



Short communication

Parallel declines in survival of adult Northern Fulmars *Fulmarus glacialis* at colonies in Scotland and Ireland

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Assessing broad-scale changes in seabird populations across the North Atlantic requires an integration of available datasets to understand the spatial extent of potential drivers and demographic change. Here, we compared survival of Northern Fulmars *Fulmarus glacialis* from a Scottish and an Irish colony from 1974 to 2009. Despite lower recapture probabilities of monel-ringed Irish birds compared with colour-ringed Scottish birds, survival probability decreased at both colonies. The extent to which the decline in survival is related to density-dependent processes or other external drivers remains uncertain, but our results suggest that these changes in survival are possibly indicative of larger-scale processes and are not confined to local colony dynamics.

Keywords: data integration, demography, large-scale processes, mark-recapture, seabird.

North Atlantic seabird populations have exhibited marked changes in abundance over the last century (Mitchell *et al.* 2004, Parsons *et al.* 2008). Although

some species such as Northern Gannets *Morus bassanus* (Montevecchi & Myers 1997) and Northern Fulmars *Fulmarus glacialis* (Fisher 1966) increased during the early 20th century, there are concerns over recent declines in a broad suite of other seabird species within this region (Parsons *et al.* 2008, Croxall *et al.* 2012). The drivers of population change remain uncertain but are known to involve both natural and anthropogenic environmental change, including climate-induced mismatches between the timing of breeding and peaks in prey availability (Durant *et al.* 2003, Burthe *et al.* 2012) and reductions in prey abundance resulting from changes in fisheries management (Frederiksen *et al.* 2004, Bicknell *et al.* 2013).

Understanding the relative importance and spatial scale of these different drivers is essential for informing conservation efforts to reduce observed declines (Grémillet & Boulinier 2009). As a first step, identification of the proximate demographic drivers of population change can focus attention either on the local waters around colonies (<400 km; Thaxter *et al.* 2012) that are likely to affect breeding success, or on more distant foraging areas that are likely to affect overwinter survival. Research in this area has been underpinned by long-term individual-based population studies (Clutton-Brock & Sheldon 2010, Lahoz-Monfort *et al.* 2014). However, for many North Atlantic seabird species, data from intensive individual-based studies are either unavailable or come from single colonies. Single colony data can inform understanding of local dynamics but limited inferences can be made about the spatial extent of the observed patterns. Efforts to integrate data from multiple study colonies have highlighted the value of using broader scale analyses to explore inter-colony variation in survival (Grosbois *et al.* 2009), but this has only been possible in a few species, such as Black-legged Kittiwake *Rissa tridactyla* (Frederiksen *et al.* 2005) and Atlantic Puffin *Fratercula arctica* (Harris *et al.* 2005). Given the lack of intensive individual-based studies for many other species of interest, it is important to identify other datasets that could be used to assess whether patterns detected at single sites using these high-resolution data also exist at sites in other parts of their range.

Population change in Northern Fulmars is of particular interest in this context, given the long debate over the drivers underlying the classic range expansion and increase in abundance within this species throughout Britain and Ireland since the late 1800s (Gordon 1936, Fisher & Waterston 1941, Salomonsen 1965, Fisher 1966). Subsequently, Cramp *et al.* (1974) initiated a series of complete censuses of seabirds in this area, the results of which suggest that the Northern Fulmar population has stabilized, with little change between the two most recent surveys made between 1985–88 (Lloyd *et al.* 1991) and 1998–2002 (Mitchell *et al.* 2004). More intensive and recent annual monitoring at a sample of

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Scottish colonies between 1986 and 2004 suggests that the species may now be in decline in this region (Parsons *et al.* 2006). However, a detailed understanding of the nature and scale of these changes is constrained because demographic studies have been made at only one NE Atlantic site (Eynhallow, Orkney), where birds using a subset of nest-sites have been colour-ringed and monitored regularly since 1950 (Dunnet 1991). Previous studies of this colony assessed how both reproduction and survival varied in relation to colony size and environmental covariates (Thompson & Ollason 2001, Grosbois & Thompson 2005). As with many other seabird species in the NE Atlantic (e.g. Frederiksen *et al.* 2004, Sandvik *et al.* 2005, 2012, Votier *et al.* 2005), demographic parameters of Fulmars at this Scottish colony were influenced by large-scale climate variation (Thompson & Ollason 2001, Grosbois & Thompson 2005). There was evidence of a long-term decline in both the probability of reproducing (Lewis *et al.* 2009) and apparent adult survival, as well as sex-specific differences in responses to climate variability (Grosbois & Thompson 2005). Intensive monitoring of known-sex individuals would therefore be required to detect whether similar fine-scale patterns in adult survival occur at other colonies, but no suitable data from other NE Atlantic colonies exist for retrospective studies of this species. However, analyses of historical ringing data could provide additional information on survival probabilities at other colonies (e.g. Sanz-Aguilar *et al.* 2009). Here, we extend the analysis of colour-ring sightings in Scotland to include data from a second colony in south-eastern Ireland, where Fulmars have been monel-ringed (but not colour-ringed) and recaptured regularly since 1974. In particular, we aim to compare temporal trends in adult survival between the two colonies by integrating recapture and resighting data, and assess whether Irish birds showed a similar decline in adult survival to that previously detected at the Scottish study colony.

