

Recruitment and survival of immature seabirds in relation to oil spills and climate variability

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Summary

1. In long-lived animals with delayed maturity, the non-breeding component of the population may play an important role in buffering the effects of stochastic mortality. Populations of colonial seabirds often consist of more than 50% non-breeders, yet because they spend much of their early life at sea, we understand little about their impact on the demographic process.

2. Using multistate capture–mark–recapture techniques, we analyse a long-term data set of individually identifiable common guillemots, *Uria aalge* Pont., to assess factors influencing their immature survival and two-stage recruitment process.

3. Analysis of the distribution of ringed common guillemots during the non-breeding season, separated by age classes, revealed that all age classes were potentially at risk from four major oil spills. However, the youngest age class (0–3 years) were far more widely spread than birds 4–6 years old, which were more widely spread than birds aged 6 and over. Therefore the chance of encountering an oil spill was age-dependent.

4. A 2-year compound survival estimate for juvenile guillemots was weakly negatively correlated with winter sea-surface temperature, but was not influenced by oil spills. Non-breeder survival did not vary significantly over time.

5. In years following four oil spills, juvenile recruitment was almost double the value in non-oil-spill years. Recent work from Skomer Island showed a doubling of adult mortality associated with major oil spills, which probably reduced competition at the breeding colony, allowing increased immature recruitment to compensate for these losses. We discuss the implications of compensatory recruitment for assessing the impact of oil pollution incidents.

Key-words: capture–mark–recapture, oil pollution, population dynamics, recruitment, sea surface temperature, seabirds

Introduction

Assessing the impact of environmental and anthropogenic perturbations on animal populations is not only important in elucidating principles of population dynamics, but is also fundamental to conservation biology and ecosystem management. Yet for long-lived iteroparous vertebrates, we still have an incomplete understanding of the demographic process, in no small part because populations of these animals change

slowly with time. To overcome this problem, much work has focused on estimating vital rates that underpin the demographic process and determining how they are influenced by environmental change, using detailed long-term studies of marked animals and sophisticated analytical techniques (Lebreton & Clobert 1991).

Seabirds are top predators in marine ecosystems and their populations tend to reflect conditions over large spatial and long temporal scales, making them important indicators of environmental change (Croxall & Rothery 1991). Recent work has demonstrated how seabird demographics can be influenced by the chronic effects of climate change (Sandvik *et al.* 2005; Crespin *et al.* 2006; Lee *et al.* 2007) and commercial

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fisheries (Frederiksen *et al.* 2004; Votier *et al.* 2004; Phillips *et al.* 2006), as well as the acute impacts of oil pollution (Peterson *et al.* 2003; Velando *et al.* 2005). However these effects appear relatively subtle, being reflected in variations in diet choice, adult survival probabilities or productivity, while breeding populations grow or remain stable. Because seabirds have long periods of immaturity, spending several years at sea before returning to breeding colonies (Croxall & Rothery 1991), little is known about vital rates of immature birds, including survival and recruitment probabilities. Understanding the demographic tactics of this age class is essential as, in a typical seabird population, non-breeders may represent more than 50% of the fully grown birds. These individuals may be responsive to environmental change (Porter & Coulson 1987), and their responses may mitigate or accentuate the effects that change has on population size.

Here we analyse resighting data of known-age, individually marked common guillemots, *Uria aalge* Pont., on Skomer Island, Wales, to estimate immature survival rates and two-stage recruitment using multistate capture–mark–recapture (CMR) techniques. By constraining models with a number of environmental covariates, we aim to identify the factors that influence immature survival and the recruitment process. In particular, we investigate the consequence of four major oil-pollution events by examining their impact on parameter estimates and comparing geographical overlap of recoveries of ringed common guillemots with oil spills in the winter quarters. Recent work from this colony found that annual variation in adult mortality of common guillemots was correlated with both climate variability and the incidence of oil spills, effects that were not apparent using population census data (Votier *et al.* 2005). It is not clear whether discrepancies between these two approaches are because of inherent variation in census data masking effects, or whether increased recruitment by non-breeders has buffered population declines (Klomp & Furness 1992; Grimm *et al.* 2005), so we specifically test whether recruitment is higher following oil spills. We discuss these findings and consider their implications for assessing the impact of stochastic events as well as changes in climatic conditions.

Methods

NON-BREEDING SEASON DISTRIBUTION AND INCIDENCE OF OIL SPILLS

Large numbers of common guillemots are marked annually at breeding colonies around Britain and Ireland with British Trust for Ornithology (BTO) rings (see Appendix S1 in Supplementary Material). Subsequent reports (recoveries) of these birds during the non-breeding season provide an indication of distribution of birds by age class and possible exposure to four major oil spills.

The location of birds ringed in Dyfed, Wales and Wexford, Ireland and subsequently recovered (either dead or alive) during the period August to April, inclusive, were plotted. The vast majority of the individuals were ringed at Skomer (Dyfed) and Great Saltee (Wexford), and as there was no discernible difference in their distribution, we pooled all 1676 recoveries. Recoveries were split

into three age classes: (1) birds in their first to third winter (age 0–3 years); (2) birds in their fourth to sixth winter (age 4–6 years); and (3) birds in their seventh winter and over (age ≥ 6 years). These age classes approximate to the stages of recruitment in common guillemots – birds in the first 3 years will, on average, not have returned to the colony (juveniles), while birds aged 4–6 years will consist primarily of non-breeders attending the colony in the first stage of recruitment (Harris *et al.* 1994). The majority of birds become breeders by the age of 6. Locations of recoveries are presented along with 95, 75 and 50% kernel density contours. GIS ARCVIEW ver. 2.0, with the animal movement extension (Hooge & Eichenlaub 2000), was used to plot the distribution of ringed common guillemots during the non-breeding season.

