Trends in seabird breeding populations across the Great Barrier Reef

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Abstract: The Great Barrier Reef is an iconic ecosystem, known globally for its rich marine biodiversity that includes many thousands of tropical breeding seabirds. Despite indications of localized declines in some seabird species from as early as the mid-1990s, trends in seabird populations across the reef have never been quantified. With a long history of human impact and ongoing environmental change, seabirds are likely sentinels in this important ecosystem. Using four decades of monitoring data, we estimated site-specific trends for nine seabird species from 32 islands and cays across the reef. Trends varied markedly among species and sites, but probable declines occurred at 45% of the 86 species-by-site combinations analyzed compared with increases at 14%. For five species, we combined site-specific trends into a multisite trend in scaled abundance, which revealed probable declines of Common Noddy (Anous stolidus), Sooty Tern (Onychoprion fuscatus), and Masked Booby (Sula dactylatra), but no long-term changes in the two most widely distributed species, Greater Crested Tern (Thalasseus bergii) and Brown Booby (Sula leucogaster). For Brown Booby, long-term stability largely resulted from increases at a single large colony on East Fairfax Island that offset declines at most other sites. Although growth of the Brown Booby population on East Fairfax points to the likely success of habitat restoration on the island, it also highlights a general vulnerability wherein large numbers of some species are concentrated at a small number of key sites. Identifying drivers of variation in population change across species and sites while ensuring long-term protection of key sites will be essential to securing the future of seabirds on the reef.

Keywords: conservation, island biodiversity, management, marine birds, ornithology, population dynamics, UNESCO World Heritage Area

Tendencias en las Poblaciones de Aves Marinas Reproductoras a lo largo de la Gran Barrera de Arrecifes

Resumen: La Gran Barrera de Arrecife es un ecosistema icónico, conocido mundialmente por la riqueza de biodiversidad marina que incluye a miles de aves marinas tropicales en reproducción. A pesar de las indicaciones de la declinación localizada de algunas especies de aves marinas que datan desde tan temprano como mediados de la década de 1990, nunca se ha cuantificado las tendencias de las poblaciones de aves marinas a lo largo del arrecife. Con una larga historia de impacto antropogénico y el cambio climático en curso, las aves marinas son los probables centinelas de este importante ecosistema. Usamos cuatro décadas de datos de monitoreo para estimar las tendencias específicas de sitio para nueve especies de aves marinas en 32 islas y cayos en todo el arrecife. Las tendencias variaron notablemente entre especies y sitios, aunque las declinaciones probables ocurrieron en 45% de las 86 combinaciones de especie por sitio analizadas en comparación con los incrementos al 14%. Combinamos las tendencias específicas de sitio para cinco especies con una tendencia multisitio con abundancia escalada. Lo anterior reveló declinaciones probables para las siguientes especies: Anous stolidus, Onychoprion fuscatus y Sula...

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Article impact statement: Four decades of monitoring reveals troubling trends for seabird breeding populations across the Great Barrier Reef. Paper submitted November 8, 2019; revised manuscript accepted August 28, 2020.

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dactylatra, pero ningún cambio a largo plazo para las dos especies con mayor distribución: Thalasseus bergii y Sula leucogaster. Para Sula leucogaster, la estabilidad a largo plazo resultó principalmente de los incrementos en una gran colonia única en la isla Fairfax del Este, la cual compensó las declinaciones en casi todos los demás sitios. Aunque el crecimiento de la población de Sula leucogaster en la isla Fairfax del Este apunta hacia el éxito probable de la restauración del hábitat en la isla, también resalta una vulnerabilidad general en la que los grandes números de algunas especies están concentrados en un número reducido de sitios importantes. La identificación de los causantes de la variación en los cambios poblacionales en las especies y en los sitios mientras se asegura la protección a largo plazo de los sitios importantes será esencial para asegurar el futuro de las aves marinas del arrecife.

**Palabras Clave:** Área de Patrimonio Mundial UNESCO, aves marinas, biodiversidad de islas, conservación, dinámicas poblacionales, manejo, ornitología

**Introduction**

Nearly one third of the world’s >300 seabird species are globally threatened (Croxall et al. 2012; BirdLife International 2018). Breeding on land but spending a large majority of their lives at sea, seabirds are supported by resources from terrestrial and marine environments while at the same time exposed to threats in both environments (Dias et al. 2019). At sea, seabirds face threats from fisheries bycatch (Anderson et al. 2011; Gianuca et al. 2017) and exploitation of prey resources (Cury et al. 2011; Grémillet et al. 2018), as well as broad-scale climatic processes (e.g., El Niño Southern Oscillation events) (Devney et al. 2009), marine heatwaves (Jones et al. 2018; Tavares et al. 2019; Piatt et al. 2020), and sea temperature changes that influence prey availability (Gjerdrum et al. 2003; Smithers et al. 2003; Weeks et al. 2013). On land, invasive species can have large negative effects on breeding colonies (Spatz et al. 2017), whereas climate change poses a threat through sea-level rise (Reynolds et al. 2015) and extreme weather events (Nicoll et al. 2017). Despite these many vulnerabilities, many of the world’s seabird populations remain unmonitored (Paleczny et al. 2015). Consequently, basic quantitative information on population size and trends is lacking for many species and regions.

