Technical Report HCSU-037

DYNAMICS OF SEABIRD COLONIES VULNERABLE TO SEA-LEVEL RISE AT FRENCH FRIGATE SHOALS, HAWAI`I

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Globally, seabirds are vulnerable to anthropogenic threats both at sea and on land. Seabirds typically nest colonially and show strong site fidelity; therefore, conservation strategies could benefit from an understanding of the population dynamics and vulnerability of breeding colonies to climate change. More than 350 atolls exist across the Pacific Ocean; while they provide nesting habitat for many seabirds, they are also vulnerable to sea-level rise. We used French Frigate Shoals, the largest atoll in the Hawaiian Archipelago, as a case study to explore seabird colony dynamics and the potential consequences of sea-level rise. We compiled a unique combination of data sets: historical observations of islands and seabirds, a 30-year time series of population abundance, LiDAR- (light detection and ranging) derived elevations, and satellite imagery. To model population dynamics for ten species at Tern Island from 1980 to 2009, we used the Gompertz model with parameters for the population growth rate, density dependence, process variation, and observation error. We used a Bayesian approach to estimate the parameters. All species increased in a pattern that provided evidence of density dependence. Density dependence may exacerbate the consequences of sea-level rise on seabirds because species that are already near the carrying capacity of the nesting habitat will be limited more than species that still have space for population growth. Laysan Albatross (*Phoebastria immutabilis*), Great Frigatebird (*Fregata minor*), Red-tailed Tropicbird (*Phaethon rubricauda*), Masked Booby (*Sula dactylatra*), Gray-backed Tern (*Onychoprion lunatus*), and White Tern (*Gygis alba*) are likely already at carrying capacity at Tern Island and therefore are most likely to be negatively impacted by sea-level rise. We project 12% of French Frigate Shoals (excluding La Perouse Pinnacle) will be inundated with +1.0 m sea-level rise or 32% with +2.0 m. Gray-backed Terns that nest along the coastal perimeters of islands and shrub-nesting species that are habitat limited are especially vulnerable to sea-level rise. However, at Tern Island, seawalls and habitat creation may mitigate projected seabird population declines due to habitat loss. We predict substantial losses in seabird nesting habitat across the low-lying Hawaiian Islands by 2100 and emphasize the need to restore higher elevation seabird colonies.

INTRODUCTION

Seabird populations are influenced globally by mortality from fisheries bycatch (de la Mare and Kerry 1994), plastic ingestion (Spear *et al.* 1995), harvesting of eggs and adults (Moller 2006), and introduced predators (Moors and Atkinson 1984, Burger and Gochfeld 1994). Breeding colonies on low-lying islands may also be threatened by sea-level rise (SLR; Baker *et al.* 2006, Woodroffe 2008, Marcelja 2010). To protect seabirds from these threats, there is an increasing emphasis on understanding seabird population dynamics for conservation and management (Nettleship *et al.* 1994, Wilcox and Donlan 2007).

Long-term monitoring of breeding colonies is one method of gathering information about the status of populations and the effectiveness of management actions. The resulting time series can be used to describe trends in seabird populations and provide insights into density dependence, carrying capacity, human disturbance, habitat loss or gain, and year-to-year variability (Lewis *et al.* 2001, Micol and Jouventin 2001, Kokko *et al.* 2004).

The Hawaiian Islands exemplify many of the challenges facing seabird conservation today. Due to predation most seabirds have been extirpated from the main Hawaiian Islands for 800 years (Olson and James 1982). In the late 19th century, there was extensive harvesting of seabird adults, nestlings, and eggs for human consumption, feather trade, and photography products (Spennemann 1998). United States legislation in 1909 ended this exploitation by creating the Hawaiian Islands National Wildlife Refuge (HINWR), encompassing all of the Northwestern Hawaiian Islands (NWHI) except Midway Atoll (Executive Order 1019). Introduced species (e.g., rabbits, rats, mice, livestock), however, continued to damage habitat on many islands during the 20th century (Ely and Clapp 1973, Amerson *et al.* 1974, Wetmore 1923 in Olson 1996). World War II military activities also had dramatic effects on many Pacific islands and their seabird populations (Fisher and Baldwin 1946). In recent decades, seabird conservation efforts have increased, including protection for the largest seabird rookery in the Pacific with the designation of Papahānaumokuākea Marine National Monument in 2006 (Presidential Proclamation 8031). Today, these small islands provide habitat for over 14 million federally protected seabirds (Fefer *et al.* 1984).

However, long-term conservation of seabird colonies is complicated by climate change. Recent estimates that include thermal expansion and ice sheet melting suggest sea levels may rise one to two meters by the end of the 21st century (Fletcher 2009, Vermeer and Rahmstorf 2009, Rahmstorf 2010). SLR could decrease the amount of nesting habitat available for seabirds on low-lying coral atoll islands, particularly in the NWHI where many islands have maximum elevations of less than 3 m (Hatfield *et al.* 2012, Krause *et al.* 2012). Nesting seabirds on low-lying islands may also suffer from the loss of nests, eggs, chicks, fledglings, and adults during severe storms and overwash events (Spendelow *et al.* 2002, U.S. Fish and Wildlife Service (USFWS) 2005, Baker *et al.* 2006, USFWS 2011). Because an increase in the frequency and severity of extreme weather events is one of the projected consequences of climate change (IPCC 2007), the negative impact of rising sea levels on seabird populations may be exacerbated by storms and El Niños.

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. Between 1963 and 2004, six of the thirteen islands that make up French Frigate Shoals (FFS) in the NWHI were inundated (Antonelis *et al.* 2006). While smaller islands were disappearing, Tern Island at FFS was expanded substantially by the U.S. military during World War II for use as a landing strip (Amerson 1971). Long-term monitoring of seabird numbers on Tern Island provides valuable information for understanding seabird population dynamics in conjunction with changes in nesting habitat (USFWS data) and human disturbance at seabird colonies. With a 30-year seabird monitoring history, FFS provides a unique opportunity to gain an understanding of disturbance and recovery of seabird colonies on low-lying Pacific islands.

Future seabird conservation will require an understanding of how and where populations are expected to decline as a result of SLR and what conservation strategies can be taken to adapt management actions to changing conditions. Quantifying the negative impacts of SLR on nesting habitat and the number of breeding seabirds requires an understanding of island topography and spatial patterns of seawater inundation (Berkowitz *et al.* 2012, Krause *et al.* 2012).

In this report, we explore seabird colony vulnerability to SLR at FFS using new topographic data, recent SLR projections, information on historical changes in seabird nesting habitat, and long-term monitoring data on seabird abundance. We use these data to: (1) quantify historical changes in the spatial extent and distribution of seabird habitat at FFS and make projections about how SLR and habitat creation could change the extent and distribution of future habitat and (2) test the assumption that seabirds would respond to habitat management by using historical information and long-term monitoring to estimate population growth rates, carrying capacities, and the strength of density dependence for ten species at Tern Island. Finally, we use our results to discuss options for future management and protection of NWHI seabird colonies in the context of SLR.

METHODS

Study Area

French Frigate Shoals (23°45’ N, 166°17’ W) is the largest atoll in the Hawaiian Archipelago (Figure 1). Eighteen seabird species, more than 202,000 breeders, nest annually at FFS (Pyle and Pyle 2009), where there are no terrestrial mammalian predators.

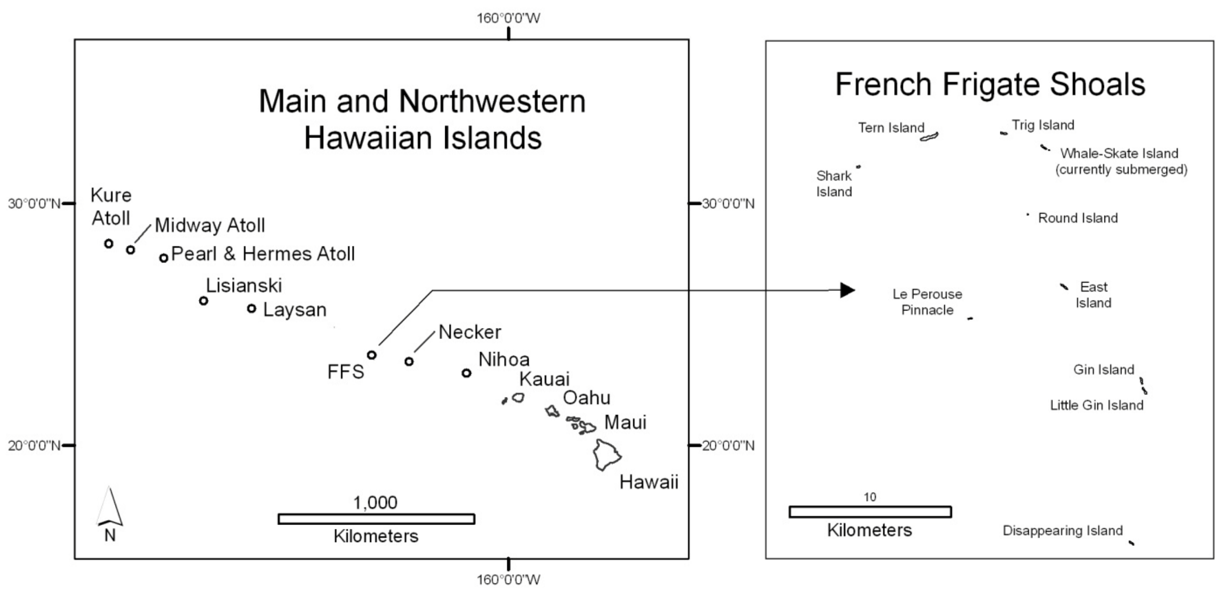


Figure 1. French Frigate Shoals (23°45’ N, 166°17’ W) is approximately 900 km northwest of Honolulu and is the largest atoll of the Northwestern Hawaiian Islands.

