Within and between species competition in a seabird community: statistical exploration and modeling of time-series data

J. M. Durant · Y. V. Krasnov · N. G. Nikolaeva · N. C. Stenseth

Abstract In a changing environment, the maintenance of communities is subject to many constraints (phenology, resources, climate, etc.). One such constraint is the relationship between conspecifics and competitors. In mixed colonies, seabirds may have to cope with interspecific and intraspecific competition for both space and food resources. We applied competitive interaction models to data on three seabird breeding populations: black-legged kittiwake (*Rissa tridactyla*), common guillemot (*Uria aalge*) and Brünnich's guillemot (*Uria lomvia*) collected over 27-years at Kharlov Island in the Barents Sea. We found a competitive effect only for the kittiwake breeding population size on the common guillemot breeding population size when kittiwakes were abundant. The timing of kittiwake breeding negatively affected the number of breeding Brünnich's guillemots. The timing of breeding was negatively correlated to biomass of the main pelagic fish in the Barents Sea, the capelin (*Mallotus villosus*), which suggests an indirect action. The community matrix shows that the community was not stable. The kittiwake population did not decrease as seen in north Norwegian populations. Likewise, the common guillemot population, after a crash in 1985, was recovering at Kharlov while Norwegian populations were decreasing. Only the Brünnich's guillemot showed a decrease at Kharlov until 1999. We suggest that the stability of the kittiwake and common guillemot populations at Kharlov is due to better feeding conditions than in colonies of the Norwegian coast, linked to a possible eastward shift of the capelin population with the temperature increase of the Barents Sea.

Keywords Black-legged kittiwake · Breeding phenology · Colonial seabirds · Guillemots · Competition

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Introduction

Shortages of adequate nesting sites and food resources are often associated in discussions of the ultimate factors controlling seabird population size, distribution and breeding success (see references in Gjøsæter 1998; Modestov 1967). Breeding site selection can strongly influence the outcome of individual breeding attempts through effects of predator exposure (e.g., Durant et al. 2010), parasitism (e.g., Andersen et al. 2009) or protection against harsh weather (e.g., Brander 2010). It is thus not

surprising that food availability (e.g., Durant et al. 2003; Frederiksen et al. 2006), and also space availability to some extent (e.g., Davoren and Montevecchi 2003; Furness and Birkhead 1984), have been used to model seabird population variation. The availability of a limited resource, whether nesting site or food, is also modified by the number of individuals that are sharing it that are conspecific (Furness and Birkhead 1984; Kokko et al. 2004) or non-conspecific (e.g., Oro et al. 2009).

In some places, seabirds form mixed colonies, i.e., groupings of different species. In such cases, seabirds compete for both food and breeding sites with conspecifics and with non-conspecifics (Croxall and Rothery 1991). For instance, black-legged kittiwakes (*Rissa tridactyla*), common guillemots (*Uria aalge*), and Brünnich's guillemots (*Uria lomvia*) all breed on vertical cliffs in spring at or near the sea shore, sometimes on the same cliff, thus creating a mixed colony, such as at Kharlov Island on the coast of the Barents Sea. All three species are small piscivorous seabirds, preferentially consuming small schooling fish (max. ca. 200 mm long), such as the capelin (*Mallotus villosus*), but differentiated by their fishing techniques and the breadth of their diet (Anker-Nilssen et al. 2000). While diet segregation can occur at some colonies (Cherel et al. 2008), this is not the case at Kharlov Island where the diets of the kittiwakes and guillemots overlap significantly (see Online Resource 1). Indeed, in the Barents Sea, kittiwakes and guillemots both seem to be very dependent on capelin as a food source (Barrett and Krasnov 1996; Krasnov and Barrett 1995). These seabirds are frequently encountered in multi-species feeding associations (Camphuysen et al. 2006), apparently sharing the same fish shoals. These three seabirds may thus be in competition for food resources at their breeding sites, making the system very well suited to test competition within a seabird community.

Competition between species may lead to a reduction of fitness and even exclusion (Chesson 2000). In other words, the species losing the competitive contest will experience a reduction of its population growth rate following the increase of the competitor population size. However, the strength of competition may not be constant through time as it is affected by changes in environmental conditions (Stenseth et al. 2002), either by effects on resource availability (Lima et al. 2006) or by different effects with competitors (spatially or temporally). Indeed, climate has been shown to affect the distribution, behavior and phenology of plants and animals (Ives 1995; Parmesan and Yohe 2003; Rosenzweig et al. 2008), as well as to disrupt tight trophic interactions between predator and prey (Durant et al. 2007).

Complete enumerations of populations are impractical or impossible. In seabirds, for instance, it is common to obtain only an estimate of the breeding population size; the number of non-breeding adults and juveniles being non-accessible. Nevertheless, competition may also be seen by the changes in the breeding population size, if it affects the whole population size by provoking a displacement of breeding birds to other breeding sites or a skipping of reproduction (e.g., in common guillemots; Kokko et al. 2004). Indeed, it is well known that a reduction of breeding success can lead to increased dispersion (Boulinier et al. 2008).

Using a 27-year time-series of black-legged kittiwakes, common guillemots and Brünnich's guillemots breeding at Kharlov Island, we have investigated competition effects both within species (intraspecific) and between species (interspecific), assuming that competition effects will be visible through changes in the breeding population size. We hypothesized that the three seabird species can compete for food (prey abundance), breeding space (population size) or both. Moreover, we supposed that, if there was space competition between species, the breeding population size will be affected by the difference in phenology of the competitors; the first species breeding potentially having an advantage. Finally, climate can affect seabirds directly, e.g., by increasing the mortality linked to extreme climatic events, but most often indirectly by affecting the distribution and abundance of lower trophic levels and modifying the available habitats (Durant et al. 2004), and was shown to affect the competition strength between birds (Stenseth et al. 2002). To separate the elements of this hypothesis, we have modeled the effects of the breeding population sizes (for both conspecifics and competitive species) and the effects of environmental variables, such as climate indices, food availability and phenology, on each breeding population size.

Materials and methods

Breeding populations (Fig. 1)

The community study was conducted at Kharlov Island using the three most abundant seabird species breeding in the Barents Sea (Kovacs et al. 2009; Krasnov et al. 1995). The birds first appear on the islands at the beginning of March (on average March 16 for black-legged kittiwakes and March 21 for both common and Brünnich's guillemots). In mid-April, they begin to reconstruct their old nests by adding new materials (e.g., grass, feathers, etc.) and building a small border around it. During surveys, a nest was considered occupied if there was a bird on it, a bird aggressively protecting it, or if it showed a reconstructed form (built on an already existing nest) with a large amount of excrement near it.
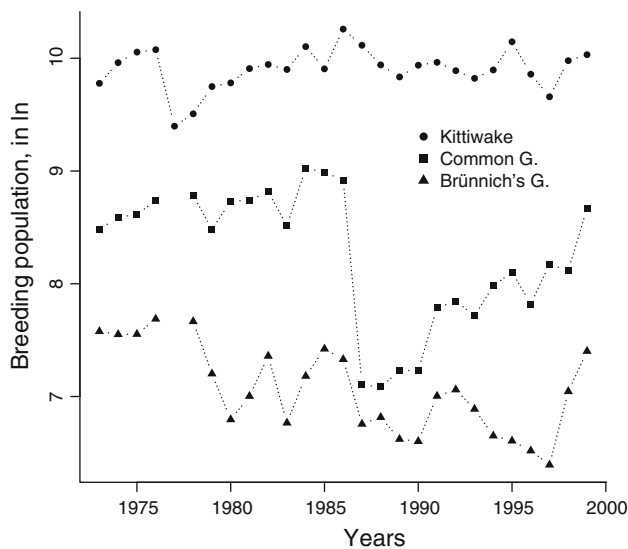
Fig. 1 Time series on breeding populations of three seabird species (black-legged kittiwake *Rissa tridactyla*, common guillemot *Uria aalge*, and Brünnich's guillemot *Uria lomvia*) breeding at Kharlov Island in the Barents Sea

To determine the breeding population of black-legged kittiwakes (hereafter kittiwake), common guillemots and Brünnich's guillemots, a census of apparently occupied nests (kittiwakes) or individuals (guillemots) was conducted annually during the incubation period (see methods in Krasnov et al. 2007a, b) between 1973 and 1999 for the whole island of Kharlov. An annual total count of Kittiwakes and Guillemots was conducted once a year. Photos were used for dense or hard to access nesting places.