Australia’s Great Barrier Reef is an ecologically and culturally significant ecosystem, known globally for its rich marine biodiversity, which includes breeding populations of 20 seabird species (Congdon 2019). Six key biodiversity areas have been identified across the reef for supporting globally and regionally significant seabird aggregations (BirdLife International 2020). The reef also has a long history of human influence. Since the mid-1800s, islands and cays have been subject to mining of guano and phosphate, lighthouse and infrastructure development, military exercises, and introductions of invasive plants and animals (Daley 2014). Although many of these destructive activities ceased with the designation of the Great Barrier Reef Marine Park in 1975, they undoubtedly influenced the biological community as it exists today (Daley and Griggs 2006; GBRMPA 2019). In addition, the reef faces broad-scale contemporary pressures of global environmental change, including repeated mass coral bleaching events from rising ocean temperatures (Hughes et al. 2018), and continued coastal development, tourism, and fisheries (GBRMPA 2019). Given that many of these changes and pressures represent known stressors to seabirds, a reef-wide analysis of population trends is needed to assess the trajectory of the seabird community and begin to prompt recovery efforts if needed.

Sporadic seabird breeding records exist from across the reef throughout the 1900s, but more consistent and widespread seabird monitoring did not start until the late 1970s. Despite the subsequent 40 years of monitoring, there has been no reef-wide assessment of trends in seabird breeding populations. Previous assessments have focused on single species or islands over relatively short periods, primarily from before 2000, and often used...
Assessing trends in reef seabird populations is important if Australia is to uphold national and international obligations. Fourteen seabird species that regularly breed on the reef are migratory and thus protected under international conservation agreements and Australia’s central environmental legislation (Environment Protection and Biodiversity Conservation Act 1999) (Australia Government, Department of Agriculture, Water and the Environment 1999). Moreover, biodiversity targets and objectives of the Reef 2050 Long-Term Sustainability Plan, the overarching framework for managing the Great Barrier Reef, require that trends in key indicator species, including seabirds, are stable or increasing at reef-wide and regionally relevant scales (Australian and Queensland Governments 2018:56).

We analyzed 4 decades of monitoring data collected by the Queensland Parks and Wildlife Service with multilevel models to evaluate temporal trends in the breeding populations of 8 seabird species from multiple sites across the Great Barrier Reef and 1 species at a single island. For each species, we estimated trends for individual sites (hereafter site-specific trends) and composite trends for 5 species with the most spatially representative data (hereafter multisite trends). Site-specific trends provide information at a scale useful for managers, whereas broader-scale multisite trends provide an overall picture of population trajectory that can be used to underpin and prioritize regional conservation efforts, assess species threat levels, and to identify more diffuse threats. By conducting the first multisite, multispecies assessment of the trajectories of seabird populations on the reef, we sought to deliver essential ecological information in support of the Reef 2050 Long-term Sustainability Plan.

**Methods**

**Study System and Monitoring Methods**

The Great Barrier Reef extends along the eastern coast of Queensland, Australia, and includes the world’s largest coral reef system (Fig. 1). It spans approximately 14 degrees of latitude (approximately 2300 km), covers approximately 346,000 km², and contains over 1000 islands and coral cays (GBRMPA 2019). The reef was declared a marine park in 1975 and a UNESCO World Heritage Area in 1981.
We analyzed breeding records collected in the Coastal Bird Atlas, the most extensive database of seabird breeding records across the reef, between 1979 and 2018. These data are held in the Queensland Government’s WildNet database (http://data.qld.gov.au) and are currently collected under the Coastal Bird Monitoring and Information Strategy: Seabirds 2015–2020 (Hemson et al. 2015). The current strategy succeeds 2 earlier iterations (Turner 2002; McDougall 2011), but was the first to be informed by a power analysis to reconcile quantitative data requirements with logistical operational constraints of scheduling site visits across the reef’s large expanse. Under the strategies, estimates of the number of breeding pairs of each species on a given island are generated from counts of numbers of active or recently active nests, chicks, young, and adults. Counts are typically total counts of the entire island but for some species estimates of breeding pairs are derived from sampling representative sections of breeding habitat based on vegetation maps for the islands.

Timing and frequency of surveys have varied considerably, but timing of site visits has been refined with each iteration of the strategy as more is understood about the breeding phenology of different species at different sites (Fig. 1). The current monitoring strategy for the reef identifies 33 islands and cays where the aim is to survey seabird breeding populations at least once per year (Hemson et al. 2015). These essential seabird sites consist primarily of sites that host large numbers of seabird species from the major seabird foraging guilds (coastal, inshore, offshore, and pelagic) and some sites that host smaller seabird numbers that are regularly visited anyway. Although breeding records exist from other islands and cays, surveys have been less frequent and thus most of them lacked enough data for trend analysis.

