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Breeding together: modeling synchrony in productivity in a seabird community

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Abstract. With environmental conditions changing rapidly, there is a need to move beyond single-species models and consider how communities respond to environmental drivers. We present a modeling approach that allows estimation of multispecies synchrony in productivity, or its components, and the contribution of environmental covariates as synchronizing and desynchronizing agents. We apply the model to long-term breeding success data for five seabird species at a North Atlantic colony. Our Bayesian analysis reveals varying degrees of synchrony in overall productivity, with a common signal indicating a significant decline in productivity between 1986 and 2009. Productivity in seabirds reflects conditions in the marine ecosystem so the estimated synchronous component is a useful indicator of local marine environment health. For the two species for which we have most data, the environmental contribution to overall productivity synchrony is driven principally by effects operating at the chick stage rather than during incubation. Our results emphasize the importance of studying together species that coexist in a community. The framework, which accommodates interspecific clutch-size variation, is readily applicable to any species assemblage in any ecosystem where long-term productivity data are available.

Key words: Bayesian analysis; breeding success; chick survival; clutch size; eastern North Atlantic seabird community; hatchability; integrative indicators; Isle of May, southeast Scotland; JAGS; long-term monitoring; marine birds; random effects.

INTRODUCTION

Demographic modeling has conventionally been carried out on a single-species basis with comparisons between different species being made a posteriori (Cury et al. 2011). However, with environmental conditions changing rapidly there is a need to move on from the “single-species vacuum” (McCarthy 2011) and develop multispecies approaches that provide insights into how communities respond to environmental drivers. Synchrony and asynchrony are important concepts in ecology, both theoretical (e.g., Moran effect in spatial synchrony, Hudson and Cattadori 1999) and applied

(e.g., effect on extinction risk, Heino et al. 1997). They are relevant in understanding community structure (Mutshinda et al. 2011) and its response to environmental changes, providing clues to guide further investigation (McCarthy 2011). The term *synchrony* has been applied in a wide variety of contexts including timing of cyclic oscillations (Cazelles and Stone 2003) and spatial synchrony of population abundance (Buonaccorsi et al. 2001). Statistical techniques used usually involve pairwise comparisons, using correlation or coincidence of peaks (Buonaccorsi et al. 2001), or model-based estimation of covariance (Mutshinda et al. 2011). Synchrony between allopatric populations of a single species has received more attention than synchrony between sympatric populations of different species; most studies have focused on variations in population abundance with few studies addressing demographic parameters (e.g., Tavecchia et al. 2008).

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Productivity, commonly defined as the average number of offspring produced per breeding attempt, is an integrated measure made up of sequential components that in birds include clutch size, hatchability, and chick survival (Rockwell et al. 1993). Here we present models that quantify multispecies synchrony in productivity (or its components), using long-term data for a seabird community typical of the eastern North Atlantic. We also explore the contribution of large- and local-scale environmental covariates to synchronizing and desynchronizing productivity in this community. The data are based on counts of fledglings (and potentially other intermediate-state variables such as eggs) produced by a known number of breeding pairs for a series of common years where clutch fate is monitored from laying until fledging, avoiding potential biases that require special care (e.g., Mayfield 1961, Heisey and Nordheim 1995). A novel feature of the models is that they can be used where the species have different clutch sizes.

Analyses are conducted within a Bayesian framework using Markov chain Monte Carlo (MCMC) methods implemented in program JAGS version 2.2.0 (Plummer 2003). We fit the models to productivity data for the five commonest members of the seabird community on the Isle of May, southeast Scotland. The species considered are three alcids (family Alcidae: Atlantic Puffin *Fratercula arctica*, Common Murre *Uria aalge*, and Razorbill *Alca torda*), which all have a clutch size of one egg, and two other species that share some ecological traits with the alcids although they lay multiple-egg clutches: the Black-legged Kittiwake *Rissa tridactyla* (Laridae) and the European Shag *Phalacrocorax aristotelis* (Phalacrocoracidae). During the breeding season the species share a common prey base, which around the Isle of May consists mainly of lesser sandeels *Ammodytes marinus* and sprat *Sprattus sprattus* (Frederiksen et al. 2006). Given their position as top predators in marine food webs, seabirds have been used as indicators to assess fish stocks, study climatic fluctuations and detect ecosystem change (Einoder 2009). Breeding success is a widely used metric since it is likely to be linked to prey availability and thus reflect changes at lower trophic levels and in abiotic conditions (Frederiksen et al. 2007). The common terms obtained from the multispecies synchrony analysis of productivity that we present can also potentially be used as community-based integrative indicators of the marine ecosystem around seabird breeding colonies.

