North Atlantic climate variation influences survival in adult fulmars

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There is increasing evidence that large scale climate variation influences reproductive parameters of seabirds, but fewer studies have investigated possible effects on adult survival. Previous work has shown that climate variation reflected by the winter North Atlantic oscillation (WNAO) influences reproductive success in northern fulmars. Here, we use a 34 year long (1962–1995) individual-based data set to investigate inter-annual and inter-individual variation in adult survival in this species. Breeding success in the previous and current seasons, and both the WNAO and one-year lagged WNAO indexes, were considered as potential sources of inter-annual variation in survival and recapture probabilities. Sex and an index of body size were considered as potential sources of inter-individual variation in survival and recapture probabilities. Body size effects were not significant, but males and females differed in both their survival and recapture probabilities. Probability of recapture of females was positively correlated with breeding success in both the current and previous breeding seasons, whereas male recapture probabilities were correlated only with previous breeding success. Male and female survival decreased over the study period, suggesting that there had been a degradation of environmental conditions. This hypothesis was supported by the detection of a negative correlation between survival and the WNAO, which, in turn, showed a positive increase over this period. The negative correlation between female adult survival and WNAO did not result only from the long term behaviour of the two time series, but persisted for higher frequency fluctuations. In contrast, the correlation between male survival and WNAO seemed to result only from the long term behaviour of the two time series. Despite uncertainties over causal mechanisms, these findings add to the body of evidence that large scale climate variation could dramatically affect seabird population dynamics. Furthermore our results suggest that climate variation can differentially influence individuals with distinct phenotypic characteristics.

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Climatic change over the past century has been shown to have important ecological consequences (Hughes 2000, Mc Carty 2001, Parmesan and Yohe 2003), but predictions concerning the impact of future climate change on biodiversity remain subject to large uncertainties. One promising avenue for understanding the biological effects of climate change is the study of the impact of past climatic variation on populations for which long term population dynamics data are available. This approach has already documented ecological impacts of climate fluctuation on millenial (Roy et al. 1996, Smith et al. 1999, Graham et al. 2003), centurial (Montevecchi and Myers 1997, Finney et al. 2002) and decadal time scales (Mc Gowan et al. 1998, Kitaysky and Golubova 2000, Barbraud and Weimerskirch 2001, Attril and Power 2002, Edwards et al. 2002, Taylor et al. 2002).

Due to the large spatial scales involved, and the high mobility of most marine organisms, investigating the dynamics of their populations is notoriously difficult

(Larkin 1978). One exception is provided by seabirds, which gather seasonally on accessible breeding grounds, providing opportunities to undertake detailed population studies (Wooler et al. 1990). Because many seabird species are marine top predators, the dynamics of their populations may reflect the state of important components of marine ecosystems, particularly forage fish (Cairns 1992, Montevecchi and Myers 1995). Furthermore, assessment of changes in the size of seabird breeding populations can be integrated with individually based studies of vital rates by applying capture mark recapture protocols. Such protocols can provide important information on the demographic processes driving population dynamics, and therefore shed light on the mechanisms through which climatic forcing may influence population dynamics (Barbraud et al. 2000, Barbraud and Weimerskirch 2001, Thompson and Ollason 2001).

Previous studies have reported significant effects of climatic variation on reproductive success in seabirds inhabiting polar (Murphy et al. 1991), temperate (Aebischer et al. 1990) and tropical marine ecosystems. However, the population dynamics of these long lived species are more sensitive to variation in adult survival than to variation in breeding parameters (Croxall and Rothery 1991, Russel 1999). Attempts to understand the demographic mechanisms by which climate change may influence trends in seabird abundance therefore require better information on the extent to which environmental variation influences adult survival. Whilst the analytical tools to detect such changes are now well developed (Lebreton et al. 1992, White and Burnham 1999), investigations of variability in survival require long time series. At least partly as a consequence of this, few studies have reported climate-driven variation in adult survival in seabirds, and these have generally been from Antarctic systems which have shown marked changes in winter sea ice cover (Croxall et al. 2002).

In the present paper we aim to apply capture mark recapture models to assess the influence of environmental factors, particularly climate variability, on the adult survival of the northern fulmar, *Fulmarus glacialis,* a pelagic seabird belonging to the Procellariidae family. The fulmar undertakes long range foraging trips to reach productive areas (Macdonald 1977, Dunnet and Ollason 1982, Weimerskirch et al. 2001). Consequently, it is difficult to define precise geographic areas where the prevailing environmental conditions should influence the fulmar's survival. In this context, proxies which integrate climatic and/or feeding conditions over large geographical scales may be particularly useful. Climate variation in the temperate North Atlantic has been shown to be related to the North Atlantic oscillation; a large scale ocean-atmosphere oscillating system (Hurrell 1995). Previous studies have already shown that the December to March north Atlantic oscillation index (WNAO)

influences the reproductive success of northern fulmars in the subsequent summer breeding season (Thompson and Ollason 2001). Furthermore, the WNAO is known to influence the dynamics and composition of several north Atlantic communities within the food chain upon which fulmars rely (e.g. phytoplankton (Edwards et al. 2001), zooplankton (Planque and Taylor 1998) and fish (Arnott and Ruxton 2002, Attril and Power 2002)). In this study, we therefore used the WNAO as a potential proxy for the climate experienced by fulmars during the winter and/or, the availability of their prey during both breeding and non-breeding seasons.

One potential problem when using capture mark recapture analysis on seabird populations is that encounters of marked individuals generally occur only on the breeding grounds, and usually only during the breeding season. The probability of encountering an individual is therefore dependent upon its breeding status: for example, like many other seabirds (Croxall and Rothery 1991, Russel 1999), fulmars are intermittent breeders (Ollason and Dunnet 1983) and only breeding individuals will be encountered in any particular season. Furthermore, pairs that fail early in the season do not relay and are unlikely to be encountered that year. Consequently, inter-annual variability in environmental conditions is also likely to influence recapture probability and it is important to model the relationship between time variation in recapture probability and variation in the environmental proxies. Furthermore, previous analysis of this capture recapture data set revealed heterogeneity of capture and/or survival rates among individuals (Carothers 1979, Buckland 1982). We therefore also explored the potential effects of two individual characteristics, sex and body size, that might underly this heterogeneity.

Material and methods

Description of the study

The study was carried out on Eynhallow, a small (75 ha) uninhabited island in Orkney, Scotland (59°8′N; 3°8′W) with low, flat coastline along which fulmars nest. Since 1950, annual visits have been made to study the fulmars. Between 1958 and 1995, visits have normally occurred at the end of May (when the number of nests with eggs is counted), in early July (when hatching success is estimated) and in early August (when fledging success is estimated). Details of the study area, and study methods are given in Dunnet (1991).

During the May and July visits, previously ringed adult birds were identified and a sample of unringed breeders were caught, and given both a uniquely numbered British Trust for Ornithology (BTO) monel ring and a unique 2 or 3 colour ring combination. We use the term encounter to refer either to the initial

capture or to the resighting of a breeding adult. We built capture recapture histories from the data on encounters of breeders gathered each year. During the period 1958–1995, 749 individuals were encountered at least once as breeders.

These fieldwork protocols have important implications for the interpretation of recapture probabilities. Previous studies have shown that fulmars can skip breeding seasons once recruited into the breeding population (Ollason and Dunnet 1983, Hatch 1987). Since encounters occur only on breeding grounds, recapture probabilities should be low in years when a high proportion of breeders skip reproduction. Attendance at the colony also tends to be lower through the rest of the breeding season following a breeding failure (Hatch 1990). In this study, the effort undertaken to encounter breeding individuals was not concentrated at the beginning of the breeding season, but involved two main sampling periods at different stages of the breeding season. The probability that a breeder remained undetected because it failed to reproduce before being encountered should therefore increase in years when reproductive failures are frequent, especially when these failures occur early in season. Finally, independently of the stage of reproduction reached, the probability of recapture is expected to be relatively low in years when nest attendance is low. Inter-annual variation in recapture probability should therefore reflect inter-annual variation in these different breeding parameters.

Candidate variables for exploring variation in survival and recapture probabilities

The covariates we considered in the analysis of survival and recapture probabilities are listed in Table 1 and described in detail below. Following the recommendation of White and Burnham (1999), we centred all covariates reflecting temporal variation in environmental conditions around the average and standardized them by the standard deviation in the time series covering the study period.