CAPTURE–MARK–RECAPTURE MODELLING

Study site and data collection

Data were collected from Skomer Island (51°40' N; 05°15' W), Wales, over the period 1985–2005. The whole island common guillemot population (including breeders, failed breeders and immatures) was counted annually at the beginning or middle of June using standardized methodologies (Birkhead & Nettleship 1980; Hatchwell & Birkhead 1991; Fig. 1a). Each year, during mid-June, a subsample of chicks (with tarsi sufficiently large to prevent ring loss) was captured at a single subcolony (Amos) and fitted with a BTO metal ring as well as a coloured Darvic ring engraved with a unique three-digit alpha-numeric code. These codes were easily observed with 8 × 30 binoculars or a 30× telescope from a nearby hide. Visits on an almost daily basis were made to the colony to search for previously ringed birds throughout the breeding season (April–July) each year. Birds seen with an egg or chick were denoted as a breeder, otherwise as a non-breeder. The youngest guillemot to breed at Skomer is 4 years old, but most do not breed until they are at least 5 or 6 years (see Appendix S6). Data analysis was therefore restricted to the 16 cohorts marked 1985–2000 at the Amos. Of 1522 chicks colour-marked over the period, 687 were resighted, and these resightings were used to build individual encounter histories for CMR analysis.

Modelling framework

To estimate simultaneously survival, resighting (or recapture) probability and transition rates, we used multistate CMR models (Brownie *et al.* 1993; Schwarz *et al.* 1993). In single-state CMR, individuals are resighted (or recaptured) during a period of observation, and between these periods they either die or survive. Apparent survival is estimated correcting for differences in resighting probability, which could otherwise bias survival estimates (Lebreton *et al.* 1992). Multistate models also allow an individual to move between a finite number of states, in this case different breeding states, the models estimating probability of transition between these. Specifically, they estimate three different parameters: p_t^r – the probability of a bird being resighted at time t in state r , given that it is alive and present at time t ; s_t^r – the probability that a bird in state r at time t is in state s at time $t + 1$, conditional on survival from time t to $t + 1$; and conditional transition ψ_t^{rs} – the probability that bird in state r at time t is in state s at time $t + 1$ (Nichols *et al.* 1994). Here all observations of birds were classified as one of three states: state 1 denotes the initial marking event as a chick and during intervening years until seen again at the colony, and is referred to herein as a juvenile; state

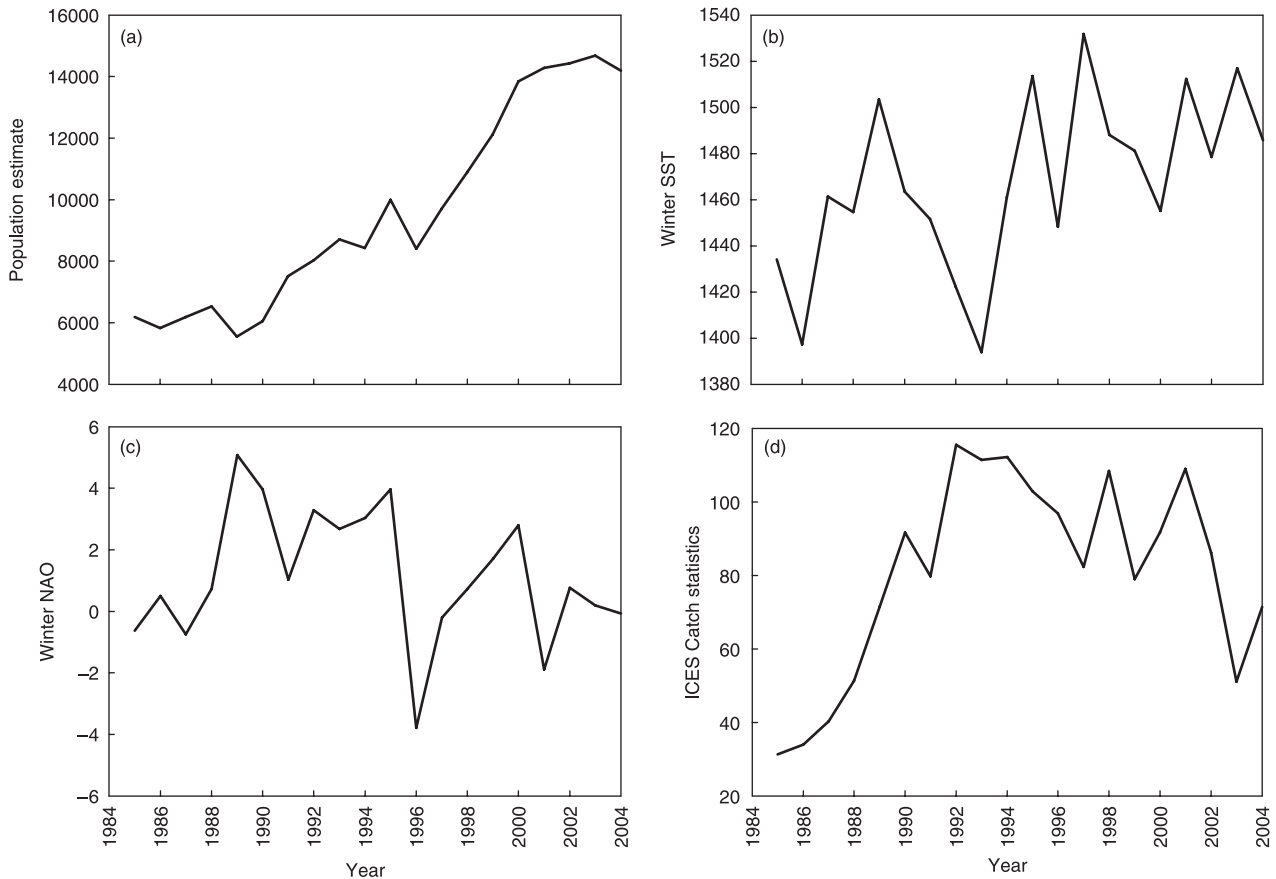


Fig. 1. Inter-annual variation in explanatory covariates. (a) Common guillemot population estimates (total number of birds at colony including breeders, failed breeders and immatures); (b) winter sea-surface temperature (<http://badc.nerc.ac.uk/browse/badc/ukmo-hadisst>); (c) winter North Atlantic Oscillation index (www.cgd.ucar.edu/cas/jhurrell/indices.html); (d) International Council for the Exploration of the Seas (ICES) annual catch statistics (FAO Fisheries Department) from common guillemot wintering areas (ICES area 27 subareas VIIa,e,f,g,h,j and VIIIa,b,c,d) for European sprat *Sprattus sprattus* L., European anchovy *Engraulis encrasicolus* L., European sardine *Sardina pilchardus* Walbaum, Atlantic herring *Clupea harengus* L. and other clupeoids (www.fao.org/fi).