PRODUCTIVITY AS A PROBABILITY: BINOMIAL MODEL

Given that clutch sizes are bound by a species-specific maximum value, we propose modeling the number of chicks fledged from $K_s(t)$ monitored pairs of species s that attempt breeding in year t , as a binomial variable: $F_s(t) \sim \text{Bin}[c_s K_s(t), \rho_s(t)]$. Here c_s is the species-specific maximum clutch size and ρ_s , the probability of each potential egg in a clutch becoming a fledgling, can be seen as a measure of productivity. This model is suitable

when only the number of fledglings is recorded, a situation that frequently occurs in seabird monitoring programs where determining clutch size is often difficult and time consuming (later we address the case where the number of eggs is also recorded). The model assumes the fate of each potential egg is an independent Bernoulli trial and as a consequence is equally applicable to obligate single-egg breeders as well as to species with variable clutch size ($c_s = 1$ and >1 , respectively). With nonindependent losses (e.g., total nest failure) the estimates of ρ obtained under the assumption of independence would still represent the mean probability of an egg resulting in a fledgling, but the dependency cannot be explicitly modeled without more detailed data.

Multispecies productivity synchrony model

In order to study synchrony in productivity in a set of species for which the total number of fledglings from a number of monitored pairs has been recorded, we adapt the structure of common and species-specific year random terms originally proposed by Grosbois et al. (2009) for multi-population synchrony, and described in Lahoz-Monfort et al. (2011) for studying multispecies synchrony in survival. Applying the binomial model above to each species, year random terms can be incorporated within productivity ρ (defined as a probability) on the logit scale: $\text{logit}[\rho_s(t)] = \beta_{0s} + \delta(t) + \varepsilon_s(t)$, where the $\delta(t)$ are random terms common to all species and $\varepsilon_s(t)$ species-specific random terms. All random terms are assumed to be independent and normally distributed, $\delta(t) \sim \mathcal{N}[0, \sigma_\delta^2(\text{tot})]$ and $\varepsilon_s(t) \sim \mathcal{N}[0, \sigma_s^2(\text{tot})]$, respectively, with no correlation between terms. For each species the year-to-year variation in productivity is effectively partitioned into common (synchronous) and species-specific (asynchronous) terms. Synchrony indices I_s , representing the amount of synchrony in the year-to-year variations in productivity on the logit scale, can be defined for each species as the ratio between the common variance to the overall variance of the random effects for that species:

$$I_s = \frac{\hat{\sigma}_\delta^2(\text{tot})}{\hat{\sigma}_\delta^2(\text{tot}) + \hat{\sigma}_s^2(\text{tot})}.$$

It represents the percentage of the year-to-year variation in productivity that is common to the other species in the set under consideration. Finally, we can introduce J covariates $c_j(t)$ in the logistic regression to estimate the contribution of the environment (Lahoz-Monfort et al. 2011):

$$\text{logit}(\rho_s(t)) = \beta_{0s} + \sum_{j=1}^J \{\beta_{js} c_j(t)\} + \delta'(t) + \varepsilon'_s(t). \quad (1)$$

The variances of the new δ' and ε'_s terms [residual variances $\hat{\sigma}_\delta^2(\text{res})$ and $\hat{\sigma}_s^2(\text{res})$] will be smaller than those estimated previously from the model without covariates

[total variances $\hat{\sigma}_\delta^2(\text{tot})$ and $\hat{\sigma}_s^2(\text{tot})$]. By comparing these, a set of coefficients can be calculated as a common $C_\delta = 1 - [\hat{\sigma}_\delta^2(\text{res})]/[\hat{\sigma}_\delta^2(\text{tot})]$ and species-specific $C_s = 1 - [\hat{\sigma}_s^2(\text{res})]/[\hat{\sigma}_s^2(\text{tot})]$. They reflect, respectively, the contribution of the set of covariates to synchronizing and desynchronizing the year-to-year variations in productivity, i.e., the amount of the synchronous and asynchronous variances explained by these covariates.

