Seabird–fish interactions: the fall and rise of a common guillemot *Uria aalge* population

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ABSTRACT: A major challenge in population ecology is the prediction of population responses to environmental variance. Food availability has long been hypothesized to play a major role in regulating seabird populations. In general, seabirds feed on small pelagic fish and/or young age classes of larger predatory fish. Here we used a logistic population model to predict the temporal variation in the population size of common guillemots *Uria aalge* in a colony in NE Norway (Hornøya) between 1987 and 2011 in relation to the variation in abundance (acoustic and trawl surveys) of important fish prey species in the Barents Sea. The fish species considered, all of which have been described in the diet of common guillemot chicks and adults on Hornøya, were capelin *Mallotus villosus* (all age classes), 1-group herring *Clupea harengus* and 0-group cod *Gadus morhua*. The guillemot population collapsed by more than 80% during the winter 1986/1987, when the abundance indices of all fish prey species were very low, but has since steadily increased. The annual variation in population growth rate after the population collapse could best be explained by the variation in abundance of 0-group cod (unlagged), and the 0-group cod and capelin 6 and 4 yr earlier, respectively (equalling the age of maturation of guillemots). We also present a numerical ocean model to identify mechanisms affecting spatio-temporal prey availability of 0-group cod around the colony during the breeding season. These results undermine earlier focus on the capelin stock as the main cause of the population crash in common guillemots.

KEY WORDS: Common guillemot · Population model · Population growth rate · North-east Arctic cod

INTRODUCTION

A major challenge in population ecology is the prediction of population responses to environmental variance. Such models are important to identify key environmental factors as management targets for threatened species and especially to predict the time to extinction or quasi-extinction of endangered species (Caughley 1994, Beissinger & McCullough 2002, Morris & Doak 2002). Among seabirds, fluctuations in food availability have long been hypothesized to play a major role in regulating populations (Lack 1966). In general, seabirds feed on small, pelagic fish species and/or young age classes of demersal fish species, many of which are heavily exploited commercially (reviewed by Croxall & Rothery 1991, Furness 2007), an exploitation that can have direct negative effects on important life history traits of the seabirds, such as survival and breeding success (e.g. Oro & Furness 2002, Frederiksen et al. 2004;

reviewed by Furness 2007). Furthermore, climate may also cause changes in seabird populations by affecting conditions such as sea temperature or the frequency of extreme weather events (Ottersen et al. 2001, Schreiber 2002, Sandvik & Erikstad 2008). Although a number of other factors such as drowning in fishing gear and oil spills may further contribute to declines in seabirds (Wiese & Robertson 2004, Votier et al. 2005, 2008, Barrett et al. 2006), there is strong evidence that fluctuations in prey fish stocks and fisheries are of major importance (reviewed by Furness 2007).

The Barents Sea is among the most productive seas in the world and is a feeding ground for huge stocks of several commercial fish species and millions of seabirds (Loeng 1989, Sakshaug et al. 1994, Anker-Nilssen et al. 2000, Barrett et al. 2006). The main fish stocks are those of capelin *Mallotus villosus*, Norwegian spring-spawning herring *Clupea harengus* and north-east Arctic cod *Gadus morhua* (e.g. Olsen et al. 2010), all of which are heavily exploited by commercial fisheries (Bergstad et al. 1987, Olsen et al. 2010 and references therein). This exploitation, plus climatic fluctuations and strong interspecific interactions have, at times, led to huge fluctuations in the stocks (e.g. Godø 2003, Gjøsæter et al. 2009) and disruptions in predator–prey interactions (Durant et al. 2004, Gjøsæter et al. 2009, Stige et al. 2010).

Many populations of seabirds that breed in the Barents Sea area are declining (Lorentsen & Christensen-Dalsgaard 2009), and common guillemot *Uria aalge* populations in particular have declined greatly along the coast of Norway, with some colonies now on the verge of extinction (Barrett et al. 2006, Erikstad et al. 2007, Lorentsen & Christensen-Dalsgaard 2009). As a result, the populations are classified as 'critically endangered' on the Norwegian Red List (Kålås et al. 2010).

Yearly population growth rates in seabirds may reflect the variance in a number of different demographic and nuisance parameters. Besides the population size, they include counting errors, the yearly variance in the degree of deferred breeding, adult survival rates and the recruitment rates of young birds into the breeding population. In common guillemots, maturation and recruitment occur at an age of 5 to 6 yr (Halley et al. 1995, Crespin et al. 2006, Munilla et al. 2007, Votier et al. 2008). Emigration and immigration of seabirds between colonies might also be extensive (Breton et al. 2006). If food availability is important in determining the fluctuations in population growth rate, the time lag in the relationship between age-specific abundance of fish prey

species and yearly seabird population growth rate may indicate which of these demographic traits are the most important in determining the population growth rate (Sandvik et al. 2012).