We based our estimates of annual breeding success (BS) at the colony scale upon the ratio of the number of chicks fledged in August to the number of nests containing an egg (the clutch size of the fulmar is one egg) in late May. Current year breeding success may show a positive and quite direct relationship with recapture probability, mediated by the influence of the frequency of early breeding failures and of nest attendance on recapture probability. Moreover, if fulmars have access early enough before the breeding season to cues about the environmental conditions that exist during the breeding season, they may decide to skip reproduction when these cues indicate unfavourable conditions. This would result in an indirect positive relationship between the current year's breeding success and recapture probability, mediated by the influence of early environmental cues on breeding decisions. The possibility that breeding success influences reproductive propensity or decisions in the next breeding season was also considered: it has been shown in other Procellariiforms that, following a breeding failure, individuals either restrain from breeding or are constrained to non breeding (Chastel 1995). At the scale of the colony, this could result in a positive relationship between recapture probability and breeding success in the previous breeding season. We accounted for this possible relationship by considering breeding success in the previous breeding season (hereafter referred to as LBS) as a potential factor influencing recapture probability. Finally, adverse environmental conditions during the breeding season may also affect subsequent adult survival. We therefore also considered the breeding success at a given capture occasion as a potential factor influencing variation in the survival of adults over the following year.

The WNAO was considered as a proxy for climatic conditions experienced outside the breeding season and/or for food abundance during and/or outside the breeding season. Because it could take time for any effect of the WNAO on low levels of the food chain to influence higher trophic levels, one year lagged WNAO (LWNAO) was also considered as a potential proxy for food abundance during and/or outside the breeding

Table 1. Covariates considered in the analysis of survival and recapture probabilities. Categorical covariates are referred to using lower case letters, and continuous covariates are referred to using capital letters.

Covariate	Notation	Type of covariate	Type of parameter
Inter-individual variation			
Recapture at the preceding occasion	d	categorical	recapture
Body size index	bsi	categorical	survival recapture
Inter-annual variation			
Year	t	categorical	survival recapture
Lagged breeding success	LBS	linear	recapture
Breeding success	BS	linear	recapture survival
Lagged North Atlantic oscillation	LWNAO	linear	survival recapture
North Atlantic oscillation	WNAO	linear	survival recapture
Effort	EF	linear logarithmic	recapture
Trend	T	linear	survival
High disturbance	hd	categorical	survival

season. We thus considered WNAO and LWNAO as potential factors affecting variation of both adult survival and recapture probabilities. Values for the WNAO were downloaded from http://www.cgd.ucar. edu/~jhurrell/nao.html#seasonal.

Although May and July field visits were made to the study area in each year, the total length of these two visits varied considerably between years (ranging from 3 to 28 days in which observers attempted to encounter breeding birds, Fig. 1). Consequently, differences in observer effort could influence year to year variation in recapture probability. We therefore used the number of days in which observers attempted to encounter breeding birds as a measure of encounter effort (EF) in each year.

Correlations among covariates

Multiple regression analysis is known to be hampered by collinearity among explanatory covariates (Graham 2003). To identify pairs of candidate covariates whose effects might be difficult to distinguish, we derived Pearson correlation coefficients (r) for all pairs of candidate covariates used in the analysis (ie WNAO, LWNAO, BS, LBS). We also derived Pearson correlation coefficients (r) between a linear trend (T) and each of the candidate covariates to identify those candidate covariates whose effect could be confounded with that of a trend in some overlooked factor (Table 2). Finally, for pairs of candidate covariates showing significant trends, we derived Pearson correlation coefficients between detrended time series. The detrended time series were computed by estimating the residuals of the least square linear regression between the focal covariate and the linear trend (T). The resulting de-trended time series were referred to by adding the letter "D" in front of the label used for the covariate. The analysis of correlation among de-trended covariates allowed us to assess whether significant correlation between candidate covariates resulted only from the co-occurrence of long term trends or whether correlations persisted for fluctuations at short time scales.

As expected from previous analysis (Thompson and Ollason 2001), breeding success correlated negatively with the previous winter's WNAO index. A negative correlation was also detected between BS and WNAO lagged by one year (LWNAO). Finally WNAO showed positive temporal auto-correlation (i.e. correlation between LWNAO and NAO). These correlations resulted mainly from the presence of long term trends in the LWNAO, WNAO and BS time series (i.e. BS, LWNAO and WNAO correlated significantly with T and correlations among detrended time series of BS, WNAO and LWNAO were weak: Table 2). Given the correlations among BS, WNAO and LWNAO, it could be difficult to determine which of these covariates has the most direct influence on adult survival or recapture probability. We therefore adopted a step up modelling approach for the selection of the covariates to include in the models inferring the factors underlying variation in survival and recapture probabilities, and assumed that the candidate covariate that correlated the most highly with the focal parameter also had the most direct link with it. Furthermore, since LWNAO and WNAO showed strong trends over the study period, we interpreted their effects on survival and recapture probability cautiously, considering possible confusion with the effects of overlooked factors which would also exhibit trends.

A negative correlation was detected between encounter effort and breeding success. This last correlation might indicate that the field protocols undertaken to encounter fulmars disturbed their breeding activities. Examination of the scatter plot (Fig. 1) reveals that the influence of effort on breeding success was limited to four years during which effort was exceptionally high. Although the decrease of breeding performances under very high levels of research effort has already been documented (Ollason and Dunnet 1980), the consequences for apparent adult survival has not yet been investigated. A factor hd (for high level of disturbance) which distinguished the time intervals following the four very high effort breeding seasons was thus considered as a potential factor of variation in adult survival.
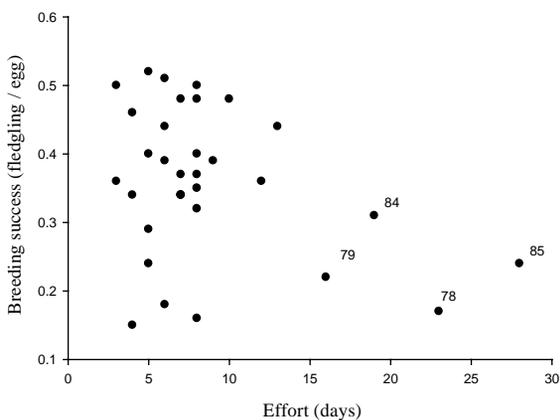

Fig. 1. Relationship between the effort undertaken to encounter ringed individuals and breeding success.

Individual characteristics

Morphological measurements were taken when breeders were first captured and ringed. Bill length and bill depth were used to calculate a discriminant function to determine the sex of the bird (Dunnet and Anderson 1961). Where discriminant functions from both members of a pair indicated that they were of the same sex, the

Table 2. Pearson correlation coefficient (r) between covariates used to explain underlying time variation in survival and recapture probabilities. Figures in italics refer to correlations between de-trended time series. Corresponding P-values are presented between brackets.

	WNAO	LBS	BS	T	EF
LWNAO	0.62; 0.24 (<0.001; 0.18)	−0.33; −0.20 (0.06; 0.27)	−0.41; −0.22 (0.02; 0.22)	0.7 (<0.001)	−0.005 (0.98)
WNAO		−0.15; 0.08 (0.41; 0.67)	−0.40; −021 (0.02; 0.25)	0.71 (<0.001)	−0.20 (0.25)
LBS			0.23; 0.14 (0.19; 0.43)	−0.28 (0.11)	−0.08 (0.66)
BS				−0.37 (0.03)	−0.35 (0.05)

larger bird was assumed to be male. Of 749 capture histories, 360 were attributed to males and 389 to females. We considered sex as a potential factor of inter-individual variations of survival and recapture probabilities.

Bill length and bill depth measurements were available for all the individuals considered in the data set, providing a potential index of body size. In addition, the weight of some (138 males and 143 females), but not all, individuals was measured at initial capture. We used these data to determine the best allometric relationship between weight and bill size. Because the weight of fulmars changes during the breeding season (Weimerskirch et al. 2001), we restricted these analyses to measurements taken within a 6 day window around the time of hatching (5th–11th of July).

We built a general linear model to test the effects on logarithm of weight (g), the logarithm of bill length, the logarithm of bill depth, sex and any interactions between sex and the two bill measurements. Interactions between sex and bill measurements were not significant (sex × log(bill depth): $F^1_{275} = 1.53$, P = 0.22; sex × log(bill length): $F^1_{275} = 1.08$, P = 0.30), whereas the effects of log(bill depth) ($F^1_{277} = 14.64$, P < 0.001), log(bill length) ($F^1_{277} = 3.87$, P = 0.05) and sex ($F^1_{277} = 29.37$, P < 0.001) were significant. The equation giving the best fit accounted for 54% of the observed variation in the logarithm of weight.

