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Lack of synchronized breeding success in a seabird community: extreme events, niche separation, and environmental variability

Casey Youngflesh, Yun Li, Heather J. Lynch, Karine Delord, Christophe Barbraud, Rubao Ji and Stephanie Jenouvrier

C. Youngflesh (https://orcid.org/0000-0001-6343-3311) ✉ (cyoungflesh@ucla.edu), Dept of Ecology and Evolutionary Biology, Univ. of California – Los Angeles, Los Angeles, CA, USA. – Y. Li, School of Marine Science and Policy, Univ. of Delaware, Lewes, DE, USA. – H. J. Lynch, Inst. for Advanced Computational Science, Stony Brook Univ., Stony Brook, NY, USA, and: Dept of Ecology and Evolution, Stony Brook Univ., Stony Brook, NY, USA. – K. Delord and C. Barbraud, Centre d'Etudes Biologiques de Chizé, UMR 7372 Centre National de la Recherche Scientifique/La Rochelle Univ., Villiers en Bois, France. – R. Ji and S. Jenouvrier, Biology Dept, Woods Hole Oceanographic Inst., Woods Hole, MA, USA.

Synchrony in ecological systems, the degree to which elements respond similarly over time or space, can inform our understanding of how ecosystems function and how they are responding to global change. While studies of ecological synchrony are often focused on within-species dynamics, synchrony among species may provide important insights into how dynamics of one species are indicative of conditions relevant to the larger community, with both basic and applied implications. Ecological theory suggests there may be conditions under which communities might exhibit increased synchrony, however, the degree to which these patterns are borne out in natural systems is currently unknown. We used long-term breeding success data from a community of Antarctic seabirds to assess the degree of interspecific, community synchrony, and the role that extreme events play in driving these dynamics. We assessed theoretical links between community synchrony, niche separation, and environmental variability using data from this and three other seabird communities as well as a simulation study. Results show that reproductive success for individual species in the Antarctic seabird community fluctuated relatively independently from one another, resulting in little synchrony across this community, outside of extreme years. While an exceptionally poor year for a given species was not necessarily associated with an exceptionally poor year for any other species, one community-wide extreme year existed. When compared to other seabird communities, this group of Antarctic seabirds exhibited lower overall synchrony and higher estimated niche separation, supporting theoretical predictions. Empirical and simulation-derived results suggest that communities where temporal variation is small for conditions in which species respond substantially differently, and large for conditions in which species respond similarly, may exhibit more synchronous dynamics. Identifying where and why synchronous dynamics might be more apparent has the potential to inform how ecological communities might respond to future global change.

Keywords: Antarctica, environmental indicators, extreme events, global change, niche separation, synchrony

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Introduction

Ecosystems are inherently dynamic systems. The degree to which aspects of these systems fluctuate similarly is often referred to as synchrony. These fluctuations in an ecological metric of interest, such as phenological (Ims 1990) or demographic (Bjørnstad et al. 1999) measures, might be considered at different scales of biological organization, including among individuals (Liebhold et al. 2004b, Carter and Rudolf 2019), among populations (Liebhold et al. 2004a, Bogdziewicz et al. 2017), or among species (Loreau and de Mazancourt 2008, Bartomeus et al. 2013, Lahoz-Monfort et al. 2013). Ecological studies of demographic synchrony have often focused on synchrony among populations of a single species (Liebhold et al. 2004a). These patterns of intraspecific synchrony inform our understanding of meta-population dynamics and the drivers of these demographic processes (Gouhier et al. 2010b) and have been linked to species' extinction risk (Heino et al. 1997).

Fluctuations among sympatric species, however, also have the potential to provide important insights into the structure and function of ecological systems (Raimondo et al. 2004, Keitt 2008, Hansen et al. 2013). For example, it has been proposed that interspecific demographic synchrony (i.e. community synchrony) is linked to the stability of ecological communities (Gouhier et al. 2010a). Community demographic synchrony also dictates to what degree the dynamics of any one species are indicative of the dynamics of any other species, or of conditions that might be relevant to the community as a whole. That is, it provides information as to how widely generalizable the dynamics or response of a single species (or group of species) might be. This might provide important information for assessing how ecosystems are changing over time and space in response to rapid global change (Walther et al. 2002). As such, it is important to quantify the degree, as well as the drivers, of synchrony in ecological systems and to identify where and when we might expect elevated levels of synchrony.

Theoretical work has proposed conditions under which higher community demographic synchrony might be expected. Species that exhibit more dissimilar responses to environmental conditions, that is higher niche separation, might be generally expected to show decreased demographic synchrony (Loreau and de Mazancourt 2008). However, in addition to the degree of niche separation, the axes (of the n-dimensional niche; Holt 2009) along which species separate may also influence synchronous dynamics. While prior theoretical work in this area has often considered environmental conditions as a single axis of variation (Loreau and de Mazancourt 2008, Lee et al. 2020), in reality, species within a community respond to many factors simultaneously (with more similar responses to some conditions than others). Ecological communities where temporal variation is small for conditions in which species respond substantially differently, and large for conditions in which species respond similarly, might be expected to exhibit more synchronous dynamics. The degree to which these theoretical patterns are borne out in natural systems, however, is currently unknown.