2 is a bird that has returned to the colony but is not breeding (herein a non-breeder); and state 3 is a bird that has returned to the colony and is breeding (herein a breeder). Much of the modelling framework used in our analysis was based on recently published work which used the detailed knowledge of guillemot breeding biology to model recruitment of common guillemots to a large Scottish colony (Crespin *et al.* 2006).

Multistate techniques necessarily result in models with a very large number of parameters. To reduce problems of redundancy and model interpretation, a number of model parameters were constrained based on biologically appropriate assumptions (Lebreton *et al.* 2003). Once a chick is marked and released as a juvenile, it can be seen at the colony again only as either a non-breeder or as a breeder. Therefore resighting probability of a juvenile was constrained to zero. Recruitment in common guillemots is a two-stage process. A preliminary visit to the colony as a non-breeder is a consistent behaviour of this species (Birkhead & Hudson 1977; Hatchwell & Birkhead 1991; Crespin *et al.* 2006), and the vast majority (93.5%) of our birds were seen as a non-breeder before joining the breeding population. A small number of individuals (6.5%) were resighted for the first time as breeders, that is, they were not seen as a non-breeder before recruiting. In the majority of cases, these birds were first resighted at age 10 or over, and most were probably missed prior to

this first resighting occasion (some parts of the colony are obscured). For this reason, they were considered anomalous and excluded from further analysis. Transition from a juvenile directly to a breeder was considered very unlikely and therefore constrained to zero.

Some birds that had already recruited into the breeding population were seen in subsequent years as non-breeders. It is unclear whether these birds were breeding but had failed before an egg or chick was noticed, or whether they were not breeding in that year. In either event, these few birds were considered as not resighted (with encounter event coded as zero), since this accounts for potential heterogeneity in the probability of recording a breeding event. Therefore transition probability from a non-breeder to a breeder was considered unidirectional.

Age can have important effects on parameter estimation, but our data allowed only limited investigation of age because of the complexity of the models. We investigated some age effects on survival of non-breeding birds (separating into birds aged 3 or 4 years and those aged ≥ 5 years) and breeders (birds aged 4 years and those aged ≥ 5 years). Transition of birds from the juvenile to non-breeder state (first stage of recruitment) included age dependence: 1-year-old birds are never seen at the colony, so the first stage of recruitment included only birds aged ≥ 2 years.

Model selection and goodness-of-fit

Recent developments in goodness-of-fit procedures for multistate CMR models now provide the opportunity to select models that fit the data well (Burnham & Anderson 2002). This is an essential process in all CMR analyses, as without the selection of an appropriate starting model, high levels of deviance and low levels of precision will result in selection of inappropriate models and biased model estimates (Pradel *et al.* 2005). We used the program U-CARE (Choquet *et al.* 2005a) to assess the fit of the data to a Jolly MoVe (JMV) model. This model is more general than the conditional Arnason–Schwartz (CAS), as it allows encounter probabilities to vary by the previous state (Choquet *et al.* 2005a). The goodness-of-fit tests are comprised of two components that: (1) examine the influence of past capture histories on individuals captured and released at the same time on the same site (test 3G); and (2) compare the encounter history of individuals caught at a given occasion with those not caught, but known to be alive, at the same occasion (test M). Subcomponents of test 3G consist of tests for transience (test 3G.SR) and memory effects (test WBWA); however, the introduction of age-dependence in survival models means goodness-of-fit is conducted excluding these components (Crespin *et al.* 2006).

Models were selected using Akaike's information criterion (AIC), modified for small sample bias, and a lack of fit (including a variance inflation factor, c , see Results: Goodness-of-fit), quasi-AIC_c (QAIC_c; Burnham & Anderson 2002). Changes in QAIC_c (termed Δ QAIC_c) were used to select the preferred model in terms of both parsimony and quality of fit, and models with Δ QAIC_c < 2 were considered to be equal. In such cases, a model with the lowest number of parameters was preferred (Lebreton *et al.* 1992). Model likelihood was also assessed by calculating QAIC_c weights (Anderson *et al.* 2000).

Multistate models necessarily require a large number of parameters, which may lead to problems of parameter redundancy and local minima in deviance. We examined parameter identifiability using the numerical Catchpole, Morgan, Freeman (CMF) approach for redundancy implemented in M-SURGE ver. 1.7 (Choquet *et al.* 2005b).

Model covariates

We examined the influence of five explanatory variables suspected to have an influence on temporal variability in recruitment and survival of juveniles and non-breeders (Fig. 1); common guillemot population size (Fig. 1a), winter sea-surface temperature (SST) (Fig. 1b), winter North Atlantic Oscillation (WNAO) index (Fig. 1c), International Council for the Exploration of the Seas (ICES) fisheries catch statistics of guillemot forage fish (Fig. 1d), and incidence of four major overwinter oil spills (*Aegean Sea*, December 1992; *Sea Empress*, February 1996; *Erika*, December 1999; *Prestige*, November 2002; Fig. 2a). More details of these explanatory variables are given by Votier *et al.* (2005). Annual whole-island counts of common guillemots on Skomer are the number of individuals on breeding ledges, and represent breeding and non-breeding individuals, which may influence survival and recruitment mediated by competition for food or nest sites. Previous studies have shown lagged effects of environmental conditions (e.g. Thompson & Ollason 2001), so we also modelled 1-year lags in all cases. We considered the influence of explanatory variables as statistically significant if their 95% CI excluded zero. Moreover, in models where unexplained residual variance exists, we multiplied confidence intervals by the square root of the mean deviance due to year: $[(\text{Dev}(\text{covariate}) - \text{Dev}(\text{time})) / ((\text{df}(\text{time}) - \text{df}(\text{covariate})))]$.