One main question related to both life history theory and the research on effects of environmental variance is the relative influence of offspring production rates and adult survival rates on population dynamics (Stearns 1992, Weimerskirch et al. 2003, Sæther et al. 2004). If the effect of adult survival is most important, the relevant time lag of prey species abundance on population growth rate should be 0 (assuming a direct effect of prey density) or 1 yr, depending on which time of year is the critical period for survival. Likewise, if the yearly variation in deferred breeding is an important parameter, a lag of 0 or 1 yr might also be expected. If, however, the effect of prey on reproduction is most important, the population dynamics will, for common guillemots, be affected most strongly by prey conditions 4 to 6 yr earlier, a lag that spans the age of recruitment. This follows from the fact that the effect of prey on reproduction will not become evident until the offspring affected have recruited into the population being censused (provided that the signal is not confounded by other factors affecting immature survival).

In this study, we used long-term monitoring data consisting of counts of individual common guillemots in study plots in the breeding colony on Hornøya in eastern Finnmark, northern Norway, from 1980 to 2011. Our aim was to explore possible effects of the variation in fish prey stocks on the variation in population growth rate. We used a logistic population model (Sæther & Engen 2002) in order to model the yearly population growth rate as a function of environmental covariates (cf. Jonzén et al. 2002, Woody et al. 2007, Sæther et al. 2009). For iteroparous species, population models should ideally be based on age- or stage-class matrix models. However, such an exercise requires access to long-term individual-based demographic data, which are available for only very few natural populations, and not from the present study population.

Since 0-group cod is an important part of the diet in adult common guillemot during the breeding season in the present study population (Bugge et al. 2011), we also utilized a numerical ocean model coupled to an individual-based model (IBM) for early stages of fish to identify mechanisms affecting spatio-temporal prey availability for common guillemots around the colony. These patterns will be discussed in a climate perspective.

MATERIALS AND METHODS

Study area and data collection

The field work was carried out from 1980 to 2011 on Hornøya (70° 23′ N, 31° 9′ E), a 0.5 km² island in northeastern Norway. Annual counts of individual common guillemots on predefined monitoring plots were made by one of us (R.T.B.) late in the incubation period or during hatching. To minimise the day-to-day variation, 5 to 10 counts were made on different days, and the mean number was used as an index of population size. The monitoring followed internationally standardized methods (Walsh et al. 1995), and more details can be found in Barrett (2001). As an index of breeding numbers, the means of all plots counted in successive years were used. Successive annual estimates of the total population on Hornøya were based on a single, total count of 1900 individuals made in 1987 and the annual rates of change documented in the monitoring plots. With a day-to-day variation in counts of 10% (R. T. Barrett unpubl.), the 1989 count was equivalent to ca. 1350 breeding pairs using a factor of 0.69 to correct for the fact that both parents are not always present in the colony (Barrett 2001). The monitoring plots cover a relatively large fraction of the total number of breeding birds on the island. From 1980 to 1989, 6 plots were monitored that, in 1989, covered 36% of the total breeding population. Because some plots appeared to be reaching maximum density of birds and because of a spread of the colony into new sites, the number of monitoring plots was then increased to 9 and, in 2001, covered ca. 40% of the total population (Barrett 2001, unpubl.). This was admittedly at the risk of variable sub-colony dynamics affecting overall results (Zador et al. 2009), but Barrett (2001) previously showed similar rates of change in total numbers and numbers of birds in the plots chosen.

We confined the analyses that included prey to age classes of fish previously described as food of guillemots in the region. For Hornøya, these include all age classes of capelin and 1-group herring and 0-group cod (Erikstad & Vader 1989, Barrett 2002, Bugge et al. 2011). These are also key fish species in the Barents Sea ecosystem and are all exploited commercially (Olsen et al. 2010). Data on fish stock variation were downloaded from www.imr.no/sjomil/index.html and from ICES (2011). Since we also focussed on the effect of recruitment on population growth rate, we lagged fish prey species counts by 4 to 6 yr, spanning the period of recruitment in common guillemots (Halley et al. 1995, Crespin et al. 2006, Munilla et al. 2007,

Votier et al. 2008). A correlation matrix of the covariates used is provided in Table S1 in the supplement at www.int-res.com/articles/suppl/m475p267_supp.pdf.