Environmental variables (Online Resource 2)

We tested environmental variables (time series between 1973 and 1999) that may affect the strength of the competition. The environmental variables were:

capelin biomass (CAPbm, in 10^6 tonnes) is estimated from acoustic stock size estimates with trawler sampling in the Barents Sea conducted by Norway and Russia each September (ICES 2006). We therefore used the biomass measured in September in year $t-1$ as an estimate of capelin biomass$_t$ available to the seabirds during the winter preceding breeding. After winter, the spawning capelin migrates to the south to breed by the northern Norway–Russian coast where they are in close proximity to seabird breeding cliffs. Capelin spawning starts in February (Gjøsæter 1998) with an average peak between March and April (Pedersen et al. 2009).

The Arctic Oscillation (AO$_t$) describes the air pressure distribution north of 20°N (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml). It is strongly correlated to the North Atlantic Oscillation

(NAO; Hurrell 1995; Stenseth et al. 2003). The variability of Atlantic water inflow into the Barents Sea strongly influences the sea temperature (ST in °C) and the oceanic Polar front is linked to the NAO/AO (Hurrell et al. 2003; Ottersen et al. 2001).

Monthly average ST was measured at 0–200 m depth in May$_t$ on the Russian Kola meridian transect (70°30′–72°30′N, 33°30′E) (see references in Hjermann et al. 2004). The sea temperature in May corresponds to the highest peak of reproduction of the three seabird species. ST is most dominant in terms of its influence on marine ecosystem processes (Drinkwater et al. 2010).

The date of first breeding (earliest date birds were observed with eggs in Julian days) is used for kittiwakes (KittiDate) and guillemots (GuillDate). Note that common and Brünnich's guillemots were not recorded separately. Kittiwake and guillemot breeding dates are strongly correlated ($r = 0.745$, $p < 0.001$; see Online Resource 3). These data were obtained during daily observations of total bird communities (several large colonies along the northern coast of Kharlov island).

Model

We assumed that competition affects each species' breeding population density, $N_{i,t}$ (where t indicates the year). To do this, we used a non-linear version of a reparameterized and transformed *Gompertz* model on the log-scale. The model can be written:

$$\ln(N_{i,t+1}) = a_{i0} + f_{ii}[\ln(N_{i,t})] + f_{ij}[\ln(N_{j,t})] + f_{i0}[E_t] + \varepsilon_t \quad (1)$$

where i and j denote different species. N_i is the breeding population size for the species i (Fig. 1). a_{i0} = intercept, E_t is an environmental variable and ε is a stochastic noise term.

All analyses were then carried out with Generalized Additive Model (GAM) formulations as implemented in the *mgcv* library of R2.11.1 (Wood and Augustin 2002). The GAM procedure automatically chooses the degrees of freedom of the smoothing function f_i (i.e., how linear is the curve) based on the Generalized Cross Validation (GCV) score. However, to smooth the resulting relationship, we set the maximum degrees of freedom for each smooth term to 2. The function can also be chosen to be linear [i.e., $f_i(X_{i,t}) = b_i \times X_{i,t}$ where b is the slope and the estimated degree of freedom (*edf*) is 1]. When f functions are linear, the Eq. 1 takes the form:

$$\ln(N_{i,t+1}) = a_{i0} + (1 + a_{ii}) \ln(N_{i,t}) + a_{ij} \ln(N_{j,t}) + \varepsilon_t \quad (2)$$

where $a_{i0} = r_i$ [the maximum per capita (intrinsic) growth rate for species i], $a_{ii} = -r_i/K_i$ (K_i is the carrying capacity for the species i), and $a_{ij} = -r_i\alpha_{ij}/K_i$ (α_{ij} represents the per

capita effect of species j on species i). That is, the ecological parameters expressed in terms of statistical parameters will then become: $r_i = a_{i0}$, $K_i = -a_{i0}/a_{ii}$, and $\alpha_{ij} = a_{ij}/a_{ii}$.

A backward selection strategy was applied based on minimization of the GCV and a measure of the model predictive squared error R^2 (see backward selection models in Online Resource 4). A covariate was retained if it caused a decrease of the model GCV.

We have limited the start model to three explanatory variables: one intraspecific competition term (N_i), one interspecific competition terms (N_j, common and Brünnich's guillemots breeding population being correlated) and one environmental variable (capelin biomass$_t$, AO$_t$, ST$_t$, kittiwake laying date$_t$, and guillemot laying date$_t$; Online Resource 2). When needed, the environmental variable was centered before being entered in the model. Following Eq. 2, a population is at equilibrium if $\exp[a_{i0} + a_{ii}\ln(N_{i,t}) + a_{ij}\ln(N_{j,t})] = 1$. We tested the equilibrium for the three seabird species using average population sizes over the studied period.

We found no auto-correlation in the residuals of the selected models. We did not take into account the potential effect of age structure in our models (Sæther et al. 2005). However, the lack of autocorrelation in the residuals indicates that time lags did not apply in our models.

Results

Some explanatory variables were correlated, such as capelin biomass and the breeding date of kittiwakes (Online Resource 3). Kittiwake laying dates significantly decreased with an increase of capelin biomass ($r_{23} = -0.44$). In other words, the higher the abundance of capelin, the earlier kittiwakes breed. While both kittiwakes and guillemots bred earlier when capelin abundance increased, breeding dates of guillemots and kittiwakes were not affected to the same degree by capelin biomass (respectively, for guillemots and kittiwake GAM: $p = 0.10$, deviance explained = 11.2% with guillemot laying date = $137.77 - 0.69 \times$ capelin biomass and GAM: $p < 0.05$, deviance explained = 19.3% with kittiwake laying date = $147.29 - 1.89 \times$ capelin biomass). As capelin abundance increases, kittiwakes shift their breeding earlier relative to the guillemots. Common and Brünnich's guillemot breeding numbers were positively correlated (Online Resource 3).

All the species were positively affected by their own species (Fig. 2a, c, f). The slope of the linear relationship between N_{t+1} and N_t was less than 1, indicating that there was a negative density dependence effect at play (Table 1; but see "Discussion"). Note that, between 1986 and 1987, a lot of common guillemots died of starvation, thereby

reducing the breeding population at Kharlov (Fig. 1; Krasnov and Barrett 1995). This event was removed from the analysis as an outlier.

Among the three seabird species studied, only the common guillemot was affected by interspecific competition, with a non-linear effect of kittiwake abundance (Table 1; Fig. 2), which became negative when the kittiwake population was over approx. 19,400 breeders [$\ln(N) > 9.9$].

The backwards selection model did retain capelin biomass, Arctic Oscillation and kittiwake laying date as variables explaining the changes in breeding population sizes for the kittiwake, common guillemot and Brünnich's guillemot, respectively. ST was not retained.

The kittiwake breeding population was affected nonlinearly by capelin abundance. The effect of capelin biomass strangely became negative for the kittiwake when the capelin biomass was above 3.08×10^6 tonnes of capelin. Notably, the common guillemot population crashed the same year as the capelin decreased below this threshold. The common guillemot was affected negatively by the Arctic Oscillation. High Arctic Oscillation values indicate higher pressures at mid-latitudes that drive ocean storms farther north. The changes in the circulation pattern linked to high Arctic Oscillation bring wetter weather to Scandinavia. The number of Brünnich's guillemot breeders decreased with the increase of kittiwake laying date. In other words, as breeding in kittiwakes was delayed, fewer Brünnich's guillemot bred (Fig. 2).