METHODS

Field data collection

In Scotland, data were collected on Eynhallow (59°8'N, 3°8'W), a 75-ha uninhabited island in Orkney (Fig. 1). At this site, breeding adults have been captured and ringed with both a British Trust for Ornithology (BTO) monel ring and a unique combination of two or three colour rings that allowed birds to be identified without capture during annual censuses.

In Ireland, data were collected on Little Saltee (52°7'N, 6°41'W), a 40-ha island off the southeast coast of County Wexford (Fig. 1). Ringing began in 1968, and became part of an annual census from 1974. At this site, breeding adults were marked only with numbered monel

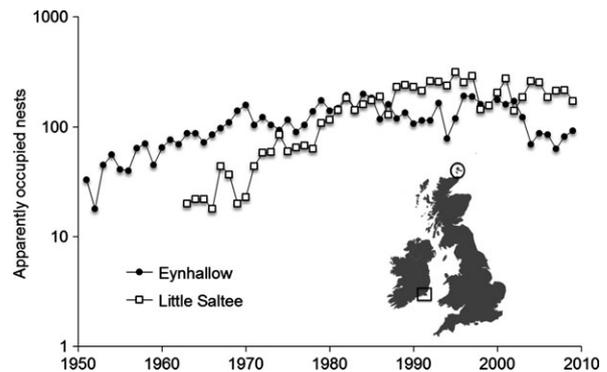


Figure 1. Trends in abundance (log scale) of Northern Fulmars at the two study colonies on Eynhallow and Little Saltee.

rings and therefore had to be recaptured to be identified. Further details of field methods and the number of birds captured or resighted at both sites are provided in Supporting Information Appendix S1.

In both Scotland and Ireland, our study colonies formed part of a larger network of sites (Mitchell *et al.* 2004). Although we have no evidence of established breeders moving between colonies, this cannot be ruled out. All estimates of survival therefore represent apparent survival.

Data analysis

Recapture and resighting data of 496 birds from Eynhallow and 1015 birds from Little Saltee were analysed using a Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) with island (Eynhallow and Little Saltee) as a group variable (*g*). These birds were all adult breeders that were either breeding for the first time or had bred previously. The analysis was restricted to the years from 1974 to 2009 to compare directly trends in adult survival during a period in which data were available for both colonies. Analyses were run within the R (R Core Team 2013) package RMARK (Laake & Rexstad 2008) to construct models in MARK (White & Burnham 1999), while the goodness-of-fit was tested within the program U-CARE (Choquet *et al.* 2009). For survival (Φ), models were constructed with (1) time-dependence (*t*) or linear time trend (*T*), (2) island effect (*g*), (3) an additive effect of time or linear time trend and island (*t+g*, *T+g*), (4) an interaction between time or a linear time trend and island (*t*g*, *T*g*) or (5) no time or island effect (.). For recapture probability (*p*), we built models with (1) island effect (*g*), (2) additive effect of time and island (*t+g*) or (3) no time or island effect (.). This resulted in 24 candidate models. For further details on modelling and model selection see Appendix S1.

RESULTS

The two study colonies each contained around 200 nests during their peak abundance. However, they differed in the pattern of change in colony size (Fig. 1). The number of occupied nests on Eynhallow increased steadily through the 1950s and 1960s, but then fluctuated at around 200 nests prior to a decline after 2000. Little Saltee was colonized later, and increased in size until the late 1990s, reaching approximately 250 occupied nests, after which it also has shown evidence of a slight decline.

The CJS analysis revealed two top models accounting for 0.98 of the QAICc weight (Table 1). The top model ($\Phi(T^*g)$, $p(t+g)$) accounted for just over half of the QAICc weight, and the second best model ($\Phi(T+g)$, $p(t+g)$) for just under half of the QAICc weight (Table 1).

Both top models supported a linear decline in survival over time as well as lower recapture probabilities on Little Saltee compared with Eynhallow (Table 2). The top model with the interaction term suggested that the decline in survival was less pronounced on Little Saltee (Table 2), whereas the second top model supported a difference in survival between islands with survival being higher on Little Saltee (Table 2). Due to the even distribution of support for these two models we present model-averaged estimates of survival and recapture probabilities (Fig. 2).

Table 1. Model selection results for the top 10 models.