Population model

To estimate the population growth rate, we used a logistic population model (Sæther & Engen 2002). The logistic population models had the form $N_{t+1} = \lambda_t N_t$, where N_t is the population size in year t, and λ_t is the population growth rate in year t:

$$\lambda_t = \exp\left(r/1 - N_t/K\right) + \sigma_d^2/(2N_t) + \sum_i \beta_i X_{i,t} + \varepsilon_t \quad (1)$$

where β_i is the slope of the ith covariate X_i; ε is an independent variable with mean zero and variance $\sigma^2 = \sigma_e^2 + \sigma_d^2/N_t$; K is the carrying capacity; r is the intrinsic population growth rate; σ_d^2 is the demographic variance; σ_e^2 is environmental variance; and X is the environmental covariate. The parameters β_i, K, r and σ_e^2 were estimated from the population time series using maximum likelihood, such that the log-likelihood

$$\ln L = -\frac{1}{2} \sum_{i=1}^{n} \{[\ln N_k - E(\ln N_k)]^2 \sigma^{-2} + \ln(2\pi\sigma^2)\} \quad (2)$$

was maximised over the n elements of the time series (Sæther et al. 2009), where $E(\ln N_k) = \ln(\lambda_{k-1} N_{k-1})$ is the predicted log-population size based on the observed population size N_{k-1} and Eq. (1). The logistic population model was chosen because it has been shown to describe the pattern of density regulation in avian population dynamics quite well (Sæther & Engen 2002). Demographic variance was assumed to be 0.1, which is a realistic value for long-lived birds (Lande et al. 2003).

Models with different covariates were compared using Akaike's Information Criterion corrected for small sample sizes (AIC$_C$), preferring models with the lowest ΔAIC$_C$ (or the highest AIC$_C$ weight or model likelihood; see Burnham & Anderson 2002). Non-nested models within 2 AIC$_C$ of each other were considered to be equally well supported. In the nested case, however, a model was disregarded when it had a higher AIC$_C$ than a model with fewer parameters. We also chose to disregard models where one of the covariates was estimated to have a negative slope (1-sided test), as we searched for direct trophic interactions between guillemots and their prey.

Confidence intervals were obtained by nonparametric bootstrapping of the model parameters using 120 000 replicates. We verified that the model residuals were normally distributed ($D = 0.12$, p = 0.84), homoscedastic ($t = 0.96$, p = 0.35), white ($\chi_6^2 = 7.58$, p =

0.27) noise (statistics provided are for the top-ranked model). Population models were run in the R environment (R Development Core Team 2011).

Modelled fish prey availability

Whereas observational juvenile distributions of fish prey were only available from autumn international 0-group fish surveys in the Barents Sea, a coupled ocean model and an IBM for ichthyoplankton (eggs, larvae and pelagic juveniles) enabled a continuous spatio-temporal description. We used the model setup for dispersal of ichthyoplankton of northeast Arctic cod and Norwegian spring-spawning herring as described by Vikebø et al. (2011). Key elements are an IBM for early stages of fish forced by the daily mean ocean weather forecast by the Norwegian Meteorological Institute produced with the 3-dimensional ocean model MI-POM (described by Engedahl 1995). In the model, fish larvae are represented by particles, and daily spatio-temporal distributions are available for overlap analysis with common guillemot feeding areas. We defined a box centred around Hornøya of 200 × 200 km (i.e. within a reasonable foraging range of common guillemots; Burke & Montevecchi 2009) and quantified the number of particles inside the box that originated from different spawning grounds along the coast at different times of the year.

RESULTS

Between 1986 and 1987, there was a very large (80%) decline in the population of common guille-

Fig. 1. *Uria aalge*. Annual variation in the approximate breeding population (no. of individuals) and in the population growth rate (ln [N_t /N_{t-1}]) of common guillemots breeding at Hornøya, NE Norway