Log(weight (g)) = 1.63 (+0.04 for males) + 0.35 × log(bill length(mm)) + 0.57 × log(bill depth(mm))

We used the right hand side of this equation as a body size index (BSI) for each of the individuals whose capture histories had been selected for the survival analysis. We then converted BSI into a categorical variable (referred to as bsi). Within each sex class, we classified individuals according to three bsi classes (small, medium, large). We chose the class boundaries to obtain approximately similar sample sizes in the three bsi groups for each sex; we then considered bsi as a potential factor of inter-individual variations of survival and recapture probabilities.

Statistical analysis

We analysed capture histories using procedures developed to provide estimates of survival probabilities (Φ), while accounting for potential biases due to variation in recapture probabilities (p). We used model notation similar to that used for generalized linear models, as advised in Lebreton et al. (1992): we used the symbol "+" to refer to additive effects and the symbol "×" to refer to interactions. We used the letter "c" to designate models in which recapture or survival probability was constant. We used a logit link function to constrain estimates of Φ and p between 0 and 1. We used the statistical package MARK 5.0 (White and Burnham 1999) to obtain maximum likelihood estimates of survival and recapture probabilities, and fit statistics, under various models.

Before using capture recapture models for hypothesis testing, a general model must be defined under which the following hypothesis are met (Lebreton et al. 1992).

1) The capture history of any given individual must be independent from the capture histories of all other individuals considered in the analysis. Our data set contains many capture histories referring to the members of a same pair. Given that the fates of paired individuals are not independent, we analysed data sets for males and females separately.

2) Within each group specified in the model, individuals must be identical with respect to their survival and recapture probabilities.

3) The fate of an individual (survives/does not survive) or the outcome of any capture–recapture session (encountered or not encountered) should not depend on the individuals' previous capture history.

To detect departures from the second two hypotheses, we conducted goodness of fit tests (GOF tests) with software U-CARE 2.0 (Choquet et al. 2001). We examined with particular attention the tests 3.SR and 2CT which detect heterogeneity in local survival and recapture probability respectively. We used the very powerful directional Z-statistic version (Choquet et al. 2001) as well as the more commonly used, but less powerful, non directional χ^2 version of these two tests.

Finally, we examined the omnibus test, which assesses the overall model fit.

For both the males and females, model Φ (bsi+t+ bsi $\times$ t) p(bsi+t+bsi $\times$ t) provided a poor fit to the data (omnibus test: female: $\chi^2_{365} = 476.7$, P <0.0001; male: $\chi^2_{351} = 497.3$, P <0.0001). Poor goodness of fit resulted mainly from highly significant component 2 CT in its directional version (females: $Z = -11.9$; P <0.0001; males: $Z = -11.6$; P <0.0001) as well as in its non directional version (females: $\chi^2_{102} = 280.9$, P <0.0001; males: $\chi^2_{99} = 258.9$, P <0.0001). This indicated heterogeneity of recapture probability either within or between capture histories. Following Pradel (1993), we addressed this heterogeneity by distinguishing two types of occasions in the model describing the variations of the recapture probabilities: 1) those following an occasion on which the individual was encountered 2) those following an occasion on which the individual was not encountered. The notation used hereafter to refer to the corresponding covariate is "d" (Table 1).

The directional version of component 3 SR was highly significant (females: $Z = 3.87$, P =0.0001; males $Z = 3.67$, P =0.0002) suggesting heterogeneity in survival probability. However the less powerful non directional version of component 3SR was far from significant (females: $\chi^2_{75} = 47.2$, P =0.99; males: $\chi^2_{75} = 51.4$, P =0.98) suggesting that heterogeneity in survival was weak. Nonetheless, it had to be taken into account. One way of eliminating heterogeneity in survival probability is to build data sets in which the first or the first n (where n >1) encounters of each individual are ignored (Pradel et al. 1997). This has the effect of eliminating from the data set the individuals that have been encountered only a few times, among which are individuals that survived relatively poorly. Here, component 3SR remained significant in its directional version in data sets in which up to the first three encounters had been ignored. We thus used data sets in which the four first encounters of each individual had been ignored for model selection and for testing the effects of the covariates listed in Table 1. The reduced data sets covered the period 1962–1995 and contained 197 capture histories for females and 183 capture histories for males. To evaluate the robustness of the results obtained from this analysis of reduced data sets, and to derive more representative results for the whole population, we also assessed key models and tests using the full data sets. Unless stated otherwise, the results presented refer to the analysis of the reduced data sets.

Model selection

We used a modified form of Akaike's information criterion, AICc (Burnham and Anderson 1998) for model selection. We considered two models with AICc differing by less than two points as models describing the data equally well. If we had to choose a unique model among several models within two AICc points, we selected the model with the lowest number of parameters (Lebreton et al. 1992).

For both sexes, the "departure model" was $\Phi(t+bsi+ t \times bsi)$ p(d+t+bsi+d $\times$ bsi+t $\times$ bsi). Prior to testing the covariates that might underly any temporal variation in survival and recapture probabilities, we built and compared the reduced models nested in the departure model (including the models in which inter-annual variation was modelled by a linear trend T). This step of the analysis permitted the definition of a "reference model" that captured the most important general sources of variation in survival and recapture probability, without relying on specific assumptions concerning the covariates underlying their temporal variation.

We performed the selection of the reference model independently for survival and recapture. In each case, we performed a step down procedure involving a series of reduced models while we held the structure for the other parameter type (recapture or survival) fixed and similar to the structure of the departure model (see Grosbois and Tavecchia 2003 for similar model selection strategies).

Detecting factors underlying temporal variations in recapture and survival

Once the reference model had been defined, we tested the covariates potentially underlying time variation (listed in Table 1). For each parameter type (survival or recapture), we built a series of models in which we held the structure for the other parameter type (recapture or survival respectively) fixed and similar to the structure of the reference model. The first model from each of these series presented a modified version of the structure of the reference model, built under the hypothesis of absence of time variation in the target parameter. Starting from this time invariant model, we performed a step up procedure in which, at each step, among the covariates considered as potentially underlying temporal variation (Table 1), we selected the one whose addition to the model lead to the best joined AICc and parsimony criterion (above). The model including all the covariates selected for describing time variation in recapture and survival probabilities will be hereafter referred to as the "final model". At each step of the selection procedure described above we computed an equivalent for maximum likelihood models of the coefficient of determination for each candidate model. This coefficient (referred to as cd) indicates the proportion of the deviance associated with temporal variation in the focal parameter accounted for by the covariates included in the focal candidate model. We computed

it as: [deviance(time invariant model) −deviance(focal candidate model)]/[deviance(time invariant model) −deviance(fully time dependent model)].

We computed P-values (referred to as P-LRT) for specific hypothesis testing using likelihood ratio tests (Lebreton et al. 1992).

Results

Model selection

Selection among the models nested within the departure model resulted in models for females and males which were similar with respect to recapture probabilities, but slightly different with respect to survival probability (Table 3). In both sexes, recapture probability varied through time (t effect), and was higher for an individual recaptured on the preceding occasion than for an individual not recaptured on the preceding occasion (d effect; Fig. 2). The probability of recapture did not seem to differ among body size index categories (bsi main effect was not retained).

The reference model for describing survival probability of males contained only a logit-linear trend (Table 3, Fig. 3). For females, the reference model contained none of the variables included in the departure model (Table 3) and survival probability was considered as constant. Nevertheless, the rejection of a categorical year effect on female survival at this step of the analysis does not mean that survival probability is strictly constant over time. Similarly the selection of a continuous trend for temporal variation in male survival rather than a categorical year effect does not mean that there is no additional temporal variation around this trend. Instead, it suggests that, given the sample sizes, time variations are small enough for a constant model and a trend model to provide a reasonable approximation of reality for females and males respectively. For the female data set, the AICc of the model containing a linear temporal trend was only 0.1 points higher than the AICc of the constant survival model (Table 3), and a logit-linear trend model was retained for both male and female data sets to provide comparable estimates of survival probability (Fig. 3).