The history of the NWHI provides an opportunity to document and understand the disturbance and recovery of seabird colonies on low-lying Pacific islands. Of the 13 islands that made up FFS in 1963, 4 had well-established vegetation (Amerson 1971). The largest vegetated island in the atoll, Whale-Skate (once 6.9 ha), had the largest seabird population during the 1960s (Amerson 1971). Over the course of the last century, Whale-Skate Island decreased in area such that after 1996 it did not support breeding birds (USFWS unpublished data). By 1999 the island disappeared entirely (Antonelis *et al.* 2006). Tern Island was expanded, relative to its 1932 shoreline (Figure 2), by the U.S. military during World War II for use as a landing strip (Amerson 1971). Despite the engineering that increased island size and doubled potential

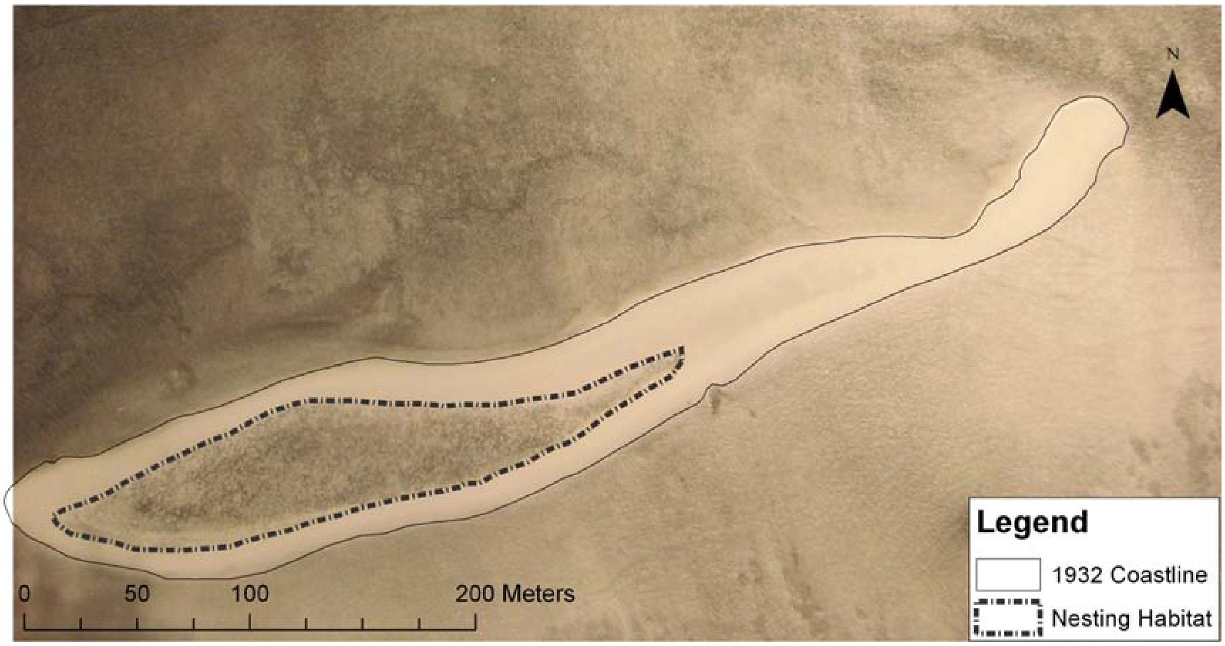


Figure 2. Aerial photograph of Tern Island, French Frigate Shoals, June 1932, taken before the August 1942 expansion to create the U.S. Naval Airfield. Photograph is from the National Archive and Records Administration Still Pictures. Nesting habitat delineation was described by Amerson (1971).

nesting habitat, human disturbance limited breeding seabird populations at Tern Island. During World War II, as many as 127 people, several dogs, and 22 planes were stationed on Tern Island (Amerson 1971). Daily patrol flights required destruction of seabird nests on the runway and only three of six historically breeding species persisted during this time (Amerson 1971). After World War II, Tern Island was used as a U.S. Coast Guard LORAN (long range navigation) station and Pacific Missile Range tracking site, with weekly flights maintained until 1979. Management of the island was transferred to the USFWS as part of the HINWR. Present day staffing fluctuates from 4–11 people and runway use is limited to emergency flights.

Geospatial Analysis to Quantify Impacts of Sea-level Rise on Seabird Nesting Habitat

Projections of inundation from sea-level rise

We used LiDAR- (light detection and ranging) derived digital elevation models (DEMs; 1-m cell size) for the land area of Shark, Tern, Gin, and Disappearing Islands (see Krause *et al.* 2012 for collection and assessment details). For islands without LiDAR data (Trig, Round, East, La Perouse, and Little Gin), we used photogrammetrically-derived DEMs from PhotoSat's geophysical processing system (Mitchell and MacNabb 2010, PhotoSat Information Ltd. 2010).

We used ArcGIS (version 10.0; ESRI 2010) to model four scenarios of SLR: +0.5, +1.0, +1.5, and +2.0 m. These scenarios of SLR assume little change in the ice sheets of Greenland and Antarctica. While the SLR scenarios presented here are presumed to occur over the next century, the actual timing for these events is unknown (Rahmstorf 2007, Merrifield *et al.* 2009, Vermeer and Rahmstorf 2009). We analyzed each SLR scenario at mean high water (MHW) based on National Oceanic and Atmospheric Administration (NOAA) tidal predictions from East Island (NOAA Station ID 1619222, scaled from the Honolulu tidal gauge, NOAA Station ID 1612340).

We used a passive SLR model to inundate all grid cells below an elevation threshold, while accounting for connectivity to a water source (Li *et al.* 2009, Krause *et al.* 2012). Specifically, only those cells connected by an eight-neighbor (grid cell) relationship to the ocean were inundated. By applying this constraint, we assumed low-elevation areas inland do not flood unless a hydrologic connection exists. Since high-resolution bathymetric data for FFS were unavailable, more complex wave run-up inundation models were not possible at this time (see Berkowitz *et al.* 2012).

Land cover and habitat classification

We used aerial and satellite photography and historical descriptions to quantify land cover on Tern Island in 1932, 1942, 1981, and 2010, and on East Island in 2011. For other islands of FFS we used aerial imagery from July 2010 collected during LiDAR data collection or DigitalGlobe WorldView-2 satellite imagery from 2010 or 2011 (Digital Globe Inc. 2010). For 1981, 2010, and 2011, we classified land cover with the IsoCluster unsupervised classification tool in ArcGIS (ESRI 2010, see Krause *et al.* 2012 for more details). We classified land cover into seven categories: (1) shrub, (2) vine/ground cover, (3) bare ground, (4) beach, (5) runway, (6) buildings, and (7) seawall. Based on a botanical survey of Tern Island (Starr and Martz 1999), we expect 'shrub' included *Scaevola taccada* and *Tournefortia argentea* and 'vine/ground cover' included *Boerhavia repens*, *Chenopodium murale*, *Chenopodium oahuense*, *Heliotropium currasavicum*, *Heliotropium procumbens*, *Ipomoea pes-caprae*, *Lepturus repens*, *Malva parviflora*, *Portulaca lutea*, *Portulaca oleracea*, *Sonchus oleraceus*, *Tribulus cistoides*, and invasive grasses including *Digitaria ciliaris* and *Eleusine indica*. 'Beach' consisted of the coastal band subject to regular wave swash and was not typically used as bird breeding habitat, while 'bare ground' consisted of sandy or rocky areas adjacent to or inland of 'beach'. Buildings at Tern Island are often used as bird breeding habitat (e.g., some species nest on or under buildings).

Historical and future land cover change

We analyzed land cover change over time using Land Change Modeler Idrisi software (Eastman 2006, IDRISI 2010). The 1981, 2010, and 2011 images were compared to quantify shoreline change (erosion or accretion) and conversion from one land cover type to another (e.g., areas with vine/ground cover that became bare ground).

We quantified potential land cover change from SLR using a vegetation response model that assumes SLR outpaces vegetation regeneration; thus inundated land cover is lost and does not shift inland. In ArcGIS, we overlaid the land cover classification with inundation extent for each SLR scenario (+0.5, +1.0, +1.5, and +2.0 m) to calculate the area of each land cover class lost. At Tern Island, we estimated the potential conversion of runway to avian breeding habitat if the runway were decommissioned (hereafter, habitat creation). We assumed that created habitat would have the same proportion of each land cover class as 2010 habitat (excluding beach, buildings, and seawall); actual habitat creation goals for the runway area may differ from these proportions.

Avifauna nesting habitat classification

We calculated species-specific potential nesting area (ha) as the sum of all utilized land cover classes (Table 1). Nesting habitat was not characterized for Brown Booby (*Sula leucogaster*)

Table 1. Known seabird nesting habitat by land cover class on Tern Island identified from aerial imagery.

Species	Shrub	Grass/ herbaceous cover	Vine/ ground cover	Bare ground	Buildings
Black-footed Albatross		X	X	X	
Laysan Albatross		X	X	X	
Bonin Petrel	X	X	X		
Bulwer's Petrel				X	
Wedge-tailed Shearwater	X	X	X	X	X
Christmas Shearwater	X	X	X		
Tristram's Storm-petrel	X	X	X	X	
Red-tailed Tropicbird	X	X			X
Masked Booby		X	X	X	
Red-footed Booby	X				
Great Frigatebird	X				
Gray-backed Tern			X	X	
Sooty Tern		X	X	X	
Brown Noddy	X	X	X	X	
Black Noddy	X				X
White Tern	X				X

and Blue Noddy (*Procelsterna cerulea*) that nest only on the rocky pinnacle of La Perouse. Habitat classification included buildings at Tern Island, as these structures are used by some birds for nesting. We classified buildings as habitat for shrub nesting White Tern (*Gygis alba*) and Black Noddy (*Anous minutus*) as they also commonly nest on window ledges or other above ground surfaces (Rauzon and Kenyon 1984). Similarly, buildings with post-and-pier foundations (a portion of the area classified as buildings) were classified as nesting habitat for three species that nest underneath them (Wedge-tailed Shearwater [*Puffinus pacificus*], Red-tailed Tropicbird [*Phaethon rubricauda*], and Black Noddy; below ground, ground, and above ground nesters respectively [Table 1]). Change in potential nesting area was calculated for SLR and habitat creation scenarios.

In defining potential habitat abundance, we assumed all known nesting habitat types were equally utilized by a given species, ignoring habitat preferences and competition between species that may vary with habitat availability among potential habitats. Land cover classification using aerial imagery did not allow for separation among soil types or substrates (e.g., sand, rubble). The three burrowing species at FFS (Bonin Petrel [*Pterodroma hypoleuca*], Wedge-tailed Shearwater, and Tristram's Storm-petrel [*Oceanodroma tristrami*]) establish nests only in areas where burrowing is possible and the soil is stable; Bulwer's Petrel (*Bulweria bulwerii*) nest in rocky crevices at FFS. Potential nesting habitat area for these four species was, therefore, overestimated because sub-surface constraints were not accounted for. For models of habitat creation on the Tern Island runway we excluded the runway area for burrow-nesting birds as they are not expected to be able to burrow into the hard-packed surface for many years. Bulwer's Petrel was also excluded from the runway area. Active management to alter or enhance habitat (e.g., artificial burrows, nest boxes, or substrate manipulation) has been successfully employed on Tern Island but was not included in the model. Finally, although land cover potentially suitable for Gray-backed Tern (*Onychoprion lunatus*) nesting exists over much of Tern Island, this species nests only near the shoreline at Tern Island (K. Courtot, P. Hartzell, M. Reynolds personal observations).

How Will Seabird Populations Respond to Changes in Nesting Habitat?

Our analysis of the vulnerability of nesting seabirds to inundation of nesting habitat from SLR assumes that (1) seabirds are limited by the amount of available nesting habitat, and (2) if new habitat is created, populations would be able to recruit into it. To test the assumption that seabird populations respond to changes in nesting habitat on FFS, we used two lines of evidence: (1) we reviewed the published literature on historical changes in seabird abundance on FFS, and (2) we used long-term nest monitoring data from Tern Island to quantify population dynamics. Land area values estimated from the land cover response models were used to calculate species-specific potential nesting area loss with SLR.