Where temporal trends occur in both demographic rates and candidate covariates, it is important to control for such effects

before reliable inference can be made. Therefore we investigated whether demographic variables had significant linear trends.

The magnitude of covariate effects was estimated using analysis of deviance (ANODEV) (Skalski *et al.* 1993):

$$r_{\text{QDev}}^2 = [\text{Dev}(\text{covariate}) - \text{Dev}(\text{constant})] / [\text{Dev}(\text{time}) - \text{Dev}(\text{constant})] \quad \text{eqn 1}$$

Covariate, constant and time refer to deviance of models constrained by covariates, fixed to be constant and to vary freely over time, respectively.

We used U-CARE (Choquet *et al.* 2005a) for conducting goodness-of-fit testing and producing M-arrays (see Appendices S2–S4), and M-SURGE (Choquet *et al.* 2005b) for multistate modelling and to assess parameter redundancy.

Results

NON-BREEDING SEASON DISTRIBUTION AND INCIDENCE OF OIL SPILLS

A total of 1676 guillemots ringed in Dyfed and Wexford were recovered during the period August–April. The distribution of ringed birds was primarily throughout the Irish Sea, but large numbers of birds were also recovered along the coast of the Bay of Biscay and eastward through the English Channel. Importantly, there was overlap between the distribution of recovered guillemots and four major oil spills that occurred during the period of this study (Fig. 2). We found marked differences in the distribution of recoveries by the three age classes. Birds aged between 0 and 3 years were very widely spread during the non-breeding season, with core recovery areas (50% kernels) within south-west England, south-east Ireland, the Atlantic coast of Brittany and the south-east coast of the Bay of Biscay (Fig. 2b). Birds aged 4–6 years shared cores of recovery with younger birds within south-west England, south-east Ireland and the Atlantic coast of Brittany, but the distribution of all recoveries was more restricted than that of younger birds (Fig. 2c). Birds aged 6 years and over showed core areas of recovery similar to birds aged 4–6, although more restricted (Fig. 2d).

CAPTURE–MARK–RECAPTURE

Goodness-of-fit tests and parameter identifiability

Goodness-of-fit tests revealed evidence of lack of fit in the data (Table 1). In particular, there was evidence of immediate trap-dependence (test M ITEC; Table 1). This type of encounter heterogeneity is the result of differences in the resighting probability of an individual dependent on whether or not it was seen on the previous occasion, resulting in biases in the estimation of survival probabilities. One way to overcome these problems is to model different resighting rates depending on whether an animal was seen at the previous observation occasion (Pradel 1993). This trap-dependence can be modelled as age-dependence but, in this data set, inclusion of trap-dependence resulted in a large number of inestimable parameters (not shown). Therefore, to reduce