Data Preparation

We selected 9 species for analysis based on a combined assessment of the quality and availability of monitoring data for each species and that would provide a representative sample of different foraging guilds. Four are pelagic foragers (Masked Booby [Sula dactylatra], Red-tailed Tropicbird [Phaethon rubricauda], Sooty Tern [Onychoprion fuscatus], and Lesser Frigatebird [Fregata ariel]), 2 offshore foragers (Brown Booby [Sula leucogaster] and Common Noddy [Anous stolidus]), and 3 inshore foragers (Greater Crested Tern [Thalasseus bergii], Lesser Crested Tern [Thalasseus bengalensis], and Roseate Tern [Sterna dougallii]) (foraging guilds from Congdon [2019]). Trends in breeding populations for the other 11 species that breed on the reef were not analyzed because either the standard monitoring method was considered unlikely to provide reliable measures of breeding pairs (e.g., for burrow-nesting species, such as Wedge-tailed Shearwaters [Ardena pacifica]) or data were too sparse.

Variation in data quality required us to undertake several cleaning steps prior to analysis. First, we removed breeding records that were flagged as unreliable counts or that were indicative of breeding presence (1 or 0) rather than abundance. For the latter, we removed records when breeding pairs equaled 1 and either the record notes indicated no count was conducted or > 100 adults of the species were simultaneously recorded. When breeding pairs equaled 1 and ≤100 adults were recorded, we considered it plausible that there might only have been 1 breeding pair or, if it was an indicator of breeding presence rather than a count, the underestimation bias would be minimal. Second, absences of breeding pairs were not explicitly recorded in the data set until recently; 0s were rarely recorded prior to 2000. We therefore created and analyzed both zero-exclusive (all 0s removed, explicit and implied) and zero-filled versions of the data set to evaluate the robustness of our results to retaining or removing 0s from the data. To zero fill the data set, we first identified all sites where breeding had been recorded for a given species and then inserted a 0 into the time series whenever a site visit was known to have occurred (based on breeding records of other seabirds), but no breeding was recorded for that species.

For both analyses, we required a minimum of 6 non-0 counts of breeding pairs from 6 different years for a species-by-site combination to be included in the analysis, which we considered a reasonable trade-off between data inclusion and minimizing the chance of detecting spurious trends. This resulted in a data set consisting of 6–326 non-0 breeding records per site per species, from 1 to 19 sites, for a total of 86 species-by-site combinations (Table 1). Site-by-species time series spanned 15–39 years (median = 35 years) and consisted of counts from 6 to 39 years (median = 14.5 years).

Modeling Trends in Breeding Abundance

We developed a hierarchical generalized linear mixed effects model to estimate site-specific and multisite trends that accounted for inconsistent sampling over time and space, seasonal and site differences in seabird breeding pairs, and overdispersion that varied by site. In the global model, we allowed the average expected number of breeding pairs to vary by site and season because counts were not taken at all sites in all years; individual sites varied in the numbers of breeding pairs they supported; counts were taken at different times of the year; and to allow for seasonal variation in the number of breeding pairs at each site. Because counts of breeding pairs were overdispersed, and dispersion varied among sites, we modeled variance in the expected numbers of breeding pairs with a negative binomial distribution with a site-specific dispersion parameter. To account for
observation error in counts, we described counts of the true number of breeding pairs with a Poisson distribution such that the magnitude of observer error was correlated with population size (Hobbs and Hooten 2015). To estimate long-term changes in breeding pairs and how they varied across sites, we allowed the slope describing linear change in numbers of breeding pairs over time to vary by site. The structure of the global model was

\[
\log \mu_i = \alpha_{k,m} + \beta_k \cdot \text{year}_i,
\]

\[
p_i = r_k / (r_k + \mu_i),
\]

\[N_i \sim \text{negative binomial} \left( p_i, r_k \right),\]

and

\[C_i \sim \text{Poisson} \left( N_i \right),\]

where \(\mu_i\) is the expected number of breeding pairs at a given site, season, and year; \(\alpha_{k,m}\) is the site- and season-specific intercept; \(\beta_k\) is the site-specific slope estimate for the relationship between number of breeding pairs and time; \(p_i\) and \(r_k\) are parameters of the negative binomial distribution (\(r_k\) describes site-specific dispersion); \(N_i\) is the true number of breeding pairs; and \(C_i\) is the observed number of breeding pairs. Terms indexed by \(i\) denote individual observations (\(i\) ranges from 1 to the total number of observations); by \(k\) denote site (\(k\) ranges from 1 to the number of survey sites \(K\)); and by \(m\) denote season (\(m\) ranges from 1 to the number of seasons \(M\)).

Site-by-season intercepts and site-specific slopes describing changes in breeding pairs over time were estimated as normally distributed random effects:

\[\alpha_{k,m} \sim \text{normal} \left( \mu_\alpha, \sigma_\alpha \right)\]

and

\[\beta_k \sim \text{normal} \left( \mu_\beta, \sigma_\beta \right).\]  

For all species excluding Roseate Tern, we fitted models with 2 seasons, October–March and April–September, corresponding approximately to the Austral summer and winter halves of the year, respectively. For Roseate Terns, we removed seasonal effects from the model because there were few observations in winter. For Lesser Frigatebird and Red-tailed Tropicbird, for which data were analyzed from 3 sites and 1 site, respectively, site-specific slopes were specified as fixed effects \(\beta_k \sim \text{normal}(0, 0.001)\).

