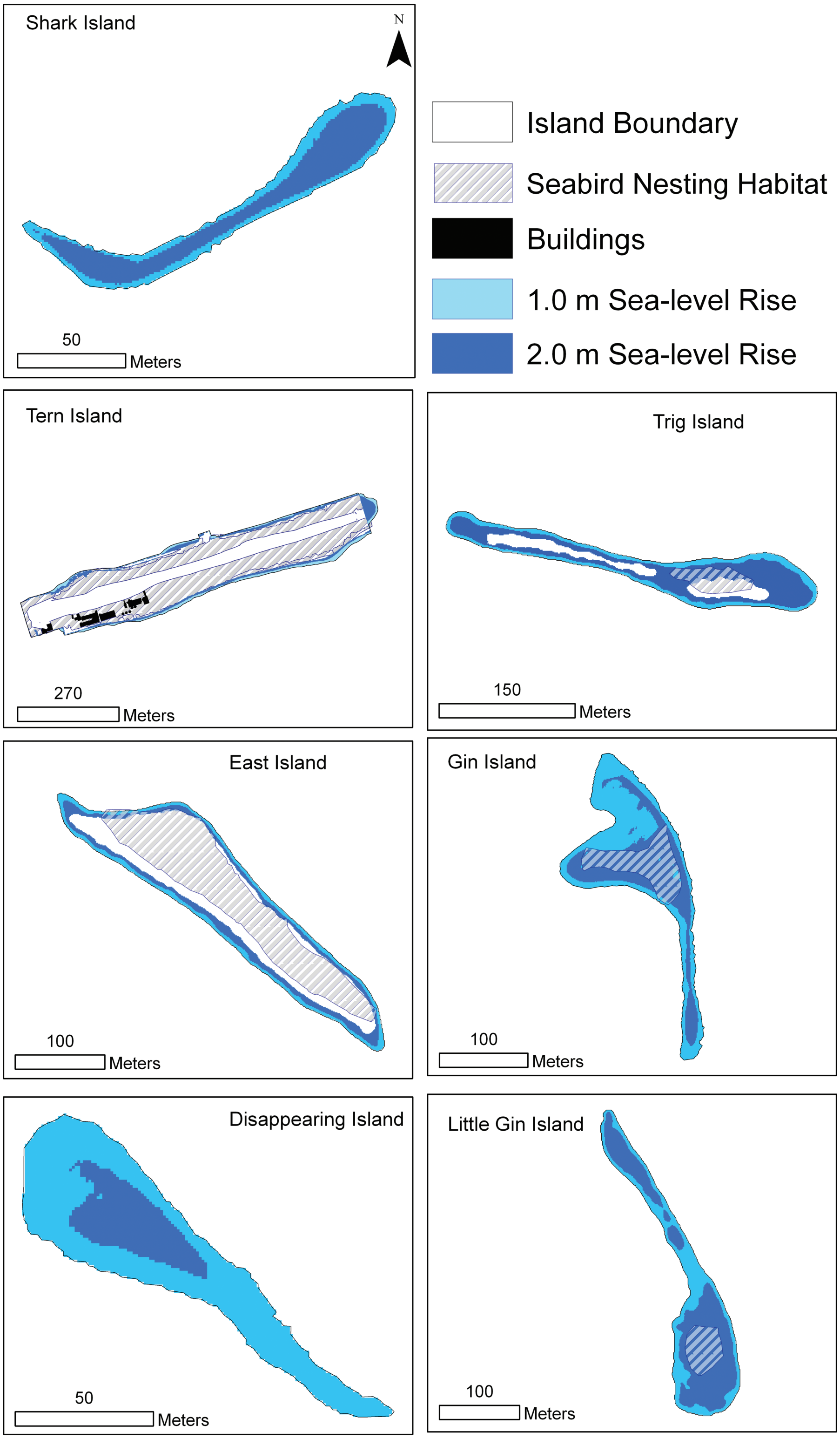


*Figure 3. Projected inundation of 7 islands of French Frigate Shoals with 1- and 2-m rises in sea level. Inundation was determined with lidar digital elevation models from July 2010 for Shark, Tern, Gin, and Disappearing Islands and with satellite digital elevation models from August 2011 for Trig, East, Little Gin, and Round Islands.*