In trying to determine how species might respond similarly to environmental variation, it is also important to consider the role of extreme events, where species exhibit exaggerated responses to perturbations (van de Pol et al. 2017). Large-scale disturbances have the potential to synchronize community dynamics (Keitt 2008, Robinson et al. 2013), though research in this area has, thus far, been relatively limited. Given the projected increase in the frequency of anomalous climatic events into the future (Jentsch et al. 2007, Rahmstorf and Coumou 2011), understanding the role of extreme events in community synchrony will be critical in developing a more complete understanding of how ecological systems are responding to global change.

Here, we use long-term data on breeding success from a community of Antarctic seabirds (Fig. 1) to assess the degree of community demographic synchrony in this community and the role that extreme events might play in driving these dynamics. Given their reliance on the marine environment and the difficulties associated with monitoring in marine ecosystems (Borja 2014), seabirds are often used as sentinels of ecosystems' responses to climate variability and change (Hazen et al. 2019). Accordingly, understanding the role of synchrony in the demographic processes of Antarctic seabirds might help to understand how Antarctic marine ecosystems function and how they are changing over time, particularly given the fact that seabirds constitute a substantial portion of the total predator biomass in the Antarctic (Ainley 1985). Using empirical data from this Antarctic seabird community, three other seabird communities around the world, as well as a simulation study, we assessed proposed theoretical links between niche separation, environmental variability and demographic synchrony. We discuss the implications of these findings for identifying systems in which community-level synchrony might be more pronounced and the relevance that this has for understanding responses to global change.

Material and methods

Description of demographic data

We collected data on five sympatrically breeding seabird species (Adélie penguin *Pygoscelis adeliae*, southern fulmar *Fulmarus glacialoides*, cape petrel *Daption capense*, snow petrel *Pagodroma nivea* and south polar skua *Stercorarius maccormicki*) at breeding sites at Pointe Géologie, Antarctica (66°40'S, 140°00'E) during the Antarctic summer (December–March). These five seabird species are highly site faithful and feed on prey items found in the marine environment (e.g. krill, fish and squid), with the exception of south polar skua, which preys primarily upon Adélie penguin eggs and young during the breeding season at Pointe Géologie (Ridoux and Offredo 1989). The number of breeding pairs and number of chicks fledged were recorded from 1980 to 2016 although data were not available for every species in all
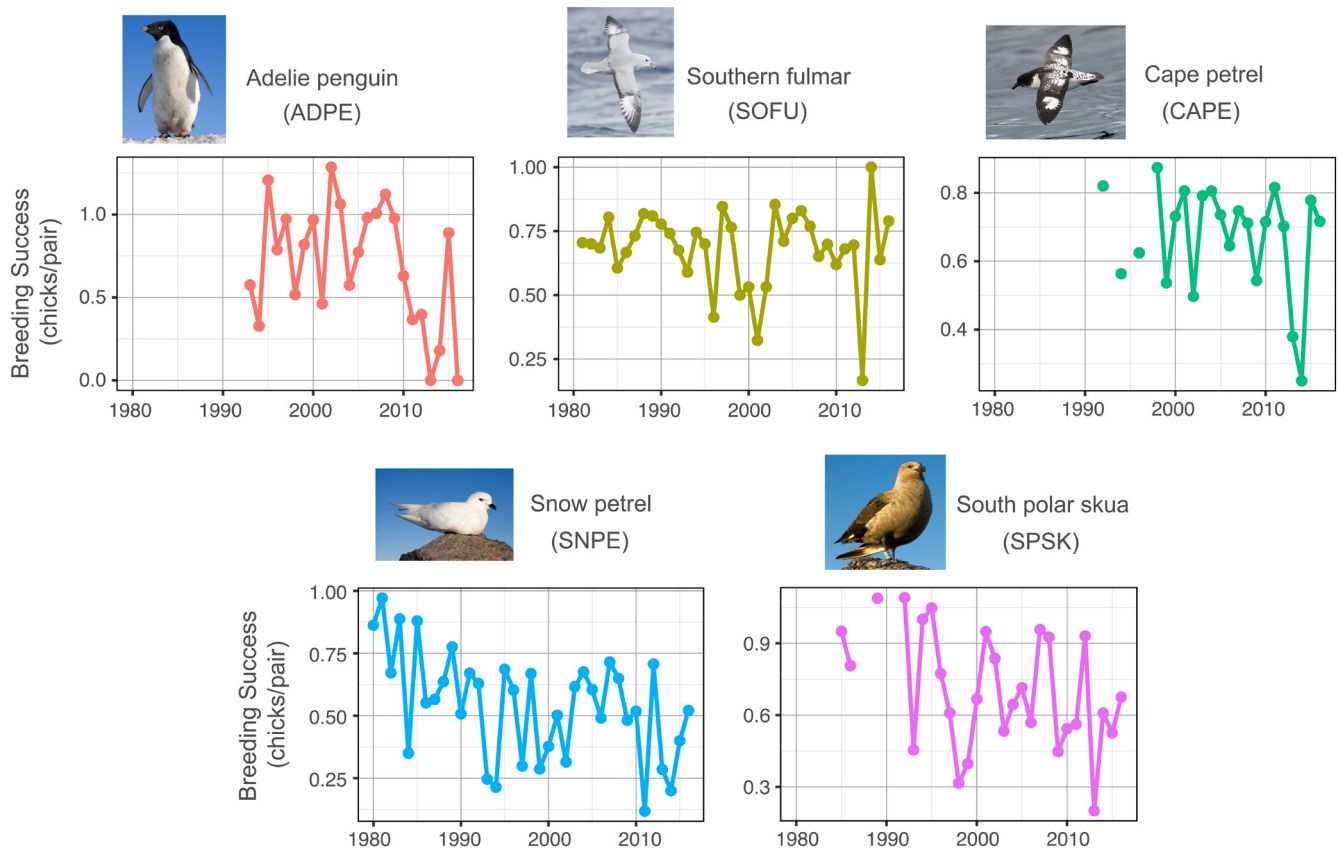
Figure 1. Fluctuations in breeding success (defined as chicks per breeding pair) for the five focal Antarctic seabird species.