Long-Term Monitoring of Nesting Seabirds on Tern Island

We analyzed abundance data collected using mean incubation counts (MIC) on Tern Island, 1980–2009, for eight species of breeding seabirds for which sufficient data were available: Black Noddy, Brown Noddy (*Anous stolidus*), Great Frigatebird (*Fregata minor*), Masked Booby (*Sula dactylatra*), Red-footed Booby (*Sula sula*), Red-tailed Tropicbird, Gray-backed Tern, and White Tern (USFWS data). MICs are the observed abundance of nests with eggs; count data are collected from visits to the colony at intervals that correspond to the mean incubation period of that species. This method has been widely applied to monitoring seabirds on Pacific islands (Megyesi and Griffin 1996, Citta *et al.* 2007, Seavy and Reynolds 2009). Because nearly all eggs would have hatched by the subsequent visit, it is unlikely that the same nest would be counted on more than a single visit. However, if pairs bred more than once in a single season or renested after failure, then the sum of nests counted during all visits in a season would overestimate the number of breeding individuals. Therefore, we followed the precedent of using the maximum MIC during a breeding season as a conservative index of the total number of breeding pairs (Megyesi and Griffin 1996, Seavy and Reynolds 2009). Additionally, we analyzed abundance data for Black-footed Albatross (*Phoebastria nigripes*) from 1980–2005 and Laysan Albatross (*Phoebastria immutabilis*) from 1982–2005 (USFWS data). Nests were directly censused annually. We refer to all counts used in the modeling as observed abundance and assume that counts provide an index of the total population.

Long-Term Changes in Observed Abundance of Nesting Seabirds on Tern Island

The description of population dynamics is complicated by two sources of variability: process variation and observation error (Shenk *et al.* 1998). Process variation represents true fluctuations in population size that result from environmental stochasticity. In contrast to process variation, observation error represents fluctuations in observed 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, Staples *et al.* 2005, Freckleton *et al.* 2006). Thus, there has been increasing emphasis on statistical methods that can estimate the contribution of each of these two sources of variation to total variation in time-series data (Clark and Bjornstad 2004, Dennis *et al.* 2006).

We used a state-space approach to investigate the temporal dynamics of breeding seabird counts (see Hatfield *et al.* 2012 for details). Briefly, density-dependent growth was modeled with the Gompertz equation:

$$X_t = a + cX_{t-1} + E_t \qquad \text{(Equation 1)}$$

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 $E_t \sim N(0,\sigma^2)$ represents the normally distributed unbiased error. Density dependence is implied when $c < 1$, with greater density dependence implied with smaller values of c (Staples *et al.* 2004, Staples *et al.* 2005, Dennis *et al.* 2006, Seavy *et al.* 2009). Process variation is represented by E_t. Observation error was incorporated by adding it to the natural logarithm of true population (resulting in the term Y_t):

$$Y_t = X_t + F_t \qquad \text{(Equation 2)}$$

where $F_t \sim N(0, \tau^2)$ and τ is the observation error (also called sampling error). Bayesian analysis (Link and Barker 2010) to estimate these parameters was conducted in WinBUGS (version 1.4.3, Lunn *et al.* 2000). We assumed vague uniform priors for σ^2, τ^2, and the first observed abundance of each species, a vague normal prior for a, and a uniform (-2, 3) prior for c. We summarized the posterior distributions for σ (process variation), τ (sampling error), a (intrinsic rate of increase), and c (strength of density dependence) by their means, standard deviations, medians, and credible intervals. Carrying capacities (K) and standard deviations (SDs) were then calculated using equations 47–51 from Dennis *et al.* (2006).

RESULTS

Geospatial Analysis to Quantify Impacts of Sea-level Rise on Seabird Nesting Habitat

Historical changes in land cover on Tern Island

Island engineering in 1942 expanded Tern Island from 6.8 ha (in 1932) to 15.5 ha, of which 46% was runway (Table 2). By 2010, 1.7 ha (11%) of the island had been lost to shoreline erosion. Vegetation encroachment reduced runway coverage to 26% of the island by 2010. Between 1981 and 2010 shrub and vine/ground cover habitat was also reduced at Tern Island because of shoreline erosion and beach encroachment. Shrubs covered only 4% (0.5 ha) of Tern Island (Table 2, Figure 3). If the runway were no longer needed for emergency evacuations at Tern Island and vegetation was allowed to encroach or be planted in this area in approximately the same proportion as the rest of the island, more shrub (0.2 ha, 40%), vine/ground cover (1.5 ha, 42%), and bare ground (1.8 ha, 45%) habitat could exist compared to 2010 (Figure 3).

Projections of inundation and land cover change from sea-level rise at Tern Island

High-resolution DEMs showed that Tern Island had a mean elevation of 2.3 ± SD 0.5 m (median = 2.4 m, range = 0–3.4 m; Table 3) in 2010. Little variation in elevation existed across Tern Island due to deliberate leveling and seawall fortification. The seawall at Tern Island may prevent inundation from SLR before 2100 because 95% of the island is ≥ 1 m in elevation and 86% of the island is ≥ 2 m (Krause *et al.* 2012). Accounting for connectivity with the ocean,

Table 2. Land cover in hectares (ha) for Tern Island, French Frigate Shoals, Hawai`i, based on aerial imagery and historical accounts. Land cover change (percent change) predicted with +1.0 m sea-level rise (SLR) with and without habitat creation.

	Area (ha)				Percent change	
	Year				+1.0 m SLR	
Tern Island	1932	1942*	1981	2010	Without habitat creation	With habitat creation
Shrub	0.0		0.7	0.5	0.0	40.0
Vine/ground cover	2.0		4.2	3.6	0.0	41.7
Bare ground	0.0	8.3	2.9	4.2	0.0	45.2
Beach	4.8	*	1.1	1.2	-41.7	-41.7
Runway (not used for nesting)	0.0	7.2	4.9	3.6	0.0	-100
Buildings	0.0		0.4	0.4	0.0	0.0
Seawall (not used for nesting)	0.0	0.0	0.0	0.3	-33.3	-33.3
Total area	6.8	15.5	14.1	13.8	-4.3	-4.3

*From Amerson (1971) description. Bare ground and beach were not differentiated.

only 4% of the total area was expected to be lost at +1.0 m SLR and 13% at +2.0 m (Tables 3 and 4).

Projections of inundation and land cover change from sea-level rise across French Frigate Shoals

In 2010, nine islands totaling 22.1 ha of land made up FFS (Table 3). The low-lying islands (excludes La Perouse Pinnacle) had a mean elevation of 1.3 ± SD 0.7 m (Table 3). Shark, Trig, Round, East, Gin, Little Gin, and Disappearing Islands combined were predicted to be reduced by 25% of their land mass with +1.0 m SLR and 64% with a +2.0 m rise (Table 3). Little to no loss of area was predicted at most islands at +0.5 m SLR; however, at SLR levels of +1.5 and +2.0 m, only Tern and East Islands are likely to support seabird breeding (Table 3, Figure 4). Within FFS, vegetation occurred only at Tern and East Islands (Tables 4–11), and as such, the only breeding habitat for seabirds on most islands was bare ground.

East Island, the second largest island of FFS (2.8 ha), had a mean elevation of 2.3 ± SD 0.5 m (Table 3). Shrubs covered <1% of the island (Table 5, Figure 5). East Island was not predicted to be reduced in size at +1.0 m SLR. At +2.0 m SLR the island was expected to be reduced in size by only 4% and only beach habitat was expected to be lost (Tables 3 and 5).

In 2010, Trig Island was 1.4 ha in size and had a mean elevation of 0.5 ± SD 0.8 m (Table 3). Total area loss of more than 21% was predicted at +1.0 m and almost 79% at +2.0 m SLR. Bare ground area, the only nesting habitat present at Trig, would not be lost at +1.5 m SLR but would be reduced by 50% at +2.0 m SLR (Table 6). Shark, Trig, Round, Gin, Little Gin, and Disappearing Islands were all less than two hectares in size with mean elevations of less than two meters (Table 3). Each of these islands, except Trig, were predicted to be reduced by more than 25% at +1.0 m SLR and completely inundated at +2.0 m SLR (Table 3).

Seabird nesting habitat change with sea-level rise

At Tern Island, no reductions in seabird habitat were predicted at +1.0 m SLR. We predicted reductions of less than 15% of potential nesting habitat for all nesting bird species at +2.0 m SLR (Table 12a). Potential habitat for species that utilize bare ground and vine/ground cover

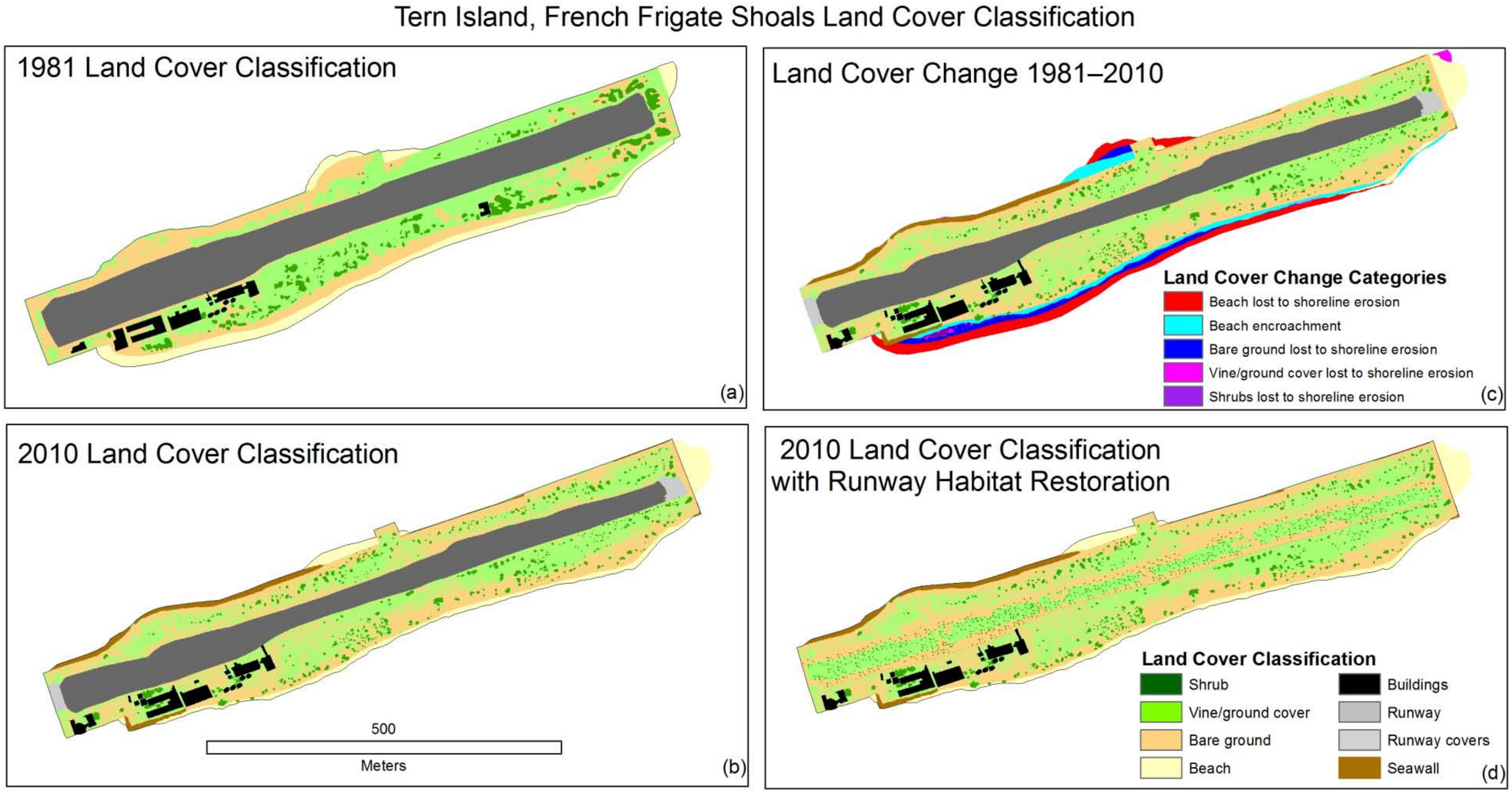


Figure 3. Land cover change analysis for Tern Island: (a) land cover classification 1981, (b) land cover classification 2010, (c) land cover change 1981–2010, and (d) potential land cover if the runway were decommissioned and seabird nesting habitat created.

