



Prey density in non-breeding areas affects adult survival of black-legged kittiwakes *Rissa tridactyla*

Tone K. Reiertsen^{1,2,*}, Kjell E. Erikstad^{2,3}, Tycho Anker-Nilssen⁴, Robert T. Barrett¹, Thierry Boulinier⁵, Morten Frederiksen⁶, Jacob González-Solís⁷, David Gremillet⁵, David Johns⁸, Børge Moe⁴, Aurore Ponchon⁵, Mette Skern-Mauritzen⁹, Hanno Sandvik³, Nigel G. Yoccoz¹⁰

¹Tromsø University Museum, Department of Natural Sciences, 9037 Tromsø, Norway

²Norwegian Institute for Nature Research,

FRAM—High North Research Centre for Climate and the Environment, Hjalmar Johansens gt 14, 9296 Tromsø, Norway

³Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, 7491 Trondheim, Norway

⁴Norwegian Institute for Nature Research, PO Box 5685 Sluppen, 7485 Trondheim, Norway

⁵Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR 5175, 1919 Route de Mende, 34293 Montpellier cedex 5, France

⁶Department of Biosciences, Aarhus University, Fredriksborgvej 399, 4000 Roskilde, Denmark

⁷Institut de Recerca de la Biodiversitat (IRBio) and Departament de Biologia Animal (Vertebrats), Facultat de Biologia, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain

⁸Sir Alister Hardy Foundation for Ocean Science (SAHFOS), Citadel Hill, PL1 2PB Plymouth, UK

⁹Institute of Marine Research, PO Box 1870, 5817 Bergen, Norway

¹⁰Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, University of Tromsø, 9037 Tromsø, Norway

ABSTRACT: In migratory birds, environmental conditions in both breeding and non-breeding areas may affect adult survival rates and hence be significant drivers of demographic processes. In seabirds, poor knowledge of their true distribution outside the breeding season, however, has severely limited such studies. This study explored how annual adult survival rates of black-legged kittiwakes *Rissa tridactyla* on Hornøya in the southern Barents Sea were related to temporal variation in prey densities and climatic parameters in their breeding and non-breeding areas. We used information on the kittiwakes' spatiotemporal distribution in the non-breeding season gained from year-round light-based tracking devices (geolocators) and satellite transmitters, and kittiwake annual adult survival rates gained from a multistate capture-mark-recapture analysis of a 22 yr time series of colour-ringed kittiwakes. In the post-breeding period, kittiwakes concentrated in an area east of Svalbard, in the winter they stayed in the Grand Banks/Labrador Sea area, and in the pre-breeding period they returned to the Barents Sea. We identified 2 possible prey categories of importance for the survival of kittiwakes in these areas (sea butterflies Thecosomata in the Grand Banks/Labrador Sea area in winter and capelin *Mallotus villosus* in the Barents Sea in the pre-breeding season) that together explained 52 % of the variation in adult survival rates. Our results may have important implications for the conservation of kittiwakes, which are declining globally, because other populations use the same areas. Since they are under the influence of major anthropogenic activities including fisheries, international shipping and the offshore oil and gas industry, both areas should be targeted for future management plans.

KEY WORDS: Black-legged kittiwake · Pteropods · Capelin · Capture-mark-recapture analyses · Non-breeding distribution

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INTRODUCTION

The relationship between adult survival in long-lived migratory species and environmental conditions in both breeding and non-breeding areas is important in understanding demographic processes and population dynamics. For many migratory birds, however, including most marine birds, the very limited knowledge of their distribution outside of the breeding season has constrained studies of the relationship between demography and environmental conditions (Runge & Marra 2005, Ratikainen et al. 2008, Schaub et al. 2011, Smith & Gaston 2012). For pelagic seabirds, of which many species are severely threatened by global extinction, such studies are crucial (Croxall et al. 2012, Frederiksen et al. 2012, Lewison et al. 2012).

The recent advance of tracking technologies, such as miniaturized year-round light-based tracking devices (GLS loggers or hereafter geolocators), has revolutionized our knowledge of the non-breeding range of migrant species (e.g. Phillips et al. 2004, González-Solís et al. 2007, Guilford et al. 2009, Egevang et al. 2010, Seavy et al. 2012, Smith & Gaston 2012). Combining such data with statistical modeling of long-term capture-mark-resighting (CMR) data now allows us to explore in detail the relationships between environmental conditions in both breeding and non-breeding areas and adult survival rates. As yet, very few studies have investigated such relationships (but see Schaub et al. 2011), and we know of only 2 seabird studies that link adult survival to environmental conditions in both the breeding and non-breeding areas (Ramos et al. 2012, Smith & Gaston 2012) and none that address temporal changes in prey availability in non-breeding areas and adult survival rates.

Even small changes in adult survival can significantly impact the population dynamics in long-lived seabirds, since adult survival has a strong effect on lifetime reproduction (Lebreton & Clobert 1991, Stearns 1992). Worrying in this respect is the growing number of studies documenting a negative impact of climate on the adult survival rates of marine birds (e.g. Harris et al. 2005, Jenouvrier et al. 2005, Sandvik et al. 2005, LeBohec et al. 2008). Climatic effects are, however, most often indirectly mediated through temporal changes in prey availability, via changes in prey abundance (e.g. Sandvik et al. 2005), but they may also affect prey availability directly through shifts in the prey's spatial distribution (e.g. Peron et al. 2010).

Most marine ecosystems show pronounced temporal and spatial variation in oceanographic processes and trophic interactions that are often driven by cli-

matic processes, and these may lead to fluctuations in important fish stocks and disruptions in predator–prey interactions (Godø 2003, Durant et al. 2005, Grebmeier et al. 2006, Gjørseter et al. 2009, Stige et al. 2010, Certain et al. 2011). Especially for top predators such as seabirds, such fluctuations in prey species may have negative effects on both survival and reproduction (Lack 1968, Cairns 1992, Furness 2003, Oro et al. 2004, Cury et al. 2011) and in some cases may even drive populations towards extinction (Erikstad et al. 2013).