years (Supporting information). Breeding success data were collected from the entire colony for southern fulmar, cape petrel, south polar skua and Adélie penguin, while a subset of nests were monitored for snow petrel (approximately 180–300 nests; Chastel et al. 1993, Barbraud et al. 2015). Given the well-defined nature of nests and survey methods, a high level of data accuracy was presumed. See Barbraud et al. (2015) for detailed data collection protocols. While data for some species exist as far back as 1952, community-wide information is not available before 1980.

To evaluate how synchrony in this seabird community compares to synchrony in other seabird communities, we obtained long-term abundance and breeding success data from the published literature and the web for three additional seabird communities from around the world. The number of species varied across sites: Isle of May (56°11'N, 2°34'W) – 1986–2009, five species (Lahoz-Monfort et al. 2013); Southeast Farallon Island (37°43'N, 123°20'W) – 1986–2004, eight species (PRBO Conservation Science); Tern Island (23°45'N, 166°17'W) – 1989–1998, six species (Dearborn et al. 2001). See the Supporting information for further details.

Community synchrony in breeding success

We modeled breeding success across the Antarctic seabird community to assess synchrony in reproductive dynamics using logistic regression fit in a hierarchical Bayesian framework. Using an approach developed by Lahoz-Monfort et al. (2013), the number of chicks F in year i for species j was modeled as binomially distributed, where E is the total number of eggs laid that season (i.e. number of trials), and p is the probability that a particular egg survives the breeding season (i.e. probability of success). The total number of eggs was determined by multiplying the number of pairs (in a given year) by the number of eggs laid per pair, a species-specific trait that is highly conserved (two eggs for Adélie penguin and south polar skua, one egg for all other species):

$$F_{ij} \sim \text{Binom}\left(E_{ij}, p_{ij}\right) (1)$$

$$\text{logit}\left(p_{ij}\right) = \mu_j + \delta_i + \epsilon_{ij}$$

$$\delta_i \sim N\left(0, \sigma_\delta^2\right)$$

$$\epsilon_{ij} \sim N\left(0, \sigma_{\epsilon_j}^2\right)$$

The logit of p is a function of a species-specific intercept (μ), year effect (δ), and residual error term (ϵ). δ and ϵ were modeled as normally distributed with variance σ_δ^2 (representing the variance in the year effect) and σ_ϵ^2 (representing the variance of each species while accounting for the year effect), respectively. We hereafter refer to the above as the L–M model. Only years in which data were available for all species were used (1994, 1996, 1998–2016). Following Palmer et al. (2017), we defined extreme years as those where the year effect was two median absolute deviations (MAD, Leys et al. 2013) away from the median, given by the equation:

$$\frac{|\hat{\delta}_i - \mathrm{median}(\hat{\delta})|}{\mathrm{MAD}} > 2 \tag{2}$$

where $\hat{\delta}$ is the posterior mean of δ. We assessed the effect of anomalous events on community-level reproductive synchrony (the degree to which reproductive success for all species varies in synchrony) by fitting a model identical to the one outlined above (Eq. 1) but excluding data from the one identified extreme year, 2013 (Supporting information).

For each of the models, estimates of variance were partitioned to calculate species-specific synchrony indices (I),

$$I_j = \frac{\sigma_\delta^2}{\sigma_\delta^2 + \sigma_{\epsilon_j}^2} \tag{3}$$

which represent the fraction of total variance for each species explained by the year effect (i.e. to what extent the variability in breeding success for that species is synchronous with the other seabird species, Lahoz-Monfort et al. 2013). Mean synchrony indices ($\bar{I}$) were calculated as a derived quantity by taking the posterior median of the arithmetic mean of the species-level synchrony indices at each iteration of the model. We use these synchrony indices as one measure of community synchrony. To facilitate direct comparisons across communities, we also calculate mean pairwise correlations among species.