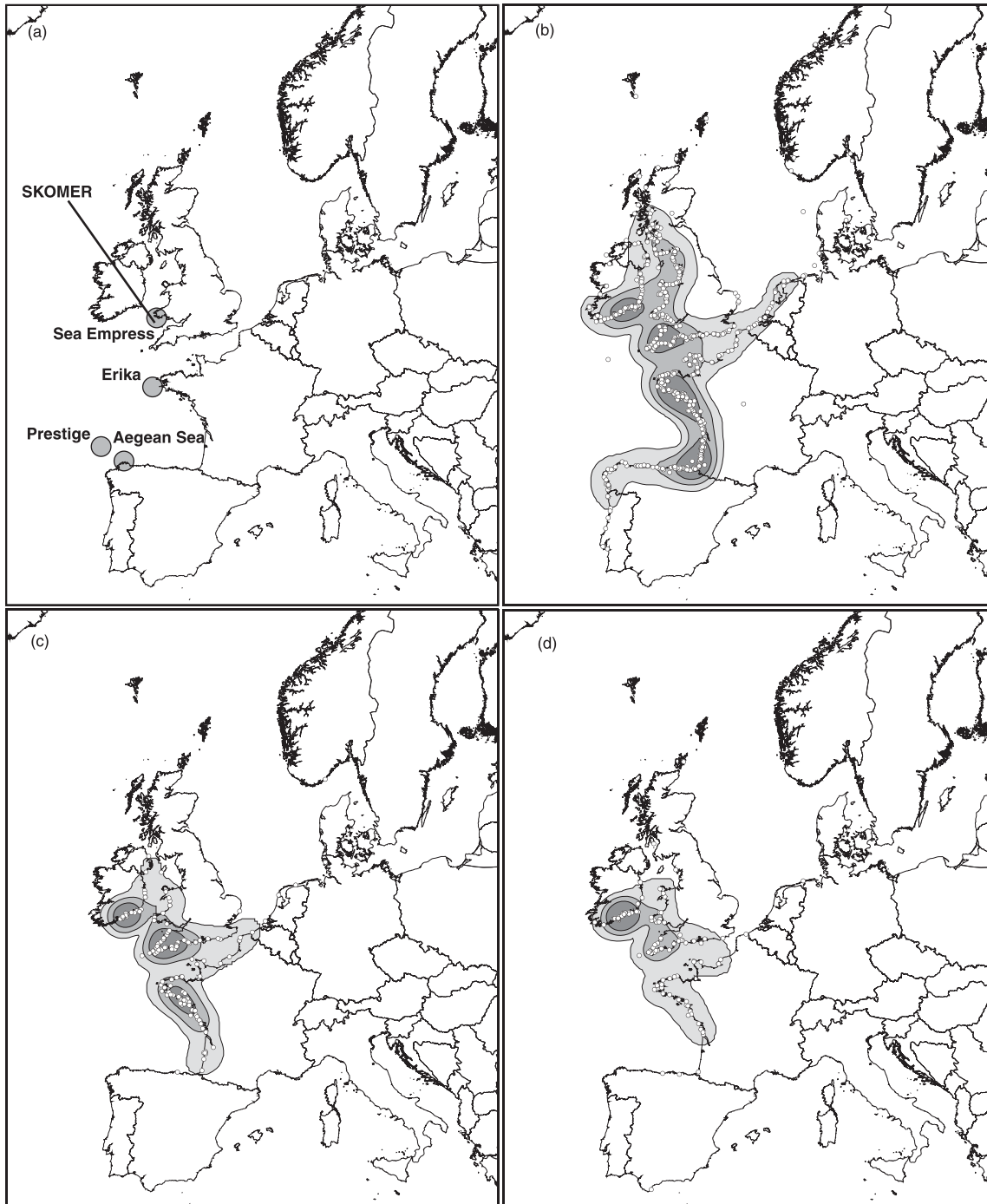


Fig. 2. (a) Location of Skomer Island, Wales and four oil tankers that ran aground, releasing >10000 t of crude oil. (b–d) 95, 75 and 50% kernel density contours (represented by increasingly dark shades of grey) for common guillemots ringed at southern Irish Sea colonies and recovered during the non-breeding season: (b) age 0–3 years ($n = 1226$); (c) age 4–6 years ($n = 290$); (d) age ≥ 6 years ($n = 160$).

problems of this nature, we incorporated a variance inflation factor (\hat{c}), based on the sum of the goodness-of-fit tests, to correct for this and other resighting heterogeneities. This value of 2.36 (calculated as the χ^2 goodness-of-fit statistic divided by the degrees of freedom) indicated high levels of overdispersion, but this adjustment results in inflated sampling variances, which reduces the risk of committing type I errors. In addition, with \hat{c} being < 3 , the use of QAIC_c is

justified and the model estimates are likely to be reliable (White & Burnham 1999).

Application of the CMF approach in M-SURGE 1.7 revealed that all parameters were identifiable, with the exception of the annual survival estimates of juvenile guillemots in 1992, 1993 and 1994. These parameters were inestimable because virtually no juveniles were marked in these years (Appendix S2). Thus, juvenile survival for the period 1992–94 was fixed

Table 1. Result of goodness-of-fit tests for the multistate capture–mark–recapture models

Test	χ^2	d.f.	<i>P</i>	Overdispersion factor (\hat{c})
3G.SM	108.726	56	<0.001	1.93
M ITEC	13.726	7	0.056	1.96
M LTEC	17.2	5	0.004	3.44
LRT (JMV vs. AS)	212.914	81	<0.001	2.63
Sum	352.095	149	<0.001	2.36

Subcomponents are described by Pradel *et al.* (2005); see text.

to the average value for the other years of this study (0.6981). The sensitivity of the analysis to this uncertainty was assessed by repeating the analysis with the upper and lower 95% CI, which produced very similar results in the final model selected.

Recapture

Models with state dependence in recapture probabilities had much greater support than those with no difference among states ($\Delta\text{QAIC}_c = 763.84$). This difference is largely because juveniles are not sighted back at the colony; non-breeders ($0.8351 \pm 95\% \text{ CI: } 0.027$) and breeders (0.8041 ± 0.039) have similar recapture probabilities. Further, models with capture varying across years received considerable support (with a decrease in QAIC_c of ≈ 27). Differences in recapture among years may be explained by our covariates influencing attendance patterns of birds. However, models constrained by oil spills, WNAO, winter SST, population size and fishery catch statistics (not shown) were not better supported than a model varying among years. Therefore state and time-dependence in recapture probabilities was used for all remaining modelling.

Table 2. Model selection to estimate factors influencing juvenile survival for common guillemots from Skomer Island

<i>p</i>	<i>S</i>	Ψ	np	QDEV	QAIC _c	ΔAIC_c	AIC weight	<i>R</i> ²	Slope ($\pm 95\% \text{ CI}$)	Description
p_t^r	$S_{\text{time, age, age}}^1 \ 2 \ 3$	General	58	8281.43	3621.08	0	0.6768	–	–	Time
p_t^r	$S_{\text{SST, age, age}}^1 \ 2 \ 3$	General	45	8341.84	3624.68	3.6	0.1119	0.32	–1.14 (0.65)	Winter SST
p_t^r	$S_{\text{SST+Oil Lag, age, age}}^1 \ 2 \ 3$	General	46	8337.21	3624.71	3.63	0.1102	0.37	–1.54 (0.86), NS	SST + Oil with 1-year lag
p_t^r	$S_{\text{SST+Oil, age, age}}^1 \ 2 \ 3$	General	46	8340.97	3626.31	5.23	0.0495	0.33	–1.14 (0.65), NS	SST + Oil
p_t^r	$S_{\text{SST+Pop, age, age}}^1 \ 2 \ 3$	General	46	8341.12	3626.37	5.29	0.0481	0.33	–1.08 (0.69), NS	SST + population size
p_t^r	$S_{\text{Pop, age, age}}^1 \ 2 \ 3$	General	45	8363.57	3633.88	12.8	0.0011	0.07	NS	Population size
p_t^r	$S_{\text{constant, age, age}}^1 \ 2 \ 3$	General	44	8370.19	3634.69	13.61	0.0008	–	–	Constant
p_t^r	$S_{\text{Linear trend, age, age}}^1 \ 2 \ 3$	General	45	8365.74	3634.81	13.73	0.0007	0.05	NS	Linear trend over time
p_t^r	$S_{\text{Oil Lag, age, age}}^1 \ 2 \ 3$	General	45	8366.88	3635.29	14.21	0.0006	0.04	NS	Oil with 1-year lag
p_t^r	$S_{\text{Oil, age, age}}^1 \ 2 \ 3$	General	45	8369.07	3636.22	15.14	0.0003	0.01	NS	Oil

np, Number of identifiable parameters; NS, non-significant slope.

General model: *p*, recapture, state-dependent, constant over time. *S*, survival, variation among states with two age classes in states 1 (juveniles) and 3 (breeder), as well as three age classes in state 2 (non-breeder). Ψ , transition: transition from juvenile to non-breeder was constrained to zero for birds <2 years old and combined for the remaining age classes, and variation explored using candidate covariates.

Top 10 models are shown constrained by candidate covariates for sea-surface temperature (SST), four major oil-pollution events (Oil), winter North Atlantic Oscillation index (NAO), Skomer guillemot population size (Pop) and a linear trend over time (models including ICES fisheries catch statistics were very poorly supported). A model with time dependence had the lowest QAIC_c value and was therefore used for subsequent modelling (bold). Variance inflation factor $\hat{c} = 2.36$, therefore AIC_c becomes the quasi-likelihood AIC_c.