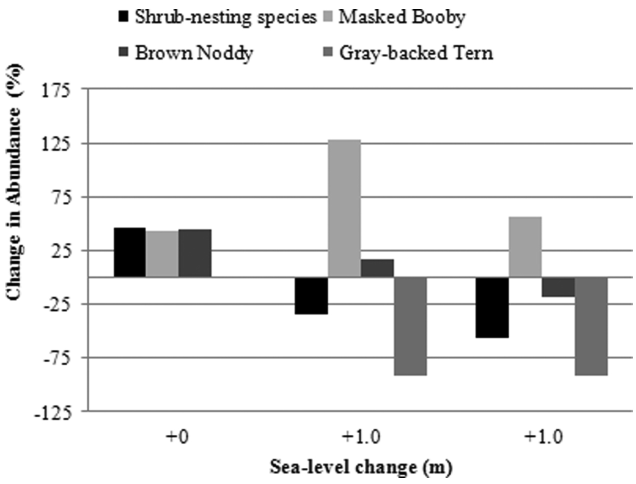


*Figure 4. Seabird abundance at Tern Island under current habitat conditions with proposed habitiat restoration (removal of runway and vegetation restoration) and no sea-level rise (0), restoration with a 1.0-m sea-level rise, and without restoration and a 1.0-m sea-level rise. Model assumes vegetation shifts upslope as sea level rises (LaFever et al. 2007). Shrub-nesting species include Black Noddy, Great Frigatebird, Red-tailed Tropicbird, Red-footed Booby, and White Tern.*

Pinnacle, these islets have a mean elevation <1.3 m (SD 0.6) (Table 1).

The seawall at Tern Island may prevent inundation from 1.0 m of sea-level rise because 95% of the island is ≥1 m in elevation and 86% of the island is ≥2 m in elevation. Shark, Trig, East, Gin, Little Gin, Round, and Disappearing Islands as a whole were predicted to lose 29.5% (area-weighted average) of their land mass with 1.0 m of sea-level rise and 72.7% of their land mass with 2.0 m of sea-level rise (Table 1). The islands with more than 1 ha of area (Tern, Trig, East, Gin, and Little Gin Islands) showed less loss of land until sea-level rise reached 1.5 and 2.0 m, after which only Tern and East Islands would be likely to support seabird breeding (Table 1 & Fig. 3). Sea-level rise models predicted the beach would become larger in all scenarios without seawall protection. In models without vegetation restoration, shrub habitat decreased almost 60% with 1.0 m of sea-level rise (Fig. 2).

For all scenarios of sea-level rise, models predicted decreases in abundance of all species except Masked Boobies, which nest on bare ground (Fig. 4). Spectacled Terns, which nests near the shoreline, and shrub-dependent species were predicted to be the most vulnerable to population declines after sea-level rise reached 1.0 m. At 2.0 m of sea-level rise, the dynamic response models projected large losses of habitat because the runway prevented vegetation shifts. Models that incorporated decommissioning the runway increased the area of potential nesting habitat and slowed losses of shrub land cover due to sea-level rise for all but the 1.5- and 2.0-m scenarios (Figs. 2 & 3).

All seabird species in our analyses were present at French Frigate Shoals from 1960 to 1969 (Amerson 1971). However, during this period, there were no breeding Great Frigatebirds, Masked or Red-footed Boobies, or Spectacled Terns on Tern Island. Only small breeding populations of Black and Brown Noddies (5 breeding pairs), Red-tailed Tropicbirds (45 pairs), and White Terns (9 pairs) persisted.