We estimated multisite trends in scaled breeding abundances (\(\hat{n}_{\text{year}}\)) for the 5 species distributed across multiple sites for which monitoring data were the most spatially and temporally representative (Brown Booby, Masked Booby, Greater Crested Tern, Common Noddy, and Sooty Tern). Assuming population closure between seasons and that individual birds breed only once per year, multisite trends were estimated by predicting breeding pairs at each site in each of \(M\) seasons, summing seasonal predictions across all \(K\) sites where the species occurred, and then dividing by \(K\) sites to produce a scaled index of breeding abundance:

\[
\hat{n}_{\text{year}} = \left\{ \sum_{k=1}^{K} \sum_{m=1}^{M} (\alpha_{k,m} + \beta_k \cdot \text{year}_i) \right\} \cdot K^{-1}. 
\]

From time series of scaled breeding abundances, we calculated average annual percent change between the first \((t = 1)\) and most recent year \((t = T)\) as 100 \cdot (\(\hat{B} - 1\)) following Link and Sauer (2002), where

\[\hat{B} = \left( \frac{\hat{n}_{\text{year}_T}}{\hat{n}_{\text{year}_1}} \right)^{1/(T-1)}.\]  

We estimated multisite trends in scaled abundance because we lacked the required data on detection probability and, in most cases, repeated counts within periods of population closure needed to accurately estimate total population size (Barker et al. 2018). We calculated annual average percent change over the full time series to align with International Union for Conservation of
Nature (IUCN) Red List Criterion A, which considers reductions in population size over 3 generations (Appendix S1; IUCN 2012). For all species, multisite trend estimates excluded site-by-season combinations for which there were no breeding records.

Models were analyzed in a Bayesian framework with MCMC implemented in JAGS (Plummer 2003) from R 3.6.2 (R Core Team 2019) with the jagsUI package (Kellner 2019). This approach takes advantage of the flexibility of Bayesian models for analyzing hierarchical data and for fully incorporating uncertainty in estimates into model predictions and because outputs are posterior distributions, which can be directly interpreted by their magnitude and probability. Vague priors were used for all model parameters: $\mu_\alpha \sim \text{uniform}(0, 500)$; $\sigma_\alpha \sim \text{uniform}(0, 100)$; $\mu_\beta \sim \text{normal}(0, 0.001)$; $\sigma_\beta \sim \text{uniform}(0, 10)$; $r_\beta \sim \text{uniform}(0, 5)$.

We ran 3 independent MCMC chains for 120,000 iterations plus an adaptive phase of 10,000 iterations to achieve model convergence. We discarded the first 40,000 samples from each chain after which every 20th sample was retained, resulting in 12,000 posterior samples for each parameter. Model chain convergence for estimated parameters was evaluated by visual inspection of trace plots and the $R$ diagnostic statistic ($R < 1.1$) (Brooks and Gelman 1998). Model fit was examined by comparing the mean, coefficient of variation, and sum-of-squares fit of observed counts to simulated data (range of Bayesian $p$-values = 0.40-0.82) (Appendix S2).

Estimated ($\beta_k, \mu_\beta$) and derived ($\hat{B}$) trend parameters were summarized by the median, 95% Bayesian credible interval (BCI), and their probabilities (i.e., the proportion of the posterior distribution $<0$ for negative estimates or $>0$ for positive estimates). We considered probabilities $\geq 80\%$ evidence of population change. Given this is the first reef-wide assessment of seabird population trends in 4 decades of monitoring, we accepted a higher chance of detecting false declines or increases over statistical certainty. However, we also provide exact probabilities of site-specific trends in Appendix S3 and present numbers of site-by-species combinations with decreasing, increasing, and no trends for a range of probabilities in Table 1 to communicate confidence at different levels (McElreath 2016). We report on the zero-exclusive analysis in the Results but summarize site-specific trends from both analyses in Appendix S2.

Results

We analyzed 3110 non-0 counts of breeding pairs of 9 seabird species from 32 sites across the reef from October 1979 to March 2018 (Fig. 1). Most breeding records came from Michaelmas Cay ($n_{\text{records}} = 1081$) and Raine Island ($n_{\text{records}} = 319$). By species, breeding sites analyzed were most widespread relative to the total number of breeding sites with $\geq 3$ breeding records for Brown Booby ($n = 19$), Greater Crested Tern ($n = 17$), Common Noddy ($n = 12$), Masked Booby ($n = 10$), and Sooty Tern ($n = 7$); thus, these species were used for the multisite trend analyses (Table 1). Red-tailed Tropicbird and Lesser Frigatebird were the most narrowly distributed species analyzed; breeding records were from 1 and 3 sites, respectively. Data for Roseate and Lesser Crested Tern were the least spatially and temporally representative, representing 40% ($n_{\text{sites}} = 8$) and 33% ($n_{\text{sites}} = 9$) of breeding sites, respectively (Table 1). The median number of years of breeding records analyzed for these 2 species was 9 and 8, respectively, compared with $\geq 12$ years for the other 7 species (range of medians = 12-33 years).