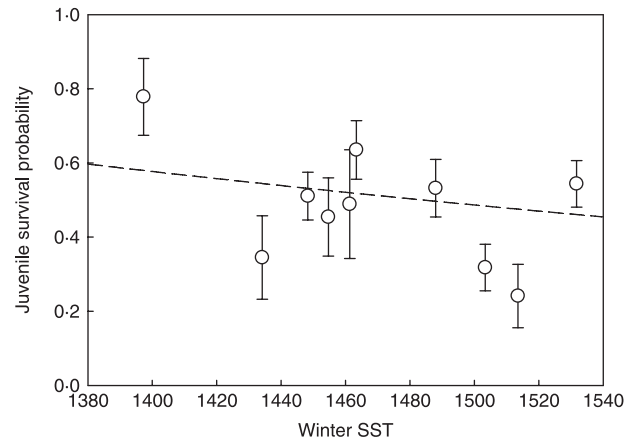


Fig. 3. Survival probability of juvenile common guillemots is weakly correlated with winter sea-surface temperature (1986–2000). Estimates are compound 2-year survival ($\pm 1 \text{ SE}$), and represent data only from the first 14 cohorts in the study, excluding data from 4 years with unreliable parameter estimates due to data sparseness. The dashed line represents estimates from the covariate model ($p_t^r, S_{\text{SST, age, age}}^1 \ 2 \ 3, \Psi_{\text{age, age}}^{1-2 \ 2-3}$).

Survival

The preferred survival model included differences among states, interannual variation for the juvenile state only, and age-dependence for the non-breeding and breeding states. Annual variation in juvenile survival may be a function of candidate explanatory variables and, although the time-dependent model had the lowest QAIC_c value, there was a negative correlation between juvenile survival and winter SST (Table 2; Fig. 3). However, when the confidence intervals were corrected for residual unexplained variation, this effect was no longer statistically significant ($\beta_{\text{SST}} = -1.14 \pm 1.39$).

Table 3. Model selection to estimate first stage of recruitment probabilities for common guillemots, *Uria aalge*, from Skomer Island

p	S	Ψ	np	QDEV	QAIC _c	Δ AIC _c	AIC weight	R^2	Slope ($\pm 95\%$ CI)	Description
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+Oil, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	57	8251.46	3610.38	0	0.5545	0.30	+0.95 (0.49)	Oil
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+Oil+SST, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	58	8249.44	3611.53	1.15	0.3120	0.32	+0.84 (0.53), NS	Oil + SST
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+Time, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	74	8178.69	3613.54	3.16	0.1142	–	–	Time
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+SST, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	57	8273.19	3619.59	9.21	0.0055	0.10	-1.36(1.31)	Winter SST
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+Oil Lag, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	57	8276.33	3620.91	10.53	0.0029	0.07	NS	Winter NAO with 1-year lag
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+Oil Lag, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	57	8277.24	3621.3	10.92	0.0024	0.06	NS	Oil with 1-year lag
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+NAO, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	57	8277.48	3621.41	11.03	0.0022	0.06	NS	Winter NAO
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+constant, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	56	8283.39	3621.91	11.53	0.0017	0	–	Constant
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+SST Lag, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	57	8279.01	3622.06	11.68	0.0016	0.04	NS	Winter SST with 1-year lag
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+Linear trend, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	57	8279.06	3622.08	11.7	0.0016	0.03	NS	Linear trend
p_t^r	$S_{time, age, age}^{1, 2, 3}$	$\Psi_{age1c, age2+POP, age}^{1 \rightarrow 2, 2 \rightarrow 3}$	57	8280.05	3622.50	12.12	0.0013	0.03	NS	Population size

p = recapture; S = survival; Ψ = transition; np = number of identifiable parameters; NS = non-significant slope. Abbreviations as in Table 2. Transition from state 1 (juvenile) to state 2 (non-breeder) was split into two age classes: birds age 1, which are never observed; and birds age ≥ 2 , which were constrained by candidate covariates. Top 10 covariate models are shown along with time-dependent and constant models. The most parsimonious model is indicated in bold type.

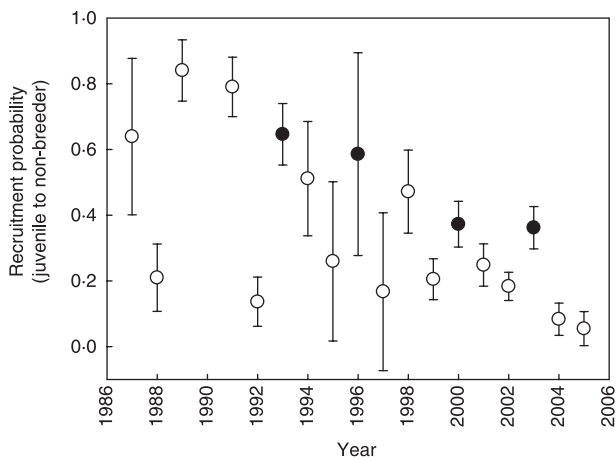


Fig. 4. Annual variation in the first stage of recruitment in common guillemots and incidence of four major oil-pollution incidents (1986–2005). Symbols indicate estimates (± 1 SE) taken from the model with transition varying by time ($p_t^r, S_{time, age, age}^{1, 2, 3}, \Psi_{age1c, age2+constant, age}^{1 \rightarrow 2, 2 \rightarrow 3}$); closed symbols indicate years following a major oil spill.

None of the other candidate covariates had a statistically significant effect on juvenile survival. No relationship between any of the candidate covariates and the survival of non-breeding guillemots was statistically supported (Appendix S7).

Transition/recruitment probabilities

Transition between the juvenile state and the non-breeder state can be viewed as the first component of recruitment. Although no 1-year-old guillemots have ever been encountered at Skomer, for the remaining age classes combined the probability of returning varied over time (Table 3; Fig. 4).