Since day length and food availability tend to be at a minimum in winter, conditions in the wintering range may strongly influence survival (Gaston 2003, Frederiksen et al. 2008a). The effects of environmental variation on adult survival may, therefore, be more profound outside the breeding season (Schaub et al. 2011, Smith & Gaston 2012). However, during the breeding season, the costs of reproduction are also known to impact survival (Golet et al. 1998, Oro & Furness 2002), and may also have direct effects on subsequent winter ecology (so called carry-over effects) (Golet et al. 1998, Ylönen et al. 1998, Harrison et al. 2010). To be able to determine what factors and time periods have the greatest impact on adult survival, it is important to consider factors in both the breeding and non-breeding seasons.

The Atlantic population of the black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake) has experienced widespread population declines in recent decades (Frederiksen 2010). The Norwegian population has decreased by 6–8% per year since the mid-1990s (Barrett et al. 2006) and is currently categorized as endangered on the Norwegian Red List (Kålås et al. 2010). The reasons for the declines over such a large scale are not fully understood, but there are indications that food shortages, possibly linked to an increase in fishery activity, are important (e.g. Frederiksen et al. 2004, 2008b, 2012).

Kittiwakes are good candidate species as sentinels of environmental change in the marine system. They are surface feeders with limited capacity to switch prey, and they seem to operate at their energetic ceiling (Welcker et al. 2010), which makes them particularly vulnerable to changes in the marine system (Furness & Tasker 2000). As such, both spatial and temporal environmental changes can affect their demographic traits. A recent study by Frederiksen et al. (2012) documented the non-breeding distribution of kittiwakes from a widespread selection of colonies across the North Atlantic (including the present study population), providing the unique opportunity to extract environmental covariates (such as sea sur-

face temperature [SST] and temporal data of prey density) from the identified non-breeding areas and combine them with important demographic traits, such as adult survival rates.

In order to collate representative data on prey availability for kittiwakes in their non-breeding areas, knowledge of their diet throughout the year is important. Such data stem, however, mainly from the breeding season, when the kittiwakes predominantly feed on invertebrates and small energy-rich schooling fish (up to 15–20 cm), the composition of which differs between different ecosystems. In the North Sea, they mainly feed on lesser sandeel *Ammodytes marinus* (Lewis et al. 2001), in the Newfoundland and Labrador Sea area on capelin *Mallotus villosus* (Carscadden et al. 2002), and in the Barents Sea they switch between capelin and herring *Clupea harengus* (Barrett 2007). In the pre-breeding season, polar cod *Boreogadus saida* have been found in stomach samples of kittiwakes (Erikstad 1990). Knowledge of their diet in the non-breeding season is poor (e.g. Frederiksen et al. 2012), but a study by González-Solís et al. (2011) of kittiwakes breeding on Hornøya suggests that they feed on a lower trophic level (zooplankton) outside of the breeding season. Some studies have shown that they may feed on a variety of large zooplankton species, e.g. *Calanus* spp., amphipods (Hyperiididae), euphausiids and pteropods (Thecosomata) (Lydersen et al. 1989, Mehlum & Gabrielsen 1993, Lewis et al. 2001, Karnovsky et al. 2008).

The aim of the present study was to explore the relationship between potential prey availability and climatic factors from known non-breeding areas and adult survival rates of kittiwakes breeding in a colony in the southern Barents Sea. Our main goal was to assess which environmental conditions and which time period had the greatest impact on this key demographic trait. By combining tracking data of kittiwakes from the colony and knowledge of kittiwake diet in their main non-breeding areas, we were able to extract data on potential important environmental factors from large-scale databases and enter them as covariates in a multistate CMR analysis and, hence, assess their impact on annual adult survival rate of kittiwakes from the study colony.

MATERIALS AND METHODS

We used a 22 yr (1990–2011) time series of resighted breeding kittiwakes that were individually marked with colour- or letter-coded rings at the colony of Hornøya (70° 23' N, 31° 09' E) in the south-

ern Barents Sea, where searches for the birds were made every year during the breeding season and where the population has declined by 70% since 1990 (Barrett et al. 2006).

Kittiwakes are long-lived, cliff-nesting seabirds that lay 1–3 eggs and have a circumpolar, subarctic and Arctic distribution (Coulson 2011). Their mean breeding life-span on Hornøya in 1989–2003 was estimated to be 8 yr (Sandvik et al. 2005); however, one individual was sighted at an age of >26 yr (Barrett 2010).

Non-breeding distribution

The non-breeding distribution of adult kittiwakes in the North Atlantic has recently been extensively mapped using light level geolocators (Bogdanova et al. 2011, González-Solís et al. 2011, Frederiksen et al. 2012). The data used in this study concern birds nesting on Hornøya, which were used in both the 2008–2009 study by González-Solís et al. (2011) and in 2008–2009 and 2009–2010 by Frederiksen et al. (2012). These data give important information on the non-breeding distribution of the study population and are used as background information for the analysis in the present study. The initial data processing is detailed in Frederiksen et al. (2012). Birds were tracked from one breeding season to the next ($n = 6$ in 2008–2009, $n = 14$ in 2009–2010) and the monthly data included in the present study are 1–10 September, 21–31 October, 1–30 November, 1–31 December, 1–31 January, 1–20 February and 4–30 April. Data from July and August were excluded because of the constant daylight in the Barents Sea. Data around the equinoxes were also excluded because latitude estimates are then unreliable (Phillips et al. 2004).

We also included data from 5 adult kittiwakes nesting in Hornøya deployed with platform terminal transmitters (PTTs or hereafter satellite transmitters; A. Ponchon et al. unpubl.) from 2010 ($n = 5$). Fixed kernel densities of kittiwake distribution were estimated with Hawth's Analysis Tools for ArcGis using the quartic approximation and a raster cell size of 20 km (Beyer 2004). The smoothing factor (also known as band width or the h statistic) was 50 and 200 km for the satellite transmitter and geolocator data, respectively. Kernel contours (%) are presented in maps with a North Pole stereographic projection.