We fit this model using the R package 'rjags' (Plummer 2016), to interface with JAGS (Plummer 2003) in R (<www.r-project.org>). The model was run for a total of 100 000 000 iterations, with a thinning rate of 500, following a 'burn-in' period of 30 000 000 draws and an adaptation phase of 8000 draws. All parameters had at least 2000 effective samples and an Gelman–Rubin convergence diagnostic (Rhat; Brooks and Gelman 1998) of <1.01. The R packages 'MCMCvis' (Youngflesh 2018a), 'dplyr' (Wickham et al. 2018) and 'ggplot2' (Wickham 2016) were used to manipulate data and model output, and to create all plots.

We assessed exceptionally poor years for breeding success on an individual species basis to serve as a comparison to community-wide dynamics. Using the same method of assessing extreme years as above (Eq. 2), for each species

we determined which years were exceptionally poor for breeding success.

Pairwise correlations in breeding success

To analyze the degree to which species' breeding success varies in synchrony on a pairwise basis, we calculated Pearson correlation coefficients for each pair of species over the set of years used above. Data were detrended (using linear regression) before analysis to remove the effect that similar long-term trends may have on correlation coefficients. Following Lillegård et al. (2005), we bootstrapped 95% confidence intervals for the correlation coefficient for each species pair. We sampled with replacement (n = 10 000) breeding success observations across years for all species and generated a Pearson correlation matrix for each of the bootstrapped samples. Correlation coefficients where the 95% confidence interval did not overlap zero were determined to be statistically significant.

Comparing synchrony across communities

For each of the four sites for which we had data (the focal site of this study [Pointe Géologie] as well as three others where data was obtained from the literature and web), we calculated Pearson correlation coefficients (ρ) for breeding success of all pairs of species after detrending the time series. For each site, only years with productivity data for all species at that site were used. We calculated the mean of the pairwise species correlation coefficients ($\bar{\rho}$) at each site to represent the overall synchrony for each seabird community (following Bjørnstad et al. 1999).

Community evenness as a measure of niche separation

Sugihara et al. (2003) showed that ecological communities where abundances were more unevenly distributed among species (i.e. most of the individuals in a community tend to belong to just a few species) tend to have higher niche separation. We calculated evenness for each of the four seabird communities and compared these values to evenness estimates for 11 other ecological communities presented in Sugihara et al. (2003) and with each other. Following Sugihara et al. (2003), we multiply abundance by body mass, which they refer to as 'abundance' to directly compare our measure to these previous estimates. We define evenness as

$$\left(\frac{N}{N-1}\right) \times \left(1 - \sum_j \left(\frac{N_j}{N}\right)^2\right) \tag{4}$$

where N_j is the median number of breeding pairs multiplied by body mass (from Billerman et al. 2020) for species j and $N = \sum_j N_j$ (Hurlbert 1971, Sugihara et al. 2003). For Southeast Farallon Island, abundance data were not available

for two of the eight species. These species were excluded when calculating evenness for this site. See the Supporting information for further details.

Simulation study

To explore how variation across multiple environmental axes can influence demographic synchrony in a community, we simulated a productivity index (p_{sim}) as a function of two hypothetical environmental variables, env_d and env_s, and some normally distributed stochastic noise (ϵ; with SD = 0.3) for six hypothetical species over 100 time steps. The simulation was setup such that each of the six hypothetical species responded differently to env_d (i.e. the effect of env_d (β_d) varied across species – β_d values for each species were drawn randomly from a normal distribution with SD = 0.1), but responded the same to env_s (i.e. the effect of env_s (β_s) was identical across species – one value for β_s was drawn randomly from a normal distribution with SD = 0.1),

$$\text{logit}\left(p_{sim_{ik}}\right) = \beta_{d_k}\text{env}_{d_i} + \beta_s\text{env}_{s_i} + \epsilon_{ik} \qquad (5)$$

$$\epsilon_{ik} \sim N\left(0, 0.3\right)$$

where i corresponds to the time step and k to each hypothetical species. A logit transform was used to bound p_{sim} between 0 and 1, to better illustrate the biological connection to p (the probability that a particular egg survives the breeding season) (Eq. 1). Two scenarios were run. In the first, values for env_d were simulated using a large degree of variation ($\sigma_d = 5$), analogous to large temporal fluctuations, while values for env_s were simulated using a small degree of variation ($\sigma_s = 1$),

analogous to small temporal fluctuations. Both environmental variables were simulated as normally distributed with a mean of 0,

$$\text{env}_{d_i} \sim N\left(0, \sigma_d\right) \qquad (6)$$

$$\text{env}_{s_i} \sim N\left(0, \sigma_s\right)$$

where σ_d and σ_s are the standard deviations for env_d and env_s, respectively. In the second scenario, the degree of variation was reversed – values for env_d were simulated using a small degree of variation ($\sigma_d = 1$) and values for env_s were simulated using a large degree of variation ($\sigma_s = 5$). In each scenario, we calculated the mean of the pairwise species correlation coefficients ($\bar{\rho}$), as was done for each seabird community. We ran each set of scenarios 100 times to account for the role that stochastic variation might play in the results. For each realization, values for β_d and β_s were identical across scenarios. However, new values were chosen for β_d and β_s at each realization.