mots on Hornøya (Fig. 1). Since then, the population has steadily increased and surpassed the 1983 level in 2003 (Fig. 1). The yearly population growth rate varied between years, but was positive or close to 0 for all years except 1987, the collapse year (Fig. 1). Coincident with the collapse in guillemot population were very low levels of all prey species (Fig. 2).
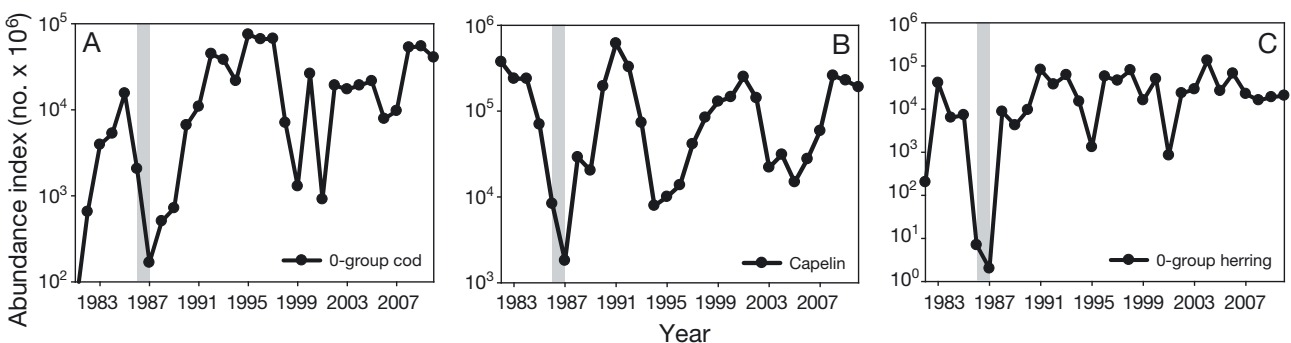
Since the crash year would have represented an extremely influential outlier, we modelled the growth of the guillemot population from 1987 onwards. Unlagged 0-group cod was the only well-supported 1-parameter model explaining guillemot population dynamics (Table 1) and accounted for 40% of the temporal variation in the population growth rates. Most of the other covariates (except for herring lagged by 6 yr) were poorer than the null model without prey covariates (Table S2 in the

Fig. 2. *Gadus morhua*, *Mallotus villosus*, and *Clupea harengus*. Annual variation in fish stock size indices (estimates of numbers, N × 10⁶) of appropriate age classes of fish species in the Barents Sea area known as important prey species for common guillemots breeding at Hornøya, NE Norway. (A) 0-group cod, (B) all age classes of capelin, (C) 0-group herring. The shaded area indicates the year when the common guillemot population collapsed (see 'Results' for details)
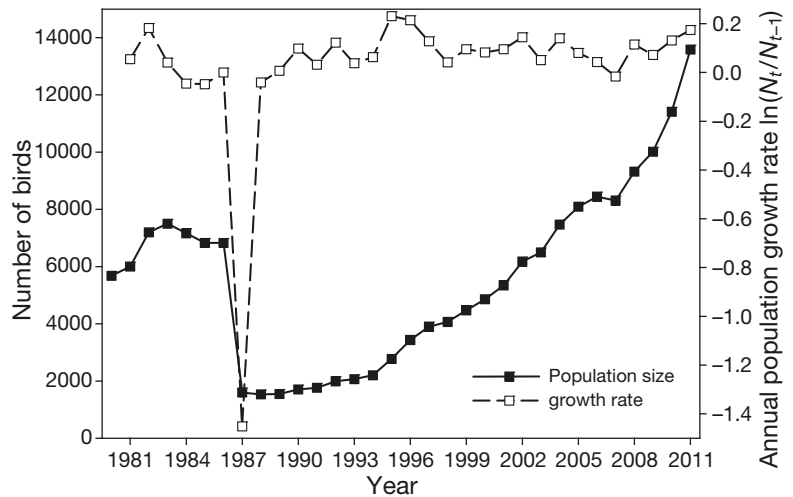
supplement at www.int-res.com/articles/suppl/m475p267_supp.pdf). However, once unlagged cod was included in the model, the latter could be further improved by adding cod lagged by 4 or 6 yr (Table 1). The top-ranked model combined 0-group cod lagged by 0 and 6 yr, and capelin lagged by 4 yr, explaining a total of 56% of the variation in guillemot population growth rates (Fig. 3, Table 2).

The 4 best models in Table 1 were within 1.3 AIC_C units of the top-ranked model (Table 1), i.e. they were approximately equally well supported. The support for the models with lagged covariates was thus somewhat equivocal. However, all slopes in the top model were estimated to be positive, i.e. 95% confidence intervals excluded 0 for all covariates (Table 2). Variable-wise evidence ratios were 0.94 for unlagged cod, 0.42 for cod lagged by 6 yr and 0.20 for capelin lagged by 4 yr. The model produced realistic estimates of population parameters (Table 2), and the high upper confidence limit of carrying capacity indicates that density regulation was rather weak in this population.