Sea-level rise and erosion contributed to the loss of seabird breeding habitat at French Frigate Shoals; nearly half the atoll's islands have been inundated since 1925, including Bare, Mullet, Near, and Whale-Skate Islands. Whale-Skate Island, inundated since 1998 (Antonelis et al. 2006), previously supported vegetation and large populations of albatrosses (500 pairs), Brown Noddies (850 pairs), Great Frigatebirds (221 pairs), Masked Boobies (140 pairs), Red-footed Boobies (14 pairs), Red-tailed Tropicbirds (8 pairs), and Spectacled Terns (120 pairs).

### Population Dynamics of Seabirds on Tern Island

The population abundance of all 8 seabird species increased at Tern Island between 1980 and 2009 (Fig. 5). Two extirpated species, the Great Frigatebird and Masked Booby, recolonized the island during this time. All species showed evidence of density dependence ($c < 1$) (Table 2). Populations of Black Noddies, Brown Noddies, and Red-footed Boobies have not reached carrying capacity. We inferred carrying capacity for the Great Frigatebird, Masked Boobies, Red-tailed Tropicbird, Spectacled Tern, and White Tern had been reached (Table 2 & Fig. 5). The strongest density dependence was evident in the Great Frigatebird population. It is likely that Tern Island cannot support more than approximately 600 nests (Fig. 5).

## Discussion

Our results suggest that even moderate amounts of sea-level rise could have profound effects on the amount of nesting habitat available to seabirds in the largest atoll of the Hawaiian Islands, French Frigate Shoals. Specifically, our topography data and sea-level rise models indicated the land areas most vulnerable to loss through inundation. Knowing which areas are most vulnerable may make it possible to anticipate where accelerated habitat loss due to sea-level rise is likely to occur, where seabird habitat is likely to persist, and where restoration activities may be most effective. Washing of waves over an island leads to loss of vegetation that may accelerate losses of land to inundation, plant dieback, increased erosion, and soil instability (Davidson-Arnott 2005). We predict French