We investigated the influence of candidate covariates on the first stage of recruitment (Table 3). The model with most support included the incidence of four major overwinter oil spills, which was 1.78 times better supported than the next

best covariate model. The positive effect of oil spills was statistically significant, and explained 30% of the total variation (Table 3), although after correcting for unexplained residual deviance, the 95% CI overlapped with zero ($\beta_{oil} = +0.9525 \pm 1.0183$). On average, recruitment from a juvenile to a non-breeder in the years following an oil spill was 0.5733 (± 0.1049) compared with 0.3413 (± 0.0547) in all other years. A significant negative effect of SST on recruitment explained 10% of the total variation (Table 3), but was not statistically significant when corrected for unexplained residual deviance ($\beta_{SST} = -1.3601 \pm 3.09$). A model including additive effects of oil and SST explained 32% of the variation in recruitment. None of the lagged covariates received strong support. Despite an apparent linear trend over time (Fig. 4), models including this covariate alone were not well supported (Table 3).

The second stage of recruitment (transition from a non-breeder to a breeder or accession to reproduction) was best modelled as constant over time (Appendix S8), but varied between birds aged 4 years (0.0056 ± 0.0118) and those aged ≥ 5 years (0.2087 ± 0.0449). None of the candidate covariates had a significant effect on this stage of recruitment (Appendix S8).

Discussion

RECRUITMENT PROBABILITY

Using a multistate CMR framework, we estimated recruitment of common guillemots as a two-stage process. The probability of a juvenile common guillemot returning to enter the non-breeding population – the first stage of recruitment – was higher in years following four major oil spills compared with ‘normal’ winters (Fig. 4). Although the effect of oil was marginally non-significant ($P < 0.056$ following correction for residual unexplained variance), the average recruitment probability postspills was almost double that in other years. Previous studies from the same colony showed a doubling of adult mortality coincident with the same oil spills but, on

average, this had no detectable effect on the number of individual birds at the colony over the same period (Votier *et al.* 2005). We believe the most parsimonious explanation for these results is that high levels of adult overwinter mortality associated with oil spills reduced levels of competition at the breeding colony, allowing increased levels of immature recruitment to compensate for these losses. These are consistent with previous studies suggesting that increased recruitment of non-breeders may be able to buffer the effects of high adult mortality (Potts *et al.* 1980; Porter & Coulson 1987; Klomp & Furness 1992; Pradel *et al.* 1997; Tavecchia *et al.* 2007). Our findings differ from previous studies, however, as we have shown an increase in the first stage of recruitment, from a juvenile to a non-breeder. It is not clear whether this is in response to higher non-breeder mortality or because non-breeders have moved to breeding ledges following increased breeder mortality. We know of no other studies that demonstrate this response to oil spills, nor of any demonstrating compensatory recruitment using current multistate CMR recruitment models.

For compensatory recruitment to occur requires that at least sites are limited in some way, and that there is a pool of potential recruits immediately available (Porter & Coulson 1987; Croxall & Rothery 1991). Non-breeding congregations are a common feature among colonial seabirds, but we know of no evidence to suggest that space is limited at non-breeding sites. Nevertheless, the patterns here suggest that recruitment of non-breeders is to some extent density-dependent. Pradel *et al.* (1997) found that recruitment of greater flamingos, *Phoenicopterus ruber roseus* Pallas, was higher following severe overwinter mortality, an effect that was observed for 3 years following the harsh winter. However, the absence of a detectable lag in the effect of oil spills on common guillemot recruitment suggests that those sites that became available following oil-related mortality were quickly occupied.

We found a weak negative relationship between winter SST and the first stage of recruitment (Table 3), which explained 10% of the variation in recruitment. Increasing sea temperatures may have negative impacts on seabirds via bottom-up effects on food availability or quality (Frederiksen *et al.* 2004; Sandvik *et al.* 2005).

Recruitment from a non-breeder to a breeder was not significantly affected by any candidate covariates (Appendix S8), and there are several possible explanations why this demographic parameter did not show patterns similar to those shown in the first stage of recruitment. Of the 1522 guillemots marked as a chick, only 12% were confirmed breeders at Skomer, compared with 45% of birds recorded as a non-breeder (Appendices S5 and S6). This difference in sample size means lower statistical power for detecting factors influencing variation in the second stage of recruitment compared with the first. Furthermore, space required for a juvenile to recruit may be contingent on two events: the death of a non-breeder, or a non-breeder recruiting to the breeding population, whereas space required for a non-breeder to recruit to the breeding population is contingent on a single event – the loss of a breeder through death or emigration.

SURVIVAL ESTIMATES

Annual variation in juvenile survival was pronounced, and although the model with the lowest QAIC_c value varied with time, there was a weak negative correlation between juvenile survival and winter SST (Table 2; Fig. 3). Previous studies have demonstrated negative relationships between SST and seabird survival, probably mediated by bottom-up effects on the food chain (Frederiksen *et al.* 2004; Sandvik *et al.* 2005). We found no influence of oil pollution on juvenile survival, despite the core distribution of ringed guillemots aged 0–3 years overlapping with three of the four major oil spills (Fig. 2). This may be because juvenile survival estimates were not available for all years (Fig. 3). Moreover, as young guillemots are far more widely dispersed than older guillemots (Fig. 2), the risk of becoming oiled is spread over a far greater area for juveniles compared with adults and non-breeders. Although analysis of oiled guillemots affected by the *Erika* and *Prestige* spills showed a high proportion of immature birds (Grantham 2004) because they probably came from a wide geographical area, it is difficult to detect population-level effects.

We converted 2-year juvenile survival rate to estimate constant annual survival as 0.6981 (± 0.0427), which is one of the highest values of juvenile survival estimated for a seabird. Using the same modelling framework, Crespin *et al.* (2006) estimated juvenile guillemot survival on the Isle of May to be 0.576 (95%, CI 0.444–0.708). Following the introduction of more sophisticated CMR analysis techniques correcting for sighting heterogeneity, estimates of annual survival tended to increase (Lebreton & Clobert 1991). Given the paucity of studies that have estimated survival rates of immature seabirds, we might anticipate a similar increase in estimated rates. Estimating juvenile survival is extremely taxing because these birds are not normally observable; however, analysing data on ringing recoveries can provide a robust estimate of this parameter (Williams *et al.* 2001).