Results

Baseline breeding success (chicks per pair: $\overline{p_j} \times E_j$), as determined from the initial L–M model (all years), was estimated as: 0.67 [95% CI: 0.67, 0.68] for Adélie penguin, 0.66 [95% CI: 0.63, 0.69] for southern fulmar, 0.67 [95% CI: 0.66, 0.68] for cape petrel, 0.48 [95% CI: 0.46, 0.49] for snow petrel, and 0.66 [95% CI: 0.62, 0.69] for south polar skua. One community-wide extreme year (2013; Eq. 2) was identified (Fig. 2a). This was excluded in the fitting of the second L–M model.
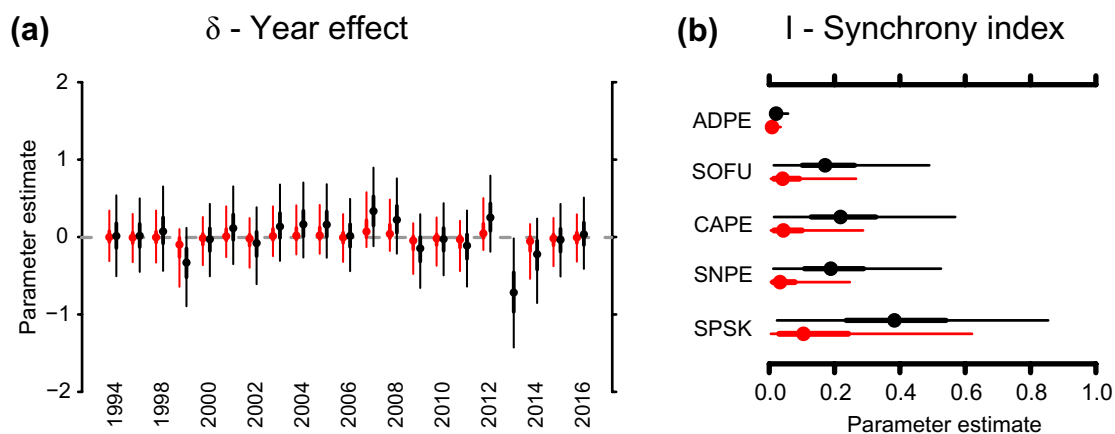

Figure 2. (a) Posterior estimates for δ (year effect) and (b) I (synchrony indices for breeding success). Synchrony indices reflect the proportion of year-to-year variation in breeding success that is explained by fluctuations among all modeled species. Results are shown for models including (black) and excluding (red) the identified extreme year (2013). In both cases, circles represent posterior medians. Thicker lines represent 50% credible intervals while thinner lines represent 95% credible intervals. ADPE – Adélie penguin; SOFU – southern fulmar; CAPE – cape petrel; SNPE – snow petrel; SPSK – south polar skua.

Synchrony indices (I), which reflect the proportion of year-to-year variation in breeding success that is explained by fluctuations among the five modeled Antarctic species, were altered substantially by the removal of the extreme year ($\bar{I}$ with extreme year = 0.20, $\bar{I}$ without extreme year = 0.04). Community-level fluctuations explained relatively little of the interannual fluctuations for any given species when excluding 2013 (Fig. 2b, Table 1).

On an individual species level, 2013 (the identified community-wide extreme year) was an exceptionally poor year for breeding success for four of the five species analyzed (Adélie penguin, southern fulmar, cape petrel, and south polar skua). All other exceptionally poor years were poor for only a single species (1996 southern fulmar, 2001 southern fulmar, 2014 cape petrel, 2016 Adélie penguin; Supporting information).

All correlation estimates of pairwise species breeding success for the Antarctic seabird community were positive, though only one of ten pairwise species breeding success associations (cape petrel–snow petrel) were statistically significant (Fig. 3).

Of the four seabird communities considered, the focal Antarctic seabird community had the lowest degree of mean pairwise correlation, one metric of community synchrony ($\bar{\rho}$; Table 2). This held true when excluding extreme years for each seabird community (Supporting information). This community had an evenness of 0.01, compared to evenness values of 0.64 for Isle of May, 0.66 for Southeast Farallon Island, 0.63 for Tern Island, and a minimum community evenness value of 0.68 for the 11 communities reported by Sugihara et al. (2003) (Supporting information). For the Antarctic seabird community, the total abundance was dominated by Adélie penguins, which contributed to the low estimated evenness (median number of breeding pairs for Adélie penguin = 14 198, southern fulmar = 41, cape petrel = 436, snow petrel = 235, south polar skua = 49.5).

Simulation study results show that the mean pairwise correlation of the simulated productivity index is lower under the scenario in which there was larger variation in the environmental variable that species respond differently to (env_{d}; median $\bar{\rho}$ across all simulation realizations = 0.01), compared to the scenario where there was larger variation in the environmental variable that species respond the same to (env_{s}; median $\bar{\rho}$ across all simulation realizations = 0.57; Fig. 4).

Table 1. Estimates for synchrony indices (I) (for each species, the proportion of interannual variation in breeding success explained by community-level fluctuations) as well as the mean synchrony index calculated across all modeled species. Removal of the extreme year resulted in a drop in estimated synchrony across the community.