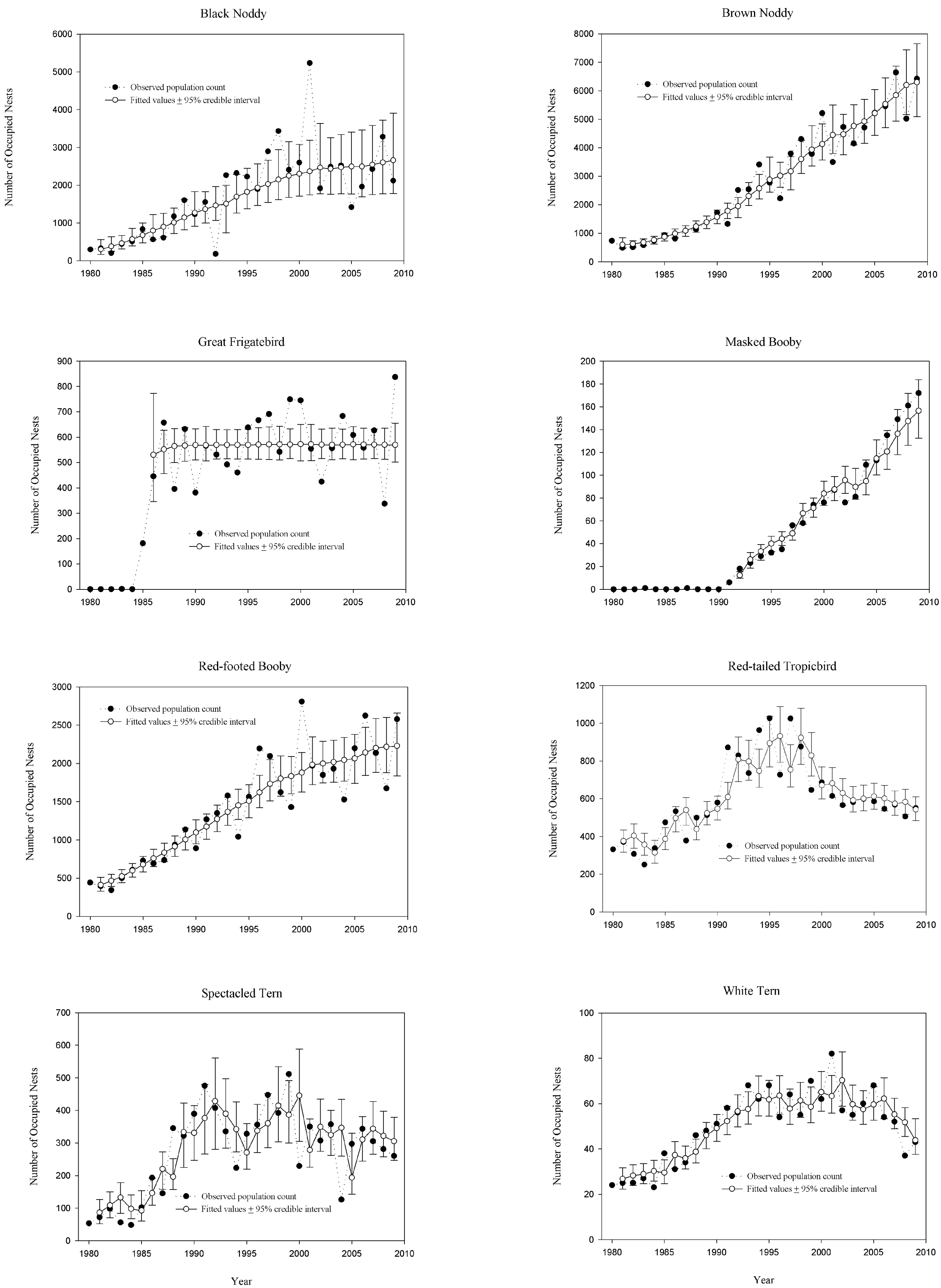


*Figure 5. Observed abundance, fitted values of abundance, and 95% credible intervals of nesting seabirds on Tern Island, 1980–2009 (U.S. Fish and Wildlife Service, unpublished data).*

**Table 2. Parameter estimates for the Bayesian analysis of the Gompertz model of 8 seabird species from Tern Island, Hawaii, 1980–2009.**

