Survival of breeders in a Danish Black-legged Kittiwake *Rissa tridactyla* colony - a capture-mark-recapture study

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Abstract

The Black-legged Kittiwake *Rissa tridactyla* is one of the most numerous seabirds in the North Atlantic, but during the last couple of decades there have been reports of widespread large declines in breeding populations. In some areas, these declines are believed to be linked to lack of prey (Lesser Sandeel *Ammodytes marinus*) due to industrial fishing and increasing sea surface temperatures. In this paper, we explore the effect of sea surface temperature and age on survival of adult breeders in a small and relatively stable Danish colony of Black-legged Kittiwakes from 1992 to 2010. We found that survival did not vary significantly over the study period (mean 0.82), but was lower than reported from other studies. This could be due to a trade-off between reproduction and survival, leading to a lower survival, or it could be due to a high emigration leading to a too low estimate. Sea surface temperature had no effect on survival, contrary to other studies. Danish Black-legged Kittiwakes may rely on a food source which is not affected by the sea temperatures, either other species of fish or fishery discards. Finally, we found that survival decreased with age, in line with other studies.

Introduction

The Black-legged Kittiwake *Rissa tridactyla* (hereafter 'Kittiwake') is one of the world's most numerous gulls, with about 2.2 million breeding pairs in the Atlantic alone (Frederiksen *et al.* 2012). The Atlantic population of Kittiwakes has been increasing from the beginning of the twentieth century until recently (Coulson 2011), but since around 1990 there have been reports of declines in survival, reproduction and population size for several species of seabirds in the North Atlantic, including the Kittiwake (Frederiksen 2010). Studies from the Isle of May in the North Sea have suggested that the decline in survival and reproduction is caused by a lack of the most important prey during the breeding season, the Lesser Sandeel *Ammodytes marinus* (Frederiksen *et al.* 2004b). This reduction in sandeel availability is believed to be linked to industrial fisheries and increasing sea surface temperatures (Frederiksen *et al.* 2004b).

The Danish breeding population of Kittiwakes is small, and the ecological pressures affecting its dynamics are poorly understood. Since the 1970s, the species has bred in only three colonies situated on the Skagerrak/North Sea coast of northern Jutland, where the population has been relatively stable over the last decades (Meltofte & Fjeldså 2002). The main colony is on Bulbjerg (57°9'N 9°1'E), a 40 m high limestone cliff where 400–500 pairs nest (Figure 1), while the two other colonies are on breakwaters and buildings in the harbours of Hanstholm and Hirtshals. Irregular counts at these two colonies indicate that they hold 80–100 pairs in total (T. Bregnballe unpublished data).

It is not known why the Danish Kittiwake population has remained stable while populations elsewhere in the North Sea have declined dramatically. In this study, we estimate for the first time survival of adult breeders at Bulbjerg and try to identify factors affecting survival. We analyse resighting data from birds observed breeding at Bulbjerg during the period 1992–2010 and test whether climatic variation may have been affecting their survival. Specifically, we test whether the negative relationship between survival and late winter sea temperature in the previous year found by Frederiksen *et al*. (2004b) at the Isle of May also applies at Bulbjerg, on the opposite side of the North Sea. In the present data set, the age of more than half of the birds was known, which made it possible to check for a decline in survival for old birds (senescence). It is highly debated whether senescence plays a role in the life history of wild animals (Bronikowski & Promislow 2005; Monaco & Silveira 2009), but studies from other Kittiwake colonies have indicated that survival decreased with age (Frederiksen *et al*. 2004a; Steiner *et al*. 2010).