Species	With extreme year	Without extreme year
Adélie penguin	0.02	0
Southern fulmar	0.17	0.04
Cape petrel	0.21	0.04
Snow petrel	0.18	0.03
South polar skua	0.38	0.1
$\bar{I}$	0.2	0.04

Discussion

Reproductive dynamics of individual species fluctuated relatively independently from one another, resulting in little synchrony, on average, across this Antarctic seabird community. While an exceptionally poor year for a given species was not necessarily associated with an exceptionally poor year for any other species, one community-wide extreme year was identified. Results suggest that, in this case, interannual dynamics of a given species are not indicative of conditions relevant for the larger ecological community, except for in extreme years. When compared to other seabird communities, this Antarctic seabird community exhibited lower overall synchrony, and higher estimated niche separation, supporting predictions made by prior theoretical work. Simulation results emphasize the importance of temporal variation along the niche axes along which these species separate for synchronous dynamics, with implications for understanding the susceptibility of ecological communities to global change.

Community synchrony, niche separation, and environmental variability

Demographic metrics from a given species are often used as indicators of the dynamics of other species in the same ecological community (Severinghaus 1981, Landres et al. 1988). A general lack of synchrony in the breeding success of this Antarctic seabird community, however, highlights that the inter-annual breeding success dynamics of one species may not be informative as to the breeding success dynamics (or the abiotic or biotic conditions relevant for the manifestation of those dynamics) of another species (Fig. 2b, Table 1).

When compared to three other seabird communities in the North Atlantic (Isle of May), East Pacific (Southeast Farallon Island), and South Pacific (Tern Island), this seabird community had the lowest degree of mean pairwise correlation among species (Table 2). Prior work has shown that ecological communities where abundances were more unevenly distributed among species tend to have higher niche separation (Sugihara et al. 2003). This Antarctic seabird community has low evenness (most of the individuals in this community belong to a small number of species) compared to the other seabird communities considered in this study as well as the ecological communities presented in Sugihara et al. (2003), suggesting substantial niche separation among these species (Fig. 4). This link between high niche separation and low community-level synchrony supports predictions made by prior theoretical work (Loreau and de Mazancourt 2008).

This high degree of niche separation may result from a number of differences apparent among the species in this Antarctic community. While all species forage within 400 km of colonies on average (Widmann et al. 2015, Delord et al. 2016, Barbraud et al. 2019), they employ different foraging strategies (Ainley et al. 1992, Widmann et al. 2015, Delord et al. 2016, Barbraud et al. 2019), rely on different proportions of similar prey species (primarily composed of fish, krill, and squid (Ridoux and Offredo 1989, Delord et al.
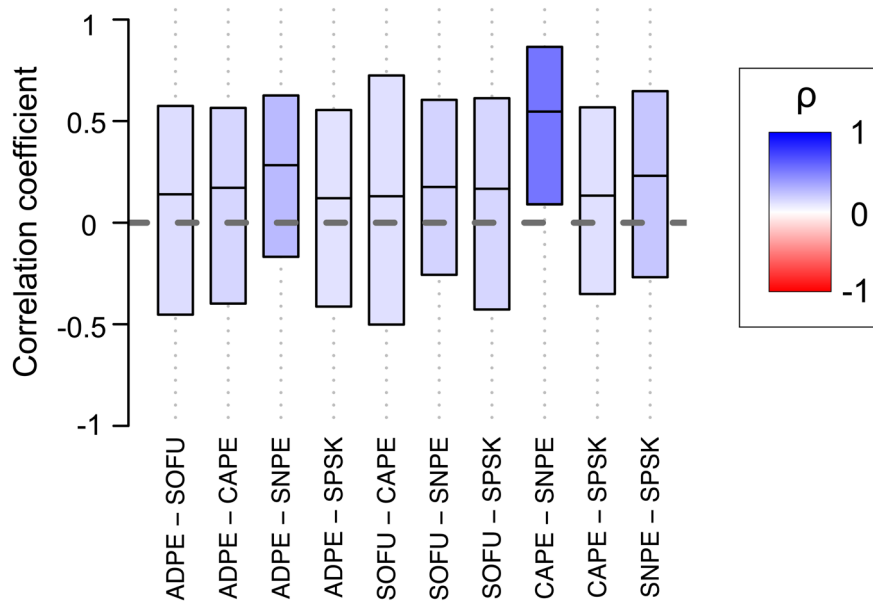
Figure 3. Pearson correlation coefficients (ρ) for breeding success for each species pair. The line bisecting each bar represents the calculated correlation coefficient – the color of each bar corresponds to this value and represents the strength of the correlation. The ends of the bars represent 95% confidence intervals. The dashed line running horizontally represents 0. ADPE – Adélie penguin; SOFU – southern fulmar; CAPE – cape petrel; SNPE – snow petrel; SPSK – south polar skua.