Overall productivity is commonly defined as the mean number of fledglings per pair, particularly for species that can lay more than 1 egg. We can derive this variable from the binomial model as $\lambda_s(t) = c_s \rho_s(t)$. For species that lay only 1 egg, $\lambda = \rho$: the mean number of fledglings per pair is equal to the probability of fledging one chick. Note otherwise that λ can take values greater than 1 but is still bounded by c_s . If the interest lies in studying synchrony in λ , an appropriate link-function would be: $\log[\lambda_s(t)/[c_s - \lambda_s(t)]] = \beta_{0s} + \delta(t) + \varepsilon_s(t)$. By substituting λ ,

$$\log\left(\frac{\lambda_s(t)}{c_s - \lambda_s(t)}\right) = \log\left(\frac{\rho_s(t)}{1 - \rho_s(t)}\right) = \text{logit}(\rho_s(t)). \quad (2)$$

Since Eq. 2 is the same as Eq. 1, we conclude that synchrony in the probability of each potential egg being laid and surviving until fledging is mathematically equivalent to that of the mean number of fledglings, and thus no specific modeling is required to estimate the latter. Note that the commonly used Poisson model for estimating λ involves an implicit approximation if maximum clutch size is taken into account (details in Appendix A). The Poisson distribution of the number of fledglings approximates the binomial under realistic conditions and we expect similar results if synchrony in λ is estimated using such a model.

THE ISLE OF MAY PRODUCTIVITY DATA SET

Data on breeding success for Atlantic Puffin, Common Murre, Razorbill, Black-legged Kittiwake and European Shag (hereafter, puffin, murre, razorbill, kittiwake, and shag) were collected between 1986 and 2009 at the Isle of May, Scotland, UK (56°11' N, 2°34' W). $K_s(t)$ pairs that attempted breeding (defined as laying a clutch) were monitored until the attempt failed or the brood fledged (details of standardized methods are in Walsh et al. [1995]), enabling the total number of fledglings $F_s(t)$ to be recorded (Appendix B). For the three alcids, which have a single-egg clutch, K equals the number of eggs, E . Clutch sizes for kittiwakes and shags are variable, but on the Isle of May typical maxima are 3 and 4 eggs, respectively. However, it was not possible to record the actual numbers of eggs laid by these two species at the monitored sites.

We first analyze the 24 years of data for the five species with the binomial model with synchrony defined for productivity ρ and no covariates. Bayesian analysis, where random effects are easily handled (Barry et al. 2003), is conducted with program JAGS (Appendix C). In this and subsequent analyses, 500 000 MCMC

samples are drawn from the marginal posterior distribution of all parameters after a conservative burn-in of 500 000. The baseline productivities $\bar{\rho}_s$ are: 0.706 for puffins; 0.728 for murre; 0.661 for razorbills; 0.139 for kittiwakes; and 0.220 for shags. Thus, in terms of probability ρ , kittiwakes and shags do poorly compared to the alcids (Appendix D: Fig. D.2). However, this reflects the fact that species that lay multi-egg clutches typically produce fewer eggs than they are physiologically capable of doing and thus even if all chicks survive productivity appears low. The more commonly reported measure of productivity as fledglings per breeding attempt $\lambda_s(t)$ can be easily derived as $c_s \rho_s(t)$ (Fig. 1).