Model	Parameters (n)	Δ QAICc	QAICc weight	QDeviance
$\Phi(T^*g)$ $p(t+g)$	40	0.000	0.535	4459.38
$\Phi(T+g)$ $p(t+g)$	39	0.369	0.445	4461.78
$\Phi(g)$ $p(t+g)$	38	6.951	0.017	4470.40
$\Phi(T)$ $p(t+g)$	38	10.408	0.003	4473.86
$\Phi(.)$ $p(t+g)$	37	15.288	<0.001	4480.77
$\Phi(t+g)$ $p(t+g)$	72	42.323	<0.001	4435.99
$\Phi(t)$ $p(t+g)$	71	52.746	<0.001	4448.47
$\Phi(t^*g)$ $p(t+g)$	106	75.228	<0.001	4397.99
$\Phi(T^*g)$ $p(g)$	6	150.046	<0.001	4678.17
$\Phi(T+g)$ $p(g)$	5	153.390	<0.001	4683.52

Table 2. β -estimates and 95% confidence intervals of parameters in the two top models (bold text denotes a significant effect). All β -estimates with an island effect denote the effect size for Little Saltee, as Eynhallow represented the baseline.

	$\Phi(T^*g)$ $p(t+g)$	$\Phi(T+g)$ $p(t+g)$
Φ_g	-0.015 (-0.389 to 0.359)	0.358 (0.209 to 0.508)
Φ_T	-0.028 (-0.040 to -0.016)	-0.020 (-0.030 to -0.010)
Φ_{T^*g}	0.020 (0.001 to 0.038)	NA
p_g	-1.753 (-1.863 to -1.643)	-1.759 (-1.869 to -1.648)

DISCUSSION

Long-term individual-based studies provide unique insights into population dynamics (Clutton-Brock & Sheldon 2010) but the effort required to run these types of studies makes them difficult to replicate at multiple sites. Only rarely, and generally when those populations are small and endangered, do such studies include a high proportion of individuals from the overall population (e.g. Inchausti & Weimerskirch 2002). For many other species, individual-based studies are restricted to particular sites and often involve only a small proportion of even the regional population. Northern Fulmars are probably an extreme case in this respect, as information on the demography of ~500 000 pairs currently breeding around Scotland (Mitchell *et al.* 2004) has been based on studies of ~200 pairs breeding on one island in Orkney where nest-sites are unusually accessible (Ollason & Dunnet 1978, Dunnet 1991, Thompson &

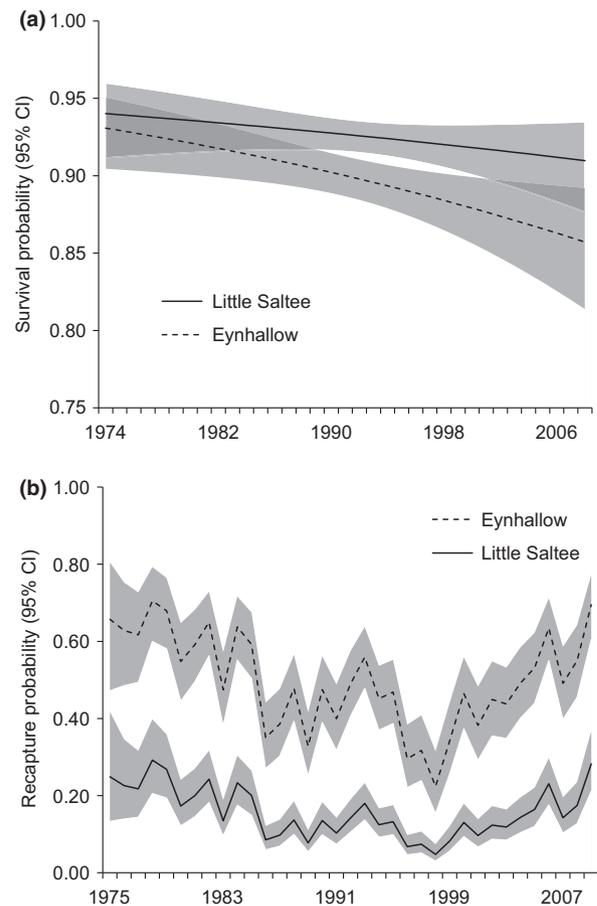


Figure 2. (a) Model-averaged (see Appendix S1) adult survival of Fulmars from Eynhallow and Little Saltee (1974–2009). (b) Annual variation in recapture probabilities at the two study colonies over this period.

Ollason 2001, Grosbois & Thompson 2005). It is therefore important to seek other sources of data that can be used to assess whether other colonies exhibit similar patterns to those detected from colour-ringing data with high recapture probabilities.