land cover classes (Black-footed Albatross, Laysan Albatross, Wedge-tailed Shearwater, Tristram's Storm-petrel, Masked Booby, Gray-backed Tern, Sooty Tern, and Brown Noddy) was reduced by 8–9% at +2.0 m SLR (Table 12a). No loss of nesting habitat was predicted for the four tree/shrub-nesting species at Tern Island (Red-footed Booby, Great Frigatebird, Black Noddy, and White Tern) at +0.5–2.0 m SLR.

Table 3. Elevation and land area (above mean high water, MHW) for islands of French Frigate Shoals, Hawai`i, derived from LiDAR and PhotoSat Digital Elevation Models (DEM). Inundation models were used to predict potential island area lost with four sea-level rise scenarios.

Island	RMSE (m)	DEM elevation (m) 2010 Mean	± SD	Max	MHW 0.0 m Area (ha)	MHW +0.5 m Area (ha)	MHW +0.5 m % change	MHW +1.0 m Area (ha)	MHW +1.0 m % change	MHW +1.5 m Area (ha)	MHW +1.5 m % change	MHW +2.0 m Area (ha)	MHW +2.0 m % change
Shark	0.05	1.2	± 0.3	1.9	0.3	0.3	0.0	0.2	-33.3	0.0	-100	0.0	-100
Tern	0.05	2.3	± 0.5	3.4	13.8	13.7	-0.7	13.2	-4.3	12.5	-9.4	12.0	-13.0
Trig*	0.15	0.5	± 0.8	2.5	1.4	1.3	-7.1	1.1	-21.4	0.8	-42.9	0.3	-78.6
Round*	0.15	1.0	± 0.6	2.0	0.1	0.1	0.0	0.0	-100	0.0	-100	0.0	-100
East*	0.10	2.3	± 0.5	3.1	2.8	2.8	0.0	2.8	0.0	2.7	-3.6	2.7	-3.6
La Perouse Pinnacle*	0.15	19.5	± 12.1	39.7	0.3	**	**	**	**	**	**	**	**
Gin	0.05	1.6	± 0.5	2.9	1.7	1.4	-17.6	0.9	-47.1	0.3	-82.4	0.0	-100
Little Gin*	0.15	1.0	± 0.4	1.8	1.6	1.5	-6.2	1.1	-31.3	0.2	-87.5	0.0	-100
Disappearing	0.05	0.6	± 0.6	2.3	0.4	0.2	-50.0	0.1	-75.0	0.0	-100	0.0	-100
Total***	-	1.3	± 0.7	3.4	22.1	21.3	-3.6	19.4	-12.2	16.5	-25.3	15.0	-32.1

*PhotoSat DEM used **Area loss due to sea-level rise not assessed for La Perouse Pinnacle ***Total excluding La Perouse Pinnacle

Table 4. Total land area (ha) and percent change for each of nine land cover types, including habitat creation on the runway, at Tern Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from aerial image (July 2010).

Land cover	0.0 m Area (ha)	+0.5 m Area (ha)	+0.5 m % change	+1.0 m Area (ha)	+1.0 m % change	+1.5 m Area (ha)	+1.5 m % change	+2.0 m Area (ha)	+2.0 m % change
Shrub	0.5	0.5	0.0	0.5	0.0	0.5	0.0	0.5	0.0
Vine/ground cover	3.6	3.6	0.0	3.6	0.0	3.6	0.0	3.5	-2.8
Bare ground	4.2	4.2	0.0	4.2	0.0	3.8	-9.5	3.6	-14.3
Beach	1.2	1.1	-8.3	0.7	-41.7	0.4	-66.7	0.3	-75.0
Buildings	0.4	0.4	0.0	0.4	0.0	0.4	0.0	0.4	0.0
Seawall	0.3	0.3	0.0	0.2	-33.3	0.2	-33.3	0.1	-66.7
Habitat creation - runway shrubs	0.2	0.2	0.0	0.2	0.0	0.2	0.0	0.2	0.0
Habitat creation - runway vine/ground cover	1.5	1.5	0.0	1.5	0.0	1.5	0.0	1.5	0.0
Habitat creation - runway bare ground	1.9	1.9	0.0	1.9	0.0	1.9	0.0	1.9	0.0
Total island size	13.8	13.7	-0.7	13.2	-4.3	12.5	-9.4	12.0	-13.0

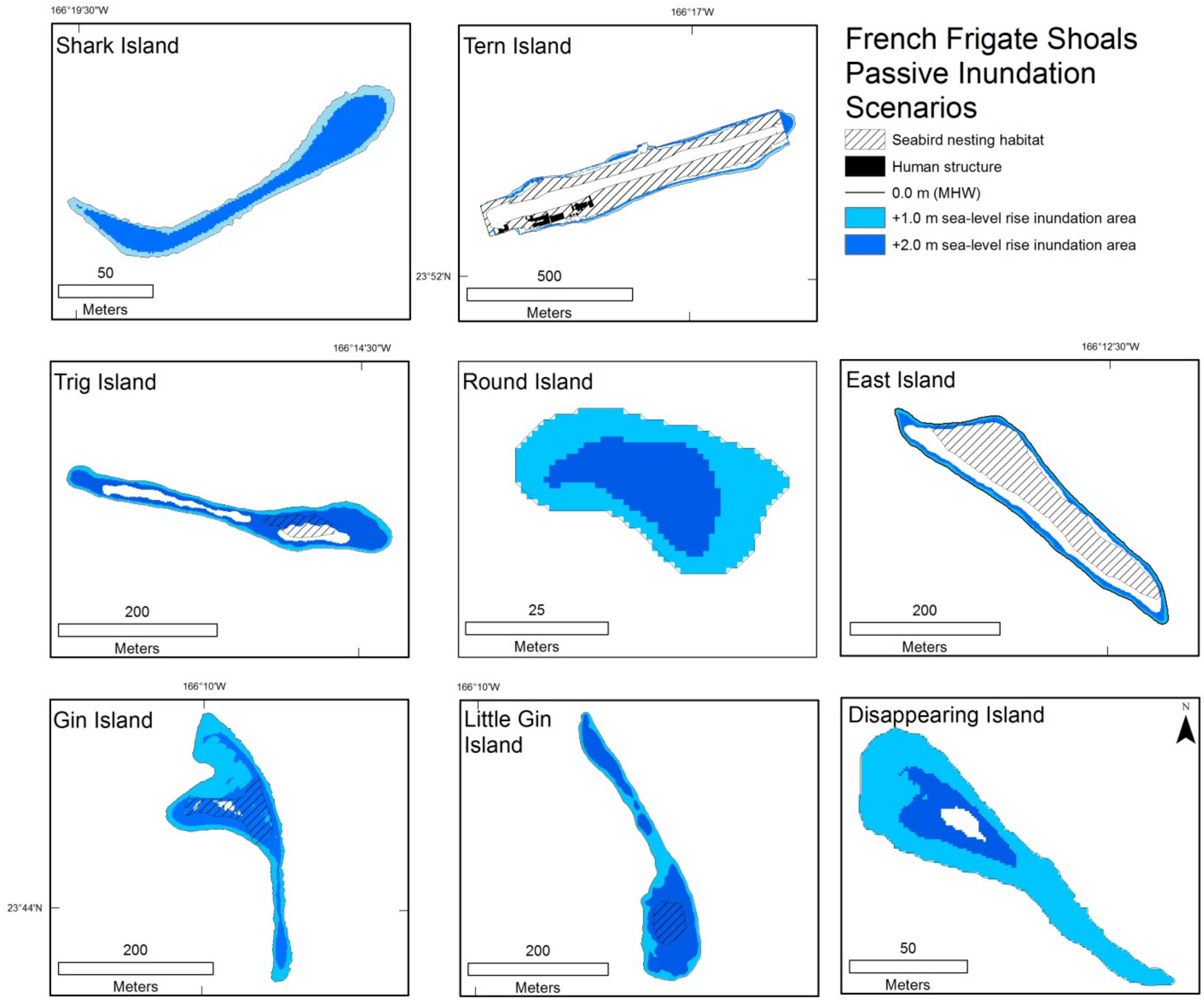


Figure 4. Passive inundation scenario maps for eight islands of French Frigate Shoals at three sea levels: mean high water (MHW), +1.0 m, and +2.0 m sea-level rise. Nesting habitat was mapped from 2011 field data (U.S. Fish and Wildlife Service, unpublished data).

Potential seabird nesting habitat could be increased by more than 22% for most nesting seabirds at Tern Island if the runway were decommissioned and vegetation established (Table 12b). However, it is likely burrow- and crevice-nesting birds (Bonin Petrel, Wedge-tailed Shearwater, Tristram's Storm-petrel, and Bulwer's Petrel) would be limited by the hard-packed substrate on a decommissioned runway (Table 12b).