These estimates show that there has been a decrease in survival probability through time for both sexes. Estimates for the first time interval of the study period (1962–1963) were 0.951 for females (95% confidence interval $=0.911$–0.973) and 0.9785 for males (0.9592–0.9888). Whereas estimates for the last time interval (1994–1995) were 0.898 (0.843–0.936) for females and 0.8674 (0.8105–0.9091) for males. Using the full data set, in which each individual's first four encounters were included, statistically significant decreases through time were detected in male as well as in female survival probability (Table 7). In addition the survival probability estimates obtained using the full data set were very similar to those based on the reduced data set: for 1962–1963, the estimates were 0.9619 (0.9446–0.9735) for females and 0.9642 (0.9483–0.9754) for males; for 1994–1995, the estimates were 0.8979 (0.8622–0.9251) for females and 0.8975 (0.8617–0.9248) for males. The similarity of results between the unmodified and the reduced data set was surprising, since the capture histories for individuals surviving relatively poorly were not included in the reduced data set. This confirms that the heterogeneity in survival probability was very weak. The results obtained with the full data set are presented in Fig. 3 as they are more representative for the population as a whole.

Covariates underlying temporal variation in recapture probability

The best model describing time variation in the recapture probability of females (Table 3, 4, Fig. 2) included

Table 3. General models for the description of survival and recapture probability variations.

| Female model	Npar	DEV	AICc	Male model	Npar	DEV	AICc
Departure model				departure model			
$\Phi(t+bsi+t \times bsi)$	148	1094.8	2655.6	$\Phi(t+bsi+t \times bsi)$	154	1080.8	2795.4
$p(d+t+bsi+d \times bsi+t \times bsi)$				$p(d+t+bsi+d \cdot bsi+t \times bsi)$			
Reference model				reference model			
$\Phi(c)\ p(d+t)$	33	1253.7	2538.2	$\Phi(T)\ p(d+t)$	34	1239.1	2670.6
Neighbourhood of the				neighbourhood of the			
reference model				reference model			
$\Phi(T)\ p(d+t)$	34	1251.7	2538.3	$\Phi(T)\ p(d+t+bsi)$	36	1236.0	2671.7
$\Phi(c)\ p(d+t+bsi)$	35	1251.4	2540.1	$\Phi(T+bsi)\ p(d+t)$	36	1237.9	2673.7
$\Phi(bsi)\ p(d+t)$	35	1253.5	2542.2	$\Phi(c)\ p(d+t)$	33	1253.2	2682.6
$\Phi(t)\ p(d+t)$	54	1219.7	2549.8	$\Phi(t)\ p(d+t)$	56	1211.5	2690.5
$\Phi(c)\ p(d+T)$	4	1342.1	2566.4	$\Phi(T)\ p(d+T)$	5	1346.6	2718.1
$\Phi(c)\ p(d)$	3	1353.3	2575.6	$\Phi(T)\ p(d)$	4	1354.1	2723.7
$\Phi(c)\ p(t)$	32	1309.4	2591.7	$\Phi(T)\ p(t)$	33	1304.1	2733.5
Final model				final model			
$\Phi(WNAO)$	7	1300.1	2530.4	$\Phi(LWNAO)$	6	1289.7	2663.2
$p(d+\log(EF)+LBS+BS)$				$p(d+\log(EF)+LBS)$			
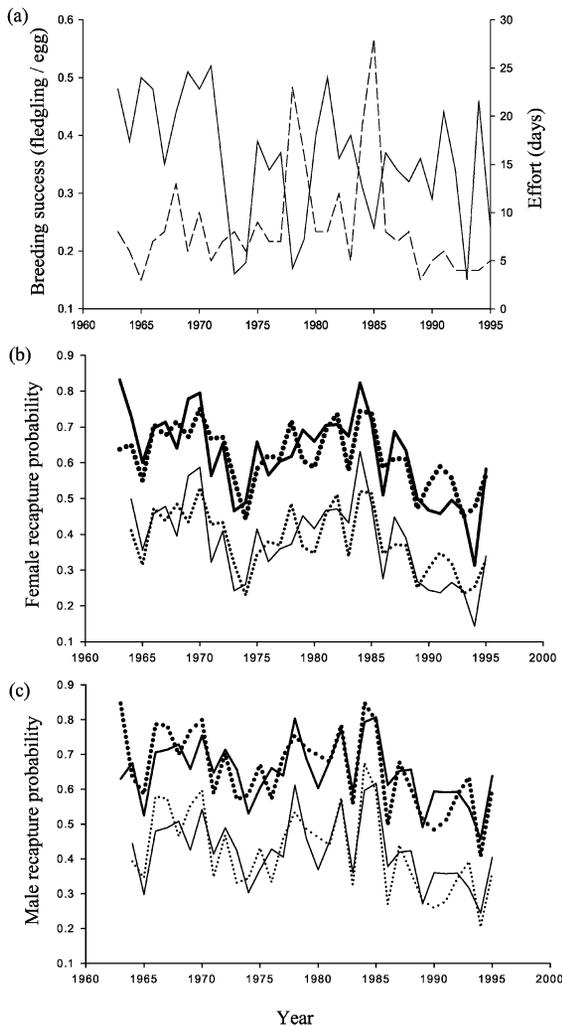
Fig. 2. Interannual variation in a) the covariates which were shown to influence recapture probability, b) estimated recapture probabilities for females and c) estimated recapture probabilities for male fulmars. In Fig. 2a), variations in breeding success are shown with a solid line and effort is shown using a dashed line. In Fig. 2b, estimates of female recapture probability obtained from the model $\Phi(c)\ p(d+t)$ are shown with thick solid line for females recaptured at the preceding occasion, and thin solid line for those femaless not recaptured at the preceding occasion. Estimates from the model $\Phi(c)\ p(d+Log(EF)+LBS+BS)$ are shown with a thick dotted line (those recaptured at the preceding occasion) and a thin dotted line (those individuals not recaptured on the preceding occasion). In Fig. 2c, estimates of male recapture probability are based upon model $\Phi(T)\ p(d+t)$, with thick solid representing males recaptured at the preceding occasion, and thin solid line those not recaptured on the preceding occasion. Estimates from the model $\Phi(T)\ p(d+Log(EF)+LBS)$ are presented as a thick dotted line (males recaptured on the preceding occasion) and a thin dotted line (males not recaptured on the preceding occasion). Estimates shown in Fig. 2b and 2c have been derived from the full data set.

the effect of effort (Log(EF), Fig. 4a), and both the current year's breeding success (BS, Fig. 4c) and the

previous year's breeding success (LBS, Fig. 4b). This model acounted for 43% of the temporal variation in recapture probability of females (Table 3, Fig. 2b). The model for males included only the effect of effort (Log(EF), Fig. 5a), and previous year's breeding success (Fig. 5b). This model acounted for 62% of the temporal variation in recapture probability of males (Table 3, Fig. 2c).

Table 6 shows the estimates of the slopes between the covariates retained in the final model and recapture probability obtained when models were based either upon the unmodified or the reduced data sets. The estimates obtained from the full data set were very close to those obtained from the reduced data set. Although we cannot state firmly from this correlative analysis that encounter effort, current breeding success and previous breeding success causally affect recapture probabilities, the consistency of the results obtained when using different data sets strongly supports the existence of direct or indirect relationships between these covariates and recapture probability.

Factors underlying temporal variation in survival probability

For both males and females, there was evidence that the observed time variation in survival was related to climate variation. For females, the final model included only the effect of the WNAO (Table 3, 5, Fig. 6a), which accounted for 21% of the temporal variation, whereas for males the final model included only an effect of lagged WNAO, which accounted for 17% of the temporal variation (Table 3, 5, Fig. 7a).