Site-specific Trends

Average site-specific trends ($\mu_\beta$) were negative with $\geq 80\%$ probability for 3 species, but trends varied markedly across species and sites (Fig. 2). Average site-specific trends were $-2.50\%$ (95% BCI: $-5.08$ to $0.02$, prob$[\mu_\beta < 0] = 0.97$) for Brown Booby; $-4.21\%$ [$-7.56$ to $-1.12$, 0.99] for Common Noddy; $-0.19\%$ ($-2.15$ to $1.84$, 0.58) for Greater Crested Tern; $-2.71\%$ ($-7.18$ to $0.01$, 0.97) for Sooty Tern; $-0.77\%$ ($-2.99$ to $1.51$, 0.78) for Masked Booby; $0.50\%$ ($-4.25$ to $5.72\%$, 0.41) for Lesser Crested Tern; and $0.93\%$ ($-3.28$ to $5.38$, 0.32) for Roseate Tern. Of the species analyzed at $>3$ sites, Sooty Tern, Common Noddy, and Brown Booby showed the most widespread evidence of decline, with probable declines ($\geq 80\%$ probability) detected at 100%, 75%, and 63% of sites, respectively. Probable declines occurred at 2 of 3 sites for Lesser Frigatebird, and at 40% or fewer sites for the remaining 5 species. Of the 86 site-by-species combinations analyzed (Table 2), 45% had probable declines ($n = 39$), 14% showed probable increases ($n = 12$), and no change was detected at 41% ($n = 35$).

Most species showed both increases and decreases at different sites (Fig. 2). The notable exceptions were Sooty Tern and Common Noddy, which showed no evidence of increase at any sites; all sites displayed probable declines or no long-term change (Fig. 2). Both Brown and Masked Booby declined at Gannet and Bylund Cays in the Swain Reefs and at large colonies on Raine Island and Moulter Cay in the north (Fig. 2). In total Brown Boobies declined at 6 of 9 sites where they occurred in the Swain Reefs, whereas Masked Boobies were stable or increased at all but 2 sites in the region (Fig. 2). Notably, Brown Booby increased at a large colony on East Fairfax Island in the southern reef as well as at a smaller colony on Michaelmas Cay. Large breeding populations of both Greater and Lesser Crested Tern were also stable or increasing at Michaelmas Cay, whereas large colonies of both Sooty Tern and Common Noddy both declined at Michaelmas. Further declines in both Common Noddy and Sooty Tern were detected across multiple northern
Figure 2. (a–f) Site-specific trends in breeding pairs of 9 seabird species across the Great Barrier Reef from October 1979 to March 2018 (circles, estimated average annual trend; thick horizontal bars, 50% Bayesian credible interval [BCI]; thin horizontal bars, 95% BCI; solid circles, trend estimates with probabilities \( \geq 80\% \); open circles, trends with probabilities <80%; color, mean number of breeding pairs counted at each site). The wider the horizontal bar, the greater the uncertainty in the trend estimate. Points to the left of the vertical dashed line indicate declining populations, whereas points to the right of the line indicate increasing populations.
Table 2. Tally of site-by-species combinations \( (n = 86) \) with declining, increasing, or no detected trends at 4 probability thresholds for 9 seabird species breeding across the Great Barrier Reef.

| Probability | decreasing (#) | increasing (#) | no change (#) | decreasing (%) | increasing (%) | no change (%) |
|-------------|----------------|----------------|--------------|---------------|---------------|--------------|
| 0.70        | 47             | 17             | 22           | 55            | 20            | 26           |
| 0.80        | 39             | 12             | 35           | 45            | 14            | 41           |
| 0.90        | 33             | 9              | 44           | 38            | 10            | 51           |
| 0.95        | 24             | 5              | 57           | 28            | 6             | 66           |

Figure 3. Scaled abundance of Greater Crested Tern, Brown Booby, Masked Booby, Common Noddy, and Sooty Tern across all analyzed sites from October 1979 to March 2018. For each species, the black line shows the median estimate and the blue ribbon shows the 95% Bayesian credible interval [BCI]. Numbers in the top left of each panel show the number of sites from which the trend was estimated and the probability of decline.

sites, including Sandbank Number 8, Davie Cay, Tydeman Cay, and Stapleton Island (Fig. 2). Probable declines also occurred for Sooty Tern at Raine Island and for Common Noddy at 2 sites in the Swain Reefs (Frigate and Price Cays) (Fig. 2).

Lesser Frigatebird and Red-tailed Tropicbird were analyzed at 3 or fewer sites and all but 1 of the sites analyzed for Roseate Tern were restricted to the Capricornia Cays. Slight declines and no change were detected for Lesser Frigatebird and Red-tailed Tropicbird at Raine Island, respectively, and no change was detected for Lesser Frigatebird at the other northern site, Stapleton Island. Trends for Roseate Tern were generally uncertain; no change was detected at all but 1 of the 8 sites analyzed (Fig. 2). There were no obvious latitudinal patterns in trends within or across species (see Appendix S3 for tables and maps of site-specific trends for each species).

Multisite Trends

Multisite trends in scaled breeding abundances \( \bar{B} \) revealed probable declines or no change for the 5 species assessed (Table 1; Fig. 3). We detected no long-term change in Greater Crested Tern and Brown Booby, the 2 most widely distributed species. However, declines at a majority of sites for Brown Booby were offset by
large recent increases on East Fairfax Island and, to a lesser extent, Michaelmas Cay (Fig. 2). Probable overall declines were detected for Masked Booby, Common Noddy, and Sooty Tern; average annual rates of change in breeding pairs ranged from \(-3.01\%\) to \(-1.37\%\) per year (Table 1; Fig. 3).