| *Species* | *Parameter*[a] | *Mean* | *SD* | *2.5% CI* | *Median* | *97.5% CI* |
|---|---|---|---|---|---|---|
| Black Noddy | *a* | 0.95 | 0.46 | 0.37 | 0.88 | 2.07 |
| | *c* | 0.88 | 0.06 | 0.72 | 0.89 | 0.96 |
| | σ | 0.08 | 0.11 | 0.03 | 0.05 | 0.52 |
| | τ | 0.50 | 0.10 | 0.20 | 0.50 | 0.67 |
| | *K* | 3008 | 1471 | – | – | – |
| Brown Noddy | *a* | 0.36 | 0.18 | 0.01 | 0.36 | 0.71 |
| | *c* | 0.96 | 0.02 | 0.92 | 0.96 | 1.01 |
| | σ | 0.07 | 0.05 | 0.03 | 0.05 | 0.23 |
| | τ | 0.17 | 0.04 | 0.05 | 0.17 | 0.24 |
| | *K* | 25,087 | 7706 | – | – | – |
| Great Frigatebird[b] | *c* | 0.08 | 0.19 | −0.29 | 0.08 | 0.45 |
| | *K* | 573 | 113 | – | – | – |
| Masked Booby | *a* | 1.01 | 0.22 | 0.59 | 1.00 | 1.46 |
| | *c* | 0.79 | 0.05 | 0.69 | 0.80 | 0.89 |
| | σ | 0.15 | 0.05 | 0.04 | 0.16 | 0.25 |
| | τ | 0.07 | 0.04 | 0.03 | 0.05 | 0.18 |
| | *K* | 141 | 37 | – | – | – |
| Red-footed Booby | *a* | 0.63 | 0.19 | 0.29 | 0.62 | 1.00 |
| | *c* | 0.92 | 0.03 | 0.87 | 0.92 | 0.97 |
| | σ | 0.05 | 0.03 | 0.03 | 0.04 | 0.13 |
| | τ | 0.19 | 0.03 | 0.13 | 0.19 | 0.25 |
| | *K* | 2774 | 623 | – | – | – |
| Red-tailed Tropicbird | *a* | 1.11 | 0.62 | −0.05 | 1.10 | 2.39 |
| | *c* | 0.83 | 0.10 | 0.63 | 0.83 | 1.01 |
| | σ | 0.17 | 0.03 | 0.10 | 0.17 | 0.24 |
| | τ | 0.06 | 0.03 | 0.03 | 0.05 | 0.13 |
| | *K* | 659 | 200 | – | – | – |
| Spectacled Tern | *a* | 1.41 | 0.59 | 0.35 | 1.37 | 2.62 |
| | *c* | 0.75 | 0.11 | 0.53 | 0.76 | 0.94 |
| | σ | 0.35 | 0.11 | 0.05 | 0.37 | 0.51 |
| | τ | 0.11 | 0.11 | 0.03 | 0.06 | 0.39 |
| | *K* | 327 | 163 | – | – | – |
| White Tern | *a* | 0.60 | 0.30 | 0.07 | 0.57 | 1.25 |
| | *c* | 0.85 | 0.08 | 0.68 | 0.86 | 0.99 |
| | σ | 0.13 | 0.04 | 0.05 | 0.12 | 0.21 |
| | τ | 0.08 | 0.04 | 0.03 | 0.08 | 0.16 |
| | *K* | 56 | 14 | – | – | – |

[a]*Key:* a*, rate of population growth in the absence of density dependence;* c*, the strength of density dependence; σ, process variation; τ, observation error;* K*, carrying capacity.*
[b]*Observation error (τ), process variation (σ), and rate of increase (*a*) are not reported for Great Frigatebird because the estimate of* c *is close to zero (Dennis et al. 2010). There is little correlation among Great Frigatebird abundance among years, which prevents reliable estimates of these parameters. Replicate counts (from either maximum mean incubation counts or other methods [Dearborn & Anders 2006]) are needed to better clarify sampling variance and the other parameters (Citta et al. 2007; Dennis et al. 2010).*

Frigate Shoals will lose additional land to erosion in areas without vegetation that are not protected by seawalls. Perhaps the greatest threat of severe island erosion to southern and eastern shores of islands is from hurricanes. On northern and western exposures most erosion occurs during large winter storms that create ocean swells that can reach heights of over 10 m (USACE 2011).

Although the seawall at Tern Island may prevent passive inundation from sea-level rise during this century because 86% of the island is ≥2 m, the other islets of French Frigate Shoals are not protected by seawalls and have a mean elevation <2 m. Despite the seawall, Tern Island is still vulnerable to sea-level rise, storm surge, and high waves. Hurricane waves in the central Pacific sometimes reach 4–9 m (Hurricane Iniki) (Fletcher et al. 1995); wave heights of this magnitude would wash over the islands in French Frigate Shoals except for La Perouse Pinnacle. This lava outcrop (0.3 ha, mean elevation 19.5 m) supports breeding Blue Noddies (*Procelsterna cerulea*), Brown Boobies (*Sula leucogaster*), Brown Noddies, Red-tailed Tropicbirds, and White Terns.