We tested whether the species were at a locally stable equilibrium, which was the case for all of them (Table 2). During the period studied, realized population growth rates were close to one for these three species, i.e., the population sizes did not show increasing or decreasing trends over time.

Table 3 presents the ecological parameters for the different models. The models estimated the local equilibrium density for kittiwakes $K_{Kittiwake}$ to be 20,219, for common guillemot K_{common} to be 428, and for Brünnich's guillemots $K_{Brünnich}$ to be ca 1,094 breeding pairs. Using the parameters of Table 3, it was possible to calculate the community matrix (Online Resource 5) and see if the community was stable, which confirmed that it was not.

Discussion

Using a 27-year time-series, we showed a competitive effect of kittiwake breeding population size on the common guillemot breeding population size at Kharlov Island. However, there was no interspecific competition between the Brünnich's guillemot and the kittiwake, nor between Brünnich's and common guillemots. All the models
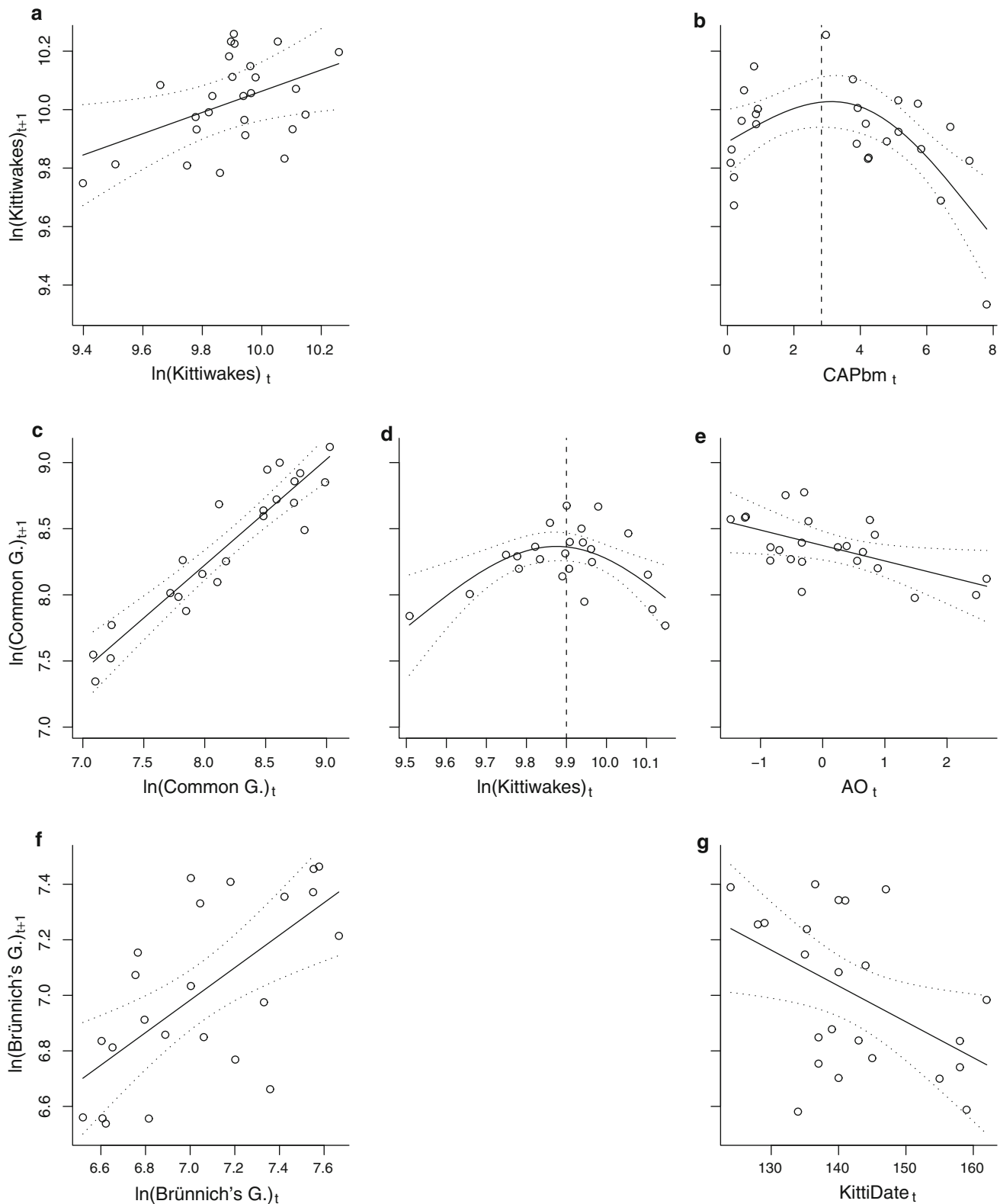
Fig. 2 Results of modeling the effects of seabird breeding density on: **a**, **b** black-legged kittiwakes ($R^2 = 0.41$), **c–e** common guillemots ($R^2 = 0.90$), and **f**, **g** Brünnich's guillemots ($R^2 = 0.58$). For (**b**), (**e**) and (**g**), the environmental variables are displayed in a non-centered form. The *dark lines* represent the model and the *dotted lines* indicate the 95% confidence intervals. *Open circles* represent the partial residuals around the significant covariate effects. For (**b**) and (**d**), the *dashed lines* locate the inflection point at 2.83×10^6 tonnes of capelin and 9.9 kittiwakes (in ln), respectively

Table 1 Regression results and estimated parameter values for the competition models for black-legged kittiwake *Rissa tridactyla*, common guillemot *Uria aalge*, and Brünnich's guillemot *Uria lomvia* (Eq. 1)

y	Intercept	x_1	x_2	x_3	DEV (gcv)
Kittiwake[a]$_{t+1}$	i***	Kittiwake$_t$*		s(CAPbm$_t$)**	50.5% (0.024)
	6.31 ± 1.59	0.36 ± 0.16		edf = 1.92	
Common[ab]$_{t+1}$	i***	Common$_t$***	s (Kittiwake$_t$)*	AO$_t$*	91.8% (0.053)
	8.27 ± 0.04	0.83 ± 0.09	edf = 1.92	−0.04 ± 0.01	
Brünnich$_{t+1}$	i*	Brünnich$_t$**		KittiDate$_t$*	57.6% (0.076)
	2.91 ± 1.14	0.58 ± 0.16		−0.013 ± 0.006	

GCV score is given between parentheses at after the deviance explained (*DEV*). When applying parameters are given with their standard error

P values for each variable (***$p < 0\ 0.001$, **$p < 0.01$, and *$p < 0.05$) are shown

[a] Kittiwake and common guillemot models have a non-linear (spline) component denoted by s(x). edf is the estimated degrees of freedom in the GAM formulation

[b] Common guillemot model was improved by removing one outlier (1986, the year when the common guillemot population crashed)

Table 2 Realized population growth rates for the three seabird species

Species	Realized population growth
Kittiwake	1.00 ± 0.03[a]
Common	1.07 ± 0.06[a]
Brünnich	0.95 ± 0.05[a]

Realized growth rates presented are mean ± SD from a bootstrap procedure

A population is at equilibrium if the realized population growth rate = 1. The realized growth rate $\{\exp[a_{i0} + a_{ii}\ln(N_{i,t}) + a_{ij}\ln(N_{j,t})]\}$ where *i* and *j* denote different species and $a_{i0} = r_i$ (the maximum *per-capita* (intrinsic) growth rate for species *i*), $a_{ii} = -r_i/K_i$ (K_i is the log-transformed carrying capacity for the species *i*) and $a_{ij} = -r_i\alpha_{ij}/K_i$ (α_{ij} represents the per-capita effect of species *j* on species *i*) is calculated for each species using the average number of breeders to obtain N_i. We created 100 bootstrap samples and estimated the parameters for the corresponding model using a linear formulation (Eq. 2) of the models in Table 1 to calculate the realized growth rate equation

[a] Indicates that the realized growth rate was not statistically different from 1. Realized growth rates were considered to be statistically not significantly different from 1 if the (0.025, 0.975) quantile interval did cover 1

incorporated the intraspecific component. The slopes of the linear relationships between N_{t+1} and N_t were all less than 1, indicating that there were negative density dependence effects at play (Table 1). However, observation error tends to cause these kinds of models to overestimate the degree of direct density dependence in populations (Viljugrein et al. 2005). For instance, when taking into account the observation error (see Online Resource 6), the common and Brünnich's guillemots may present positive density dependence in our study, while the strength of the negative density dependence in the kittiwakes becomes less secure. Such a positive density dependence was shown for common guillemots breeding on the Isle of May (Ashbrook et al. 2010), and was interpreted as a mechanism that

improves breeding success when conditions are good by, e.g., allowing both parents to forage at the same time while neighboring adults defend the nest.