In 2008, 2009 and 2010, all kittiwakes nesting in Hornøya equipped with geolocators and satellite transmitters went straight north after the breeding season to an area east of the Svalbard archipelago

(EOS hereafter) (between 75° N and 80° N, and 15° E and 35° E) and stayed there until October (Figs. 1A,B & 2C). In October they started to migrate west towards the Grand Banks/Labrador Sea area (GBLS hereafter) in the NW Atlantic (Fig. 1B), where most birds stayed from November to February (Fig. 1C). In February, the first birds migrated back to the Barents Sea (BS), and by March all birds had returned. In April, all birds were close to the breeding colony (Fig. 1D).

CMR modeling of adult kittiwake survival

The CMR analysis started with the Cormack–Jolly–Seber (CJS) model (Lebreton et al. 1992). All birds were captured only once, and attempts made to resight them in the following years. We, therefore, denote the recapture rate as resighting rate.

We assessed the goodness-of-fit (GOF) of the CJS model using U-CARE software (Choquet et al. 2009a). By doing so, we examined whether the model fitted the data and whether there was any heterogeneity in the resighting probabilities. This was done by evaluating the overdispersion coefficient, \hat{c} . Test 3.SR, a test component in the GOF test that tests the assumption that all marked individuals alive at time i have the same probability of surviving to $i + 1$ (transient effect), showed that there was a transient effect in the data ($N[0,1] = -0.105$, $df = 13$, $\chi^2 = 87.98$, $p \approx 0$, $\hat{c} = 6.77$), and test 2.CT, which tests the assumption of independence in the resighting rate (i.e. trap-happiness or trap-shyness) showed that there was trap-happiness in the data ($N[0,1] = -23.40$, $df = 19$, $\chi^2 = 677.09$, $p \approx 0$, $\hat{c} = 35.64$). We, therefore, used the method proposed by Gimenez et al. (2003), who used a multi-state model, with 3 states, adding an unobservable state for non-resighted birds in the previous year (the probability of having not been seen before), to correct for heterogeneity in resighting probabilities (details in Reiertsen et al. 2012).

To estimate and compare the annual survival rates of adult kittiwakes, we used the program E-SURGE (Choquet et al. 2009b). A time-dependent model was the starting point for the model selec-

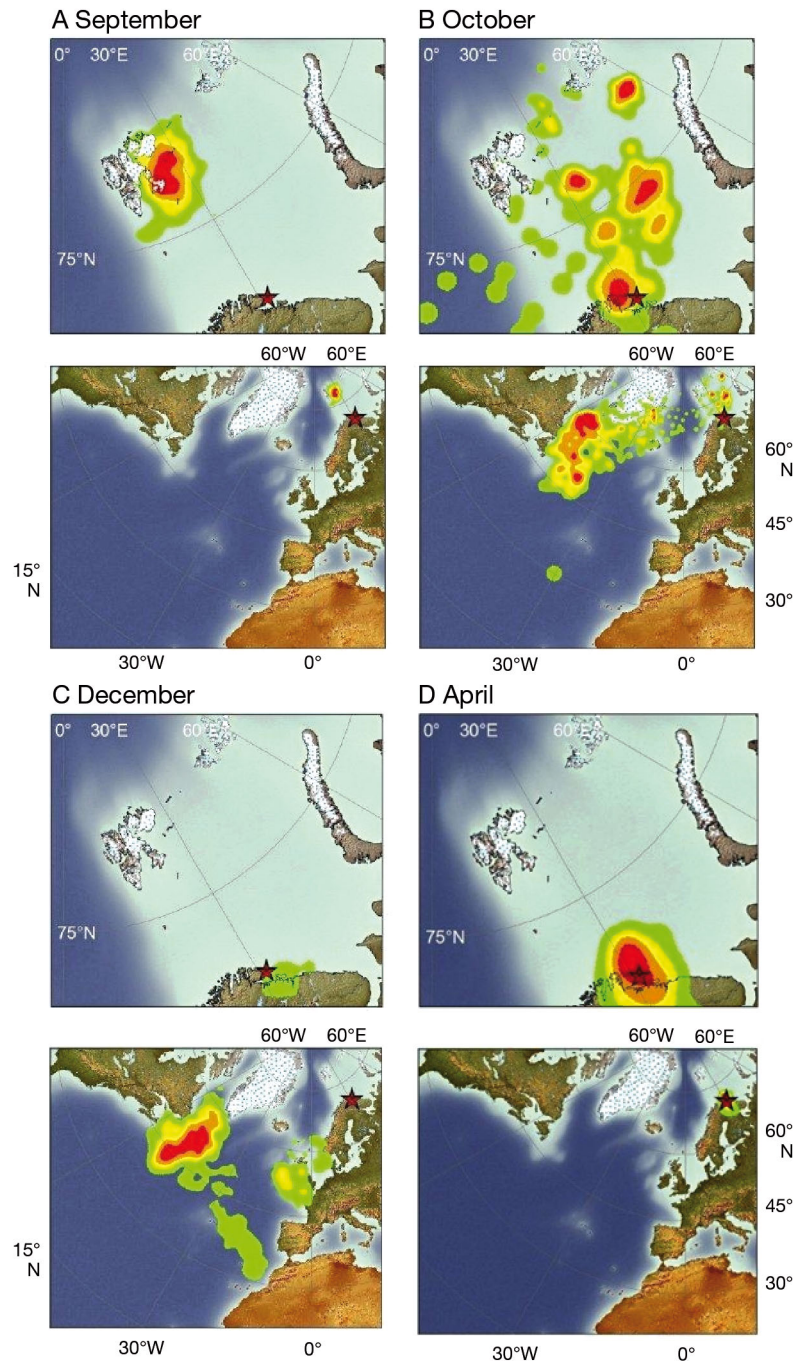


Fig. 1. Distribution of adult kittiwakes from Hornøya at different times of the year, as revealed by geolocators over 2 non-breeding seasons. The panels in the first row show an overview of the Barents Sea, and those in the second row show an overview of the North Atlantic including the Barents Sea. The 25, 50, 75 and 90% kernel contours (red, orange, yellow and green, respectively) are shown for the periods (A) 1–10 September, (B) 21–31 October, (C) 1–31 December and (D) 4–30 April. $n = 6$ (2008–2009), $n = 14$ (2009–2010)