Based on the strong relationship found between 0-group cod abundance and common guillemot population growth, we also focused on cod in the coupled ocean model and IBM of early stages of fish. Cod larvae were produced at spawning grounds SG 1 to 8 along the Norwegian Coast (Fig. 4A, Vikebø et al. 2011), and the model system describes individual trajectories of larvae from the respective spawning grounds into the Barents Sea and to the west of Spitsbergen following the Norwegian Coastal Current (NCC) and partly in the Norwegian Atlantic Slope Current (NASC; Fig. 4B,C). Inflow to the Barents Sea occurs on both sides of a major bank structure, Tromsøflaket, and along the Bear Island Trough. Near-coast transport increases the likelihood of being transported close to Hornøya. Larvae from the northernmost spawning ground (SG 8; Fig. 4A) reach the box defined around Hornøya first, arriving in late March, with a maximum occurrence in early May and gradually decreasing to half the maximum value in late July (Fig. 4D). Farther west, the next spawning ground (SG 7; Fig. 4D) supplies prey items from early April, increasing until mid-June before levelling off at about 80% of the maximum values from the northern-most spawning ground farther east (SG 8; Fig. 4D). Moving even farther west, the spawning

Table 1. *Uria aalge*. Comparison of population models of common guillemot on Hornøya, Norway, with fish stocks at different time lags as covariates. Models are sorted by ascending ΔAIC_C (change in Akaike's Information Criterion corrected for small sample sizes). All models that are better (i.e. have a lower AIC_C) than a model with fewer parameters are shown. See Table S2 in the supplement for an exhaustive list of models tested

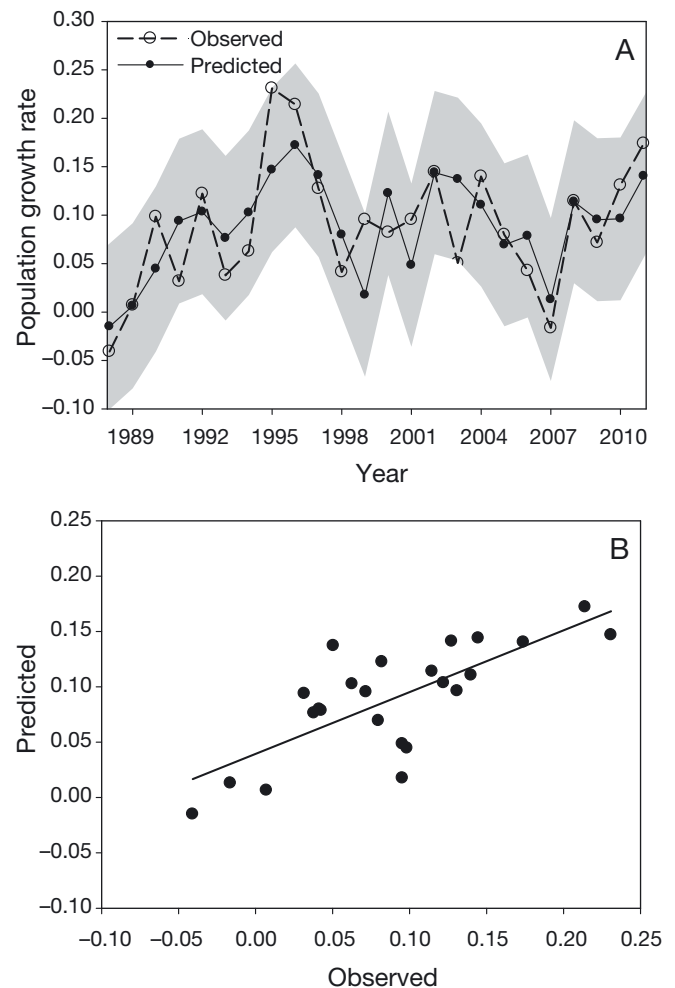| Model: fish (lag in years)	ΔAIC_C	AIC_C weight	Model likelihood	r^2
Cod (0) + cod (6) + capelin (4)	0.00	0.118	1.000	0.559
Cod (0) + cod (6)	0.22	0.105	0.895	0.489
Cod (0) + cod (4)	0.35	0.099	0.839	0.487
Cod (0)	1.31	0.061	0.520	0.396
Herring (6)	10.11	0.001	0.006	0.128
[Null model]	10.70	0.001	0.005	0.048

Fig. 3. *Uria aalge*. (A) Annual population growth rate of common guillemots at Hornøya, NE Norway, and the fitted values from the top ranked model (see Tables 1 & 2) that best describe the population growth rate for the whole time period, with 95% CI. (B) The same data as in (A), but predicted values of growth rate from the model are plotted against the observed values

Table 2. *Uria aalge*. Covariates explaining common guillemot population growth rate on Hornøya, and parameters describing the population dynamics. For each parameter, the estimate, lower (LCL) and upper (UCL) 95% confidence levels are provided, as well as the partial variance explained by and the significance level of each covariate. Estimates are from the top model in Table 1