Observation error can also affect the interspecific competitive term. However, such an effect is only visible for a strong competition effect. In our study, the only interspecific competition found was the small effect of kittiwakes on the common guillemot breeding population (see Supplementary Materials). To conclude, apart from the case of the common guillemot, there was no apparent interspecific competition in our system. Using statistical modeling of long-term population data, we were able to describe the relationship of three sympatric seabird species. While observation errors can bias the parameter estimates, the use of series with a high level of system noise (e.g., demographic or environmental noise) can bypass this problem (Lande et al. 2003). In our system, the coefficients of variation were always higher than 18%, and in the case of common guillemots, where both intra- and interspecific competition was at play, the CV was ca. 50% indicating a strong stochasticity as illustrated by the crash in the population in 1986–1987 (see Fig. 1).

Common guillemots have been considered to have low sensitivity to changes in prey availability due to their ability to access prey throughout the water column (Carscadden et al. 2002) and to increase parental foraging effort when prey becomes scarce (Furness and Tasker 2000). This is not what we found in this study where changes in capelin biomass explained changes in common and Brünnich's guillemot populations (Online Resource 4). The main plankton feeder in the Barents Sea, the capelin is well known to play a key role in this marine ecosystem (Hjermann et al. 2010). Capelin population fluctuations and collapses were responsible for the loss of 85–90% (more than 200,000 pairs) of the common guillemot breeding colony at Bear Island in the west of the Barents Sea

Table 3 Ecological parameters for the different models

Species	Kittiwake	Common	Brünnich	r_i	K_i
N_i = Kittiwake	$\alpha_{i,i} = -0.637$	$\alpha_{i,j} = 0$	$\alpha_{i,j} = 0$	6.312	9.91
N_i = Common[a]	$\alpha_{i,j} = -0.272$	$\alpha_{i,i} = -0.152$	$\alpha_{i,j} = 0$	0.919	6.06
N_i = Brünnich	$\alpha_{i,j} = 0$	$\alpha_{i,j} = 0$	$\alpha_{i,i} = -0.415$	2.905	6.99

We used the linear form of the Eq. 1 (Eq. 2)

$$\ln(N_{i,t+1}) = a_{i0} + (1 + a_{ii})\ln(N_{i,t}) + a_{ij}\ln(N_{j,t}) + \text{Env}$$

With $a_{i0} = r_i$ (the maximum *per-capita* (intrinsic) growth rate for species i) + a_0 (intercept change due to environment), $a_{ii} = -r_i/K_i$ (K_i is the log transformed local equilibrium density in the absence of heterospecifics), $a_{ij} = -r_i\alpha_{ij}/K_i$ (α_{ij} represents the per-capita effect of species j on species i) so that $r_i = a_{i0}-a_0$, $K_i = -(a_{i0}-a_0)/a_{ii}$, $\alpha_{ii} = -r_i/K_i$, and $\alpha_{ij} = a_{ij}/a_{ii}$ where i and j denote different species. In case of centered environment variables $a_0 = 0$. Note that we report here two α_{ij} per species i. In Eq. 2 the strength of the competition (α_{ij}) was modelled for only one competitive species at the time, the effect of the other competitive species being equal to 0. In other words, per species i were estimated a_{ij} two times, once for each competitive species, the effect of the other being assumed to be null in the model

[a] In order to estimate a_{ij} on the Common Guillemot' equation, we have forced the effect of kittiwake on Common guillemots to be linear (DEV = 86.8% gcv = 0.086), see Table 1

(Anker-Nilssen et al. 2000; Vader et al. 1990), and assumed to be responsible for the severe decrease of common guillemot breeding individuals at Kharlov Island (Fig. 1). Capelin biomass seems not to affect Brünnich's guillemots as strongly as it affects common guillemots. One explanation of this difference can be that the majority of Kharlov's common guillemots overwinter above the Polar Circle, i.e., they remain in the Barents and northern Norwegian Seas where the capelin population decline was observed (Gjøsæter et al. 2009), while Brünnich's guillemots overwinter in the Barents Sea and also near the southwestern coast of Greenland (Nikolaeva et al. 1996) where feeding conditions were better. The common guillemots breeding at Kharlov Island may thus be more capelin-specialist birds during winter (Vader et al. 1990) than kittiwakes or Brünnich's guillemots (Krasnov et al. 1995), and consequently more sensitive to changes in capelin availability. In Norway, west of Kharlov, where capelin availability is lower, common guillemots seem to be in a critical situation (Lorentsen and Christensen-Dalsgaard 2009).

The competition model shows that the number of breeding kittiwakes can have a negative effect on common guillemots when kittiwake breeders exceed a threshold number (above 19,000 pairs, i.e., 19 years out of the 27 years of our study; Table 1). Note that the kittiwake population did not show a trend with time (GAM $p > 0.30$ and Fig. 1) and the negative effect of kittiwakes on common guillemots occurred irregularly over the studied period. Likewise, the competitive model shows that a late kittiwake breeding date negatively affects the size of the Brünnich's guillemots breeding population. During our study, kittiwakes usually started to breed after the two species of guillemots, and this difference tended to increase in time following the general decline of capelin (see Online Resource 2). Since the change of capelin biomass had a

stronger effect on the kittiwake breeding dates than on the guillemot breeding dates (-1.89 vs. -0.69), such changes led to a modification of the breeding synchrony. In other words, kittiwakes are more sensitive to changes in capelin biomass (Fig. 1b) and are better at tracking its changes. Note that the highest value of kittiwake laying date corresponded to the recent years when capelin abundance was generally low (Online Resource 2), confirming the effect of capelin abundance on kittiwakes. We assume that the negative effect of kittiwake laying date on Brünnich's guillemot is an indirect effect linked to prey abundance: the scarcer the abundance of food, the later the kittiwakes breed (see Moe et al. 2009). However, this may not be the only effect since neither capelin biomass nor guillemot laying date were part of the final model. The increase in kittiwake laying date also coincided with an increase in the difference between kittiwake laying date and the guillemots laying date. In other words, the kittiwakes bred later relative to the guillemots as kittiwake laying date increased (ca 1.7 days later before 1985 to ca 8.7 days later after 1985). This again suggests that the negative effect of kittiwake laying date on the Brünnich's guillemot breeding population is an indirect effect linked to prey abundance at a critical period for guillemots.