2016)), and utilize different nesting substrate and micro-habitats (Prévost 1963). Other factors, such as the degree of synchronicity in the timing of breeding among conspecifics (Youngflesh et al. 2017, 2018), small-scale stochastic variation in the distribution of prey (Weimerskirch 2007), and heterogeneity in the quality of individuals within each of these populations (Vindenes et al. 2008, Jenouvrier et al. 2015, 2017), might further mediate this degree of niche separation.

Simulation results highlight the theoretical importance of not only niche separation (i.e. similarities in species' responses to environmental conditions) but also variation in the conditions that these species experience, for synchronous community-level dynamics. Small temporal variation in conditions to which species respond more differently (env_d in the simulation study), and large temporal variation in conditions to which species respond more similarly (env_s in the simulation study) resulted in higher degrees of synchrony (Fig. 4). Higher variability in ocean productivity (Supporting information) and lower community-level synchrony (Table 2) in the Antarctic seabird community compared to the other three seabird communities considered here, supports this notion that the magnitude

of environmental variability could play an important role in synchronous dynamics. However, parsing the degree to which species separate along different niche axes is a challenging task given the complexity inherent in the n-dimensional niche concept (Holt 2009). While we consider the observed relationship in the empirical data largely anecdotal (as results are based on data from only four communities), in conjunction with results from the simulation study, this evidence suggests conditions under which community-level synchrony might be more pronounced. This also highlights the importance of considering multiple environmental axes in theoretical studies (Loreau and de Mazancourt 2008, Lee et al. 2020) exploring how communities might respond to environmental variation.

Pairwise dynamics among species

While community-level synchrony was low, more closely related species pairs might be expected to show higher pairwise synchrony (and lower niche separation). Of all pairwise species, comparisons for interannual breeding success, the cape petrel–snow petrel pair was found to have the highest correlation and the only to be statistically significant (Fig. 3). These species are also the most closely related pair in this assemblage (Kennedy et al. 2002), consistent with the idea that more closely related species may respond more similarly (though it should be noted that previous work has shown segregation in the diet of chicks of these species (Delord et al. 2016)).

Given that the south polar skua preys upon the eggs and young of other species in this community, most notably Adélie penguins (Young 2005, Pacoureau et al. 2019), it might be expected that productivity for this species would be inversely

Table 2. Estimates of the mean pairwise correlation (an estimate of community synchrony) for four seabird communities.

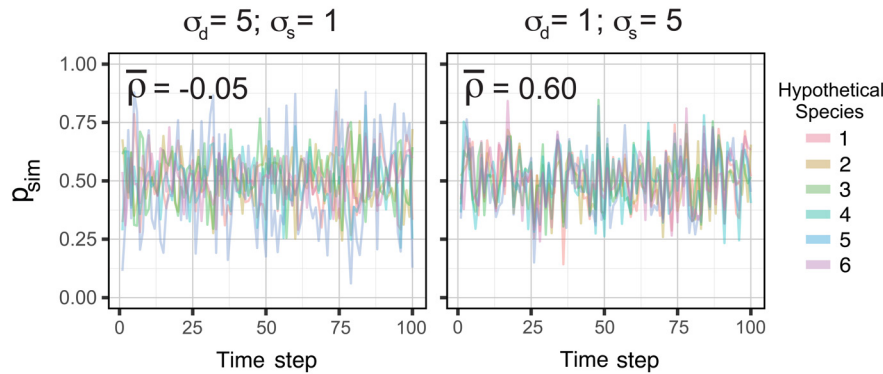| Site	ρ̄
Pointe Géologie (with extreme year)	0.21
Pointe Géologie (without extreme year)	0.03
Isle of May	0.26
Southeast Farallon Island	0.31
Tern Island	0.32

Figure 4. One realization (of the 100 total realizations) for a simulated productivity index (p_{sim}) over time for six hypothetical species. Data were simulated under two scenarios. At left, high temporal variation ($\sigma_d = 5$) for conditions to which species responded differently to (env$_d$) and low variability ($\sigma_s = 1$) in conditions to which species responded similarly to (env$_s$) was used. At right, the degree of variability was reversed for simulated values of env$_d$ and env$_s$. The mean pairwise correlation coefficients ($\bar{\rho}$) for each scenario are shown.

related to the rest of the community. However, there are relatively few breeding pairs of south polar skua relative to other species (e.g. the Adélie penguin), and density-dependent processes in the south polar skua populations (Pacoureau et al. 2019) may have masked pairwise correlations for this species. These predators likely have little influence on the overall productivity of these other species. Elevated estimates for the synchrony index (I) for south polar skua, which captures to what extent fluctuations of a given species are synchronous with the larger community, may suggest the opposite is true (i.e. productivity of prey species may influence south polar skua productivity; Fig. 2b). However, no statistically significant positive pairwise associations were found between south polar skua and any other species (Fig. 3).