The estimated random-effects variances and synchrony indices (Table 1) indicate that productivity is appreciably synchronized for razorbills (87% of the year-to-year variation is synchronous with the other four species) but less so for puffins (30%) and murre (29%); kittiwakes and shags show even lower values (9% and 12%, respectively). Razorbill productivity shows relatively less year-to-year variation, which limits the amount of synchronous variation of the set. Indeed Razorbill's productivity variation is mostly explained as common variance, which gives its high synchrony index. The opposite occurs for kittiwakes and shags, where most year-to-year variation is species-specific and thus not shared with all the other species. Puffins and murre show intermediate results. It is important to realize that synchrony is inherently related to the set of species used. Thus if the analysis is conducted with a subset of, e.g., puffins, kittiwakes, and shags, estimated synchrony differs ($I_{\text{PUF}} = 41\%$, $I_{\text{KIT}} = 21\%$, $I_{\text{SHA}} = 25\%$). To support our theoretical results, we repeat the analysis with synchrony defined directly in the derived parameter λ (fledglings per pair). As predicted, the estimates of synchrony obtained are identical (second decimal place) to those for synchrony defined in ρ . We also analyze productivity for kittiwakes and shags defining synchrony in a Poisson model (Appendix A), obtaining very similar synchrony indices (first decimal place) to the binomial model.

The estimated common terms $\delta(t)$ show a significant decline over the study period (Fig. 2). They represent the part of the yearly variation that is synchronous to all the species in the set and thus this result indicates a generalized decline in the productivities of the community. This common trend can be estimated directly (see model in Appendix E): we obtain a slope $\hat{\alpha} = -0.303$ $[-0.425, -0.197]$ and smaller indices of synchrony from the residual common terms ($I'_1 = 0.077$, $I'_2 = 0.084$, $I'_3 = 0.618$, $I'_4 = 0.017$, $I'_5 = 0.022$), indicating that this trend accounts for an important part of the common variation.

We next investigate the effect of two environmental covariates on synchrony of productivity ρ : Hurrell winter NAO (North Atlantic Oscillation) index, an indicator of climate conditions over northwestern Europe, and a local measure of sea surface temperature,