East Island provided the second largest amount of breeding bird habitat of the islands of FFS in 2010. As much as 2.1 ha of habitat was available for species that use bare ground and vine/ground cover habitats (Black-footed Albatross, Laysan Albatross, Wedge-tailed Shearwater, Tristram's Storm-petrel, Masked Booby, Gray-backed Tern, and Brown Noddy; Table 13). For all

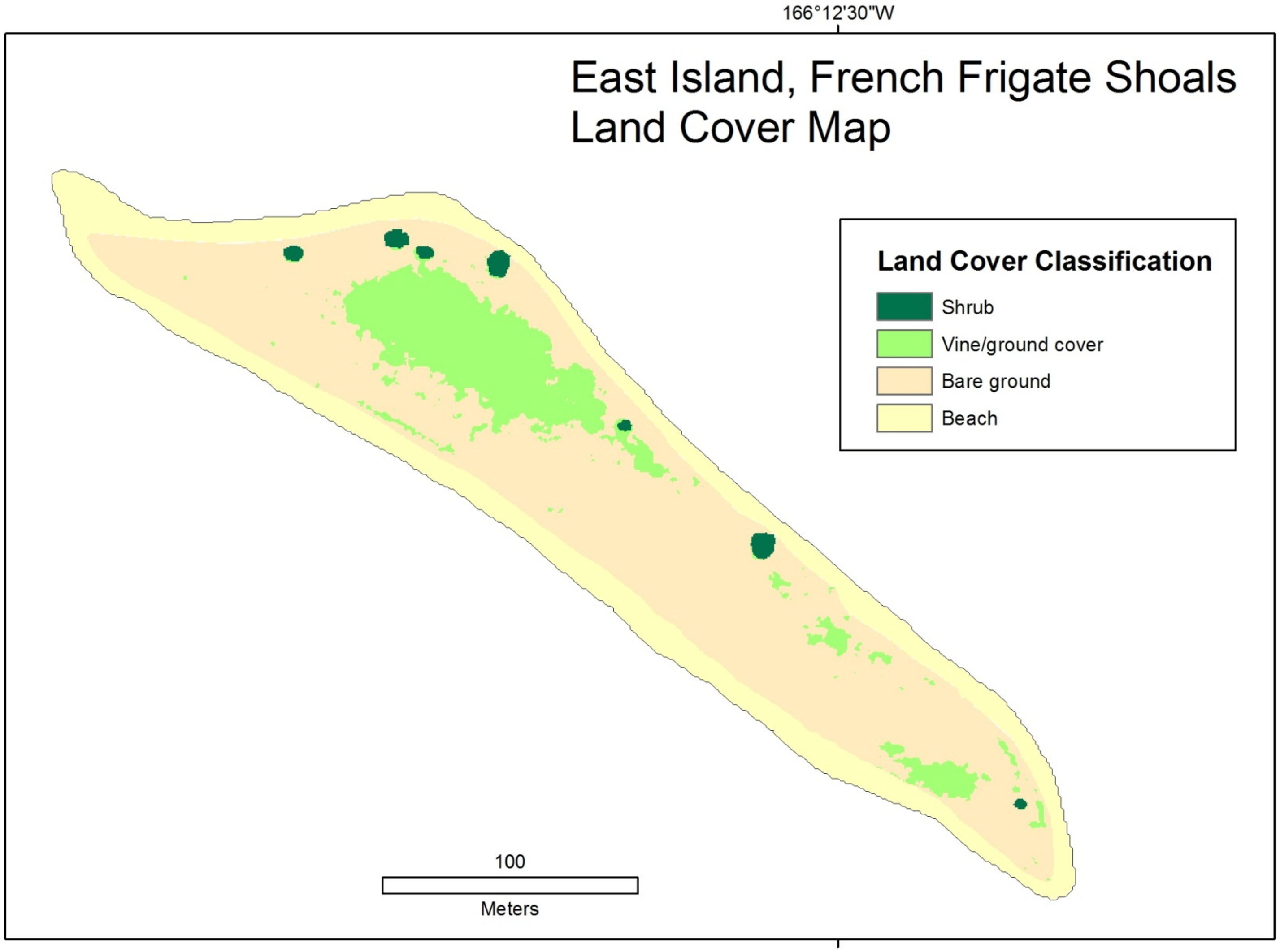


Figure 5. East Island, French Frigate Shoals, land cover classification map developed using primarily unsupervised classification methods from DigitalGlobe Worldview-2 satellite imagery (August 2011).

Table 5. Total land area (ha) and percent change for each of four land cover types at East Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from DigitalGlobe WorldView-2 satellite imagery (August 2011).

	0.0 m	+0.5 m		+1.0 m		+1.5 m		+2.0 m	
Land cover	Area (ha)	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change
Shrub*	0.03	0.03	0.0	0.03	0.0	0.03	0.0	0.03	0.0
Vine/ground cover	0.4	0.4	0.0	0.4	0.0	0.4	0.0	0.4	0.0
Bare ground	1.7	1.7	0.0	1.7	0.0	1.7	0.0	1.7	0.0
Beach	0.7	0.7	0.0	0.7	0.0	0.6	-14.3	0.6	-14.3
Total island size	2.8	2.8	0.0	2.8	0.0	2.7	-3.6	2.7	-3.6

*Additional decimal place displayed to quantify small amount of shrub habitat present

Table 6. Total land area (ha) and percent change for each of two land cover types at Trig Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from DigitalGlobe WorldView-2 satellite imagery (August 2011).

	0.0 m	+0.5 m		+1.0 m		+1.5 m		+2.0 m	
Land cover	Area (ha)	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change
Bare ground	0.2	0.2	0.0	0.2	0.0	0.2	0.0	0.1	-50.0
Beach	1.2	1.1	-8.3	0.9	-25.0	0.6	-50.0	0.2	-83.3
Total island size	1.4	1.3	-7.1	1.1	-21.4	0.8	-42.9	0.3	-78.6

Table 7. Total land area (ha) and percent change for one land cover type at Shark Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from aerial image (July 2010).

	0.0 m	+0.5 m		+1.0 m		+1.5 m		+2.0 m	
Land cover	Area (ha)	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change
Beach	0.3	0.3	0.0	0.2	-33.3	0.0	-100	0.0	-100
Total island size	0.3	0.3	0.0	0.2	-33.3	0.0	-100	0.0	-100

Table 8. Total land area (ha) and percent change for one land cover type at Round Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from DigitalGlobe WorldView-2 satellite imagery (August 2011).

	0.0 m	+0.5 m		+1.0 m		+1.5 m		+2.0 m	
Land cover	Area (ha)	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change
Beach	0.1	0.1	0.0	0.0	-100	0.0	-100	0.0	-100
Total island size	0.1	0.1	0.0	0.0	-100	0.0	-100	0.0	-100

Table 9. Total land area (ha) and percent change for each of two land cover types at Gin Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from aerial image (July 2010).

	0.0 m	+0.5 m		+1.0 m		+1.5 m		+2.0 m	
Land cover	Area (ha)	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change
Bare ground	0.4	0.4	0.0	0.4	0.0	0.2	-50.0	0.0	-100
Beach	1.3	1.0	-23.1	0.5	-61.5	0.1	-92.3	0.0	-100
Total island size	1.7	1.4	-17.6	0.9	-47.1	0.3	-82.4	0.0	-100

Table 10. Total land area (ha) and percent change for each of two land cover types at Little Gin Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from DigitalGlobe WorldView-2 satellite imagery (August 2011).

	0.0 m	+0.5 m		+1.0 m		+1.5 m		+2.0 m	
Land cover	Area (ha)	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change
Bare ground	0.2	0.2	0.0	0.2	0.0	0.1	-50.0	0.0	-100
Beach	1.4	1.3	-7.1	0.9	-35.7	0.1	-92.9	0.0	-100
Total island size	1.6	1.5	-6.2	1.1	-31.3	0.2	-87.5	0.0	-100

Table 11. Total land area (ha) and percent change for one land cover type at Disappearing Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from aerial image (July 2010).

	0.0 m	+0.5 m		+1.0 m		+1.5 m		+2.0 m	
Land cover	Area (ha)	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change	Area (ha)	% change
Beach	0.4	0.2	-50.0	0.1	-75.0	0.0	-100	0.0	-100
Total island size	0.4	0.2	-50.0	0.1	-75.0	0.0	-100	0.0	-100

SLR scenarios considered (+0.5–2.0 m), breeding habitat at East Island was not lost (Table 13). The islands of Trig, Gin, and Little Gin each provided ≤ 0.4 ha of bare ground nesting habitat for Black-footed Albatross, Laysan Albatross, Masked Booby, and Brown Noddy (Brown Noddy at Gin only; Tables 14–16). At Gin and Little Gin Islands, 50% of breeding habitat was lost at +1.5 m SLR and 100% at +2.0 m SLR. Trig Island lost 50% of nesting habitat area at +2.0 m SLR. Shark, Disappearing, and Round Islands were not used as seabird breeding sites in 2010.

Population Dynamics Inferred From Analysis of Long-Term Monitoring on Tern Island

Viable population monitoring analysis

All ten of the seabird populations, for which there were sufficient long-term data to conduct

Table 12. Total potential nesting habitat area (ha) and percent change for breeding avifauna at Tern Island, French Frigate Shoals, with four sea-level rise (SLR) scenarios (+0.5, +1.0, +1.5, and +2.0 m) with (a) active runway and (b) habitat creation on the runway. Areas calculated from land cover classes with aerial imagery (July 2010). We assumed percent change from a uniform density across nesting habitat. Additional assumptions of this model are described in the methods.

a) Tern Island, French Frigate Shoals, with active runway conditions

	Area (ha)	Percent change with SLR			
Species	0.0 m	+0.5 m	+1.0 m	+1.5 m	+2.0 m
Black-footed Albatross	7.8	0.0	0.0	-5.1	-9.0
Laysan Albatross	7.8	0.0	0.0	-5.1	-9.0
Bonin Petrel	4.1	0.0	0.0	0.0	-2.4
Bulwer's Petrel	4.2	0.0	0.0	-9.5	-14.3
Wedge-tailed Shearwater	8.7	0.0	0.0	-4.6	-8.0
Christmas Shearwater	4.1	0.0	0.0	0.0	-2.4
Tristram's Storm-petrel	8.3	0.0	0.0	-4.8	-8.4
Red-tailed Tropicbird	0.9	0.0	0.0	0.0	0.0
Masked Booby	7.8	0.0	0.0	-5.1	-9.0
Red-footed Booby	0.5	0.0	0.0	0.0	0.0
Great Frigatebird	0.5	0.0	0.0	0.0	0.0
Gray-backed Tern	7.8	0.0	0.0	-5.1	-9.0
Sooty Tern	7.8	0.0	0.0	-5.1	-9.0
Brown Noddy	8.3	0.0	0.0	-4.8	-8.4
Black Noddy	0.9	0.0	0.0	0.0	0.0
White Tern	0.9	0.0	0.0	0.0	0.0

b) Tern Island, French Frigate Shoals, with habitat creation on the runway

	Area (ha)	Percent change with SLR and habitat creation				
Species	0.0 m	0.0 m	+0.5 m	+1.0 m	+1.5 m	+2.0 m
Black-footed Albatross	7.8	43.6	43.6	43.6	38.5	34.6
Laysan Albatross	7.8	43.6	43.6	43.6	38.5	34.6
Bonin Petrel	4.1	0.0	0.0	0.0	0.0	-2.4
Bulwer's Petrel	4.2	0.0	0.0	0.0	-9.5	-14.3
Wedge-tailed Shearwater	8.7	0.0	0.0	0.0	-4.6	-8.0
Christmas Shearwater	4.1	41.5	41.5	41.5	41.5	39.0
Tristram's Storm-petrel	8.3	0.0	0.0	0.0	-4.8	-8.4
Red-tailed Tropicbird	0.9	22.2	22.2	22.2	22.2	22.2
Masked Booby	7.8	43.6	43.6	43.6	38.5	34.6
Red-footed Booby	0.5	40.0	40.0	40.0	40.0	40.0
Great Frigatebird	0.5	40.0	40.0	40.0	40.0	40.0
Gray-backed Tern	7.8	43.6	43.6	43.6	38.5	34.6
Sooty Tern	7.8	43.6	43.6	43.6	38.5	34.6
Brown Noddy	8.3	43.4	43.4	43.4	38.6	34.9
Black Noddy	0.9	22.2	22.2	22.2	22.2	22.2
White Tern	0.9	22.2	22.2	22.2	22.2	22.2

Table 13. Total potential nesting habitat area (ha) and percent change for breeding avifauna at East Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from land cover classes with DigitalGlobe WorldView-2 satellite imagery (August 2011). We assumed percent change from a uniform density across nesting habitat.