Parameters	Estimate	LCL	UCL	Partial r^2	p
Cod, 0-group, unlagged (slope 1)	0.0297	0.0173	0.0426	0.403	0.000025
Cod, 0-group, lag 6 yr (slope 2)	0.0177	0.0048	0.0303	0.082	0.0083
Capelin, lag 4 yr (slope 3)	0.0164	0.0002	0.0331	0.074	0.049
Population growth rate (*r*)	0.121	0.084	0.162		
Carrying capacity (*K*)	18700	10900	3.77×10^9		
Environmental variance (σ_e^2)	0.00183	0.00068	0.00257		

ground south of Tromsøflaket (SG 6; Fig. 4A) supplies larvae from late May that increase steadily in number off Hornøya throughout the period of interest. In late July, the abundance of 0-group cod from SG 6 is at about twice the level of SG 7 and about 4 times the level of SG 5 and 8 (Fig. 4A). The remaining spawning grounds SG 1 to 5 contribute much less to the prey items available for common guillemot feeding than SG 6 to 8.
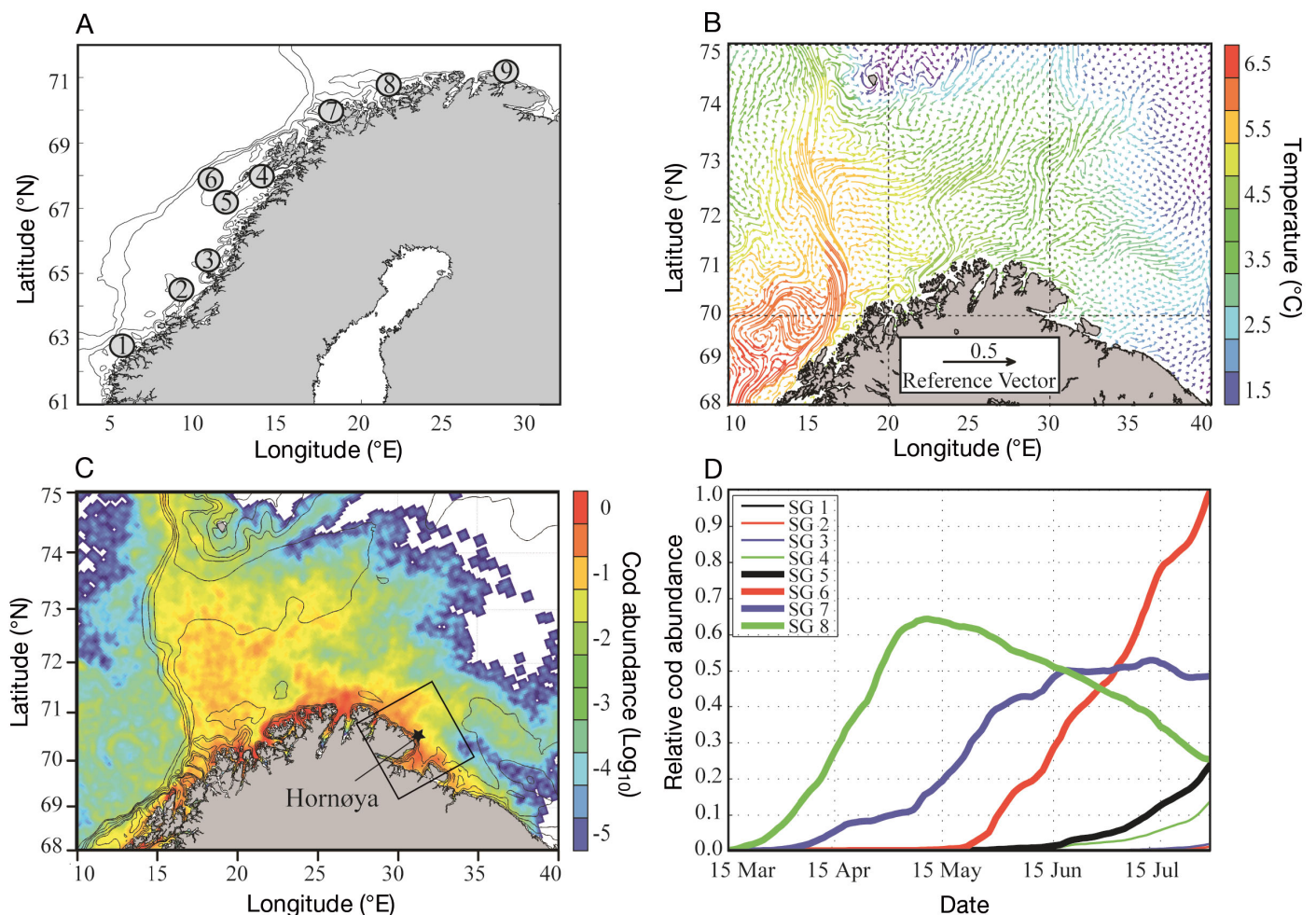