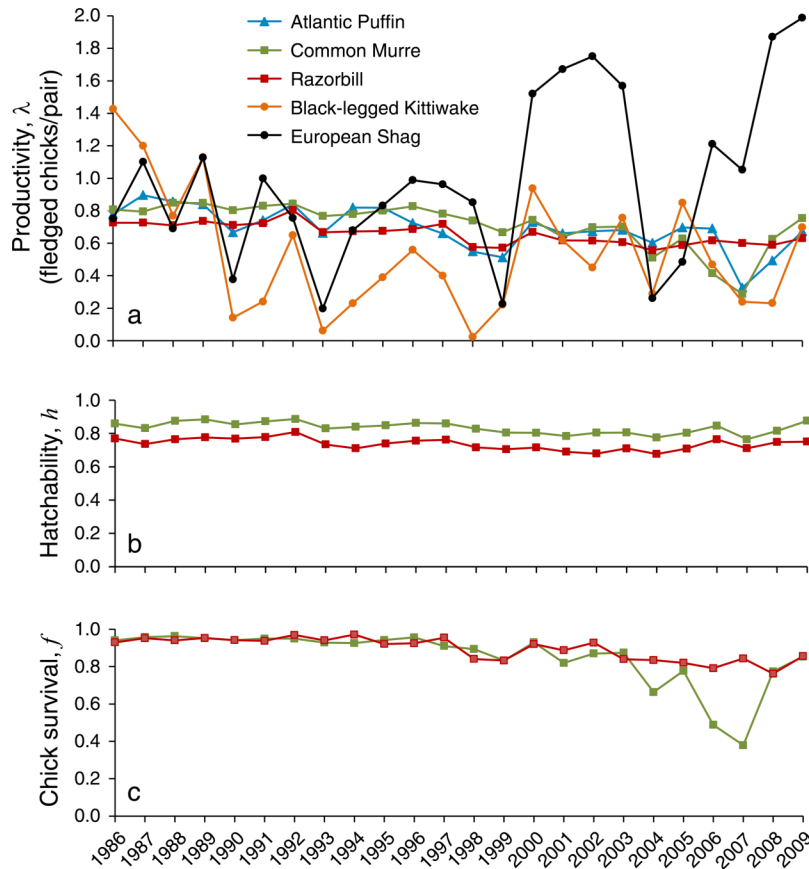


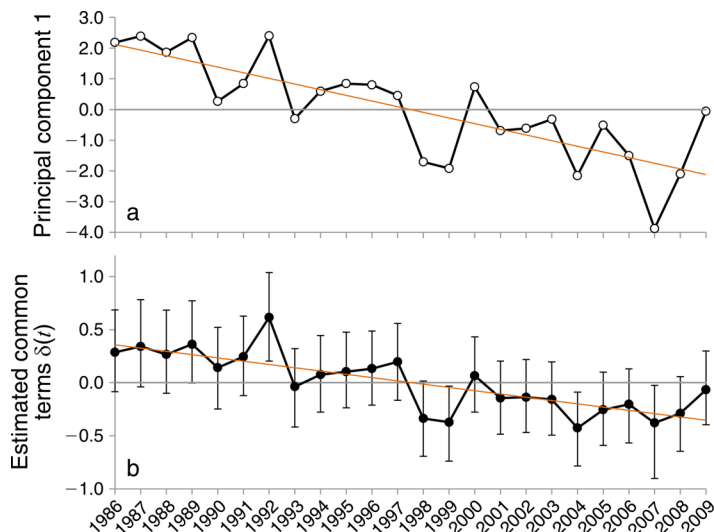
FIG. 1. (a) Estimates (medians of marginal posterior distributions) of annual productivity for five species of colonial seabirds on the Isle of May, southeast Scotland, with productivity $\lambda_s(t)$ defined as the mean number of fledglings per breeding pair. See Appendix D for an equivalent plot on the probability scale [productivity $\rho_s(t)$] as well as separate plots for each species with 95% credible intervals. (b, c) Estimates of the components of productivity (hatchability, h , and chick survival, f , respectively) for Common Murres and Razorbills.

TABLE 1. Estimates of random effects variances, indices of synchrony (I_s) and contribution of covariates to synchronizing (C_δ) and desynchronizing (C_s) overall productivity.

Synchronous component	Asynchronous component	Derived indices I_s and coefficients C_s and C_δ
Model without covariates		
$\hat{\sigma}_\delta^{-2}(\text{tot}) = 0.115$ [0.046, 0.278]	$\hat{\sigma}_1^{-2}(\text{tot}) = 0.272$ [0.114, 0.623]	$I_1 = 0.295$ [0.097, 0.636]
	$\hat{\sigma}_2^{-2}(\text{tot}) = 0.277$ [0.139, 0.581]	$I_2 = 0.292$ [0.102, 0.594]
	$\hat{\sigma}_3^{-2}(\text{tot}) = 0.018$ [0.000, 0.125]	$I_3 = 0.870$ [0.448, 1.000]
	$\hat{\sigma}_4^{-2}(\text{tot}) = 1.127$ [0.627, 2.240]	$I_4 = 0.092$ [0.030, 0.234]
	$\hat{\sigma}_5^{-2}(\text{tot}) = 0.833$ [0.456, 1.686]	$I_5 = 0.120$ [0.044, 0.276]
Model with covariates		
$\hat{\sigma}_\delta^{-2}(\text{res}) = 0.041$ [0.005, 0.125]	$\hat{\sigma}_1^{-2}(\text{res}) = 0.159$ [0.057, 0.401]	$C_1 = 0.413$
	$\hat{\sigma}_2^{-2}(\text{res}) = 0.213$ [0.096, 0.509]	$C_2 = 0.232$
	$\hat{\sigma}_3^{-2}(\text{res}) = 0.014$ [0.000, 0.104]	$C_3 = 0.183$
	$\hat{\sigma}_4^{-2}(\text{res}) = 0.506$ [0.261, 1.105]	$C_4 = 0.551$
	$\hat{\sigma}_5^{-2}(\text{res}) = 0.762$ [0.379, 1.730]	$C_4 = 0.085$
		$C_\delta = 0.643$

Notes: Estimates show the median and 95% CI. The synchrony indices I_s are based on the MCMC samples while the contributions of covariates to synchronizing (C_δ) and desynchronizing (C_s) productivity are based on point estimates of the variances. Total variances are estimated from the model without covariates while residual variances come from the model with the covariates included. Species key: 1, Atlantic Puffin; 2, Common Murre; 3, Razorbill; 4, Black-legged Kittiwake; and 5, European Shag. Convergence of the MCMC chains is assessed with the Gelman–Rubin diagnostic \hat{R} (Gelman and Rubin 1992) calculated in the R package CODA (Plummer et al. 2006) with three overdispersed chains for all variables. For both models, the statistic suggests that a burn-in period of 100 000 samples ensures convergence ($\hat{R} < 1.02$ for all parameters).