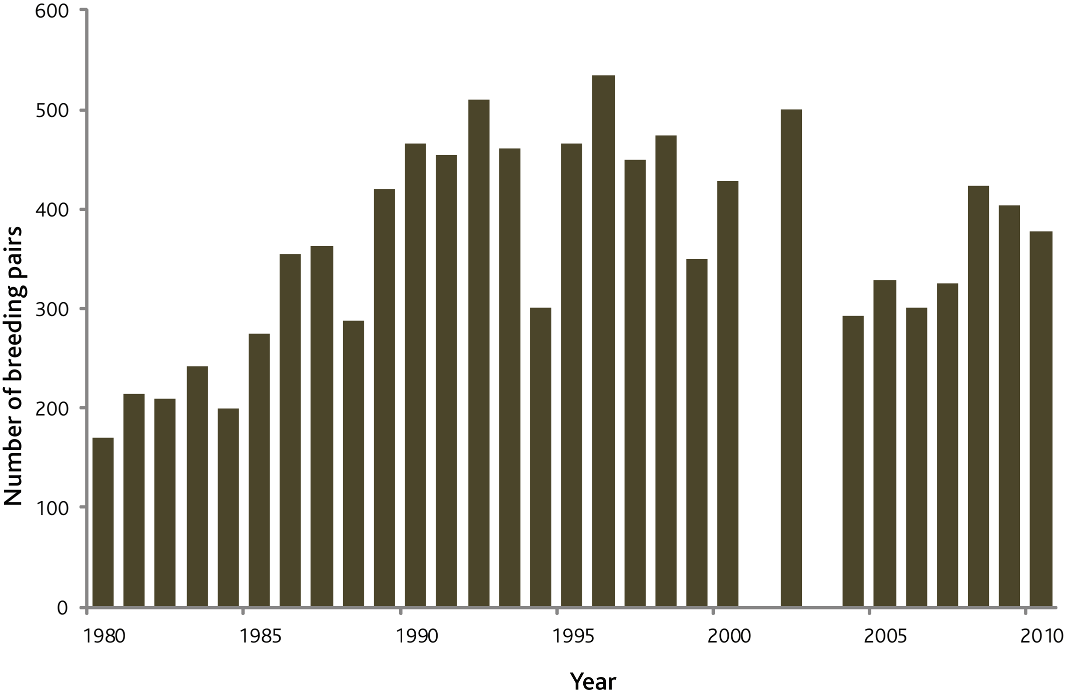

Figure 1. Number of breeding pairs of Black-legged Kittiwakes *Rissa tridactyla* at Bulbjerg, 1980 to 2010. No counts were available for 2001 or 2003. Source: Thomas Bregnballe unpublished data.

Figure 2. A section of the Black-legged Kittiwake *Rissa tridactyla* colony at Bulbjerg, Denmark, June 2009. © Per Frederiksen.

Methods

Resightings of metal-ringed Kittiwakes were made during 5–7 annual visits to the colony throughout the breeding season (April to August) 1992–2010, mainly by one observer (JLP). Visits preferentially took place when low water level allowed access to the foreshore, from which birds in all parts of the colony could be observed, typically at distances < 50 m (Figure 2). Ringed birds were located using binoculars, and ring numbers read using a Kowa telescope with a 20–60x zoom lens. The data consisted of resightings of birds observed at least once as breeding adults at Bulbjerg. The data set included 152 birds ringed in Denmark between 1976 and 1995, and 11 birds ringed in other countries between 1983 and 2009; 113 of the birds were ringed as chicks, and their age was thus known. Sea surface temperatures (SST) for the area around Bulbjerg (56–59°N 6–10°E) were downloaded from the Meteorological Office Hadley Centre homepage (Rayner *et al*. 2006), and the yearly mean temperature for the coldest months (February and March) was calculated.

We used standard capture-mark-recapture (CMR) techniques to estimate probabilities of survival and resighting (Lebreton *et al*. 1992). Initially, a goodness-of-fit test was performed in U-CARE 2.3.2 (Choquet *et al*. 2009) to check that the data followed the assumptions of a CMR model, namely that all individuals should have the same probability of surviving and being resighted. CMR modelling was performed in MARK 6.0 (White & Burnham 1999). We used the Cormack-Jolly-Seber (CJS) model with time-dependent survival and resighting probabilities as a starting point for the analysis. 'Trap-dependence' (different resighting probability for birds seen, respectively not seen, on the previous occasion) was included in the model following results from the goodness-of-fit test, using a multi-state approach (Gimenez *et al*. 2003; Frederiksen *et al*. 2004b). In order to ensure estimability of the model, trap-dependence was modelled as additive, i.e. with a constant difference between birds seen and not seen the previous year (Pradel 1993).

Subsequently, we tested whether winter SST had an immediate or lagged effect on survival by including SST in the same or the previous winter as a covariate of survival. For the subset of birds of known age, we also tested whether survival varied as a linear or quadratic function (on the logit scale) of age. Models were ranked using AIC_C (Akaike's Information Criterion adjusted for sample size; Burnham & Anderson 2002).