Overall, similar percentages of site-by-species combinations with decreasing, increasing, and no change as well as multisite trends were revealed by the zero-filled and zero-exclusive analyses (Tables 1 & 2 in Appendix S2).

**Discussion**

Our results reveal variable but troubling trajectories for breeding populations of several seabird species across the Great Barrier Reef. Probable declines (\(\geq 80\%\) probability) were detected at 39 of 86 (45%) site-by-species combinations, and multisite trends revealed probable reef-wide declines in at least 3 of 5 species assessed (Common Noddy, Sooty Tern, and Masked Booby). Although evidence of reef-wide long-term change was weakest for Greater Crested Tern and Brown Booby, the 2 most widely distributed species analyzed, stability in Brown Booby populations was largely due to increases on East Fairfax Island in the southern reef that offset losses at a majority of other sites. Although growth of the Brown Booby population on East Fairfax Island represents a likely management success story, the increasing reliance on a single site highlights a potential vulnerability whereby impacts to a handful of key sites, such as Michaelmas Cay, Raine Island, and East Fairfax Island, could have large repercussions for the reef’s seabird community. Ensuring effective long-term management and protection of these sites seems essential to securing a future for seabirds on the reef.

The observed variability in site-specific trends likely reflects a complicated ecological and environmental context. Specifically, we considered a suite of species with a diversity of life histories, foraging strategies, and habitat preferences, occupying an environment with a long history of human impact, both disruptive (e.g., mining) and beneficial (e.g., marine park designation), that now faces pressures of intensifying global environmental change. Although it was beyond the scope of our analysis to explicitly analyze drivers of population change, variability in trends considered within this ecological and environmental context suggests drivers at multiple spatiotemporal scales. That probable declines were observed across sites spanning large latitudinal ranges for species such as Common Noddy, Brown Booby, and Sooty Tern, suggests that broad-scale factors, such as marine heatwaves and El Niño events, and their influence on prey availability, may be important drivers of seabird population trends (reviewed in Congdon et al. 2007). Considering that multiple marine heatwaves have occurred across the reef in the past 20 years, including those that caused well-documented mass coral-bleaching events (Hughes et al. 2018), increasing sea temperatures could be a persistent stressor to seabird populations on the reef.

Although broad-scale pressures may be affecting seabird populations regionally, human activities have undoubtedly contributed to local changes. The reef has a long history of human impact, including mining, military activities, and non-native species introductions. Although most localized threats ceased with marine park designation in the 1970s, their impacts on the geomorphology, habitats, and biological communities of islands and cays are likely still being felt. For example, introduced rats and goats were not eradicated from East Fairfax Island until the mid-1990s and prior to this the island was used for bombing practice (Daley 2014). It seems likely that growth in brown booby breeding populations at this site is due in part to the removal of these threats. Had such actions not been taken, Brown Booby breeding populations at East Fairfax Island may have faced declines similar to those observed for this species in other parts of the reef. On Raine Island, a navigation beacon was first constructed in 1844 and extensive mining of rock phosphate and guano occurred here, and at several other islands and cays across the reef, in the years that followed. Despite mining having stopped long before our time series began, long-term impacts of mining on the island’s geomorphology and vegetation have likely contributed to seabird trends observed during and preceding the past 4 decades (Daley and Griggs 2006). Erosion and overwashing of cays are other factors whose impacts are felt locally, but which could have been accelerated by interacting local-scale impacts of vegetation destruction, broader-scale impacts of sea-level rise, and greater frequency and intensity of extreme weather. Michaelmas Cay and multiple sites in the Swain Reefs have suffered erosion, overwashing, and cyclone damage over the past 20 years.

Determining the scales at which environmental variation and threats affect population dynamics is essential for efficient management of seabird breeding populations (Oppel et al. 2018). Extracting coarse data on local changes, as we have started to do here, combined with broad-scale environmental data on sea surface temperature and prey abundance could be a fruitful first avenue for developing a comprehensive understanding of drivers of trends. Ultimately, however, causes of population change cannot be diagnosed solely on counts of breeding pairs. Future analyses of seabird population health on the reef would benefit from higher resolution measures of multiple demographic components, including monitoring nestling food provisioning and juvenile recruitment (Emmerson et al. 2015; Scopel et al. 2019); individual-based tracking to understand energy budgets and foraging distributions (Pollet et al. 2014; Miller et al.
2018); and mark-recapture studies to quantify variation in survival and breeding participation (Genovart et al. 2018; Gianuca et al. 2019). Mark-recapture and tracking studies targeted at species and regions of concern could also help to understand the extent of movements among sites and, in turn, the relevant scale at which populations should be managed.