Whilst these results provide support for an influence of the WNAO on both male and female survival, they must be considered in the light of the marked tendency of WNAO to increase over the study period (Table 2, Fig. 3). It is important to distinguish between a genuine effect of WNAO on survival, and co-variation with another factor that had been overlooked, but that also showed a significant trend over this period. To make this distinction possible we tested, using likelihood ratio tests, the effect of de-trended WNAO (DWNAO) and de-trended LWNAO (DLWNAO) on adult survival in the presence of a trend effect. Analysis of both the reduced and the full data sets produced similar results (Table 7). Whereas the effect of the WNAO on female survival was robust to the de-trending (Table 7, Fig. 6b), neither the de-trended version of WNAO nor the de-trended version of the LWNAO was significantly correlated with male adult survival in the presence of a trend effect (Table 7, Fig. 7b).
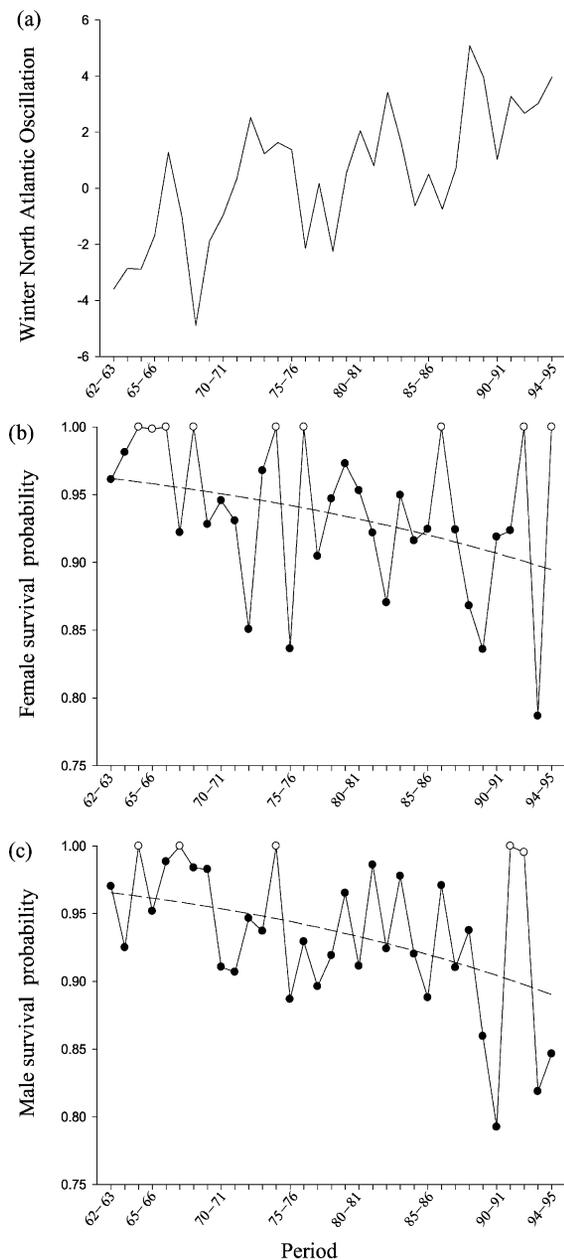
Fig. 3. Interannual variation in (a) covariates correlating with survival probability (b) survival probability of females (c) survival probability of males. In Fig. 3a, the WNAO is represented as a solid line. In Fig. 3b and 3c estimates of survival probability from model $\Phi(y)$ $p(d+t)$ are shown as filled circles. Open circles represent estimates at the boundary displaying abnormal confidence intervals. Estimates from the model $\Phi(T)$ $p(d+t)$ are shown as a dashed line. Estimates shown in (b) and (c) have been derived from the full data set.

Discussion

Heterogeneity in recapture and survival probabilities

Whilst the major aim of our study was to assess the influence of environmental variation on survival, pre-

vious work on this and similar data sets had highlighted the importance of accounting for individual heterogeneity in recapture and survival probabilities. In other studies of adult survival in seabirds, estimates have often had to be based upon all adults in the sample (Harris et al. 2000, Jones et al. 2002), despite the most obvious potential source of heterogeneity being the sex of these individuals. Unfortunately, due to high partner fidelity in fulmars, building models that could test for sex differences in survival and/or recapture probabilities would have violated one of the key assumptions underlying capture–recapture model: independence among capture–recapture histories. We therefore built separate models for known males and females. An alternative approach, if larger data sets were available, would be to conduct the analysis on a subset of males and females which had never paired. This would allow one to build and compare various models based on a data set containing capture histories of individuals from both sexes. The advantage of this approach would be the possibility of testing the interactions between sex and other individual and environmental characteristics.

Other sources of heterogeneity were eliminated by data selection prior to the analysis rather than by integrating them in the survival and recapture probability models. This was the case of the heterogeneity in survival revealed by the GOF tests. However, whilst this effect was statistically significant when using a very powerful test, the results obtained from a data set from which the poorly surviving individuals had been eliminated were strikingly similar to those obtained from the full data sets. The heterogeneity in survival detected thus has little, if any, biological significance.

Evidence for heterogeneity in recapture probability was much stronger and clearer than that for heterogeneity in survival probability. This effect had been detected in previous analysis of parts of this dataset (Carothers 1979, Buckland 1982), and was characterised by a higher probability of encountering an individual if it had been encountered during the previous breeding season. This may reflect heterogeneity in recapture probability within individual capture histories and/or inter-individual heterogeneity. Heterogeneity between capture histories would not be surprising since recapture probability was related to breeding performance (Table 4, 5) and numerous seabird's studies have demonstrated inter-individual heterogeneity in phenotypic quality that results in some individuals surviving and reproducing less well than others (Wooler et al. 1990, Harris and Wanless 1995, Calladine and Harris 1997, Cam et al. 1998). Heterogeneity within individual capture histories would reflect a positive temporal autocorrelation of breeding performances within individuals and could be explained, for example, by age related variation which had been documented in many seabird species, including fulmars from this study population

Table 4. Models exploring the covariates underlying time variation in recapture probability.

Female model	Npar	DEV	AICc	cd (%dev)	Male model	Npar	DEV	AICc	cd (%dev)
Full time variation model					full time variation model				
Φ(c) p(d+t)	33	1253.7	2538.2		Φ(T) p(d+t)	34	1239.1	2670.6	
Constant model = step 0					constant model = step 0				
Φ(c) p(d)	**3**	**1353.3**	**2575.6**		**Φ(T) p(d)**	**4**	**1354.1**	**2723.7**	
Covariate selection step 1					covariate selection step 1				
Φ(c) p(d+log(EF))	**4**	**1330.4**	**2554.7**	**23**	**Φ(T) p(d+log(EF))**	**5**	**1303.5**	**2675.0**	**44**
Φ(c) p(d+WNAO)	4	1334.1	2558.4	19	Φ(T) p(d+EF)	5	1310.0	2681.6	38
Φ(c) p(d+EF)	4	1342.0	2566.3	11	Φ(T) p(d+LBS)	5	1335.7	2707.2	16
Φ(c) p(d+LBS)	4	1342.6	2566.9	11	Φ(T) p(d+NAO)	5	1339.8	2711.3	12
Φ(c) p(d+LWNAO)	4	1346.1	2570.4	7	Φ(T) p(d+LWNAO)	5	1348.3	2719.9	5
Φ(c) p(d+BS)	4	1350.2	2574.5	3	Φ(T) p(d+BS)	5	1349.9	2721.5	4
Covariate selection step 2					covariate selection step 2				
Φ(c) p(d+log(EF)+BS)	**5**	**1319.1**	**2545.5**	**34**	**Φ(T) p(d+log(EF)+LBS)**	**6**	**1283.9**	**2657.5**	**61**
Φ(c) p(d+log(EF)+LBS)	5	1319.5	2545.8	34	Φ(T) p(d+log(EF)+LWNAO)	6	1299.9	2673.5	47
Φ(c) p(d+log(EF)+WNAO)	5	1324.6	2550.9	29	Φ(T) p(d+log(EF)+WNAO)	6	1303.0	2676.6	44
Φ(c) p(d+log(EF)+LWNAO)	5	1324.6	2550.9	29	Φ(T) p(d+log(EF)+FS)	6	1303.4	2677.0	44
Covariate selection step 3					covariate selection step 3				
Φ(c) p(d+log(EF)+BS+LBS)	**6**	**1310.1**	**2538.5**	**43**	Φ(T) p(d+log(EF)+LBS+LWNAO)	7	1282.8	2658.4	62
Φ(c) p(d+log(EF)+BS+LWNAO)	6	1317.0	2545.3	36	Φ(T) p(d+log(EF)+LBS+BS)	7	1283.2	2658.8	62
Φ(c) p(d+log(EF)+BS+WNAO)	6	1317.3	2545.6	36	Φ(T) p(d+log(EF)+LBS+WNAO)	7	1283.7	2659.3	61
Covariate selection step 4									
Φ(c) p(d+log(EF)+BS+LBS+LWNAO)	7	1307.9	2538.3	46					
Φ(c) p(d+log(EF)+BS+LBS+WNAO)	7	1308.7	2539.1	45					