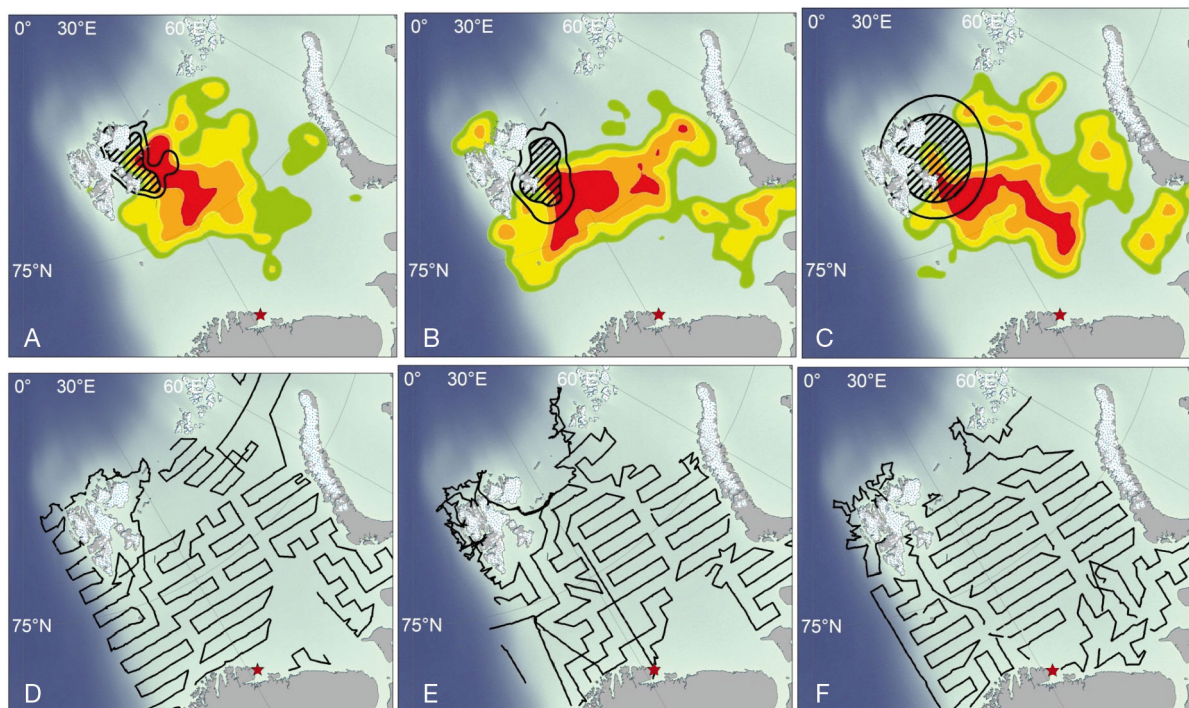


Fig. 2. Spatial distribution of capelin (coloured areas) and kittiwakes (black-contoured areas) in (A) 2008, (B) 2009 and (C) 2010. The data from 2008 ($n = 6$) and 2009 ($n = 14$) are based on light level geolocators, and the data from 2010 ($n = 5$) are based on satellite transmitters. The lower 3 panels show the survey areas of capelin between 20 and 30 August in (D) 2008, (E) 2009 and (F) 2010. Kernel contours for capelin are 25, 50, 75 and 90% (red, orange, yellow and green, respectively) and for kittiwakes 50 and 75% (black, hatched and unhatched, respectively). Red stars: Hornøya

tion, denoted as $\phi(t)p(f+t)$, where ϕ was the annual adult survival and p was the re-sighting probability, t was time dependence and f was the transition between states when we took into account trap-happiness in the model. By comparing the time-dependent model with the constant survival, denoted as $\phi(i)p(f+t)$, the constant re-sighting model $\phi(t)p(f)$, or both, $\phi(t)p(f)$, where i denotes a constant model, we assessed the appropriate model for annual survival and re-sighting probability.

Inclusion of covariates

We included covariates in the models to examine whether they could explain the variation observed in the kittiwake adult survival rates. We started by including only one covariate at a time to assess the impact of each covariate on the survival rate, and then we extended the models using 2 covariates.

In wild populations, adult survival is most likely to be influenced by multiple factors (e.g. Burnham & Anderson 2002), and models with full time variation usually provide the best description for rich data sets.

Finding a model with covariates that explain all the variation in survival is, therefore, unlikely, and residual unexplained variation after accounting for the effect of covariates can be expected (Grosbois et al. 2008). We assessed the ability of each covariate to describe significant variation in survival, using analysis of deviance tests (ANODEV: F -test statistic with n_{cov} and $n - n_{\text{cov}} - 1$ degrees of freedom, where n_{cov} represents the number of covariates included and n is the number of parameters of the time-dependent model) (Skalski et al. 1993, Grosbois et al. 2008, Lebreton et al. 2012), which is an established way of evaluating the significance of covariates. To assess the effect of the covariates on the kittiwake adult survival rate, we used an approximated R^2 statistic, which compared the constant and the time-dependent survival models, which is done using the formula $[\text{Deviance (covariate model)} - \text{Deviance (constant model)}] / [\text{Deviance (time-dependent model)} - \text{Deviance (constant model)}]$ (Gaillard et al. 1997, Barbraud et al. 2000, Jouvrier et al. 2006). This gives us the proportion of explained variation (Grosbois et al. 2008, Lebreton et al. 2012), which is denoted as R^2 in Tables 1 & S3 (in the Supplement at www.int-res.com/articles/suppl/m509p289_supp.pdf).