Our case study demonstrated both the resilience and the vulnerability of Pacific seabird populations. The population growth of seabird colonies at Tern Island despite a long history of disturbance suggests that some species can recover from intense human activity, including the dredge and filling operation that changed a sandy spit in 1941 into an auxiliary airfield subject to 38 years of weekly aircraft traffic. The engineered expansion of Tern Island benefitted seabirds half a century later by increasing the area of predator-free breeding habitat and reducing vulnerability to sea-level rise by increasing the island's mean elevation. At Tern Island, increases in seabird populations and the recolonization of extirpated species may be correlated with increases in nesting habitat, decreases in human disturbance at nesting colonies, and inundation of other islands of French Frigate Shoals. Despite the dramatic nature of seabird population increases we observed at Tern Island, there is also evidence that density dependence is now limiting population growth for many species.

The mechanisms by which population density may act to regulate the rate of population growth in seabirds has large implications for how these populations will respond to the creation of habitat. It is possible that density dependence could operate independently of the amount of available nesting habitat at the colony. Density-dependent foraging success may also be a factor in reduced reproductive success of colonial seabirds (Ashmole 1963; Lewis et al. 2001; Ballance et al. 2009). However, for the species at French Frigate Shoals, we believe it is more likely that density dependence is associated with the availability of nesting habitat. A shortage of nest sites may prevent pairs from breeding or reduce the reproductive success of birds that breed. Limited nest sites may affect species that nest in or under small trees or shrubs (e.g., Black Noddies, Great Frigatebirds, Red-footed Boobies, Red-tailed Tropicbirds, and White Terns). Even for ground-nesting species that can nest in areas with no vegetation, if bird densities are high the rate at which eggs are broken or nestlings are killed, either by adjacent adults (Schaffner 1991) or competing species, may increase.

### Mitigating the Effects of Sea-Level Rise

French Frigate Shoals are representative of Pacific atolls and islets in general. Over 358 atolls and islets span the Pacific (World Atlas 2011), and their elevations are on average <3 m (Dickinson 2009). Baker et al. (2006) predicted that a sea-level rise of 88 cm would cause Northwestern Hawaiian Islands shorelines to lose 5–75% of their land area. New evidence suggests that a sea-level rise of 1.0 m by 2100 is more likely (Fletcher 2009). Our preliminary analysis of sea-level rise in the Northwestern Hawaiian Islands (including Kure Atoll, Midway Atoll, Pearl and Hermes Atoll, Lisianski Island, Laysan Island, and French Frigate Shoals) predicted 4% of land area may be lost to inundation with a 1.0 m rise in sea level (U.S. Geological Survey, unpublished data). This loss of land area could leave more than 200,000 tropical seabirds without nesting habitat.

Our model results for habitat loss at moderate levels of sea-level rise (1.0 m) provide an example of how habitat limitation may affect population persistence. The models with habitat restoration showed that restoration may be beneficial even under moderate levels of sea-level rise. Opportunities for near-term mitigation exist in areas less vulnerable to inundation (island interiors and at maximum elevations), where trees and shrubs can be restored or artificial nest structures can be built to increase the carrying capacity for some species (Rauzon & Drigot 1999). We also expect vegetation restoration of the runway at Tern Island would be beneficial for nesting seabirds (Fig. 2). Island building, previously implemented for military operations at Tern Island and Midway Atoll, has also been used to restore habitat for colonial seabirds and may offset decreases in area of habitat losses associated with climate change (D. Roby, personal communication). Most seabird colonies have been extirpated from the main Hawaiian Islands (Olson & James 1982; Burney et al. 2001; USFWS 2005). However, over the long-term, if seabirds can be protected from introduced mammalian predators, restoration of Pacific seabird colonies on higher-elevation islands may represent a more enduring conservation solution for Pacific seabirds. For example, Kaho'olawe, one of the main Hawaiian Islands, is relatively high in elevation and would provide much-needed habitat for nesting seabirds if it were restored (Lindsey et al. 1997).

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