While during the period studied kittiwakes tended to lay eggs later than guillemots (see Online Resource 2), they usually arrive earlier at Kharlov Island to breed [note that at Kharlov, kittiwakes usually lay eggs earlier than guillemots: the mean date for kittiwake was 18.05 ($n = 48$), and for guillemots was 20.05 ($n = 49$). During years of good food abundance this difference is even larger, e.g., in 1970 when the date of egg laying for kittiwakes was 11.05 and for guillemots was 18.05]. However, the date of breeding did not seem to affect the relationship between kittiwakes and common guillemots as it does for Brünnich's guillemots. As shown by our results, it is only after a certain level of filling

of the breeding space is reached (ca. 19,000 pairs) that a competition effect occurs between kittiwakes and common guillemots. One hypothesis may be that the two species are in contact only after reaching this threshold (see photo in Online Resource 1). In other words, before this threshold is reached, the positive relationship between the common guillemot and kittiwake populations may be an indirect effect that indicates an improvement of the feeding conditions, i.e., capelin abundance. After the threshold is reached, the breeding space is full and a negative effect on the guillemot population can appear, perhaps due to increased aggressiveness (e.g., López-Sepulcre et al. 2010), or increased parasitic loads (e.g., Boulinier and Danchin 1996; Hudson et al. 1998). The kittiwake abundance did not have a similar impact on the Brünnich's guillemot. There are two possibilities for this: (1) the Brünnich's guillemot population is much smaller in number than the two other species and its population was decreasing regularly throughout the period studied, hiding any effect of kittiwake population abundance, and (2) although there is a clear overlap in diet, Brünnich's guillemots depend less on capelin and pelagic schooling fish in general than common guillemots do (Barrett et al. 1997), thus decreasing the competition with kittiwakes during periods of low capelin abundance. For instance, during periods of low capelin abundance, Brünnich's guillemots brought many more benthic fish species indicating other foraging areas than kittiwakes (Krasnov et al. 1995).

Following the multi-species feeding associations theory (Camphuysen et al. 2006), the kittiwake is described as a catalyst that discovers and exploits fish schools driven to the surface by small auks such as common guillemots. By feeding on a fish ball, kittiwakes attract scroungers, such as herring gulls (Larus argentatus) and great black-backed gulls (L. marinus), forcing smaller seabirds (i.e., guillemots) to swim away. We suggest that, in times of high abundance of kittiwakes, the presence of kittiwakes might become limiting for the guillemots by attracting scrounger birds both more rapidly and in larger numbers. Although, to our knowledge, there is no evidence for a competitive effect between kittiwakes and guillemots at sea, competition for foraging space has been shown between pursuit-diving seabirds (e.g., Ronconi and Burger 2011).

Kittiwake populations in western breeding places in the Barents Sea have been declining since 1975 (Anker-Nilssen et al. 2000; Lorentsen and Christensen-Dalsgaard 2009). This was not the case at Kharlov Island, although data collection stopped in 1999 (Fig. 1). In Labrador, associated with the demise of the capelin population, the breeding success of kittiwakes declined while the population remained stable (Carscadden et al. 2002). This was also documented for the Norwegian populations (Barrett 2007). Breeding success is not available for our

population. However, the number of occupied nests and brood size did not change significantly during the period studied (Krasnov and Nikolaeva 1998). In addition, opposite to what we expected, capelin biomass affected the number of kittiwake breeders negatively when capelin biomass increased over 3×10^6 tonnes per year. This is related to the fact that the high capelin abundance corresponds to earlier years and low capelin abundance to the later years. We suggest that the stable population of kittiwakes at Kharlov Island between 1973 and 1999 is due to better feeding conditions, especially during the more recent years, than in the western colonies of the Norwegian coast. Indeed, capelin data are global and no information on local abundances are available, although it represents a better index of the food available for breeding birds than typical prey assessments conducted on scientific cruises (Durant et al. 2010). With the warmer current coming from the Atlantic to the Barents Sea during "warm years", the spawning ground of capelin is displaced north- and eastward (Gjøsæter 1998), leading the fish away from the Norwegian seabird colonies, but nearer Kharlov Island. The eastward migration of capelin spawning grounds and adult population may continue following the model of future climate scenario (Huse and Ellingsen 2008). If our hypothesis is correct, it suggests that the warming of the Barents Sea has, irrespective of the capelin abundance, contributed to maintaining the eastern kittiwake populations. While data collection ended at Kharlov Island in 1999, Krasnov et al. (2007a) reported that, since 2002, Russian kittiwake populations west of Kharlov Island were decreasing while to the east of the island they were increasing. Individual birds may be able to track spatio-temporal variation in the quality of breeding patches and disperse from patches where the local reproductive success is low and recruit to patches where the local reproductive success is high (Danchin et al. 1998). Alternatively, the high breeding success led to a better recruitment rate in the colonies closest to areas with available resources. In other words, Barents Sea kittiwakes may exhibit an eastward shift of their population following the capelin similar to what was observed in other seabird species confronted with resource migration (e.g., South Africa; Crawford et al. 2008). Concerning inter-specific competition, although common guillemots were never numerous (1.8–3.2% of the total number of breeding birds), the number breeding at the Dvorovaya Bay's colony (most eastern colonies of the Murman coast) has decreased to 25% of the population level in 1960 (Krasnov et al. 2007b). This suggests that the competition between guillemots and kittiwakes will intensify with time. East of Dvorovaya Bay, there is a large colony of kittiwakes where no guillemots can be found, an outcome possibly related to an eastward shift in kittiwakes.

References

Andersen T, Carstensen J, Hernandez-Garcia E, Duarte CM (2009) Ecological thresholds and regime shifts: approaches to identification. Trends Ecol Evol 24:49–57

Anker-Nilssen T, Bakken V, Strøm H, Golovkin AN, Bianki VV, Tatarinkoa IP (2000) The status of marine birds breeding in the Barents Sea region. Norwegian Polar Institute, Tromsø

Ashbrook K, Wanless S, Harris MP, Hamer KC (2010) Impacts of poor food availability on positive density dependence in a highly colonial seabird. Proc R Soc Lond B 277:2355–2360

Barrett RT (2007) Food web interactions in the southwestern Barents Sea: black-legged kittiwakes *Rissa tridactyla* respond negatively to an increase in herring *Clupea* harengus. Mar Ecol Prog Ser 349:269–276

Barrett RT, Krasnov YV (1996) Recent responses to changes in stocks of prey species by seabirds breeding in the southern Barents Sea. ICES J Mar Sci 53:713–722

Barrett RT, Bakken V, Krasnov JV (1997) The diets of common and Brünnich's guillemots *Uria aalge* and *U. lomvia* in the Barents Sea region. Polar Res 16:73–84

Boulinier T, Danchin E (1996) Population trends in Kittiwake *Rissa tridactyla* colonies in relation to tick infestation. Ibis 138: 326–334

Boulinier T, McCoy KD, Yoccoz NG, Gasparini J, Tveraa T (2008) Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. Biol Lett 4:538–540

Brander KM (2010) Cod Gadus morhua and climate change: processes, productivity and prediction. J Fish Biol 77:1899–1911

Camphuysen CJ, Scott BE, Wanless S (2006) Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multispecies foraging assemblages and habitat-specific feeding strategies. In: Boyd IL, Wanless S, Camphuysen CJ (eds) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge, pp 82–97

Carscadden JE, Montevecchi WA, Davoren GK, Nakashima BS (2002) Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. ICES J Mar Sci 59:1027–1033

Cherel Y, Ducatez S, Fontaine C, Richard P, Guinet C (2008) Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. Mar Ecol Prog Ser 370:239–247

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366

Crawford RJM, Sabarros PS, Fairweather T, Underhill LG, Wolfaardt AC (2008) Implications for seabirds off South Africa of a long-term change in the distribution of sardine. Afr J Mar Sci 30:177–184

Croxall JP, Rothery P (1991) Population regulation of seabirds: implications of their demography for conservation. In: Perrins CM, Lebreton J-D, Hirons GJM (eds) Bird population studies: relevance to conservation and management. Oxford University Press, Oxford, pp 272–296

Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79:2415–2428

Davoren GK, Montevecchi WA (2003) Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres *Uria aalge*. J Avian Biol 34:44–53

Drinkwater KF et al (2010) On the processes linking climate to ecosystem changes. J Mar Syst 79:374–388