Fig. 4. *Gadus morhua*. (A) Well-known northeast Arctic cod spawning grounds, indicated by numbers, along the coast of Norway used in the numerical dispersal study of cod larvae. Their relative importance is the same as in Vikebø et al. (2011). (B) Monthly mean circulation and temperatures in the ocean forecast by the Norwegian Meteorological Institute at 20 m depth for April 2008 to 2011. (C) Modelled distribution of larval northeast Arctic cod on 1 July averaged over the years 2008 to 2011 based on daily mean circulation from the Norwegian Meteorological Institute. Colours indicate abundance relative to maximum abundance on a logarithmic scale. The black box indicates a 200 × 200 km area centred on Hornøya. (D) Abundance of larvae from the respective spawning grounds (SG) within a 200 × 200 km box centred on Hornøya as function of date relative to maximum abundance occurring in late August for spawning products from SG 6. The main pre-laying and breeding season for the common guillemot at Hornøya is from 1 May to 15 July

DISCUSSION

The population collapse of common guillemots on Hornøya in 1986/1987 coincided with very low stock estimates of all important fish prey species such as capelin, herring and cod (Fig. 3). Since then, the Hornøya population has steadily increased, reaching and surpassing the 1980 level in 2003. Other common guillemot populations in Norway (including Bear Island) also collapsed in 1987, but the subsequent population trends have varied greatly between populations (Vader et al. 1990, Lorentsen & Christensen-Dalsgaard 2009). Such a sudden and large decline followed by an initially slow recovery (thus ruling out deferred breeding) for the Hornøya population can only have been caused by a mass mortality of adults (breeding and non-breeding birds).

After the collapse year in 1986/1987, the logistic population model shows that unlagged 0-group cod could explain much of the variance in population growth rate over time. Additionally, 0-group cod lagged by 6 yr and capelin lagged by 4 yr contributed positively. Also a model with unlagged 0-group cod and cod lagged by 4 yr contributed positively and was within the range of 2 AIC_C units. Since we do not have enough demographic data to build matrix models and since we do not know the wintering areas of sub-adult and adult guillemots, we cannot give any conclusive evidence on which demographic traits are most affected, but we do suggest some possible pathways which need to be considered in the future.

In general, any unlagged contribution of prey on growth rate suggests an effect via adult survival and/or rate of non-breeding events, whereas a lagged effect equal to the age of recruitment in common guillemots suggests an effect via reproduction (Sandvik et al. 2012). The unlagged effect of 0-group cod apparently had the highest influence on population growth rate, but a direct effect on adult survival (except for the crash year) seems unlikely. Adult survival rate during the period 1988 to 2011 was high and constant (0.96 ± 0.01 SE, Reiertsen et al. 2012). The unlagged effect of 0-group cod may thus instead reflect the yearly variation in deferred breeding during the study period. Although adults feed their chicks with capelin, herring and sandeels *Ammodytes* sp., they feed themselves almost exclusively on 0-group cod (Bugge et al. 2011). As such, the availability of 0-group cod is probably critical for whether birds decide to breed. To abstain from breeding under unfavourable conditions is an important strategy for long-lived species to cope with a variable environment in order to minimise the cost of repro-

duction and to maximise their residual fitness (e.g. Erikstad et al. 1998, 2009, Jenouvrier et al. 2003). Another possible but indirect effect of unlagged 0-group cod on population growth rates could be that birds breeding during years of low cod abundance spend more time searching for food, thus reducing their attendance at breeding ledges and thereby being missed during census counts (Harding et al. 2007).

The lagged effects of cod and capelin suggest an effect on the recruitment of immature birds to the colony. The lagged effect of 0-group cod is also consistent with a recent analysis from the present study population that shows that the body condition of chicks leaving the colony increases with the availability of 0-group cod in the Barents Sea (Barrett & Erikstad 2013). Although we have no data on reproductive success and recruitment to the colony in our study population, previous studies from other colonies have described recruitment in detail (Halley et al. 1995, Crespin et al. 2006, Votier et al. 2008). The general trend is that the return rate is slow and, although some birds may visit the colony after only 2 and 3 yr, they are subsequently not observed at breeding ledges but instead on intertidal rocks below the colony (Halley et al. 1995). Most birds, however, settle on the breeding ledges at the age of 4 yr (Halley et al. 1995), although most of them do not start breeding until they are 5 to 6 yr old (Crespin et al. 2006, Munilla et al. 2007). This suggests that most recruits settle at the ledges in the monitoring plots in this study after 4 yr and that a lagged effect of 4 to 6 yr of capelin and cod may well be an effect of the reproductive success 4 to 6 yr earlier. Fish data lagged by 5 yr did not, however, have any effect. This may be incidental or could be an effect of recruits temporarily leaving the colony before they start breeding, as shown for the Atlantic puffin *Fratercula arctica* at Hornøya (Sandvik et al. 2008).