	Area (ha)	Percent change			
Species	0.0 m	+0.5 m	+1.0 m	+1.5 m	+2.0 m
Black-footed Albatross	2.1	0.0	0.0	0.0	0.0
Laysan Albatross	2.1	0.0	0.0	0.0	0.0
Bonin Petrel	0.4	0.0	0.0	0.0	0.0
Bulwer's Petrel	1.7	0.0	0.0	0.0	0.0
Wedge-tailed Shearwater	2.1	0.0	0.0	0.0	0.0
Christmas Shearwater	0.4	0.0	0.0	0.0	0.0
Tristram's Storm-petrel	2.1	0.0	0.0	0.0	0.0
Red-tailed Tropicbird*	0.03	0.0	0.0	0.0	0.0
Masked Booby	2.1	0.0	0.0	0.0	0.0
Red-footed Booby*	0.03	0.0	0.0	0.0	0.0
Great Frigatebird*	0.03	0.0	0.0	0.0	0.0
Gray-backed Tern	2.1	0.0	0.0	0.0	0.0
Brown Noddy	2.1	0.0	0.0	0.0	0.0

*Additional decimal place displayed to quantify small amount of shrub habitat present.

Table 14. Total potential nesting habitat area (ha) and percent change for breeding avifauna at Trig Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from land cover classes with DigitalGlobe WorldView-2 satellite imagery (August 2011). We assumed percent change from a uniform density across nesting habitat.

	Area (ha)	Percent change			
Species	0.0 m	+0.5 m	+1.0 m	+1.5 m	+2.0 m
Black-footed Albatross	0.2	0.0	0.0	0.0	-50.0
Laysan Albatross	0.2	0.0	0.0	0.0	-50.0
Masked Booby	0.2	0.0	0.0	0.0	-50.0

Table 15. Total potential nesting habitat area (ha) and percent change for breeding avifauna at Gin Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from land cover classes with aerial image (July 2010). We assumed percent change from a uniform density across nesting habitat.

	Area (ha)	Percent change			
Species	0.0 m	+0.5 m	+1.0 m	+1.5 m	+2.0 m
Black-footed Albatross	0.4	0.0	0.0	-50.0	-100
Laysan Albatross	0.4	0.0	0.0	-50.0	-100
Masked Booby	0.4	0.0	0.0	-50.0	-100
Brown Noddy	0.4	0.0	0.0	-50.0	-100

Table 16. Total potential nesting habitat area (ha) and percent change for breeding avifauna at Little Gin Island, French Frigate Shoals, with four sea-level rise scenarios (+0.5, +1.0, +1.5, and +2.0 m). Areas calculated from land cover classes with DigitalGlobe WorldView-2 satellite imagery (August 2011). We assumed percent change from a uniform density across nesting habitat.

	Area (ha)	Percent change			
Species	0.0 m	+0.5 m	+1.0 m	+1.5 m	+2.0 m
Black-footed Albatross	0.2	0.0	0.0	-50.0	-100
Laysan Albatross	0.2	0.0	0.0	-50.0	-100
Masked Booby	0.2	0.0	0.0	-50.0	-100

population growth analyses, increased at Tern Island between 1980 and 2009, in some cases dramatically (Figure 6). Two extirpated species, Great Frigatebird and Masked Booby, recolonized the island during this time. Three species, Red-tailed Tropicbird, Gray-backed Tern, and White Tern, declined from the mid-1990s to 2009, however (Figure 6). For the Black-footed Albatross, Red-footed Booby, Brown Noddy, and Black Noddy, the populations have not yet reached carrying capacity. We infer that carrying capacity has been reached for the Laysan Albatross, Great Frigatebird, Red-tailed Tropicbird, Gray-backed Tern, and White Tern since the observed nesting pairs exceed the values derived for these species (Table 17, Figure 6). All species showed evidence for density dependence (Table 17, $c < 1$). The strongest density dependence was evident in the Great Frigatebird population (mean $c = 0.08$), for which it appears that Tern Island is unable to support more than ca. 600 nests (Figure 6f).

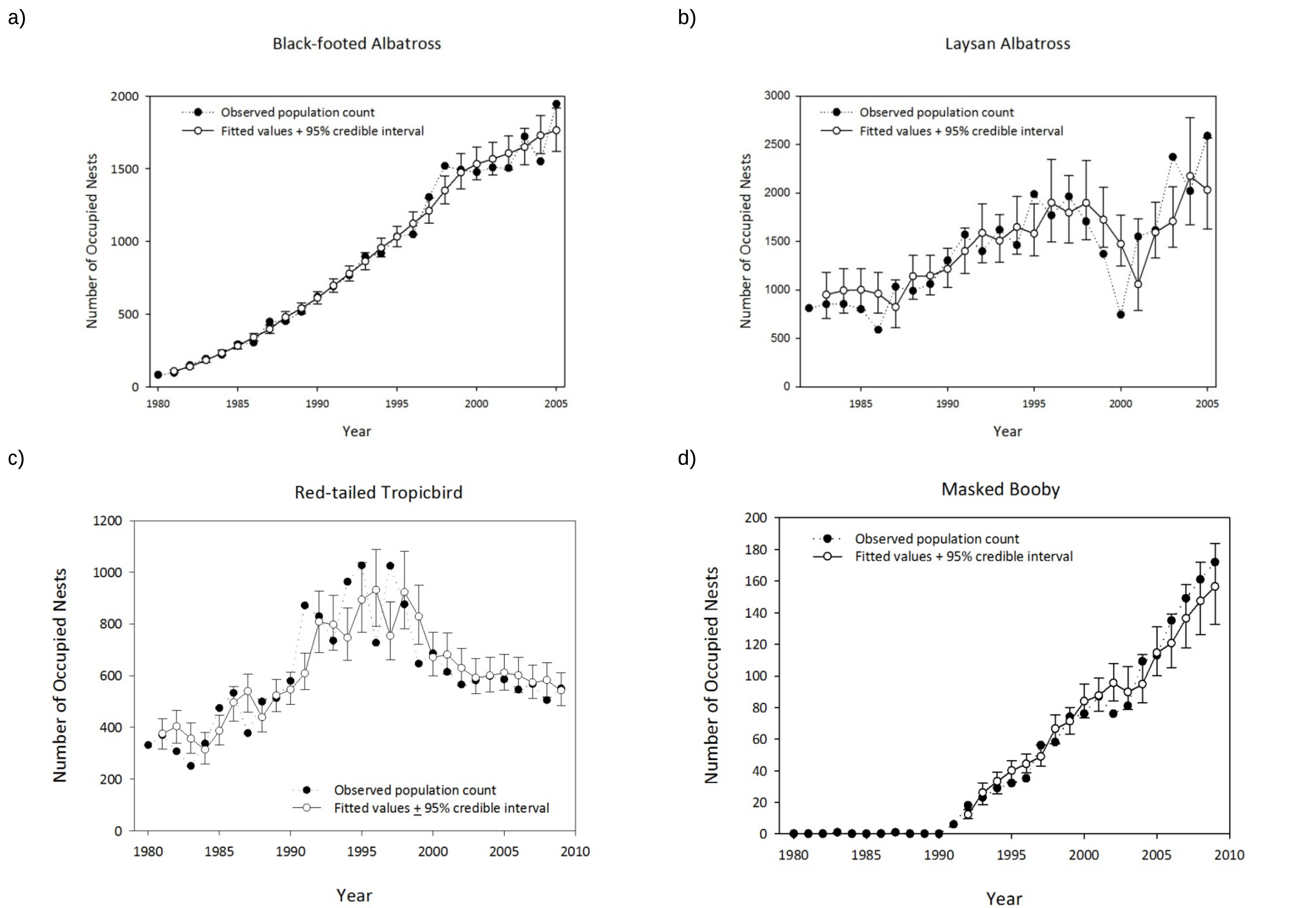
Potential changes in seabird abundance

We assumed changes in nesting area abundance would be proportional to the changes in species-specific abundance for the 10 species at Tern Island that showed evidence of density-dependent growth or that had reached carrying capacity (Table 17). Abundance of Black-footed and Laysan Albatross, Masked Booby, Gray-backed Tern, and Brown Noddy is expected to decrease by as much as 9% with current habitat conditions and +2.0 m SLR (Table 12a). However, with habitat creation on the runway, abundance of these 10 species was predicted to increase by more than 20%, even with an increase in sea levels of +2.0 m (Table 12b).

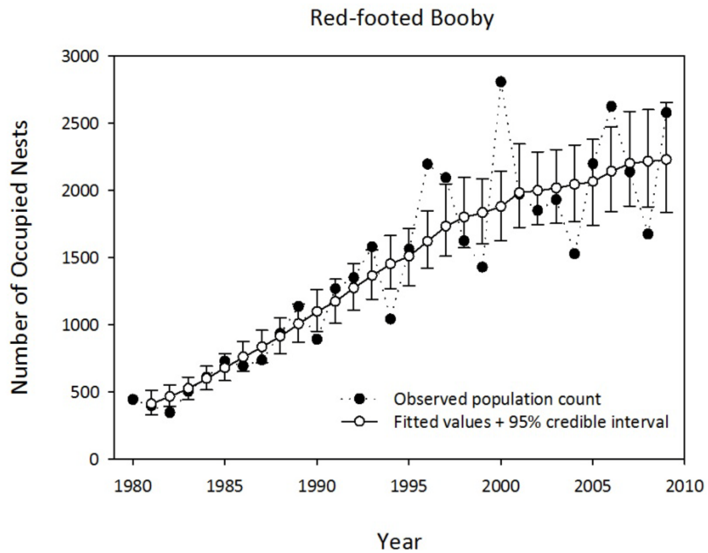
Historical changes in seabird abundance

All seabird species included in analyses of population growth were present at FFS during 1960–1969 (Smithsonian Pacific Ocean Biological Survey Program; Amerson 1971). However, there were no breeding Masked or Red-footed Booby, Great Frigatebird, Gray-backed Tern, Black Noddy, or Brown Noddy on Tern Island at that time. Only small breeding populations of Black-footed Albatross (7 pairs), Laysan Albatross (200 pairs), Red-tailed Tropicbird (45 pairs), and White Tern (9 pairs) persisted on Tern Island (Amerson 1971). These populations have increased dramatically, now exceeding 1500, 2500, 500, and 40 breeding pairs, respectively (Figure 6a–c & j).