Durant JM, Anker-Nilssen T, Stenseth NC (2003) Trophic interactions under climate fluctuations: the Atlantic puffin as an example. Proc R Soc Lond B 270:1461–1466

Durant JM, Stenseth NC, Anker-Nilssen T, Harris MP, Thompson P, Wanless S (2004) Marine birds and climate fluctuation in North Atlantic. In: Stenseth NC, Ottersen G, Hurrell JW, Belgrano A (eds) Marine ecosystems and climate variation: the North Atlantic. A comparative perspective. Oxford University Press, Oxford, pp 95–105

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271–283

Durant JM et al (2010) Influence of feeding conditions on breeding of African penguins—the importance of adequate local food supplies. Mar Ecol Prog Ser 420:263–271

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75: 1259–1268

Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311:655–656

Furness RW, Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar Ecol Prog Ser 202:253–264

Gjøsæter H (1998) The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. Sarsia 83:453–496

Gjøsæter H, Bogstad B, Tjelmeland S (2009) Ecosystem effects of the three capelin stock collapses in the Barents Sea. Mar Biol Res 5: 40–53

Hjermann DO, Stenseth NC, Ottersen G (2004) Indirect climatic forcing of the Barents Sea capelin: a cohort effect. Mar Ecol Prog Ser 273:229–238

Hjermann DØ et al (2010) Trophic interactions affecting a key ecosystem component: a multi-stage analysis of the recruitment of the Barents Sea capelin. Can J Fish Aquat Sci 67:1363–1375

Hudson PJ, Dobson AP, Newborn D (1998) Prevention of population cycles by parasite removal. Science 282:2256–2258

Hurrell J (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitations. Science 269:676–679

Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (eds) (2003) The North Atlantic Oscillation: climate significance and environmental impact. American Geophysical Union, Washington

Huse G, Ellingsen I (2008) Capelin migrations and climate change—a modelling analysis. Clim Change 87:177–197

ICES (2006) Report of the Arctic Fisheries Working Group (AFWG), 19–28 April 2006, ICES Headquarters. ICES CM 2006/ ACFM:25

Ives AR (1995) Predicting the response of populations to environmental-change. Ecology 76:926–941

Kokko H, Harris MP, Wanless S (2004) Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. J Anim Ecol 73:367–376

Kovacs KM, Haug T, Lydersen C (2009) Seabirds in the Barents Sea. In: Sakshaug E, Johnsen G, Kovacs KM (eds) Ecosystem Barents Sea. Tapir, Trondheim

Krasnov YV, Barrett RT (1995) Large-scale interactions among seabirds, their prey and humans in the southern Barents Sea. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP (eds) Ecology of fjords and coastal waters. Elsevier, Amsterdam, pp 443–470

Krasnov YV, Nikolaeva NG (1998) Some results of the multidisciplinary study of the kittiwake in the Barents Sea. In: Krasnov YV, Matishov GG, Galaktionov KV, Saninova TN (eds) Biology and oceanography of the Kara and Barents Seas (along the Northern marina route). KSC RAS, Apatity, pp 180–260

Krasnov YV, Matishov GG, Galaktionov KV, Savinova TN (1995) *Morskiye kolonialniye ptitsi Murmana* (The colonial seabirds of Murman). Nauka, St. Petersburg

Krasnov YV, Barrett RT, Nikolaeva NG (2007a) Status of black-legged kittiwakes (*Rissa tridactyla*), common guillemots (*Uria aalge*) and Brunnich's guillemots (*U-lomvia*) in Murman, north-west Russia, and Varanger, north-east Norway. Polar Res 26: 113–117

Krasnov YV, Nikolaeva NG, Goryarev YI, Ezhov AV (2007b) Current status and population trends in the Kittiwake (*Rissa tridactyla*), Common (*Uria aalge*) and Brunnich's (*U. lomvia*) guillemots at Kola Peninsula, European Russia. Ornithologia 34: 65–75 (in Russian)

Lande R, Engen S, Sæther B-E (2003) Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford

Lima M, Previtali MA, Meserve PL (2006) Climate and small rodent dynamics in semi-arid Chile: the role of lateral and vertical perturbations and intra-specific processes. Clim Res 30:125–132

López-Sepulcre A, Kokko H, Norris K (2010) Evolutionary conservation advice for despotic populations: habitat heterogeneity favours conflict and reduces productivity in Seychelles magpie robins. Proc R Soc Lond B 277:3477–3482

Lorentsen SH, Christensen-Dalsgaard S (2009) Det nasjonale overvåkingsprogrammet for sjøfugl. Resultater til og med hekkesesongen 2008. NINA Rapport 439:1–53

Modestov VM (1967) The ecology of colonial nesting birds (based on observations on the Eastern Murman Coast and in the Volga river delta). Trans Kandalaksha State Reserv 5:49–154 (in Russian)

Moe B et al (2009) Climate change and phenological responses of two seabird species breeding in the high-Arctic. Mar Ecol Prog Ser 393:235–246

Nikolaeva NG, Krasnov YV, Barrett RT (1996) Movements of common *Uria aalge* and Brünnich's Guillemots *U. lomvia* breeding in the southern Barents Sea. Fauna Norveg Ser C Cinclus 19:9–20

Oro D, Perez-Rodriguez A, Martinez-Vilalta A, Bertolero A, Vidal F, Genovart M (2009) Interference competition in a threatened seabird community: a paradox for a successful conservation. Biol Conserv 142:1830–1835

Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC (2001) Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42

Pedersen OP, Tande KS, Pedersen T, Slagstad D (2009) Advection and retention as life trait modulators of capelin larvae—a case study from the Norwegian coast and the Barents Sea. Fish Res 97:234–242

Ronconi RA, Burger AE (2011) Foraging space as a limited resource: inter- and intra-specific competition among sympatric pursuit-diving seabirds. Can J Zool 89:356–368

Rosenzweig C et al (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 453:353–357

Sæther B-E et al (2005) Generation time and temporal scaling of bird population dynamics. Nature 436:99–102

Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. Science 297: 1292–1296

Stenseth NC et al (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proc R Soc Lond B 270: 2087–2096

Vader W, Barrett RT, Erikstad KE, Strann K-B (1990) Differential responses of common and thick-billed murres to a crash in the capelin stock in the southern Barents Sea. Stud Avian Biol 14: 175–180

Viljugrein H, Stenseth NC, Smith GW, Steinbakk GH (2005) Density dependence in North American ducks. Ecology 86:245–254

Wood SN, Augustin NH (2002) GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecol Model 157:157–177

Electronic Supplementary Material

Within and between species competition in a seabird community: statistical exploration and modeling of time-series data

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Online Resource 1. Trophic niche segregation among the three seabird species breeding at Kharlov Island.

Mixed colony at Kharlov Island (Common guillemots *Uria aalge* breeding over kittiwakes *Rissa tridactyla*). Photo taken by Y Krasnov.

At Kharlov Island, kittiwakes and guillemots are essentially piscivores targeting capelin and herring. Diet composition was collected on Kharlov Island between 1982-1999 for kittiwakes (lacking data for 1984 and 1985), between 1984-1999 for common guillemots (lacking data for 1985), and between 1992-1999 (lacking data for 1996 and 1997) for Brünnich's guillemots. Using these time series, we have calculated the diet overlap *O* using Schoener's index (Schoener 1968, Mysterud 2000):

$$O_{jk} = 1 - 0.5 * \Sigma |\, P_{ij} - P_{ik} \,|$$

where O_{jk} is the overlap between the bird species j and k; p_{ij} is the proportion of species j feeding on prey species/group i; and p_{ik} is the proportion of species k feeding on prey species/group i. Overlap in diet between species j and k is complete when $O_{jk} = 1$ and is absent when $O_{jk} = 0$ (Mysterud 2000).