FIG. 2. (a) Comparison of the first principal component from PCA of the productivity estimates time series of the five species, obtained applying the methods in Frederiksen et al. (2007) and (b) the common random terms $\delta(t)$ estimated in the analysis of the model without covariates (with 95% credible intervals). The estimated linear trends are (a) $\widehat{PC1} = 2.299 - 0.184t$ and (b) $\widehat{\delta}(t) = 0.388 - 0.031t$, respectively, both showing significant declines over the study period ($R^2 = 0.622$ and 0.619 , respectively, $P < 0.001$). Note that the random terms are shown and estimated on the logistic scale.



SST (details in Appendix D). We include time-lagged versions (1 and 2 years, denoted by subscripts in our covariates) to allow for potential indirect effects acting through the food chain (Frederiksen et al. 2006). Finally, we consider a binary covariate that indicates the occurrence of a commercial sandeel fishery that operated close to the Isle of May between 1990 and 1998 since this influences breeding success of kittiwakes in this region (Frederiksen et al. 2007). The analysis of productivity synchrony is repeated including these covariates. The estimated regression coefficients whose 95% CIs do not include 0 (or is close to the limit) are, for puffins, NAO_1 (0.180 [-0.057, 0.420]) and SST_1 (-0.566 [-0.849, -0.290]); for murrens, only SST_2 (-0.297 [-0.583, -0.019]); for razorbills, NAO_0 (0.129 [0.004, 0.256]) and NAO_2 (0.173 [0.025, 0.325]); for kittiwakes, NAO_2 (0.372 [-0.012, 0.764]), SST_1 (-0.464 [-0.826, -0.069]) and “fishery” (-1.880 [-2.654, -1.101]); and no significant covariates for shags. Although different species appear affected by different aspects of the climatic variables, the direction of the responses is consistent, with the contribution of NAO always positive and SST always negative. The presence of the local sandeel fishery is only significant for kittiwake productivity, as previously noted by Frederiksen et al. (2007). Figs. D3 and D4 in Appendix D plot the effect of the covariates NAO and SST on productivity.

In terms of their contribution to synchrony (Table 1), the analysis shows evidence of climatic covariates explaining a large part (64%) of the common signal (although this variance was originally small). The contribution to desynchronizing productivity varies from species to species, from 18% for Razorbills to 55% for kittiwakes (the only species clearly affected by the sandeel fishery), and is very small for shags, consistent with the lack of significant covariates.

MODELING THE COMPONENTS OF PRODUCTIVITY

The results presented above are based on data restricted to the number of chicks fledging from the monitored breeding sites. However, in some cases information about intermediate stages of breeding may be available and thus multispecies synchrony can be estimated for components of productivity. There is a tradition of modeling “nest survival” based on the successive stages, including when not all nests are observed from nest construction through to fledging (Mayfield 1961, Heisey and Nordheim 1995). The compartment model in Rockwell et al. (1993) can be adapted for our case study. Defining fledglings as chicks that survive to leave the breeding site, synchrony can be estimated for any *transition probability* in the model, including egg survival, hatchability, and chick survival (or compounds of these) depending on data availability for the different *state variables* (eggs laid, eggs at hatch, chicks hatched, and fledglings, respectively).

We illustrate this using a model to quantify synchrony for two particular components (details and data in Appendix F): (a) hatchability $h_s(t)$, the probability of a chick hatching from a laid egg and (b) chick survival $f_s(t)$, the probability of a hatched chick surviving until fledging. The model can be modified easily for other stages of productivity. We apply the model to murrens and Razorbills at the Isle of May (1986–2009), for which we have appropriate data: eggs laid $E_s(t)$, hatched chicks $H_s(t)$ and fledglings $F_s(t)$. The two last counts can be modeled as $H_s(t) \sim \text{Bin}[E_s(t), h_s(t)]$ and $F_s(t) \sim \text{Bin}[H_s(t), f_s(t)]$. To estimate synchronies, we again use logistic regressions with common and species-specific year random terms: $\text{logit}[h_s(t)] = \beta_{hs} + \delta_h(t) + \epsilon_{hs}(t)$ and $\text{logit}[f_s(t)] = \beta_{fs} + \delta_f(t) + \epsilon_{fs}(t)$. As explained for $\rho_s(t)$, synchrony indices can be defined for h and f , and the contribution of environmental covariates quantified.