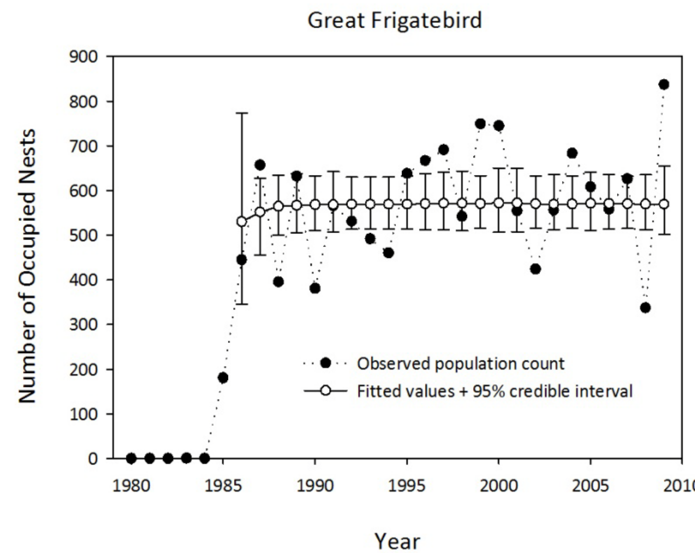
Elsewhere in FFS, the loss of six islands and overwash events have contributed to the loss of seabird breeding habitat within FFS since 1964. Forty years ago, prior to inundation, Whale-Skate Island (separate and later joined as one island) supported native vegetation and breeding seabird colonies of Black-footed Albatross (50 pairs), Laysan Albatross (500 pairs), Red-tailed Tropicbird (8 pairs), Masked Booby (140 pairs), Red-footed Booby (14 pairs), Great Frigatebird


a)
Black-footed Albatross
Observed population count
Fitted values + 95% credible interval
Number of Occupied Nests
Year
b)
Laysan Albatross
Observed population count
Fitted values + 95% credible interval
Number of Occupied Nests
Year
c)
Red-tailed Tropicbird
Observed population count
Fitted values + 95% credible interval
Number of Occupied Nests
Year
d)
Masked Booby
Observed population count
Fitted values + 95% credible interval
Number of Occupied Nests
Year

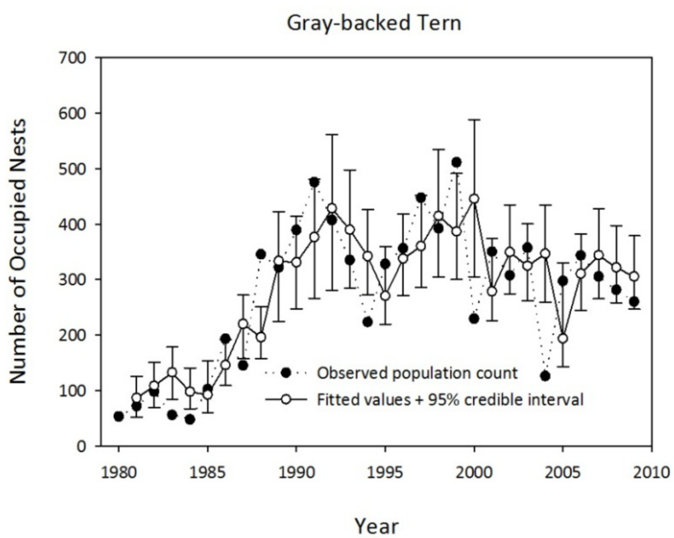
e)


Red-footed Booby
Number of Occupied Nests
Year
Observed population count
Fitted values + 95% credible interval

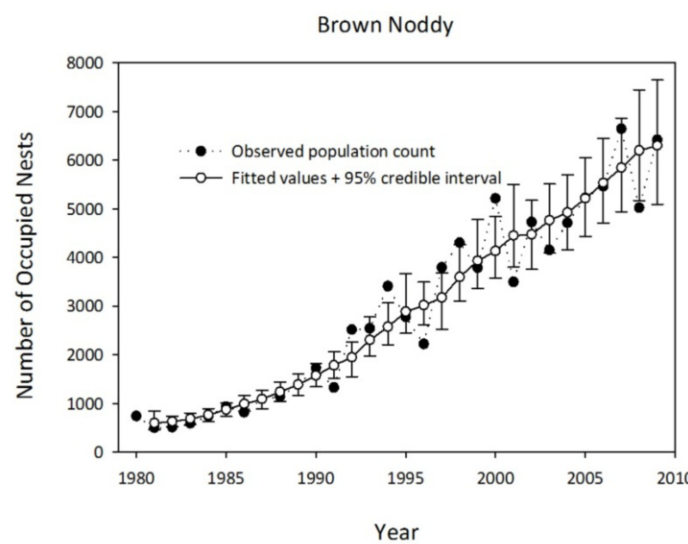
f)


Great Frigatebird
Number of Occupied Nests
Year
Observed population count
Fitted values + 95% credible interval

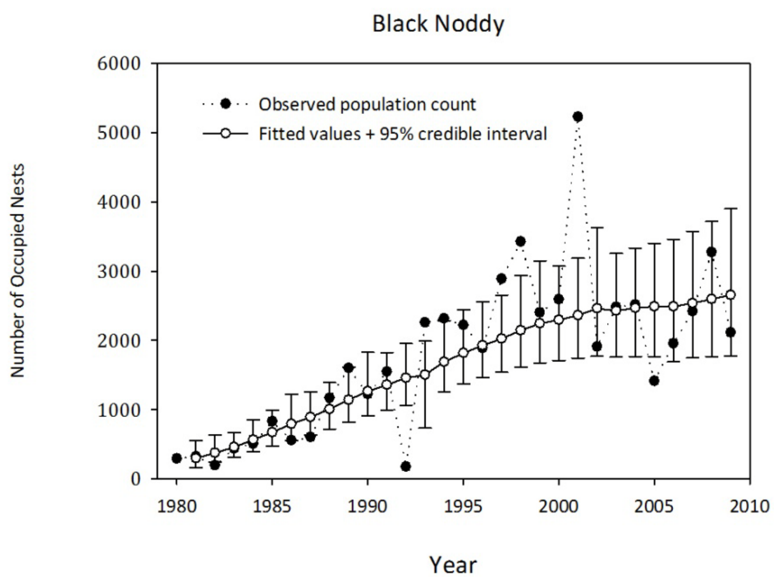
g)


Gray-backed Tern
Number of Occupied Nests
Year
Observed population count
Fitted values + 95% credible interval

h)


Brown Noddy
Number of Occupied Nests
Year
Observed population count
Fitted values + 95% credible interval

i)



j)

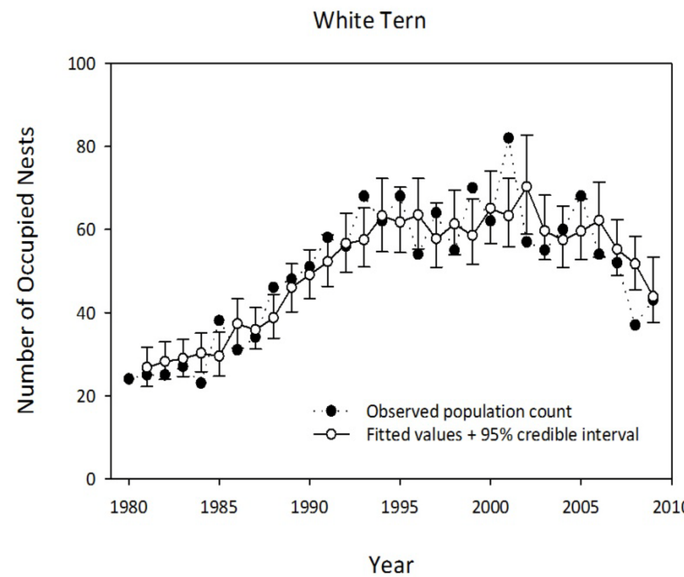


Figure 6. Observed seabird abundance, Tern Island, French Frigate Shoals, 1980–2009, and fitted values ± 95% credible intervals. Species include (a) Black-footed Albatross, (b) Laysan Albatross, (c) Red-tailed Tropicbird, (d) Masked Booby, (e) Red-footed Booby, (f) Great Frigatebird, (g) Gray-backed Tern, (h) Brown Noddy, (i) Black Noddy, and (j) White Tern.

(221 pairs), Gray-backed Tern (120 pairs), and Brown Noddy (850 pairs; Amerson 1971). No seabirds nested at Whale-Skate Island after 1996 (USFWS unpublished data), which has been inundated since 1998 (Antonelis *et al.* 2006).

Discussion

Our results suggest that even moderate amounts of SLR could have profound effects on the amount of nesting habitat available to seabirds at FFS. Specifically, the SLR model indicates a loss of land area along specific shorelines of Tern Island and substantial loss of land area at the other islands of FFS, allowing managers to anticipate where accelerated habitat loss from SLR is likely and where habitat restoration or creation activities might be most effective. Frequent wave overwash may accelerate habitat losses from inundation, as overwash can lead to upslope vegetation shifting, plant dieback, increased erosion, and soil instability (Davidson-

Table 17. Parameter estimates (*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) for the Bayesian analysis of the Gompertz model for 10 seabird species from Tern Island, Hawai`i, with standard deviations (SD) and credible intervals (CI). Data for Black-footed Albatross are from 1980–2005, Laysan Albatross from 1982–2005, and for all other species from 1980–2009.