In this study, the analysis of conventional monel ringing data from a second colony on Little Saltee allowed us to detect parallel declines in apparent adult survival (Fig. 2a) that had previously only been identified on Eynhallow (Grosbois & Thompson 2005). Recapture probabilities on Little Saltee were much lower (Fig. 2b) because they depended upon direct captures of ringed birds to read the monel rings. Although annual effort put into recaptures and/or resightings at each colony varied independently, the temporal variation in recapture probabilities within the colonies followed a similar pattern (Fig. 2b). This is perhaps not surprising, as previous work indicates that larger-scale processes, such as the North Atlantic Oscillation (NAO), affect the likelihood of established breeders attending the colony in any one year (Thompson & Ollason 2001).

The range and abundance of Northern Fulmars increased dramatically through the early part of the 20th century. More recently, Seabird 2000 census data have indicated that abundance at colonies in Britain and Ireland has stabilized (Mitchell *et al.* 2004), whereas detailed monitoring across Scottish sites detected a 29% decline in occupied nests between 1984 and 2004 (Parsons *et al.* 2006). Previous studies have highlighted local (Eynhallow; Lewis *et al.* 2009) and broader-scale (Scotland; Parsons *et al.* 2008) declines in productivity over this period. As outlined above, our study colonies represent only a tiny fraction of these regional populations, and there is limited information available to assess whether they are representative. Nevertheless, these parallel trends are not unexpected, given that an increasing number of similar individual-based studies of other seabird species in the NE Atlantic are demonstrating covariation in adult survival both across species at single colonies (Lahoz-Monfort *et al.* 2011) and within species using colonies that are separated at large spatial scales (Harris *et al.* 2005, Reynolds *et al.* 2011). Given the lack of studies of Northern Fulmars at other sites, it may only be possible to determine whether our results are representative through continuation of the broader time-series of colony counts reported in Mitchell *et al.* (2004) and Parsons *et al.* (2006). We cannot rule out the possibility that the trend in apparent adult survival at one or both of these sites is the result of a trend in adult emigration. However, if the reductions in apparent adult survival that we observed at our two study colonies represent a widespread decline in survival, this may have been the proximate driver underlying the stabilization of these populations following their rapid increase earlier in the 20th century. If so, the total Northern Fulmar population of Britain and Ireland is likely to show

evidence of decline by the time of the next national seabird census.

The ultimate drivers underlying our observed trends in adult survival remain less clear. Parallel trends in the reproductive probabilities of other NE Atlantic seabird populations suggest that there have been reductions in key prey populations (Parsons *et al.* 2008). Survival of many other species in this region varies in relation to environmental covariates, such as sea surface temperature (SST) and the NAO (Sandvik *et al.* 2012). Such relationships are also likely to reflect responses to changes in prey availability, although there may be interactions with other anthropogenic stressors (e.g. Frederiksen *et al.* 2004, Votier *et al.* 2005). Previous analyses of the Eynhallow dataset explored the effects of different environmental variables on adult survival and demonstrated that there were important sex differences in responses to different environmental variables (Grosbois & Thompson 2005). We were unable to extend our analyses to incorporate environmental variables because observations from the Irish colony were sparse and sex was unknown. Northern Fulmars are also subject to uncertain levels of fisheries by-catch in parts of their Atlantic range (Anderson *et al.* 2011). At the same time, given the species' earlier increase in abundance (Fig. 1), more recent declines in both reproduction and survival could result from density-dependent competition for food resources. Mitchell *et al.* (2004) showed that there is a much larger regional population in Scottish waters (c. 500 000 pairs) than in Irish waters (< 40 000 pairs). Although our two study colonies were of similar size (Fig. 1), Scottish birds may experience greater intraspecific competition for food resources due to this larger regional population, which may explain the stronger decline in survival in Eynhallow birds (Fig. 2a). Recent tracking work demonstrated that breeding Northern Fulmars may forage many hundreds of kilometres from breeding sites during incubation (Edwards *et al.* 2013). There is also evidence of overlap in wintering areas used by birds from these Scottish and Irish colonies (Quinn 2014). This overlap highlights that the trend in adult survival at two distant colonies may be a response to common environmental signals, as seen in Common Guillemots *Uria aalge* that bred at distant colonies but shared common wintering areas (Reynolds *et al.* 2011). Nevertheless, resource availability within the 400-km foraging range of breeding Fulmars (Thaxter *et al.* 2012) could of course also be influenced by broader-scale processes. Both tracking and isotopic studies indicate that Northern Fulmars travel widely across the North Atlantic, but also spend a significant amount of the year in these relatively local waters around their colonies (Quinn 2014). Further studies are now required to characterize individual and colony-specific variation in foraging areas to identify appropriate environmental covariates and suitable measure of density, which will

permit a more integrated exploration of the different drivers influencing survival in this species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:
 Appendix S1. Methods.