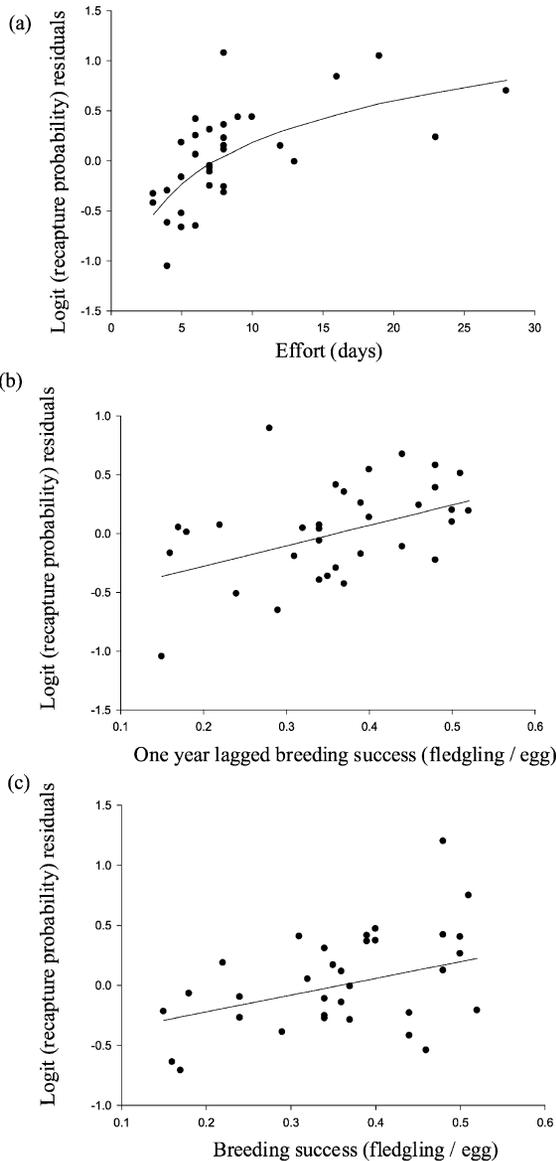Notes: the model selected at each step is highlighted in bold.

Fig. 4. Relationship between logit of recapture probability of females and covariates retained in the final model: (a) log(EF), (b) LBS (c) BS. For each covariate, the relationship is shown with the residuals of a model relating logit(recapture probability) with the two other covariates. The survival part of the models from which these residuals are taken is the reference model $\Phi(c)$. All estimates have been derived from the full data set.

(Ollason and Dunnet 1978). Alternatively a positive temporal autocorrelation of breeding performance within individuals could arise from constraints or strategic decisions conditional on breeding success in the previous year. This possibility is discussed later in relation to temporal variation in recapture probability.

We also hypothesised that body size might explain at least some of the inter-individual heterogeneity in recapture and survival probabilities, particularly given that the fulmar exhibits marked geographical variation in body size, suggesting that this trait is subjected to selection pressures that vary geographically (Wynne-Edwards 1952). We detected no such effects, but this may at least partly be because our index of body size is likely to be only weakly correlated with true body size. Ideally, future studies should gather data on other morphometric or physiological variables so that individual heterogeneity in recapture and survival rates can be explored in relation to a broader suite of individual co-variates.

Temporal variation in recapture probability

The number of days in which observers attempted to encounter breeding birds had a significant effect on recapture probability of both males and females. However, the relationship between recapture probability and effort was not linear, as recapture probability levelled off at around 0.8 even when effort was very high. This suggests that, in any year, at least 20% of individuals are not recaptured because they deserted the colony early in the season or did not attempt to breed that year. Intermittent breeding has been documented in many long lived seabirds (Wooler et al. 1990, Chastel 1995, Harris and Wanless 1995, Catry et al. 1998) including the northern fulmar (Ollason and Dunnet 1983, Hatch 1987), and is believed to be a tactic to avoid jeopardizing future survival when environmental conditions are unfavourable for breeding (Ollason and Dunnet 1983, Hatch 1987).

In females, but not males, we also detected a relationship between recapture probability and the current year's breeding success that may reflect a strategic decision to skip breeding when environmental conditions are unfavourable. However it is difficult to explain why such decisions would be made by females and not by males. One alternative possibility is that recapture probability is generally lower in years when more breeders failed early in the season, and that this leads to sex-differences in recapture probability. Male fulmars undertake a long incubation stint soon after the female has laid the egg (Dunnet and Ollason 1978), which tends to overlap with the study's first field trip of the season. Males are therefore more likely to be encountered at the beginning of the breeding season, when effort is highest, before most of the breeding failures have occurred.

Breeding success in the previous year also had a strong effect on recapture probabilities for both males and females, with recaptures being higher after successful breeding seasons. This may reflect a relationship between former breeding success and probability of early breeding failure in the next breeding season. However we did not detect any temporal auto-correlation of breeding success (e.g. correlation between BS and LBS in Table 2)
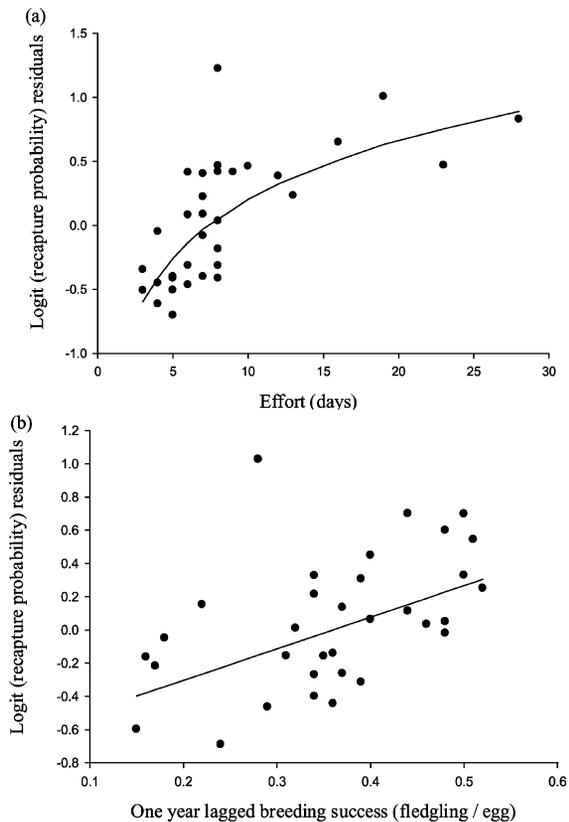
(a)

(b)

Fig. 5. Relationship between logit of recapture probability of males and covariates retained in the final model: (a) log(EF), (b) LBS. For each covariate, the relationship is shown with the residuals of a model relating logit(recapture probability) with the other covariate. The survival part of the models from which all these estimates are taken is the reference model $\Phi(T)$. All the estimates have been derived from the full data set.

which suggests that unfavourable environmental conditions during a given breeding season is not a predictor of unfavourable conditions in the next season. Furthermore, this interpretation depends upon the existence of a relationship between breeding success and recapture probability. However, this was only detected in females, whereas the relationship between former breeding success and recapture probability was significant for both sexes. Alternatively, the relationship between former breeding success and recapture probability may result from an increase in the likelihood of skipping breeding following a breeding failure. This relationship has been seen in other Procellariiformes (Chastel 1995), and could result either from individuals restraining themselves from breeding, or being constrained to non-breeding, after a failure. Strategic decisions to skip reproduction following a breeding failure would be beneficial if environmental conditions during the breeding season are temporally auto-correlated. This is unlikely to be the case here since we failed to detect any temporal auto-correlation in breeding success (Table 2) and since the

temporal auto-correlation detected in WNAO resulted from the presence of a long term trend in the time series rather than from a strong dependence of the WNAO in one year on the WNAO in the previous year (i.e. there was no temporal auto-correlation in the WNAO de-trended time series: Table 2). The alternative constraint hypothesis is supported by results from the literature. For example, divorce or a change in nest site after a breeding failure has been documented in many seabirds (Reed and Oring 1993, Bried and Jouventin 1999, Danchin and Cam 2002) and can act as a constraint on breeding propensity in the next breeding season because it can take more than one season for a bird to secure a new mate or nest site (Hatch 1987, Weimerskirch 1992, Harris and Wanless 1995, Catry et al. 1998, Bried and Jouventin 1999).

Whilst outside the scope of this study, these results suggest that further analysis of these capture–recapture data could explore the causal mechanisms underlying observed variability in recapture probability. Ideally, this requires analytical tools that would allow us to disentangle breeding frequency from the probability of encountering a breeding individual. Such analytical developments would allow one to address, for example, the relationship between breeding success and probability of skipping reproduction in the next breeding season. Further development of multistate capture recapture models provides a promising avenue to address this problem.