Species	Parameter	Mean	SD	2.5% CI	Median	97.5% CI
Black-footed Albatross	*a*	0.97	0.07	0.52	0.67	0.82
	c	0.91	0.01	0.89	0.92	0.94
	σ	0.06	0.01	0.04	0.06	0.09
	τ	0.04	0.01	0.03	0.04	0.08
	K	2,662	331	-	-	-
Laysan Albatross	*a*	1.5	1.1	-0.60	1.14	3.72
	c	0.81	0.16	0.49	0.81	1.09
	Σ	0.87	0.07	0.03	0.06	0.26
	T	0.23	0.08	0.04	0.24	0.35
	K	1,780	674	-	-	-
Red-tailed Tropicbird	*a*	1.11	0.62	-0.05	1.1	2.39
	c	0.83	0.1	0.63	0.83	1.01
	Σ	0.17	0.03	0.1	0.17	0.24
	T	0.06	0.03	0.03	0.05	0.13
	K	659	200	-	-	-
Masked Booby	*a*	1.01	0.22	0.59	1.0	1.46
	c	0.79	0.05	0.69	0.8	0.89
	Σ	0.15	0.05	0.04	0.16	0.25
	T	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	1.0
	c	0.92	0.03	0.87	0.92	0.97
	Σ	0.05	0.03	0.03	0.04	0.13
	T	0.19	0.03	0.13	0.19	0.25
	K	2,774	623	-	-	-
Great Frigatebird*	*a*	-	-	-	-	-
	c	0.08	0.19	-0.29	0.08	0.45
	Σ	-	-	-	-	-
	T	-	-	-	-	-
	K	573	113	-	-	-

Species	Parameter	Mean	SD	2.5% CI	Median	97.5% CI
Gray-backed 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	-	-	-
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
	T	0.17	0.04	0.05	0.17	0.24
	K	25,087	7,706	-	-	-
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
	T	0.5	0.1	0.2	0.5	0.67
	K	3,008	1,471	-	-	-
White Tern	*a*	0.6	0.3	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
	T	0.08	0.04	0.03	0.08	0.16
	K	56	14	-	-	-

*Future seabird monitoring could be improved with independent replicate counts, especially for the Great Frigatebird (Citta *et al.* 2007). Observation error (τ), process variation (σ), and rate of increase (*a*) are not reported for Great Frigatebird since the estimate of *c* is close to zero (Dennis *et al.* 2010). There is little correlation among Great Frigatebird abundance among years, preventing reliable estimates of these parameters. Replicate counts (either using maximum MIC or other methods, see Dearborn and Anders 2006) are needed to better clarify sampling variance and the other parameters (Citta *et al.* 2007, Dennis *et al.* 2010).

Arnott 2005). We predict FFS will lose additional habitat to erosion in areas not protected by seawalls. Additionally, species such as the Gray-Backed Tern that nest near the shoreline will be particularly vulnerable to storm-wave overwash. La Perouse Pinnacle, an unvegetated lava outcrop with a mean elevation of 19.5 m that supports populations of Red-tailed Tropicbird, Brown Booby, Red-footed Booby, Blue Noddy, Brown Noddy, and White Tern, is unlikely to be affected by SLR.

While the seawall at Tern Island may prevent passive inundation from SLR before 2100 (because 86% of the island is ≥ 2 m), the other islands of FFS are not protected by seawalls and have mean elevations of < 2.5 m. Despite the seawall, Tern Island is still vulnerable to inundation in places where the seawall is eroding, especially during extreme events such as winter waves that can reach heights of greater than 10 m (USACE 2011) and from major hurricanes that occasionally occur in the Central Pacific. While only five category-five hurricanes have occurred in the Central Pacific since 1950 and none have made landfall, future storms may make landfall in the NWHI, or at least come close enough to produce damaging storm surges and wave heights (Businger 2012, Central Pacific Hurricane Center 2012). As a reference level of potential impact, Hurricane Iniki, a category-four storm in 1992, produced combined water heights of 4–9 m on the island of Kaua`i (Fletcher *et al.* 1995). In terms of storm paths, major hurricanes have occurred within the Hawaiian Archipelago (Businger 2012, Central Pacific Hurricane Center 2012) to either side of FFS (Hurricane Iniki to the west and Hurricane Patsy, which approached Midway in 1959, to the east); thus the possibility remains that a major hurricane and its associated storm surge and overwash potential will affect FFS at some point in the future.

This case study from the NWHI demonstrated both the resilience and the vulnerability of Pacific seabird populations. The population growth of seabird colonies at Tern Island revealed the ability of some species to recover from intense human disturbance, including the 1941 dredge and filling operations that changed a sandy spit into an auxiliary airfield subject to 38 years of regular aircraft traffic. Engineering to expand Tern Island benefitted seabirds half a century later by increasing predator-free breeding habitat and reducing vulnerability to SLR by increasing the island's mean elevation. At Tern Island, increases in many seabird populations may be correlated with increases in nesting habitat, decreases in human-caused nesting disturbance, and the inundation of other FFS islands. Despite the dramatic nature of these increases, there is evidence that density dependence is now limiting population growth for many species.

The mechanisms by which density may act to regulate the rate of population growth in seabirds has important implications for how these populations will respond to the creation of new habitat. It is certainly possible that density dependence could operate independently of the amount of available nesting habitat at the colony. Density-dependent foraging success has also been suggested as a factor that may reduce the reproductive success of colonial seabirds (Ashmole 1963, Lewis *et al.* 2001, Ballance *et al.* 2009). However, for these species at FFS we find it more likely that density dependence is associated with the availability of suitable nesting habitat. A shortage of nest sites may prevent pairs from breeding or reduce the reproductive success of birds that do breed. Nest-site limitation may be important for species that nest in or under small trees or shrubs (e.g., Black Noddy, Great Frigatebird, Red-footed Booby, Red-tailed Tropicbird, and White Tern). Even for ground-nesting species that do not rely on vegetation for nesting habitat, nest-site limitation is important if high bird densities increase the rate at which eggs are broken or nestlings are killed, either by adjacent adults (Schaffner 1991) or by competing species.

To better detect trends in breeding populations by providing a measure of observation error that currently cannot be distinguished from process error, future seabird monitoring could be improved with independent replicate counts, especially for the Great Frigatebird (Citta *et al.* 2007). Observation error (τ), process variation (σ), and rate of increase (a), are not reported for Great Frigatebird since the estimate of c is close to zero (Dennis *et al.* 2010). There is little correlation found in Great Frigatebird abundance among years, preventing reliable estimates of these parameters. Replicate counts (either using maximum MIC or other methods, see Dearborn and Anders 2006) are needed to better clarify sampling variance, which cannot be distinguished from process error, and the other parameters (Citta *et al.* 2007, Dennis *et al.* 2010).

Options for Adapting Pacific Seabird Conservation to Sea-level Rise

French Frigate Shoals are representative of Pacific atolls and islets in general. A recent study notes that more than 350 atolls and islands span the Pacific (World Atlas 2011) with elevations generally lying < 3 m above mean sea level (Dickinson 2009). Evidence suggests that a SLR of +1.0 m by 2100 is an appropriate planning target (Fletcher 2009). An analysis of SLR of the NWHI (including Kure Atoll, Midway Atoll, Pearl and Hermes Atoll, Lisianski Island, Laysan Island, and FFS) predicted 4% of habitat may be lost to inundation from +1.0 m SLR and 26% from +2.0 m SLR (Krause *et al.* 2012). This could leave many seabirds without nesting habitat.

Our predictions of habitat loss at moderate levels of SLR (+1.0 m) provide a scale of likely habitat limitation and link habitat limitation with population persistence. Our results also suggest that habitat creation could be beneficial to seabirds even under moderate levels of SLR or after extreme events (e.g., severe winter storms; Figure 3). Opportunities for near-term mitigation exist in areas less vulnerable to inundation (i.e., atoll interiors and maximum elevations) by restoring habitat or establishing artificial nest structures to increase the carrying capacity for some species. Indeed, artificial nest boxes deployed at Tern Island have been readily used by burrow- and crevice-nesting species such as Tristram's Storm-petrel and Bulwer's Petrel (USFWS unpublished data). Habitat creation on the runway at Tern Island is also expected to increase seabird habitat (Figure 3). Island expansion, previously implemented for military operations at Tern Island and Midway Atoll, has been used specifically to restore colonial seabirds and could be considered to offset declining critical habitat resources in the face of climate change (D. Roby, U.S. Geological Survey, personal communication). Most seabird colonies have been extirpated from the main Hawaiian Islands (Olson and James 1982, Burney *et al.* 2001); however, in the long-term, if seabirds can be protected from introduced mammalian predators, restoration of colonies on higher elevation islands represents a more enduring conservation solution for Pacific seabirds. For example, Kaho`olawe, which is one of the main Hawaiian Islands and relatively high in elevation, has the potential to provide such a refuge for nesting seabirds (Lindsey *et al.* 1997).

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APPENDIX I

This appendix describes differences in this analysis and an earlier analysis published in *Conservation Biology 2012* ("Population dynamics of Hawaiian seabird colonies vulnerable to sea-level rise", by Jeff S. Hatfield, Michelle H. Reynolds, Nathaniel E. Seavy, and Crystal M. Krause, DOI: 10.1111/j.1523-1739.2012.01853.x). Both examine the potential impacts of sea-level rise (SLR) at French Frigate Shoals, but with different data, models, and results. In this appendix we summarize differences in the two publications.

Land Area Change

Land area (ha) loss values for the islands of French Frigate Shoals under four scenarios of SLR published in Table 1 of the *Conservation Biology* manuscript (2012, Volume 26(4)) were revised using updated and corrected imagery. The updated values are presented in Table 3 of this report and a correction has been published in *Conservation Biology* (February 2013).

Land Cover Loss Models

Land cover response to SLR is uncertain. Among many factors, the timescale on which SLR occurs, underlying habitat conditions (e.g., soil type), and species characteristics and composition will affect how the land cover of an island will change with rising sea levels. Analyses and results in the *Conservation Biology* manuscript focused on a land cover response model that assumed land cover would shift inland with rising sea levels (referred to as the "dynamic" vegetation response model). With this model, as an elevation bin (e.g., 0.0–0.5 m) was inundated the land cover within the elevation bin was assumed to shift to a higher elevation and, likewise, land cover at higher elevations were also shifted. Comparatively, in this report we assumed a "static" vegetation response in which SLR outpaces a shift in vegetation and inundated land cover was lost. The two vegetation response models present extreme examples of how land cover might respond to SLR inundation. In general, results of the "static" model showed the greatest reduction in the beach land cover class, whereas, results of the "dynamic" model showed more equal reductions across all land cover classes.

Seabird Nesting Habitat Area Change Analysis

The *Conservation Biology* analyses of population dynamics and nesting habitat area (ha) loss due to SLR at Tern Island were conducted for a subset of eight nesting species for which long-term population monitoring data were available. In this report we expanded analyses of nesting habitat area (ha) loss to include all seabird species at all low-lying islands of French Frigate Shoals. The report was also expanded to include two additional species (Black-footed and Laysan albatross) in analyses of population dynamics.

Estimates of species-specific nesting habitat loss to SLR presented differ because different land cover response models were applied. Seabird nesting habitat losses were greater for all species when the "dynamic" model (*Conservation Biology*) was applied compared to the "static" model (this report). The "dynamic" models assumed the beach land cover class, which is mostly in the lowest elevation range (0.0–0.5 m), would shift inland and replace land cover classes that are used as nesting habitat. Conversely, the "static" models assumed the beach land cover class, which is not used as nesting habitat, did not shift inland as it was inundated with SLR.

To maintain consistency across all the islands of the atoll included in this more comprehensive report, total potential nesting habitat area values for all species were calculated as the sum of all utilized land cover classes. However, in the *Conservation Biology* manuscript in which only Tern Island was analyzed, species-specific spatial nesting distribution data from 2010 were used to quantify nesting area for Gray-backed Tern (referred to as Spectacled Tern in *Conservation Biology*) and Brown Noddy (USFWS unpublished data). For all other species included in the *Conservation Biology* manuscript, potential nesting habitat area was calculated as the sum of all utilized land cover classes.