Table 1. Overview of the most important models of kittiwake adult survival and their neighbouring models, with different environmental covariates. ϕ is the survival rate and p is the re-sighting rate. The notation t indicates time-dependent, f indicates the transition between 2 states and is a model where the re-sighting rate has been corrected for trap-happiness and transience, and i indicates a constant model. The notations and explanations for the covariates are given in Table 2. Models are sorted by ascending QAIC_c (quasi-likelihood Akaike's information criterion corrected for small sample size and overdispersion) and Δ QAIC_c (the difference between the QAIC_c of a given model and the QAIC_c of the best model) is given for covariate models only. QAIC_c wt: QAIC_c weight. A total overview of the model selection is given in Table S3 in the Supplement (see www.int-res.com/articles/suppl/m509p289_supp.pdf)

Model	k	Deviance	QAIC _c	Δ QAIC _c	QAIC _c wt	F	p	R ²
$\phi(t)p(f+t)$	42	10349.93	10434.58					
$\phi(\text{CapelinTot}+\text{ThecoDec})p(f+t)$	25	10405.13	10455.36	0	0.97	9.17	0.002	0.52
$\phi(\text{CapelinTot}+\text{PcodEOS})p(f+t)$	25	10412.01	10462.24	6.87	0.03	7.21	0.005	0.46
$\phi(\text{CapelinTot}+\text{EuphDec})p(f+t)$	25	10417.54	10467.77	12.41	0.00	5.93	0.01	0.41
$\phi(\text{ThecoDec}+\text{PcodEOS})p(f+t)$	25	10429.32	10479.55	24.19	0.00	3.78	0.041	0.31
$\phi(\text{PcodEOS})p(f+t)$	24	10432.47	10480.68	25.32	0.00	7.02	0.016	0.28
$\phi(\text{CapelinTot})p(f+t)$	24	10433.87	10482.08	26.71	0.00	6.61	0.019	0.27
$\phi(\text{EuphDec})p(f+t)$	24	10451.51	10499.72	44.36	0.00	2.33	0.143	0.11
$\phi(\text{ThecoDec})p(f+t)$	24	10458.36	10506.58	51.21	0.00	1.05	0.318	0.05
$\phi(i)p(f+t)$	23	10464.66	10510.86	55.49	0.00	0.00	0	0

The model selection was performed using QAIC_c (quasi-likelihood Akaike's information criterion corrected for small sample size and overdispersion) (Burnham & Anderson 2002), where the model with the lowest QAIC_c value was considered the best. Δ QAIC_c is the difference between the QAIC_c of a given model and the QAIC_c of the best model. According to Burnham & Anderson's (2002) scale of Δ QAIC_c model interpretation, models with scores of Δ QAIC_c ≤ 2 are strongly plausible, 4–7 less plausible and ≥ 10 improbable. Survival and resighting probability estimates are given with 95% confidence intervals. We also used model averaging to assess the effect of each covariate on adult survival rate. Model averaging provides an average weighted estimate of the covariates used in a given number of models (Burnham & Anderson 2002).

A detailed description of how the covariates from the different areas and time periods were selected is given in the Supplement (see www.int-res.com/articles/suppl/m509p289_supp.pdf), and a list of all the covariates used in the CMR analysis is given in Table 2. For EOS in the autumn, we used acoustic data of capelin (CapelinEOS) and polar cod (PcodEOS) from the yearly joint Norwegian–Russian ecosystem surveys as covariates (for a detailed description see Skern-Mauritzen et al. 2011). An overview of the survey area covered in 2008, 2009 and 2010 and the resulting capelin distribution is given in Fig. 2. The acoustic data of capelin used in the figures were log-transformed and are from 20 August to 30 September. Kernel contours (%) were calculated and presented for capelin distribu-

tion using the same method as described for kittiwakes (smoothing factor was 50 km). We also used SST data (SSTautEOS), which were extracted from the Extended Reconstruction SST data set (available on a $2^\circ \times 2^\circ$ grid; Smith et al. 2008, NOAA 2012), for EOS (75° N, 80° N, 15° E and 35° E) during the post-breeding period (mean of August–September). For GBLS, we used data from the continuous plankton recorder survey (CPR data) from the winter period (November–February) from 1990 to 2010. The data were provided by the Sir Alister Hardy Foundation (SAHFOS) and consisted of monthly mean number of individuals of amphipods (Hyperiidia), euphausiids (Euphausiacea total), *Calanus finmarchicus* and pteropods (Thecosomata total). The area from which we extracted CPR data was within 40° N, 62° N, 38° W and 60° W. CPR methods are described in Lindley (1982). We also used SST from the same area in winter (mean of October–January) and the principal-component-based indices of the North Atlantic Oscillation (NAO) (NCARS 2012) as climatic covariates for this area and time period.

For the pre-breeding in BS, we used the data from ICES (2011) for the total biomass of capelin, (1-group) herring, and the eastern and the western distribution of polar cod in BS, which is defined as stock numbers of a given age on 1 January multiplied by weight at age and reflect the estimated densities of the fish species on 1 January. Additionally, for the area around Hornøya in the pre-breeding (monthly means of February–April) and breeding periods (means of May–July) (between 70° N, 72° N, 28° E and 34° E) SST was used as climatic covariate. Average breeding

Table 2. Overview of all covariates used in the capture-mark-resighting analysis with time periods and areas of interest. The notation used in the model selection is explained, and data sources are indicated. IMR: Norwegian Institute of Marine Research; NOAA: National Oceanic and Atmospheric Administration (USA); SAHFOS: Sir Alistair Hardy Foundation (UK); ICES: International Council for the Exploration of the Sea (Denmark)