Results

The global test in U-CARE showed no overall lack of fit ($\chi^2 = 60.22$, df = 54, P = 0.26). However, the specific test for trap-dependence was highly significant (z = -3.3, P < 0.001). Including trap-dependence into the model, there was no evidence of lack of fit ($\chi^2 = 24.65$, df = 38, P = 0.95).

We found no evidence for an effect of SST on survival (Table 1). The model fitting the data best was the one with constant survival and time-dependent resighting probabilities. Individuals seen in the previous year had a higher probability of being

Table 1. Model selection for the full data set. Additive trap dependence was included in the model. Covariates used for survival were sea surface temperature in the same year (SST) and in the previous year (SST-1). The model with the lowest AIC_C included constant survival, time-dependent resighting probability and additive trap dependence. None of the sea surface temperature parameters decreased AIC_C.

Survival	Resighting	Deviance	No. Parameters	ΔAIC_C
Constant	Time, additive trap-dependence	505.89	20	0
SST-1	Time, additive trap-dependence	504.99	21	1.33
SST	Time, additive trap-dependence	505.71	21	2.06
Constant	Time	521.23	19	13.12
Time	Time, additive trap-dependence	496.96	36	28.21
Time	Time	511.96	35	40.79

Table 2. Model selection for the subset of known-age birds. Age was used as either a linear or quadratic term. The model with the lowest AIC_C included a linear age effect on survival, with resighting probability varying over time and additive trap-dependence.

Survival	Resighting	Deviance	No. Parameters	ΔAIC_C
Age, linear	Time, additive trap-dependence	726.55	21	0
Constant	Time, additive trap-dependence	728.94	20	0.07
Age, quadratic	Time, additive trap-dependence	725.67	22	1.47
Age, linear	Time	738.79	20	9.92

seen than those not seen in the previous year (Figure 3). Resighting probabilities varied between years, but were generally surprisingly high considering that birds were metal-ringed only. The mean survival estimate from the model was 0.82 ± SE 0.02, giving an estimated mean life expectancy of 5.03 years. There was no support for models with constant resighting probability.

Model selection for the known-age individuals showed that the model with the lowest AIC_c was the one with survival as a linear function of age, although the AIC_c for this model was only slightly lower than for the model with constant survival (Table 2). Survival declined with age, from 0.89 in the second year of life to 0.71 in the twentieth year.

Discussion

We found that adult survival of Kittiwakes breeding at Bulbjerg seemed to remain constant over the 18-year study period (1992–2010). This may be related to the relatively low sample size, but at least indicates that no major fluctuations or trends have occurred, in contrast to the Isle of May at the other side of the North Sea, where survival declined markedly from 1986 to 2002 (Frederiksen *et al.* 2004b). Another contrast to the Isle of May was the lack of a relationship between survival and sea temperature around Bulbjerg. This could be due to a difference in prey selection between the two sites. The diet of Kittiwakes in Denmark has not been studied, but it is possible that Kittiwakes at Bulbjerg differ in their main food