Temporal variation in survival probabilities

Several earlier studies estimated the survival of adult fulmars from this study population (Dunnet and Ollason 1978, Carothers 1979, Buckland 1982), focussing on the 15 year period that corresponds to the first half of the time series used in our study. These studies concluded that survival was constant over time and did not differ between sexes, with estimates of survival probability ranging from 0.9511 (95% confidence interval =0.943–0.956, Dunnet and Ollason 1978) to 0.968 (0.960–0.976, Buckland 1982). Although using different modelling frameworks, these estimates are close to those from the present study, as the estimates derived from the trend model applied to the full data set were 0.962 (0.9464–0.9732) and 0.966 (0.9511–0.9758) for females and males respectively over the period 1958–1959, and 0.944 (0.934–0.953) and 0.9462 (0.936–0.955) over the period 1974–1975. As in the previous studies, our estimates suggest that, on average, survival probability of males and females is similar. Two of the earlier studies (Carothers 1979, Buckland 1982) detected a decrease in survival at the end of their time series, but both authors attributed this to biases generated by the strong inter individual heterogeneity in recapture probabilities. Our

Table 5. Models exploring the covariates underlying time variation in survival probability.

Female model	Npar	DEV	AICc	cd (%dev)	Male model	Npar	DEV	AICc	cd (%dev)
Full time variation model					full time variation model				
Φ(t) p(d+t)	54	1219.7	2549.8		Φ(t) p(d+t)	56	1211.5	2690.5	
Constant model = step 0					constant model = step 0				
Φ(c) p(d+t)	**33**	**1253.7**	**2538.2**		**Φ(c) p(d+t)**	**33**	**1253.2**	**2682.6**	
Covariate selection step 1					covariate selection step 1				
Φ(WNAO) p(d+t)	**34**	**1246.7**	**2533.2**	**21**	**Φ(LWNAO) p(d+t)**	**34**	**1246.0**	**2677.5**	**17**
Φ(LWNAO) p(d+t)	34	1253.0	2539.6	2	Φ(WNAO) p(d+t)	34	1248.9	2680.4	10
Φ(hd) p(d+t)	34	1253.2	2539.8	2	Φ(LBS) p(d+t)	34	1251.9	2683.4	3
Φ(LBS) p(d+t)	34	1253.3	2539.9	1	Φ(BS) p(d+t)	34	1251.9	2683.5	3
Φ(BS) p(d+t)	34	1253.7	2540.3	<1	Φ(hd) p(d+t)	34	1253.1	2684.6	<1
Covariate selection step 2					covariate selection step 2				
Φ(WNAO+LWNAO) p(d+t)	35	1245.4	2534.2	4	Φ(LWNAO+hd) p(d+t)	35	1244.8	2678.5	20
Φ(WNAO+LBS) p(d+t)	35	1246.1	2534.9	2	Φ(LWNAO+LBS) p(d+t)	35	1245.2	2678.8	19
Φ(WNAO+BS) p(d+t)	35	1246.6	2535.3	<1	Φ(LWNAO+BS) p(d+t)	35	1245.5	2679.2	18
Φ(WNAO+hd) p(d+t)	35	1246.7	2535.4	<1	Φ(LWNAO+NAO) p(d+t)	35	1246.0	2679.6	17

Notes: the model selected at each step is highlighted in bold.

analyses used new models designed to overcome such biases (Pradel 1993), and we suggest that the decrease in survival over the study period is a real effect. This conclusion is re-enforced by our finding that there is a negative correlation between adult survival and the WNAO, which has increased over the study period.

Influence of climate variation on survival

The increase in the WNAO over the last 50 years has been demonstrated to modify winter climate in the northern hemisphere, characterized in the UK by stronger westerlies bringing warmer and wetter meteor-ological conditions (Hurrell 1995). Such conditions may be unfavourable for the fulmar which is near the southern limit of its range around UK coast. Further-more, the WNAO has been demonstrated to influence the dynamics and the composition of several commu-nities upon which fulmars either directly or indirectly depend (Planque and Taylor 1998, Edwards et al. 2001, Arnott and Ruxton 2002).

Considered alone, the fact that fulmars' adult survival declined over a period during which the WNAO increased would provide only weak evidence of a link between this measure of climate variation and adult survival. Indeed the longer term decline in adult survival could be attributed to factors, independent from climate, which may have been overlooked in the present analysis. For example, modifications in anthropogenic factors such as a reduction in fish offal availability (Votier et al. 2004), or an increase in the risk of bycatch due to the development of long-line fisheries (Lokkeborg and Robertson 2002) could explain the decline in adult survival of fulmars. However, the correlation between WNAO and adult survival of female fulmars remained significant after both time series had been de-trended (Fig. 6). The correlation between WNAO and females' survival is thus not limited to the long term behaviour of the two time series, and persists for higher frequency fluctuations. This provides support for the hypothesis that the observed decrease in survival stems, more or less directly, from climatic and oceanographic changes that are captured by the increase in WNAO.

Table 6. Point estimates and 95% confidence intervals (between square brackets) from the model containing all covariates retained for recapture probabilities.

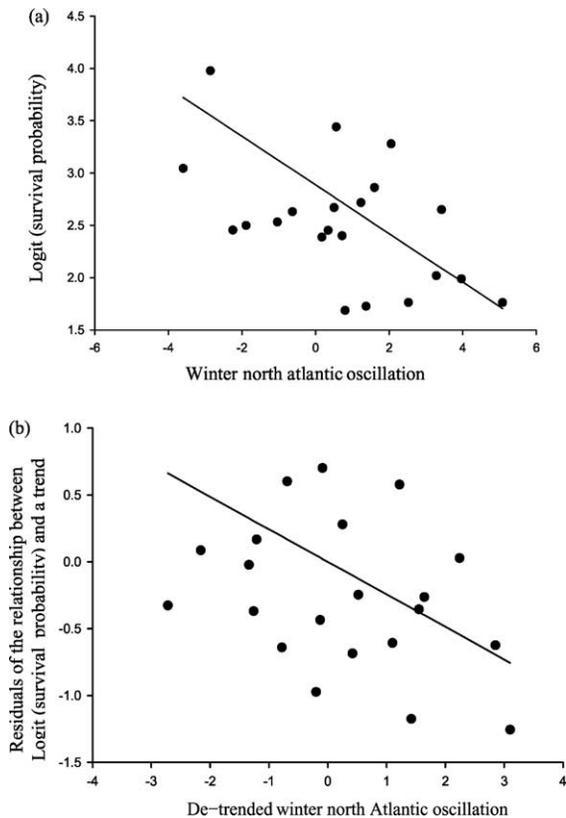|	Reduced data set	Full data set
a) Females		
Log (EF)	0.32 [0.21; 0.44]	0.31 [0.23; 0.39]
BS	0.19 [0.07; 0.31]	0.15 [0.07; 0.22]
LBS	0.17 [0.06; 0.29]	0.18 [0.11; 0.25]
b) Males		
Log (EF)	0.41 [0.30; 0.53]	0.34 [0.27; 0.42]
LBS	0.24 [0.13; 0.35]	0.20 [0.13; 0.27]

Fig. 6. (a) Relationship between logit of survival probability of females and WNAO (b) Relationship between de-trended WNAO and the residuals of a model relating the logit(survival probability) of females to a trend covariate. The recapture part of the models from which all these estimates are taken is the reference model p(d+t). All the estimates have been derived from the full data set.

Investigation of the mechanisms underlying the effect of the WNAO is made difficult because the WNAO is likely to integrate information on climate outside the breeding season and/or on feeding conditions both outside and/or during the breeding season. Recent results obtained by Oro and Furness (2002) and Ratcliffe et al. (2002) on the factors influencing adult survival respectively of kittiwakes (*Rissa tridactyla*) and of great skuas (*Catharacta skua*) suggest that prey abundance (in their case sandeels, *Amnodytes maritimus*) is one of the factors driving variation in adult survival of many seabird species. However, neither study assessed the impact of climate variation, and it remains possible that climate variation also influences adult survival in these species either directly or through its impact on prey abundance. Indeed, an indirect influence on adult survival of the WNAO through its impact on prey abundance might be expected in some sandeel-dependent populations since the WNAO has recently been demonstrated to impact sandeels' abundance in the North Sea (Arnott and Ruxton 2002).