Time period	Area	Covariate notation	Covariate explanation	Source
Autumn (Sep)	East of Svalbard (EOS)	CapelinEOS	Acoustic assessment of the capelin stock	IMR
		PcodEOS	Acoustic assessment of the polar cod stock	IMR
		SSTautEOS	Sea surface temperature	NOAA
Winter (Nov–Dec)	Grand Banks/ Labrador Sea (GBLS)	ThecoDec	Continuously plankton recorded (CPR) data of the suborder Thecosomata	SAHFOS
		ThecoNov	CPR data of Thecosomata	SAHFOS
		HypDec	CPR data of Hyperiiidea	SAHFOS
		HypNov	CPR data of Hyperiiidea	SAHFOS
		EuphDec	CPR data of Euphausiacea	SAHFOS
		EuphNov	CPR data of Euphausiacea	SAHFOS
		CalDec	CPR data of <i>Calanus finmarchicus</i>	SAHFOS
		CalNov	CPR data of <i>Calanus finmarchicus</i>	SAHFOS
		SSTwinterGBLS	Sea surface temperature	NOAA
		Winter (Dec–Mar)	North Atlantic	NAOPC
Spring (Mar–Apr)	Barents Sea (BS)	CapelinTot	Total biomass of capelin	ICES
		Herring1Y	1-group herring	ICES
		PcodEast	Total biomass of polar cod in the eastern part of the Barents Sea	ICES
		PcodWest	Total biomass of polar cod in the western parts of the Barents Sea	ICES
Summer (breeding season)	Around Hornøya	SSTspringHorn	Sea surface temperature	NOAA
		SSTsummerHorn	Sea surface temperature	NOAA
		BSL1	Breeding success, lagged 1 yr	

success in the previous year (BSL1) was also used as a population-level covariate for the breeding season.

Some of the covariates had missing values for some years. These included *Calanus finmarchicus*, Hyperiiidea, Euphausiacea and Thecosomata in December 1991. To obtain a complete time series, we used the method developed by Colebrook (1975), which multiplies the long-term monthly mean corresponding to a missing month in a given year by the ratio of the sum of the non-missing values in that year to the sum of the corresponding long-term monthly means. Fish and plankton covariates were log-transformed prior to analysis to achieve a linear relationship on a log scale.

Covariates with linear temporal trends were detrended, using the residuals from the regression between the parameter and the year (Table S2 in the Supplement). All covariates were checked for autocorrelation after detrending (see Table S1 and Fig. S1 in the Supplement for an overview of colinearities between and temporal variation in the covariates), and we did not enter covariates with high correlation in the same model (Table S1 in the Supplement). Significant autocorrelation ($p < 0.05$) was when $R \geq 0.44$.

RESULTS

An overview of the best models in the model selection and their neighbouring models is given in Table 1, and a total overview of the model selection is given in Table S3 in the Supplement.

Overall, the model with the lowest QAIC_c (Table 1) was the model with time dependency in both the survival rate and the resighting rate, where we had corrected for transience and trap-happiness (Fig. 3). Survival varied extensively with time (mean $\phi = 0.85$, range = 0.66–0.98). There were 2 severe drops in the survival rate; one in 1994 ($\phi = 0.66$, SE = 0.05) and one in 2003 ($\phi = 0.74$, SE = 0.04; Fig. 3). Models corrected for trap-happiness were clearly better (lower Δ QAIC_c) than models without such a correction (Table S3 in the Supplement).

None of the models with covariates improved the model with full time-dependency of both the survival probability and the re-sighting rate, because of the presence of residual unexplained variation as explained in the methods. We, therefore, only compared the difference between the QAIC_c values (Δ QAIC_c) for models that included covariates.

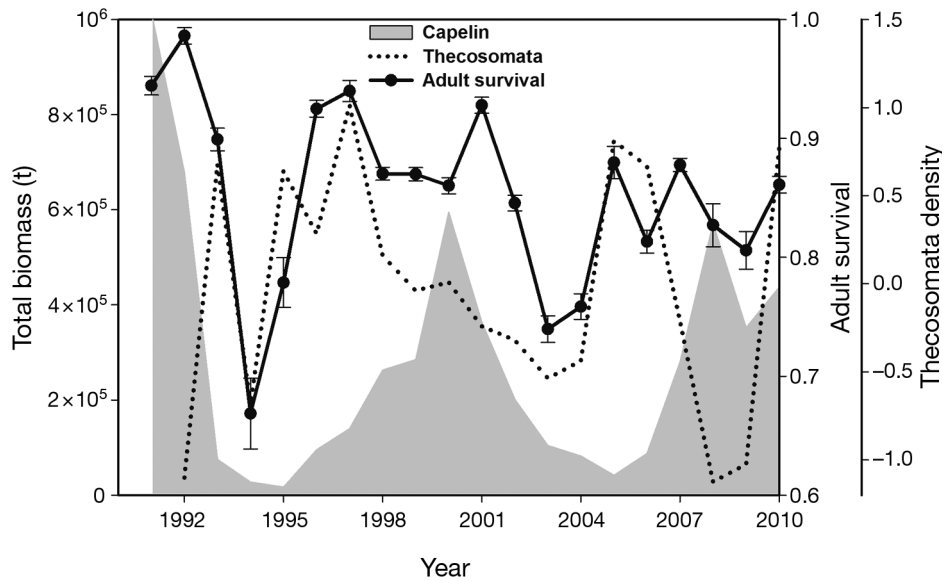


Fig. 3. Temporal variation of kittiwake adult survival rates (solid line; error bars are $\pm 95\%$ confidence limits) and the best covariates, total biomass of capelin in the Barents Sea (grey area) and detrended Thecosomata density (monthly mean no. of ind. for specified area; see 'Materials and methods') in December in the Grand Banks/Labrador Sea area (dotted line) between 1990 and 2010

Among the covariate models, the model that included temporal variation of the total biomass of capelin in BS (CapelinTot) and the temporal variation of Thecosomata density in December in the GBLs (ThecoDec) was clearly the best (QAIC_c weight = 0.97; Table 1). This model was 6.87 Δ QAIC_c units better than the second best covariate model that included the total biomass of capelin in BS and the acoustic data of polar cod in EOS (PcodEOS) (QAIC_c weight = 0.03; Table 1). Model averaging of the 3 covariates included in these models gives estimates of 0.40, 0.50 and -0.008 for CapelinTot, ThecoDec and PcodEOS, respectively. The effect of both Thecosomata in GBLs in December and the total biomass of capelin in BS on adult kittiwake survival are thus very strong compared with polar cod in EOS in the post-breeding period. Estimates of the covariates from the top model explaining adult survival were both positive (0.41 [range = 0.30–0.52] and 0.52 [range = 0.33–0.70] for CapelinTot and ThecoDec with 95% confidence intervals). The temporal trends in both the time-dependent model and the best covariate model are shown in Fig. 4.