The variations in h are more similar in both species than those of f (Fig. 1). Particularly notable is 2006–2007, when murre chick survival declines dramatically, while for razorbill it is only slightly lower than average. The differences in overall productivity ρ are driven by chick survival, with hatchability playing a minor role. Synchrony indices are: $I_h = 0.612$, $I_f = 0.509$ for murre; $I_h = 0.874$ and $I_f = 0.888$ for razorbills; i.e., a large part of the razorbill year-to-year variation in both hatchability and chick survival is shared with murre, while for murre most of the variation is species specific. These results suggest that under the conditions that have operated over the last 24 years, the chick stage has been more sensitive than the egg stage to environmental variations, probably some aspect of food availability, with murre less well buffered than razorbills, resulting in the latter displaying larger variation, particularly at the chick stage. In terms of the environmental contribution, we find no significant covariates for h ($\alpha = 0.05$, two-tailed) while for f , winter NAO₀ was significant for razorbill and SST₂ for murre; these coincide with the ones found significant for overall productivity ρ , including the sign. For f , we estimate a large contribution to synchrony ($C_{f\delta} = 0.855$), a medium contribution to asynchrony in razorbills ($C_{fR} = 0.435$) and a low contribution to asynchrony in murre ($C_{fM} = 0.095$); possibly because none of the covariates properly explains the drop in 2006–2007). The relationship of overall productivity with these covariates appears to be driven primarily by chick survival.

We finally use simulations to verify that the framework proposed for studying synchrony in components of productivity is able to recover the parameters of interest. We simulate and analyze data for two different components of productivity: the probability of laying an egg, γ , and fledging success, ϕ , probability of an egg surviving until fledging. The model is able to separate the random terms of these two components, with 95% CI of intercepts, variances and synchrony indices including the true value (Appendix G).

DISCUSSION

We present a modeling approach to estimating multispecies synchrony in productivity or its components that incorporates interspecific variation in clutch sizes. The method is widely applicable, as we demonstrate in a case study representative of many seabird monitoring programs (Walsh et al. 1995, Dragoo et al. 2006). The study and modeling of productivity components is an area of interest in ecology (Martin et al. 1989) and conservation (Rockwell and Barrowclough 1995), and asynchronous allocations of reproductive effort in response to environmental change have been recorded even in closely related sympatric species (e.g., Wilson and Martin 2010). Our study also highlights that observed changes in overall productivity can be driven by particular stages of breeding, which can help identify key environmental or intrinsic mechanisms.

The proposed multispecies synchrony framework, which can be readily applied to other demographic parameters, is based on a comparison with the common signal from all species considered and is thus not limited to pairwise comparisons as in other traditional methods. However, the approaches should be regarded as complementary as they provide different insights that are both potentially informative. The multispecies framework can also be adapted to single-species multi-population cases (synchrony of geographically separated populations; Grosbois et al. 2009) and to different age classes based on age-specific data (Rockwell et al. 1993). The binomial form makes it possible to consider synchrony between productivity and other demographic rates like survival, or between different components of productivity for a single species. When temporal autocorrelation is anticipated in the random variation (as in Ripa and Lundberg [1996]), it can be accounted for using a multivariate normal distribution to model each random effect, with the covariance structure representing correlation between successive years (details in Appendix E).