The results presented by Oro and Furness (2002) furthermore suggest that the period during which sandeel abundance is limiting for adult survival is not the breeding season but the few months following it. Our results support the hypothesis that food availability during the breeding season is not a limiting factor for seabird adult survival. If the key influence of the WNAO on adult survival was through the influence of WNAO on food abundance during the breeding season, we would have expected survival to correlate more strongly with breeding success than with WNAO. In addition, the influence of environmental conditions during the breeding season on survival was not expected, a priori, because pelagic seabirds are believed to allocate resources towards self maintenance, at the detriment of reproduction during unfavourable breeding conditions (Croxall and Rothery 1991, Saether et al. 1996, Russel 1999). We therefore suggest that future work aiming to understand causal links between climate variation and survival should focus on the birds' behaviour and feeding ecology outside the breeding season. Considering the hypothesis proposed by Oro and Furness (2002), investigation of the feeding ecology during the few months following reproduction should be a good starting point.

As the mechanisms through which WNAO influences fulmar survival are unclear, so are those explaining why there is a correlation between high frequency fluctuations of the WNAO and survival in females but not in males. The species is slightly sexually dimorphic (Wynne-Edwards 1952), and this could result in differences in foraging energetics that lead to sex differences in foraging areas, as observed in wandering albatross (Weimerskirch and Wilson 2000, Shaffer et al. 2001). Under this hypothesis, environmental conditions in areas used by the females could be more directly linked to the WNAO than in areas used by the males. At present there is no information on where adult fulmars from this colony forage during and outside the breeding season. However, recent developments in tracking devices (Weimerskirch and Wilson 2000, Weimerskirch et al. 2001) should in future permit the identification of areas used by male and female fulmars during and outside the breeding season.

Although there remains uncertainty over the mechanisms through which WNAO influences survival, our findings add to the body of evidence that suggests that large scale climate variation can dramatically affect seabird population dynamics (Croxall et al. 2002, Jones et al. 2002, Durant et al. 2003, Jenouvrier et al. 2003). Previous work on northern fulmar has already documented a negative correlation between WNAO on the probability of adults making a breeding attempt, and on their subsequent breeding success (Thompson and Ollason 2001). The relationship between the WNAO and survival found in the present study is in the same
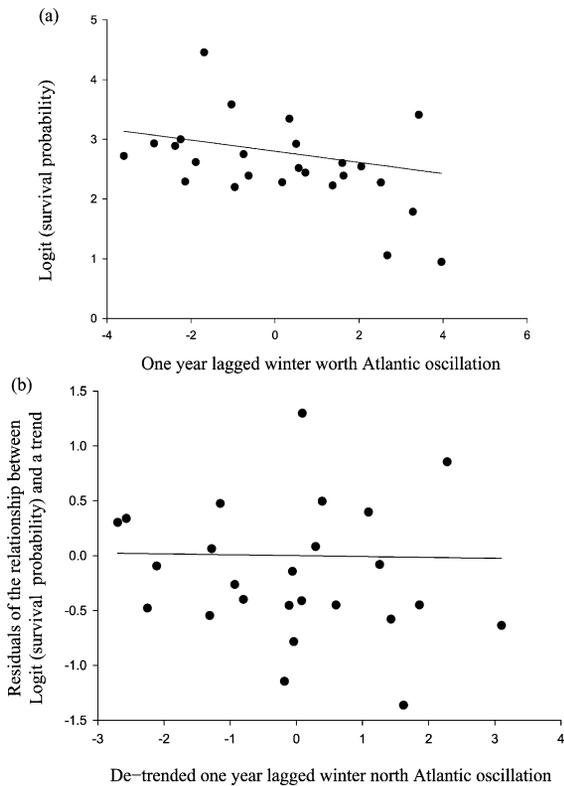
Fig. 7. (a) Relationship between the logit of survival probability of males and LWNAO, (b) Relationship between de-trended LWNAO and the residuals of a model relating logit(survival probability) of males to a trend covariate. The recapture part of the models from which all these estimates are taken is the reference model p(d+t). All the estimates have been derived from the full data set.

direction, and the tendency for the WNAO to increase is therefore expected to result in a substantial depression of population growth rate. Interestingly, following the dramatic range expansion and population explosion of

fulmars over the last century, recent reports suggest that some European populations are now in decline (Mitchell et al. 2004). Recent work on southern fulmars (*Fulmarus glacialoides*) has highlighted the value of using Leslie matrix models to integrate similar data on adult survival and reproduction to quantify the impacts of climate variability on recent trends in abundance (Jenouvrier et al. 2003). However, preliminary attempts to explore the effect of WNAO on the growth rate of the more open population of northern fulmars in Eynhallow have highlighted the importance of key demographic parameters for which we still lack estimates; particularly the input of immigrants to the colony. Further work aims to extend analysis of this data set using other recent developments of capture–recapture models which permit the estimation of recruitment rates (Pradel and Lebreton 1999).

An increasing number of studies have now reported an influence of large scale climatic phenomena on seabird demography. However, most have been concerned with the influence of the warming trend in Antarctica (reviewed by Croxall et al. 2002) and the influence of El Niño southern oscillation (Oedekoven et al. 2001). Studies in temperate oceanic systems are rarer and tend to focus on effects on reproduction (e.g. north-western Pacific; Kitaysky and Golubova 2000, Gjerdrum et al. 2003, north-western Atlantic; Montevecchi and Myers 1997). In the north eastern Atlantic, several studies found relationships between breeding or foraging success and local weather conditions. For example, Aebischer et al. (1990) detected a correlation between the frequency of westerly weather and kittiwake's breeding parameters, Aebisher and Wanless (1992) detected a relationship between the timing of breeding and the frequency of easterly winds, and Finney et al. (1999) showed that the feeding behaviour of common guillemots was sensitive to the occurrence of stormy weather.

Table 7. Point estimates, 95% confidence intervals (between square brackets), and statistical significance for covariates potentially underlying temporal variation in adult survival.

	Reduced data set		Full data set	
	Slope	P-LRT	Slope	P-LRT
a) Females				
WNAO	−0.46 [−0.80; −0.12]	0.008	−0.55 [−0.78; −0.32]	<0.001
LWNAO	−0.15 [−0.50; 0.20]	0.41	−0.39 [−0.64; −0.15]	0.001
T	−0.23 [−0.54; 0.08]	0.15	−0.31 [−0.51; −0.11]	0.002
DWNAO	−0.34 [−0.65; −0.03]	0.03	−0.41 [−0.65; −0.17]	<0.001
DLWNAO	−0.002 [−0.30; 0.29]	0.99	−0.18 [−0.42; 0.06]	0.14
b) Males				
WNAO	−0.38 [−0.75; −0.02]	0.04	−0.25 [−0.48; −0.01]	0.04
LWNAO	−0.50 [−0.87; −0.13]	0.007	0.22 [−0.49; 0.05]	0.03
T	−0.58 [−0.88; −0.28]	<0.001	−0.33 [−0.53; −0.14]	0.001
DWNAO	0.05 [−0.25; 0.36]	0.73	0.02 [−0.20; 0.23]	0.87
DLWNAO	−0.07 [−0.37; 0.23]	0.66	−0.01 [−0.23; 0.21]	0.90

Notes: for the effects of WNAO, LWNAO and T, the reduced model for the computation of P-LRT was $\Phi(c)$. For the effects of DWNAO and DLWNAO, the reduced model was $\Phi(T)$. The model for recapture probability is the reference model: p(d+y).

In spite of the widely recognized sensitivity of seabird population dynamics to changes in adult survival on the one hand and of the dramatic change in climatic conditions over the past 50 years on the other hand, few studies have previously explored the influence of climatic variation on seabirds' adult survival. In Antarctic and Pacific systems, effects of large scale climate variation have been detected (Hodder and Graybill 1985, Barbraud and Weimerskirch 2001, Jones et al. 2002). But in the Atlantic, studies of adult survival in other seabirds have either concluded that survival was constant (Harris et al. 1994, Frederiksen and Petersen 1999), found temporal variation without being able to link it to environmental factors (Harris et al. 1997), or detected relationships with more local environmental factors such as prey abundance (Oro and Furness 2002, Ratcliffe et al. 2002) without addressing the impact of climatic variation. The long time series used in the present study undoubtedly improved the statistical power of our attempts to detect an influence of the WNAO on adult survival. The continuation of individual based studies at a wide range of seabird colonies around the North Atlantic should provide exciting opportunities to explore the generality of these findings for other species, enabling us to understand the influence of environmental changes on different components of this community of marine top predators.

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