When considering models with single covariates, they all had a very high QAIC_c, and QAIC_c weights were very close to zero. Thus models with 2 covariates were clearly better than single-covariate models (Table 1). The best single-covariate model was the one with acoustic data of polar cod in EOS, which explained 28% of the variation in adult survival but was 26.32 Δ QAIC_c units higher than the overall best covariate model (Table 1). Capelin in BS and the density of Thecosomata in GBLs were

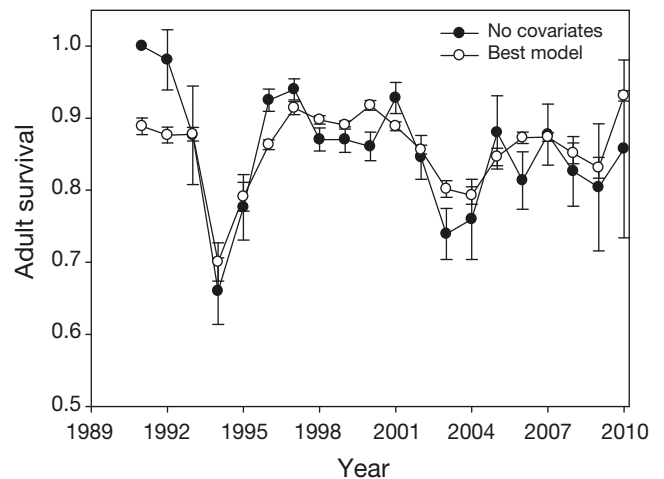


Fig. 4. Temporal variation in kittiwake adult survival from the time-dependent model with no covariates (●) and the model with total biomass of capelin in the Barents Sea and Thecosomata in the Grand Banks/Labrador Sea in December (○) between 1991 and 2010

26.71 and 51.21 Δ QAIC_c units higher, respectively, than the overall best covariate model (Table 1). None of the models that included climatic covariates was ever better than models including prey densities. The best climatic model included ThecoDec and SST in EOS in the post-breeding season (SSTautEOS) (Δ QAIC_c = 22.48, R^2 = 0.32; Table S3 in the Supplement). The models including covariates from the breeding season had a much higher QAIC_c than the best covariate models (Δ QAIC_c = 55.19 and 56.71, R^2 = 0.02 and 0.01, for SSTsummerHorn and BSL1, respectively).

DISCUSSION

The best covariate model explaining the temporal variation of kittiwake adult survival included the total biomass of capelin in the BS and the monthly mean density of Thecosomata in GBLS in December. This suggests that prey densities in the BS and the GBLS area, which both seem to be important non-breeding areas for kittiwakes from Hornøya (and many other kittiwake populations, e.g. Bogdanova et al. 2011, Frederiksen et al. 2012), affect adult survival of kittiwakes.

Capelin in the Barents Sea

Capelin is one of the most abundant fish species in the BS (Orlova et al. 2010), and the stocks fluctuate greatly (Ushakov & Ozhigin 1987). During the period of the present study, the capelin stock collapsed twice (around 1994 and 2003) (Gjøsæter et al. 2009), and both collapses coincided with a corresponding drop in the adult survival rate of kittiwakes (Fig. 2). The collapse in 2003 was accompanied by an exceptional die-off of adult birds in the region in early spring (Barrett et al. 2004). Capelin plays a key role in the pelagic ecosystem of the Barents Sea (Orlova et al. 2010) and follows a characteristic seasonal migration pattern (Fauchald et al. 2006, Gjøsæter et al. 2011). It is an important grazer of zooplankton (Hassel et al. 1991, Gjøsæter et al. 2002, Stige et al. 2009) and an important food source for Atlantic cod *Gadus morhua*, seabirds and marine mammals (Folkow et al. 2000, Nilssen et al. 2000, Bogstad & Gjøsæter 2001, Fauchald et al. 2011).

In general, kittiwakes are known to feed on schooling fish (Lewis et al. 2001, Carscadden et al. 2002), and in the southwest BS (Hornøya), capelin is the main prey during the breeding season (Furness & Barrett 1985, Barrett 2007). It has also been shown that kittiwake breeding success on Hornøya decreases when the abundance of capelin is low (Barrett 2007, A. Ponchon et al. unpubl.). Although we do not know in detail the diet of kittiwakes during the non-breeding season, the results of this study and those of Barrett et al. (2004) show that the temporal variation in the BS capelin stock may have a strong impact on the yearly variation in kittiwake survival rates. Kittiwakes from Hornøya stay in the BS from March to October, i.e. the pre-breeding season, the breeding season and post-breeding season, when they move to EOS. It is likely that the capelin densities in the BS when the kittiwakes return in March–

April are critical for their survival. This return coincides with the capelin spawning migration towards the coast of Norway and Russia in March–April (Gjøsæter et al. 2011), a time when the fish are full of energy-rich gonads (Montevecchi & Piatt 1984). In the pre-breeding season, the northern BS is still covered with ice and primary production is low, such that the seabirds are constrained to feed on mainly pelagic fish such as 1-group herring and capelin (Fauchald et al. 2011). The capelin spawning migration is highly concentrated in space and time (Fauchald et al. 2011), and it is very likely that kittiwakes are especially sensitive to the abundance and distribution of this energy-packed fish at this time of the year, since they need to build energy reserves prior to reproduction.

After the breeding season, the kittiwakes move quickly to EOS (Figs. 1A & 4C). Capelin distributions in the post-breeding period show a limited overlap with the kittiwake distribution (Fig. 4). Acoustic data of capelin and polar cod from this area in this time period did not, however, correlate with kittiwake survival, which suggests that kittiwakes find other prey, e.g. zooplankton in EOS in the post-breeding period, as also suggested by González-Solís et al. (2011). Unfortunately, there are no temporal plankton data from EOS that could have been used to test directly whether conditions from this area also were important for kittiwake survival. Another implication is that capelin seems to have the highest impact on kittiwake survival during the pre-breeding and/or breeding season.