Our five seabird species share a common long-term productivity decline. Superimposed on this trend is year-to-year variation that tends to be only weakly synchronized among the species, although some good (e.g., 2000) and poor (e.g., 2004) breeding seasons are shared by all. Extreme nonlinear cases of only exceptionally bad or good seasons inducing synchrony may require different model structures (Cattadori et al. 2005). Food supply is an important extrinsic factor affecting seabird breeding success (Frederiksen et al. 2007), often acting via thresholds in prey availability (Cury et al. 2011). Given that productivity of our species is thought to differ in sensitivity to variation in prey abundance (with kittiwakes considered the most sensitive and shags the least; Furness and Tasker 2000), varying responses with different thresholds are plausible. In addition, the species with multiple-egg clutches show greater capacity for year-to-year variation, with recurrent seasons of low productivity. There are also marked differences in breeding strategies e.g., murre and razorbill chicks only spend three weeks at the colony and leave when unable to fly, completing their development at sea, while in the other three species chicks fledge when only slightly below adult size.

In terms of climate influences, despite consistency among the species in the direction of the responses to winter North Atlantic Oscillation (NAO) and local sea surface temperature (SST), these do not have great explanatory power overall. These climate indices are assumed to reflect food availability, but direct measures of relevant local prey populations would ideally be incorporated into the model. The fact that different lags are important for different species highlights the need for more detailed studies of the mechanisms involved, including differences in species and/or age classes of prey taken or differences in feeding area or foraging depth.

Moreover, extreme but short-lived climate events such as storms, not reflected in these covariates, may affect the species in contrasting ways (e.g., heavy rain will flood puffin burrows while gales are more likely to impact on cliff-nesting species), which will further contribute to asynchrony. The marked differences in wintering areas could also desynchronize productivity, with species potentially starting the breeding season in different body condition due to carry-over effects. Finally, in addition to environmental and trophic covariates, intrinsic covariates such as density may also affect productivity via competition for high-quality breeding sites and/or food. We are currently developing a multispecies integrated population model (Besbeas et al. 2002) that jointly estimates true abundance and demographic parameters; such a framework would allow incorporating abundances as covariates to account for interactions among species (e.g., interspecific density-dependence from competition for resources).

The common terms may convey information about variations in the marine environment around the Isle of May that affect the breeding success of our five species synchronously, and the long-term decline found probably reflects a general deterioration in conditions in the North Sea. The validity of this result is reinforced by the fact that, despite important methodological differences, it coincides broadly with the decline seen in the “seabird index” proposed by Frederiksen et al. (2007) based on a posteriori PCA (principal-component analysis) of the productivities of our five species (Fig. 2). Being model-based, our method has the advantage of obtaining measures of uncertainty, and permits the explicit estimation of the asynchronous components, that is, the differing response of each species with respect to the set. It also provides a way of generating multispecies-based indices, although more careful examination of their properties would be required on a case-by-case basis before their application in management (Einoder 2009).

In conclusion, the framework presented here to quantify multispecies synchrony in productivity is flexible, and we have demonstrated that it can be easily adapted for different components of productivity, as long as suitable data are available. Although the terminology in this paper refers to avian breeding, the methods are equally valid for non-avian communities. The study of productivity synchrony may help to generate ecological hypotheses, and such models can be important tools in understanding the response of species communities in the face of environmental change. Finally, the study of synchrony and its potential role in the development of multispecies environmental indicators highlights the relevance of long-term monitoring programs from which long time series of demographic parameters like productivity can be estimated.

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LITERATURE CITED

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SUPPLEMENTAL MATERIAL

Appendix A

Poisson model: specification, JAGS code, and a figure summarizing kittiwake and shag productivity estimates obtained with the Poisson model (*Ecological Archives* E094-001-A1).

Appendix B

A table presenting the Isle of May breeding success raw data set for the five species of seabirds (*Ecological Archives* E094-001-A2).

Appendix C

Binomial model: specification and JAGS code (*Ecological Archives* E094-001-A3).

Appendix D

Binomial model: four figures presenting Isle of May results for overall productivity (*Ecological Archives* E094-001-A4).

Appendix E

Extensions of the binomial synchrony model: estimating a trend in the common random terms and dealing with autocorrelated random terms (*Ecological Archives* E094-001-A5).

Appendix F

Modeling two components of productivity, hatchability, and chick survival, with real data set for murre and Razorbills (*Ecological Archives* E094-001-A6).

Appendix G

Modeling two components of productivity, probability of laying an egg and of fledging success (simulation study) (*Ecological Archives* E094-001-A7).