A very surprising result of this study was the strong positive relationship between 0-group cod abundance and the variation in guillemot population growth rate. Much focus has previously been put on the capelin stock as being the key prey species for common guillemots in the Barents Sea and playing a significant role in the 1986/87 population crash (Vader et al. 1990, Barrett & Krasnov 1996). The capelin stock, however, subsequently collapsed twice, in 1994/1995 and 2004/2005 (Fig. 2; Gjøsæter et al. 2009), with no effect on the population growth rate of the common guillemot. Although we cannot exclude the possibility that lack of capelin may have contributed to the population collapse in 1987, it is un-

likely that it was the sole or major factor, especially since the guillemot population continued to strongly increase through both periods of low capelin abundance. As such, and as mooted by Bugge et al. (2011), it seems that the availability of 0-group cod may be a very important factor determining the population dynamics of the common guillemot in the southern Barents Sea.

Cod, herring and capelin are among the commercially and ecologically most important fish species in the Norwegian Sea and Barents Sea. The stock dynamics of these species are closely interlinked and coupled to broad-scale climatic changes (e.g. Hjermann et al. 2004a, Stige et al. 2010). In addition to oceanographic oscillations and complex predator–prey interactions, commercial overexploitation has caused dramatic changes in these fish stocks (Hjermann et al. 2004b, Sissener & Bjørndal 2005, Lehodey et al. 2006, Stige et al. 2010). As suggested in the present study, all 3 stocks are important prey species for common guillemots in the study area (Erikstad & Vader 1989, Barrett 2002, Bugge et al. 2011). However, the single most important prey species driving the population fluctuation is the amount of 0-group cod both through its influence on the rate of nonbreeding events and its effect on the number of recruits entering the population 4 to 6 yr later.

The modelled arrival of 0-group cod in areas around Hornøya shows that the different spawning grounds contributed to the supply of prey items for common guillemots at different temporal and quantitative scales. This is particularly relevant, as we know that the spawning distribution of northeast Arctic cod varies on a multi-annual scale (Sundby & Nakken 2008). In warm years, the spawning distribution tends to shift northwards, and in cold years it shifts southwards. Opdal et al. (2011) suggested that the distribution is also linked to fisheries, and argued that demographic changes in the cod stock due to size-selectivity may result in maturation at a younger age and a shorter spawning migration southwards along the Norwegian coast. If this is the case, both size-selective fishery on cod and a warming trend may favour 0-group availability near Hornøya. Natural variations, however, such as inter-annual variation in the NCC (Skagseth at al. 2011) and the inflow of the NASC to the Barents Sea (Ingvaldsen et al. 2004), affect the distribution of 0-group cod and constitute the dominating signal on a year-to-year basis. Our findings motivate further studies of inter-annual variation in spatio-temporal larval and juvenile cod distribution involving biophysical models. These should span the entire observational periods of sea-

birds, allowing quantification of inter-annual variation in overlap with common guillemot feeding areas.

To conclude, this study shows that cod may be more important than previously anticipated in driving population trends in common guillemots at Hornøya. This undermines the earlier focus on the capelin stock as the main cause of the population crash of the Hornøya population as well as other guillemot colonies along the Norwegian coast (Vader et al. 1990). This study also shows that monitoring data on the number of breeding birds could successfully be used to model the population growth rate and the effect of environmental variance. Although such monitoring data are relatively inexpensive to gather, it has been claimed they are a poor proxy of environmental variance (Cairns 1987, Parsons et al. 2008). Seabirds have long life spans, low reproductive rates and delayed maturity. As a result, a marked change in food abundance during the breeding season is not necessarily followed up by a change in numbers the following season (Furness & Camphuysen 1997, Parsons et al. 2008). Moreover, possible sub-colony dynamics (e.g. Zador et al. 2009) may affect the shape of time series when samples of plots are surveyed to infer overall population changes. However, as shown in this study, such models may help to identify important environmental factors that should be the focus of more detailed studies on environmental variance and the effect on specific life history traits. For guillemots, such focus should include factors determining the spawning success of cod along the coast of Norway and the path and survival of larvae as they drift northwards past the colonies and into the Barents Sea (Vikebø et al. 2007, Olsen et al. 2010).

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