Thecosomata in the GBLS

The other prey covariate which entered the top-rank model was the density of Thecosomata in GBLS in December, a time when most of the kittiwakes from Hornøya were present in that area. There is some earlier evidence that kittiwakes feed at lower trophic levels in winter and that they probably feed more on a variety of large zooplankton species, such as amphipods, pteropods and euphausiids (Mehlum & Gabrielsen 1993, Karnovsky et al. 2008, González-Solís et al. 2011, Frederiksen et al. 2012), than in the breeding season when their main prey is fish (e.g. Lewis et al. 2001, Carscadden et al. 2002, Barrett 2007, A. Ponchon et al. unpubl.). Furthermore, Karnovsky et al.'s (2008) study from the North Water Polynya showed that kittiwakes there fed extensively on the pteropod *Limacina helicina* and that they had fatty acid signatures resembling the signatures of the

little auks *Alle alle* that feed exclusively on zooplankton (Karnovsky et al. 2008). This supports our hypothesis that Thecosomata is a likely food for kittiwakes.

Thecosomata is a taxon of pelagic swimming sea snails also called sea butterflies or pteropods. They are rich in lipids, live their whole life in a planktonic form, and can be found in large concentrations in the upper layer of the water. They play an important role in the marine food web, in particular at high latitudes (Comeau et al. 2012), and are important food sources for herring and capelin and for higher predators, such as whales and seabirds (Hunt et al. 2008, Orlova et al. 2011, Comeau et al. 2012). The density of Thecosomata in December declined steeply between 1990 and 2011 (Fig. 2), possibly as a result of ocean acidification (Lischka et al. 2011). Thecosomata, such as *Limacina helicina*, have an aragonitic shell, which makes them particularly sensitive to acidification, a process that is expected to be most serious in Arctic oceans (Steinacher et al. 2009, Comeau et al. 2012) and which will be more severe when ocean temperatures increase (Lischka et al. 2011). Kittiwakes from most of the breeding colonies in the north Atlantic spend their winter in this area (Frederiksen et al. 2012); hence, the steep decline in Thecosomata abundances could be an important driver of the overall decline in the North Atlantic kittiwake populations.

SST

Since both the temporal and spatial variance in SST may influence the distribution of prey independent of total density, we used un-lagged SST from the different areas and time periods together with prey category data in the models but found no apparent direct effects of SST. Although kittiwakes are very sensitive to changes in the marine system, they are also highly mobile, especially in the non-breeding period, when they are not constrained by the need to return regularly to the colony and can easily move around searching for available food (Fauchald 1999, Pinaud & Weimerskirch 2005, Certain et al. 2011). This could indicate that kittiwakes are more sensitive to overall prey density as such and not to small-scale changes in the spatial distribution of prey linked to oceanographic changes. Increasing SST, however, could also result in a vertical shift of preys in the water masses (i.e. prey move to deeper and colder water), thus making them inaccessible to kittiwakes that cannot dive, even if prey densities are high.

None of the models that included any climatic covariates (SST and NAO) could compete with the

best models in the model selection. This may indicate that kittiwakes are not directly affected by the climate factors in these areas and that their abilities to move around may buffer this effect. Additionally, this may give some support to the explanation that kittiwakes are more sensitive to overall prey densities in these areas than to the spatial changes of the prey.

None of the breeding-season covariates (i.e. breeding success or SST in the summer near the colony) could explain any temporal variability in adult survival, which is in contrast to other studies (Oro & Furness 2002, Frederiksen et al. 2004). However, as stressed by Frederiksen et al. (2004), identifying factors outside the breeding season was very difficult at that time because of the limited knowledge of kittiwakes' non-breeding distribution, and the importance of the conditions in the non-breeding areas could not be ruled out as an explanation of the adult survival variability.

CONCLUSIONS

This study demonstrates the importance of linking the knowledge of the winter distribution of seabirds and density of the prey they feed on in their wintering areas to temporal variation of adult survival rates. Although it has been suggested that adult survival may be primarily influenced by prey densities and oceanographic conditions in the wintering area (Gaston 2003, Daunt et al. 2006, Wanless et al. 2007, Frederiksen et al. 2008a, Harris et al. 2010), lack of data on migration patterns and the whereabouts of important wintering areas has precluded the search for causal explanations. This study is among the first to examine the influence of prey densities in non-breeding areas on the survival of seabirds. The study is highly exploratory and based on scarce loggerhead data, but it suggests that Thecosomata in the GBLs and capelin in the BS are important prey species for kittiwakes in the non-breeding season. This needs to be tested further. Both the BS and the GBLs are impacted by intense anthropogenic activities, such as fisheries, international shipping and the offshore oil and gas industry, with several reports of operational and accidental discharges of hydrocarbons (Hedd et al. 2011). All these activities pose risks to seabirds, and the knowledge of how important these areas are to a species that is globally declining has strong implications for conservation and management of both these areas.

The migration part of our study is based on only 3 yr of data and a rather low number of tracked

individuals. There is therefore a strong need for a larger sample of logger data over more years to examine the stability and evidence of winter migration patterns. However, although the sample size from Hornøya is small, there is evidence that birds from several populations return to the same areas in different years (Frederiksen et al. 2012, B. Moe et al. unpubl., A. Ponchon et al. unpubl.). Also, the time series of CMR data is 22 yr long, and since we found such strong correlations between the survival rate and the covariates from the main areas revealed by migration data, it is plausible that there is some stability in the migration pattern. A challenge for future studies of demography and causal mechanisms will be to map both the stability of wintering areas over time and not only the density of prey, but also the spatial distribution of the prey in different areas. Such information is essential for the conservation and management of any seabird, including the kittiwake, a species that is declining globally.

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