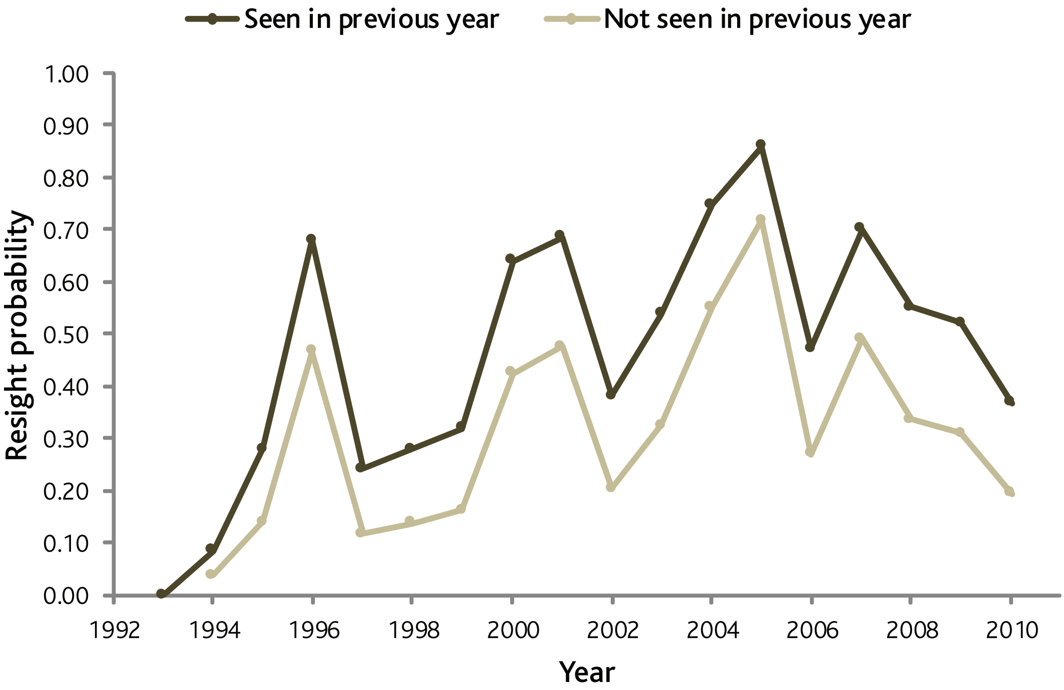

Figure 3. Resighting probabilities of breeding Black-legged Kittiwakes *Rissa tridactyla* at Bulbjerg for birds seen, respectively not seen, in the previous year.

source from those at the Isle of May. The waters off the west coast of Jutland are very shallow, and it is likely that the Lesser Sandeel in this area is replaced by its close relatives, the Small Sandeel *Ammodytes tobianus* and the Great Sandeel *Hyperoplus lanceolatus*, which typically occur in shallower waters close to the coast (Muus *et al.* 1999). Kittiwakes at Helgoland in the south-eastern North Sea, where the population is also stable, were found to feed mainly on Whiting *Merlangius merlangus* (Markones *et al.* 2009). These alternative prey species may be less affected by increasing sea temperatures, due to e.g. differences in spawning habitat and behaviour, or in diet. Furthermore, Kittiwakes may also feed on offal and discharges from fishing boats (Garthe & Hüppop 1994). Hanstholm, one of Denmark's most important fishery harbours, is about 26 km west of Bulbjerg, and thus well within typical Kittiwake foraging range (Daunt *et al.* 2002; Kotzerka *et al.* 2010). The diet of Danish Kittiwakes should be studied, since such studies could clarify the difference between Bulbjerg and other areas of the North Sea where Kittiwakes show population declines, and thereby help understand the problems causing the decline of the Kittiwake in further detail.

The mean survival found at Bulbjerg (0.82) was relatively low compared to many other studies in both the Atlantic and the Pacific (range of means 0.80–0.93; Frederiksen *et al.* 2005). However, survival was similarly low at the small colony in North Shields studied by Coulson (2011) over several decades (1954–1990), which nevertheless remained stable in size throughout this period. It is possible that this represents alternative trade-offs between survival and reproduction in small and large colonies, since a negative correlation between colony size and breeding success has been suggested for seabirds in general (Hunt *et al.* 1986), or alternatively differences in food supply which may affect this trade-off (Coulson 2002). Unfortunately, no data on breeding success have been collected at Bulbjerg, so we could not test this hypothesis. Another explanation could be high levels of emigration from and immigration to the colony at Bulbjerg, which could maintain a stable population while inducing low survival estimates, since emigrants appear as dead in single-site CMR studies. Survival may also have been biased low if some individuals moved to the upper part of the colony, where rings are very difficult to read from the beach.

Finally we found an apparent effect of senescence on the life history of Kittiwakes in the Danish colony, in the form of a decline in survival with age. This result is supported by other studies (Frederiksen *et al.* 2004a; Steiner *et al.* 2010). However, the support for this effect was not very strong, as the model only had a slightly lower AIC_c than the model with constant survival. The tendency we found was thus not as strong as in other studies; e.g. Frederiksen *et al.* (2004a) found a quadratic relationship between survival and age at the Isle of May. The biological meaning of senescence has been highly debated, because it is unclear how natural selection can favour the evolution and maintenance of senescence (Bronikowski & Promislow 2005; Monaco & Silveira 2009). This study, however, can be added to the accumulating evidence of the existence of senescence in wild populations (Nussey *et al.* 2008).

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