For Common G. *vs* Kittiwake; $O_{jk} = 0.511 \pm 0.197$ (period 1986-1999)

For Kittiwake *vs* Brünnich's G.; $O_{jk} = 0.449 \pm 0.156$ (period 1992-1999)

For Common G. *vs* Brünnich G.; $O_{jk} = 0.678 \pm 0.141$ (period 1992-1999)

If we consider that when overlap $O > 2*SD$ of the diet overlap is significant, all the diets are significantly overlapping during the studied periods.

Mysterud A (2000) Diet overlap among ruminants in Fennoscandia. Oecologia 124:130-137

Schoener TW (1968) Anolis lizards of Bimini - Resource partitioning in a complex fauna. Ecology 49:704-726

Online Resource 2. Times series used as explanatory variables in the analysis.
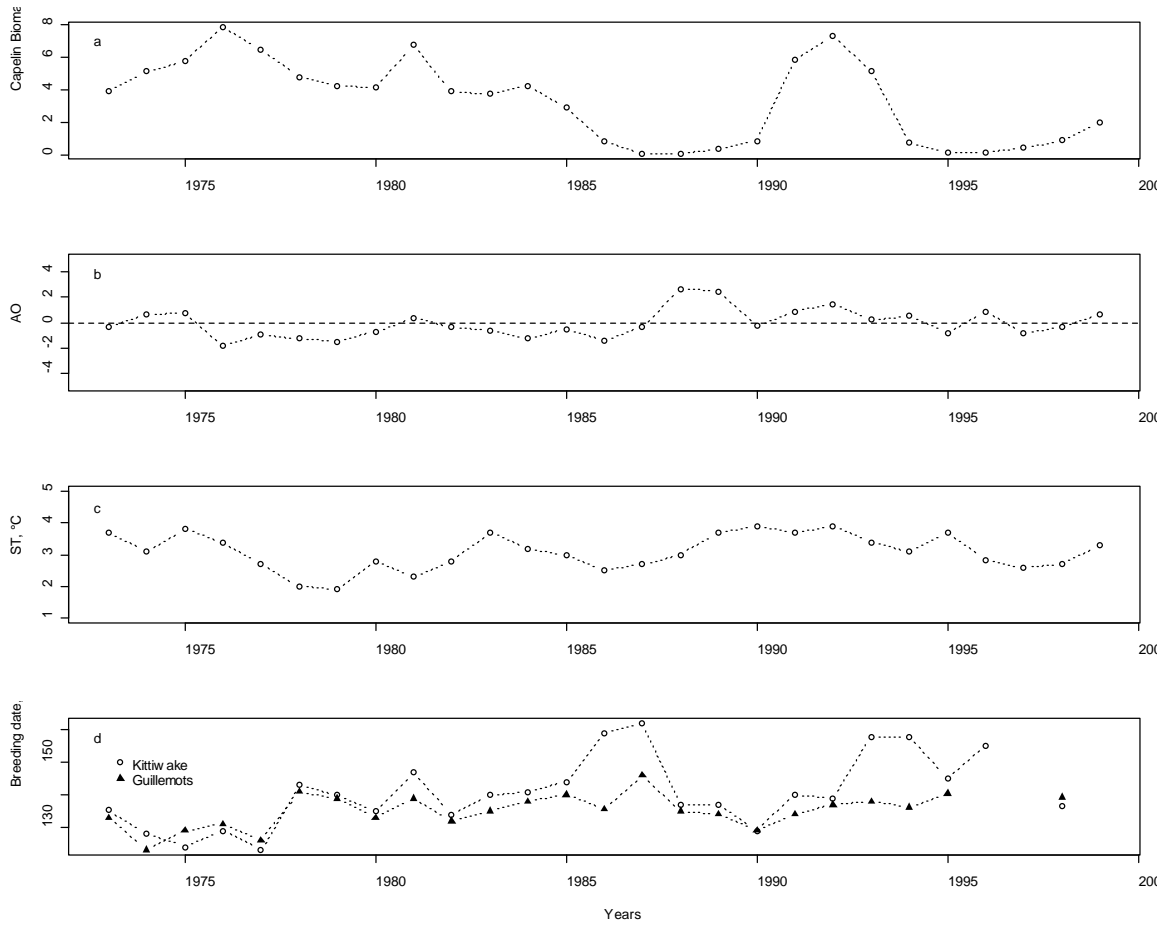
(**a**) CAPbm is the capelin stock biomass (in million tonnes). Capelin data are coming

from acoustic stock size estimates in September in the Barents Sea (ICES, 2006). (**b**) AO

$_t$ is the Arctic Oscillation index (average of AO from January year $_t$ to March year $_{t+1}$).

(**c**) ST $_t$ is the monthly average sea temperature in °C measured in May $_t$ on the Russian

Kola meridian transect (33° 30' E, 70° 30' N to 72° 30' N). (**d**) Average breeding dates

for Kittiwake and Guillemots (Common and Brünnich's merged) in Julian date.

4

Online Resource 3. Pearson's product moment correlations between the different explanatory variables in year $_t$ used to model the population changes of kittiwake, common guillemot and Brünnich's guillemot.

	Kittiwake	Common	Brünnich	CAPbm	AO	ST	KittiDate	GuillDate	
Kittiwake		0.03[24]	0.08[24]	-0.24[25]	0.05[25]	0.33[25]	0.28[23]	0.18[22]	
Common	0.895		**0.65**[24]	**0.47**[24]	**-0.61**[24]	-0.31[24]	-0.19[22]	-0.12[21]	**r-values** [d.f.]
Brünnich	0.692	<0.001		**0.60**[24]	-0.29[24]	-0.11[24]	-0.40[22]	-0.27[21]	
CAPbm	0.234	0.015	0.001		-0.18[25]	0.06[25]	**-0.44**[23]	-0.34[22]	
AO	0.801	0.001	0.151	0.371		**0.40**[25]	-0.02[23]	-0.14[22]	
ST	0.095	0.127	0.597	0.755	0.040		-0.28[23]	-0.33[22]	
KittiDate	0.182	0.382	0.053	0.028	0.933	0.184		**0.75**[22]	
GuillDate	0.407	0.600	0.218	0.109	0.517	0.119	<0.001		
					***p*-values**				

Values for Kittiwake, Common, and Brünnich are $\log_e$ transformed.

Kittiwake (n=27), Common (n=26), Brünnich (n=26), CAPbm (n=27), AO (n=27), ST (n=27), KittiDate (n=25), and GuillDate (n=24). In bold are presented the variables significantly correlated.

Note that the breeding dates for Kittiwake can be modelled (GAM, R^2=0.52) using herring abundance (slope: 8.75 ± 2.21), the capelin abundance (slope: -1.82 ± 0.62), and the Sea temperature (slope: -8.05 ± 2.81). Likewise, the guillemots the breeding dates can be modelled (GAM, R^2=0.38) using the capelin abundance (slope: -0.72 ± 0.35), the herring abundance (edf = 1.53, increase) and the Sea temperature (edf = 1.70, decrease).

Online Resource 4. Result from fitting a GAM to the variation in population of three species of seabirds (black-legged kittiwake, common guillemot and Brünnich's guillemot) breeding at Kharlov Island in the Barents Sea. Models are linear when the estimated degree of freedom (edf) by GAM is equal to 1.

y_{t+1}	x_t	n	edf	GCV	R^2	p-value
	CAPbm	26	1.88	0.028	0.30	0.007
	Common	25	1	0.033	-0.03	0.614
	Brünnich	25	1.21	0.033	-0.02	0.839
Kittiwake	Kittiwake	26	1.61	0.034	0.13	0.190
	AO	26	1.78	0.035	0.12	0.169
	ST	26	1	0.039	-0.03	0.544
	GuillDate	24	1	0.039	-0.02	0.442
	Common	24	1.53	0.201	0.53	0.000
	CAPbm	25	1.91	0.219	0.49	0.000
	AO	25	1.66	0.336	0.21	0.022
Common	Brünnich	24	1	0.366	0.13	0.049
	KittiDate	24	1	0.373	0.14	0.040
	Kittiwake	25	1	0.382	0.08	0.093
	ST	25	1	0.420	-0.01	0.399
	Brünnich	24	1	0.093	0.37	0.001
	Common	24	1	0.111	0.25	0.008
	KittiDate	24	1	0.112	0.33	0.002
Brünnich	CAPbm	25	1.18	0.113	0.30	0.007
	AO	25	1.32	0.154	0.05	0.204
	Kittiwake	25	1	0.159	0.01	0.293
	ST	25	1	0.167	-0.04	0.967

Values for Kittiwake, Common guillemot, and Brünnich's guillemot are log transformed.