Extreme year

Despite low synchrony, one community-wide extreme year did exist. Initial estimates of community synchrony were largely driven by one extreme year (2013) in which exceptionally poor breeding success was observed for all species (Fig. 2a). This previously documented event was hypothesized to be due to high sea ice coverage near the breeding site and on the foraging areas (Barbraud et al. 2015). Large disturbances such as this may lead to a synchronized response in a community (Hansen et al. 2013), as community dynamics may be more likely to exhibit a shared response in exceptionally poor years as opposed to exceptionally favorable years. These extreme community-level responses may highlight the vulnerability of these systems to disturbance (Robinson et al. 2013) and have important implications for understanding how this system is likely to respond to future global change (Jentsch et al. 2007). Given the projected increase in the frequency of anomalous climatic events (Rahmstorf and Coumou 2011), extreme events could become more common in this system, resulting in higher degrees of overall synchrony.

However, not all extreme years for a given species are shared across the community (i.e. the worst year in terms of breeding success for a given species may be an average year for all other species; Palmer et al. 2017). For instance, the Adélie penguin had a near complete breeding failure in 2016 at this site (attributed to sea ice dynamics near the colony (Ropert-Coudert et al. 2018)) while other species exhibited an average year (with a year-effect estimate near 0; Fig. 1, 2) for breeding success (Supporting information). Punctuated environmental events may exhibit pronounced effects on some species, while affecting others very little. For example, large snowstorms can result in increased chick mortality when nests are inundated with snow – species that nest in areas prone to inundation, such as pygoscelid penguins or snow petrels (Chastel et al. 1993, Youngflesh 2018b, Youngflesh et al. 2021a) are likely more susceptible to these events than species that nest in well-draining areas, such as southern fulmars. This is one dimension of the niche separation which appears to be pronounced among the seabird species in the community. Understanding these (both single-species and community-wide) extreme event dynamics may be particularly important for understanding how colonial species respond to future global change, as many individuals in a population of a given species experience very similar conditions in a given year and little variation may exist among nests at a given breeding colony.

Implications for understanding responses to global change

Given the link between community synchrony and the stability of ecological communities (Isbell et al. 2009), this work has implications for understanding which systems might be more susceptible to environmental perturbations (Hooper et al. 2005). While it has been proposed that increased environmental variability can stabilize ecological dynamics (i.e. result in lower temporal variation in metrics such as overall community biomass) (McNaughton 1977), simulation results presented here show that the opposite effect may occur under conditions of low niche separation along the axes in which that variation is occurring (Fig. 4).

In trying to understand and manage ecological systems in the face of global change, surrogates or indicators, are often used to represent metrics in ecological systems that cannot, or simply are not, measured directly (Landres et al. 1988). Measures of synchrony within a community provide insight into the degree to which the dynamics of one species might represent conditions relevant to the larger ecological community with both basic and applied implications. Dynamics may be more easily generalized in systems in which synchrony tends to be higher. While the lack of synchrony in breeding success in this Antarctic seabird community illustrates that single-species dynamics should not be assumed to be representative of the larger community a priori, there are conditions under which communities might be expected to be more synchronous. Results suggest that both niche separation and environmental variability play a role in the degree of synchrony that might exist. All else being equal, similar responses among species to conditions that exhibit large temporal variation, and dissimilar responses among species to conditions that exhibit small temporal variation, may result in increased community-level synchrony. Quantifying this differentiation, however, remains a difficult task, and other factors, such as competition (Loreau and de Mazancourt 2008, Lee et al. 2020) and predation (Raimondo et al. 2004, Robertson et al. 2015), might further mediate this synchrony among species. Additional empirical and theoretical work may shed light on the varying importance of these factors and confirm the degree to which these patterns are exhibited across a range of ecological communities.

For systems where synchrony is low, aggregating information across species provides a way to more effectively generalize demographic dynamics. Various methods of aggregation have been proposed in environmental management frameworks, using approaches such as principal component analysis to derive multivariate indices (Zador et al. 2013, Sydeman et al. 2017) across species (Durant et al. 2009), or separating species by ecological guilds (Parsons et al. 2008). Community-wide extreme events (necessarily identified through aggregation across species) also provide information in this regard, representing phenomena that are relevant to the entire assemblage (as opposed to single-species events). These exceptional events might indicate substantial changes in the ecosystem state. This approach may be increasingly useful in the future, as the frequency of anomalous climate events continues to grow (Rahmstorf and Coumou 2011, van de Pol et al. 2017). In the absence of substantial community synchrony, however, these approaches that rely on aggregation across species will require sustained, high-resolution monitoring of ecological systems in order to effectively assess ecosystem change, capture biological extreme events, and implement subsequent conservation management efforts.

Author contributions

Casey Youngflesh: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead). **Yun Li**: Conceptualization (supporting); Investigation (supporting). **Heather J. Lynch**: Conceptualization (lead); Funding acquisition (lead); Methodology (supporting); Project administration (lead). **Karine Delord**: Data curation (lead); Investigation (supporting); Methodology (supporting). **Christophe Barbraud**: Data curation (lead); Investigation (supporting); Methodology (supporting). **Rubao Ji**: Conceptualization (supporting); Investigation (supporting). **Stephanie Jenouvrier**: Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (lead).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5068/D1KT10> (Youngflesh et al. 2021b). Code to reproduce analyses is available via Github (https://github.com/caseyyoungflesh/seabird_demo_synchrony). This code is archived on Zenodo (<http://doi.org/10.5281/zenodo.5271851>).

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