Although our analyses were based on the most spatially, temporally, and taxonomically extensive data set of seabird breeding populations across the reef, gaps in our understanding of seabird trends remain. For example, several common species had insufficient monitoring data for long-term trend analysis, such as Bridled and Black-naped Terns. Second, the first 2 decades of data collection were not guided by a consistent monitoring strategy, which led to variability in the spatial distribution, timing, and frequency of surveys. Modern modeling approaches can allow reliable trend estimation from data generated by nonstandard sampling designs, but ongoing consistent and representative monitoring will improve trend estimation certainty going forward. The most recent iteration of the strategy provides the most rigorous and consistent approach to monitoring from 2015 onward, and will continue to be refined in an adaptive manner. Third, for most of the time series breeding absences were not explicitly recorded. Analysis of both zero-filled and zero-exclusive versions of the data set revealed largely similar results, but adherence to more consistent data recording protocols, as is currently happening (Hemson et al. 2015), will also further help to alleviate uncertainty in trend estimates.

Our results revealed variable but concerning trends in breeding populations of 9 seabirds across the Great Barrier Reef, with likely reef-wide deterioration in populations of at least 3 of the 5 species assessed across multiple sites. Taxonomic and spatial gaps remain in our understanding of population changes in the reef’s seabirds, including the drivers of observed population changes, but our study greatly expands the spatial and temporal breadth of past analyses of seabird population trends on the reef. Although continued consistent monitoring of essential seabird breeding sites will enable future population trajectories to be estimated with increasing precision, our analysis suggests that considering the environmental history of human activities at specific sites, coupled with data on more diffuse threats, could help to reveal drivers of population trends and guide interventions to mitigate these drivers.

**Acknowledgments**

We thank the many individuals who contributed to seabird monitoring across the Great Barrier Reef over the past 4 decades. We also thank J. Dutoit and D. Shearer for their help with gathering information on island threats. This work was supported by funding from the Queensland Parks & Wildlife Service. B.K.W. was supported by ARC Linkage Project LP150101059 (awarded to R.A.F.) and a postdoctoral fellowship from the Natural Sciences and Engineering Research Council of Canada. M.L. was supported by the Swedish Research Council Formas (Grant 2017-00384).

**Supporting Information**

Table 1: Conservation status and decline thresholds for the 9 seabird species breeding across the Great Barrier Reef that were analyzed in this study.

Table 1: Tally of site-by-species combinations (n = 86) with decreasing, increasing, or no detectable trends at 4 probability thresholds for all 9 species from the zero-filled and zero-exclusive analyses.

Table 2: Multisite trends in scaled abundance of 5 seabird species across the Great Barrier Reef from 1979 to 2018 from the zero-filled and zero-exclusive analyses.

Figure 1: Average site-specific trends estimated from the zero-filled and zero-exclusive analyses for Greater Crested Tern.

Figure 2: Site-specific trends estimated from the zero-filled and zero-exclusive analyses for Greater Crested Tern.

Table 3: Tally of site-by-species combinations (n = 17) with decreasing, increasing, or no detectable trends at 4 probability thresholds for Greater Crested Tern from the zero-filled and zero-exclusive analyses.

Figure 3: Predicted numbers of breeding pairs by site and season estimated from the zero-exclusive analysis for Greater Crested Tern.

Figure 4: Model fit plots and Bayesian p-values from the zero-exclusive analysis for Greater Crested Tern. Bayesian p-values close to 0 or 1 indicate poor model fit.

Figure 5: Average site-specific trends estimated from the zero-filled and zero-exclusive analyses for Brown Booby.

Figure 6: Comparison of site-specific trends estimated from the zero-filled and zero-exclusive analyses for Brown Booby.

Table 4: Tally of site-by-species combinations (n = 19) with decreasing, increasing, or no detectable trends at 4 probability thresholds for Brown Booby from the zero-filled and zero-exclusive analyses.

Figure 7: Predicted numbers of breeding pairs by site and season estimated from the zero-exclusive analysis for Brown Booby.

Figure 8: Model fit plots and Bayesian p-values from the zero-exclusive analysis for Brown Booby. Bayesian p-values close to 0 or 1 indicate poor model fit.

Figure 9: Average site-specific trends estimated from the zero-filled and zero-exclusive analyses for Masked Booby.

Figure 10: Site-specific trends estimated from the zero-filled and zero-exclusive analyses for Masked Booby.
Table 5: Tally of site-by-species combinations \((n = 10)\) with decreasing, increasing, or no detectable trends at 4 probability thresholds for Masked Booby from the zero-filled and zero-exclusive analyses.

Figure 11: Predicted numbers of breeding pairs by site and season estimated from the zero-exclusive analysis for Masked Booby.

Figure 12: Model fit plots and Bayesian \(p\)-values from the zero-exclusive analysis for Masked Booby.

Figure 13: Average site-specific trends estimated from the zero-filled and zero-exclusive analyses for Common Noddy.

Figure 14: Site-specific trends estimated from the zero-filled and zero-exclusive analyses for Common Noddy.

Table 6: Tally of site-by-species combinations \((n = 12)\) with decreasing, increasing, or no detectable trends at 4 probability thresholds for Common Noddy from the zero-filled and zero-exclusive analyses.

Figure 15: Predicted numbers of breeding pairs by site and season estimated from the zero-exclusive analysis for Common Noddy.

Figure 16: Model fit plots and Bayesian \(p\)-values from the zero-exclusive analysis for Common Noddy. Bayesian \(p\)-values close to 0 or 1 indicate poor model fit.

Figure 17: Comparison of average site-specific trends estimated from the zero-filled and zero-exclusive analyses for Sooty Tern.