NAO is the winter North Atlantic Oscillation index (December year $_{t-1}$ to March year $_t$).

KittiDate and GuillDate are the dates of first breeding for kittiwakes and guillemots respectively (in Julian day). AO is the Arctic Oscillation index (January year $_t$ to March year $_t$). ST is the temperature average for May $_t$ measured at Kola. CAPbm is the Capelin stock biomass measured by acoustic survey in the Barents Sea in September year $_{t-1}$.

GCV: Generalized Cross Validation Criterion.

Online Resource 5. Community matrix

The community matrix was computed using the ecological parameters found in Table 3.

$$\begin{bmatrix} -6.313 & 0 & 0 \\ 3.182 & 1.776 & 0 \\ 0 & 0 & -2.905 \end{bmatrix}$$

The eigenvalues of the matrix are -6.313, -2.905, and 1.776. In order to have a stable equilibrium, all eigenvalues need to be negative. The largest eigenvalue of the community matrix being positive the community is not stable (Gillman 2009) .

Gillman, M. (2009) An introduction to mathematical models in ecology and evolution: Time and Space. - Wiley-Blackwell.

Online Resource 6. Reflection on the effect of observation error on estimates of intraspecific competition (density dependence) and interspecific competition: results of simulation

Sampling error has been shown to affect the estimation of the direct density dependence effect (Carroll et al. 1995) and can also affect the estimation of the effect of the interspecific term. In their supplementary materials, Hjermann et al. (2010) show that measurement errors can indeed lead to an underestimation of the slope and thereby an overestimation of the density dependence effect. However, they also show that the underestimation is negligible if the variance in the population is strong.

We simulated the effect of observation errors on estimates of density dependence or competition in the following way: Let the abundance at two stages be X_t and X_{t+1} and of competitor species Y_t. For density dependence (intra-specific competition), we simulated that X_{t+1} depends on X_t by the following formula: $\log(X_{t+1}) = b*\log(X_t) + \varepsilon$ (where ε represents random variation in survival; ε is normally distributed around zero). For interspecific competition, we let X_{t+1} depend on Y_t by the following formula: $\log(X_{t+1}) = b1*\log(X_t) + b2*\log(Y_t) + \varepsilon$. In both cases, we simulated a measurement error in X_t and in Y_t, so we observe $X_t' = X_t + \gamma$ (γ is measurement error) or $Y_t' = Y_t + \gamma$ respectively, and estimated b using linear regression between X'_{t+1} and X_t' and b2 using linear regression between X'_{t+1} and X_t' and Y_t', simulation 1 and simulation 2 respectively. We let the standard deviation of $\log(X_t)$ and of $\log(Y_t)$, the real value of b, and the degree of measurement (observation) error γ vary. The figures show the estimated values of b and

b2 (ordinate axis) compared to the real values (abscissa axis); unbiased estimates should lie on the black line (indicating ordinate=abcissa).

Results for simulation 1 are presented on Panel *a* and the ones for simulation 2 on Panel *b*. We show only results with a large observation error (γ), given as the coefficient of variation (CV; standard deviation in γ as percentage of X_t (or Y_t); i.e., a coefficient of variation of 20% means that 95% of the observed X_t values are within +/- 40% of the real X_t values). An observation error of 20% is quite large following the methods used for estimating the seabird population at Kharlov Island (basically a complete count; see Methods). The use of a smaller observation error would have given less deviation of the slope to the real slope (see Hjermann et al. 2010). It is clear that as long as the variation of X_t or Y_t is modest (low system noise), b is strongly underestimated in simulation 1 when there is observation error (and density dependence, given as 1-b, is overestimated). However, if the variation in X_t is large (standard deviation of $\log(X_t) \geq 1$), bias is reduced even for a strong observation error. For the competition term, the underestimation of b2 is less strong and affects the estimation significantly only for a strong competitive effect. We show that the slope of the effect of interspecific competition is not underestimated in the range we are considering (-0.2 to -0.3, see panel *b*).

The slope of the density dependence effect is always underestimated, especially when the system noise is small. For example, the slope of b=0.83 observed for common guillemots corresponds to a real slope b ranging between 1.03-1.10 (thus for a positive density dependence effect) for a system noise ranging from 0.1-2. In a similar way, the slope of b = 0.36 observed for kittiwakes corresponds to a real slope ranging from 0.45 to

0.82 a system noise ranging from 0.1-2. While greatly overestimated in its strength (for an unrealistic system noise <0.2), the direction of the density dependence effect is retained.

For info, in our system, kittiwake has a CV= 0.18, Common guillemot a CV = 0.50 (0.19 and 0.49 if cutting the time series in two at 1986), and Brünnich's guillemot a CV= 0.39.
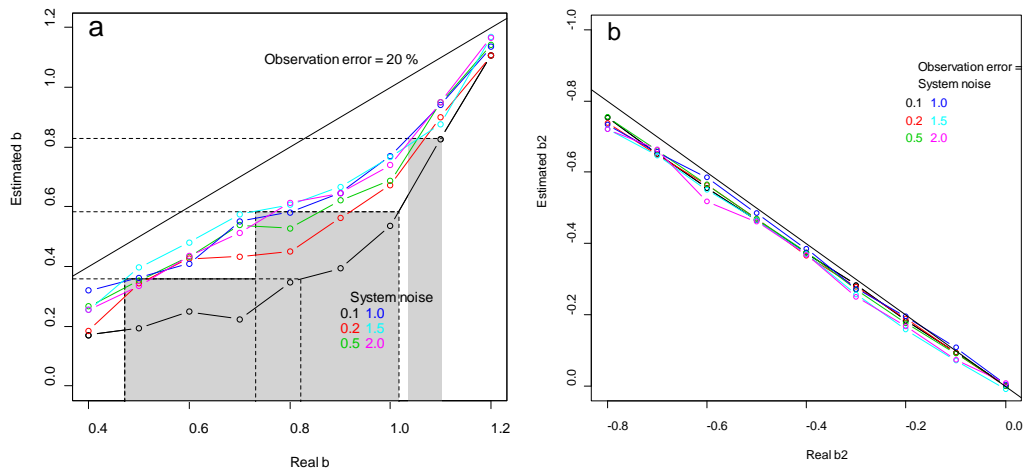

Figure S2. Simulation of the observation error on estimates of intraspecific competition and interspecific competition effect estimate. (**a**). Difference between the real slope b (intraspecific effect) and the estimated slope when $\log(X_{t+1}) = b*\log(X_t) + \varepsilon$ (where ε represents random variation in survival; ε is normally distributed around zero). Horizontal lines indicate the slopes estimated for the density dependence for the three species considered. The grey shaded area corresponds to the real value of X_t depending on the system noise. (**b**) Difference between the real slope b (interspecific effect) and the estimated slope when $\log(X_{t+1}) = b1*\log(X_t) + b2*\log(Y_t) + \varepsilon$.

Carroll RJ, Ruppert D, Stefanski LA (1995) Measurement error in non-linear models.

Chapman and Hall, London,UK.

Hjermann DØ, Bogstad B, Dingsør GE, Gjøsæter H, Ottersen G, Eikeset AM, Stenseth NC (2010) Trophic interactions affecting a key ecosystem component: a multi-stage analysis of the recruitment of the Barents Sea capelin. Can J Fish Aquat Sci 67:1363-1375.