Figure 18: Comparison of site-specific trends estimated from the zero-filled and zero-exclusive analyses for Sooty Tern.

Table 7: Tally of site-by-species combinations \((n = 7)\) with decreasing, increasing, or no detectable trends at 4 probability thresholds for Sooty Tern from the zero-filled and zero-exclusive analyses.

Figure 19: Predicted numbers of breeding pairs by site and season estimated from the zero-exclusive analysis for Sooty Tern.

Figure 20: Model fit plots and Bayesian \(p\)-values from the zero-exclusive analysis for Sooty Tern. Bayesian \(p\)-values close to 0 or 1 indicate poor model fit.

Figure 21: Average site-specific trends estimated from the zero-filled and zero-exclusive analyses for Roseate Tern.

Figure 22: Site-specific trends estimated from the zero-filled and zero-exclusive analyses for Roseate Tern.

Table 8: Tally of site-by-species combinations \((n = 8)\) with decreasing, increasing, or no detectable trends at 4 probability thresholds for Roseate Tern from the zero-filled and zero-exclusive analyses.

Figure 23: Predicted numbers of breeding pairs by site and season estimated from the zero-exclusive analysis for Roseate Tern.

Figure 24: Model fit plots and Bayesian \(p\)-values from the zero-exclusive analysis for Roseate Tern. Bayesian \(p\)-values close to 0 or 1 indicate poor model fit.

Figure 25: Average site-specific trends estimated from the zero-filled and zero-exclusive analyses for Lesser Crested Tern.

Figure 26: Site-specific trends estimated from the zero-filled and zero-exclusive analyses for Lesser Crested Tern.

Table 9: Tally of site-by-species combinations \((n = 9)\) with decreasing, increasing, or no detectable trends at 4 probability thresholds for Lesser Crested Tern from the zero-filled and zero-exclusive analyses.

Figure 27: Predicted numbers of breeding pairs by site and season estimated from the zero-exclusive analysis for Lesser Crested Tern.

Figure 28: Model fit plots and Bayesian \(p\)-values from the zero-exclusive analysis for Lesser Crested Tern. Bayesian \(p\)-values close to 0 or 1 indicate poor model fit.

Figure 29: Site-specific trends estimated from the zero-filled and zero-exclusive analyses for Lesser Crested Tern.

Table 10: Tally of site-by-species combinations \((n = 3)\) with decreasing, increasing, or no detectable trends at 4 probability thresholds for Lesser Crested Tern from the zero-filled and zero-exclusive analyses.

Figure 30: Predicted numbers of breeding pairs by site and season estimated from the zero-exclusive analysis for Lesser Crested Tern.

Figure 31: Model fit plots and Bayesian \(p\)-values from the zero-exclusive analysis for Lesser Crested Tern. Bayesian \(p\)-values close to 0 or 1 indicate poor model fit.

Figure 32: Site-specific trend estimated from the zero-filled and zero-exclusive analyses for Red-tailed Tropicbird.

Table 11: Tally of site-by-species combinations \((n = 1)\) with decreasing, increasing, or no detectable trends at 4 probability thresholds for Red-tailed Tropicbird from the zero-filled and zero-exclusive analyses.

Figure 33: Predicted numbers of breeding pairs by site and season estimated from the zero-exclusive analysis for Red-tailed Tropicbird.

Figure 34: Model fit plots and Bayesian \(p\)-values from the zero-exclusive analysis for Red-tailed Tropicbird. Bayesian \(p\)-values close to 0 or 1 indicate poor model fit.

Figure 1: Alternative visualization of the site-specific trends shown in Figure 2 that facilitates cross-species and cross-site comparisons.

Figure 2: Site-specific trends in breeding abundance of Greater Crested Tern.

Table 1: Site-specific breeding abundances and trends of Greater Crested Tern across the Great Barrier Reef.

Figure 3: Site-specific trends in breeding abundance of Brown Booby.

Table 2: Site-specific breeding abundances and trends of Brown Booby across the Great Barrier Reef.

Figure 4: Site-specific trends in breeding abundance of Masked Booby.

Table 3: Site-specific breeding abundances and trends of Masked Booby across the Great Barrier Reef.
Figure 5: Site-specific trends in breeding abundance of Common Noddy.
Table 4: Site-specific breeding abundances and trends of Common Noddy across the Great Barrier Reef.
Figure 6: Site-specific trends in breeding abundance of Sooty Tern.
Table 5: Site-specific breeding abundances and trends of Sooty Tern across the Great Barrier Reef.
Figure 7: Site-specific trends in breeding abundance of Roseate Tern.
Table 6: Site-specific breeding abundances and trends of Roseate Tern across the Great Barrier Reef.
Figure 8: Site-specific trends in breeding abundance of Lesser Crested Tern.
Table 7: Site-specific breeding abundances and trends of Lesser Crested Tern across the Great Barrier Reef.
Figure 9: Site-specific trends in breeding abundance of Lesser Frigatebird.
Table 8: Site-specific breeding abundances and trends of Lesser Frigatebird across the Great Barrier Reef.
Figure 10: Site-specific trends in breeding abundance of Red-tailed Tropicbird.
Table 9: Site-specific breeding abundances and trends of Red-tailed Tropicbird across the Great Barrier Reef.

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