Our explanatory covariates did not explain a significant proportion of the variance in the survival of non-breeding guillemots (Appendix S7). This may be because this age class is not susceptible to oil pollution, climate-related effects or competition with fisheries, or because survival was influenced by some other, unmeasured factor. Alternatively, we cannot exclude the possibility of a type II statistical error because of the relatively small number of birds resighted in this age class.

Survival of non-breeding adult guillemots was 0.9534 (± 0.0770) for 3-year-olds; 0.8744 (± 0.0586) for 4-year-olds; and 0.7815 (± 0.0449) for birds aged 5–20 combined. These values are similar to, but slightly higher than, those estimated in the same manner on the Isle of May (Crespin *et al.* 2006). Decreasing non-breeder survival with age may be a result of individuals that remain in the non-breeding component being of lower phenotypic quality compared with those that recruit to become breeders.

Estimates of adult breeder survival are significantly lower (0.859 \pm 0.027) than those reported previously from Skomer (0.955 \pm 0.006) by Votier *et al.* (2005). The earlier study on Skomer analysed birds marked as established breeders, which

have lower rates of emigration compared with first-time or inexperienced breeders, as evidenced by the transience effect observed in this study (Test 3G.SM, Table 1). This difference in dispersal is consistent with lower survival estimates found in the present study, and highlights the importance of transience in seabird populations (Tavecchia *et al.* 2007).

IMPLICATIONS FOR ASSESSING THE IMPACT OF OIL POLLUTION

Previously, we showed that four major oil spills doubled adult common guillemot mortality but had no significant effect on the number of individuals counted at the breeding colony (Votier *et al.* 2005). The results here suggest this discrepancy was because of compensatory recruitment rather than variance in colony counts, and further highlights the value of CMR studies. Juvenile guillemots are an abundant subset of the population (Appendices S5 and S9), which perhaps explains why they are able to compensate for relatively large numerical losses to the total population due to stochastic mortality. Nevertheless, a significant reduction in this age class may compromise their ability to buffer environmental stress.

Another adverse impact of increased juvenile recruitment may be an increase in the number of inexperienced breeders in the population. However, detecting such an effect at a population level may be difficult. It is unlikely that both members of a breeding pair would be lost as a result of oil spills unless both members of a pair winter together, and there is no evidence that they do, therefore the most likely route for recruitment is to pair with an established breeder. Work has shown that breeding success of divorced guillemots that retain their original territory and obtain a new mate remains largely unaffected (Jeschke *et al.* 2007). Therefore incoming birds are unlikely to reduce breeding success unless both members of a breeding pair are new recruits.

Despite four major oil spills (as well as the impact of environmental perturbations), the common guillemot population at Skomer has increased significantly over the past two decades (Fig. 1a). From a management point of view, one might argue that oil spills are not deleterious at the population level, as common guillemots are able to buffer their impact. However, we do not know how the Skomer population would have changed in the absence of these events, and there is good evidence that common guillemots used to be far more abundant on Skomer in the past than they are now (Birkhead & Ashcroft 1975). An important future avenue of research would be to model the number of common guillemots when free from oil spills using population projection matrices (Hodgson & Townley 2004). A similar iterative approach could be used to quantify the impact of repeated oil spills of differing intensity on population trends of common guillemots and other top marine predators potentially affected.

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References

- Anderson, D.R., Burnham, K.P. & Thompson, W.L. (2000) Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, **64**, 912–923.
- Birkhead, T.R. & Ashcroft, R.E. (1975) Auk numbers on Skomer Island. *Nature in Wales*, **14**, 223–233.
- Birkhead, T.R. & Hudson, P.J. (1977) Population parameters for the Common Guillemot *Uria aalge*. *Ornis Scandinavica*, **8**, 145–154.
- Birkhead, T.R. & Nettleship, D.N. (1980) *Census Methods for Murres, Uria spp.: A Unified Approach*. Occasional Paper No. 43. Canadian Wildlife Service, Ottawa.
- Brownie, C., Hines, J.E., Nichols, J.D., Pollock, K.H. & Hestbeck, J.B. (1993) Capture–recapture studies for multiple strata including non-Markovian transition probabilities. *Biometrics*, **49**, 1173–1187.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Choquet, R., Reboulet, A.M., Pradel, R., Gimenez, O. & Lebreton, J.-D. (2005a) *U-CARE 2.2 User's Manual*. CEFE, Montpellier, France. <http://www.cefe.cnrs.fr/biom/en/software.htm>
- Choquet, R., Reboulet, A.M., Pradel, R., Gimenez, O. & Lebreton, J.-D. (2005b) *M-SURGE 1.7 User's Manual*. CEFE, Montpellier, France. <http://www.cefe.cnrs.fr/biom/en/software.htm>
- Crespin, L., Harris, M.P., Lebreton, J.-D., Frederiksen, M. & Wanless, S. (2006) Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology*, **75**, 228–238.
- Croxall, J.P. & Rothery, P. (1991) Population regulation of seabirds: implications of their demography for conservation. *Bird Population Studies* (eds C.M. Perrins, J.-D. Lebreton & G.J.M. Hiron), pp. 272–296. Oxford University Press, Oxford, UK.
- Frederiksen, M., Wanless, S., Harris, M.P., Rothery, P. & Wilson, L.J. (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology*, **41**, 1129–1139.
- Grantham, M.J. (2004) Age structure and origins of British and Irish Guillemots *Uria aalge* recovered in recent European oil spills. *Atlantic Seabirds*, **6**, 95–108.
- Grimm, V., Revilla, E., Groeneveld, J. *et al.* (2005) Importance of buffer mechanisms for population viability analysis. *Conservation Biology*, **19**, 578–580.
- Harris, M.P., Halley, D.J. & Swann, R.L. (1994) Age of first breeding in Common Murres. *Auk*, **111**, 207–209.
- Hatchwell, B.J. & Birkhead, T.R. (1991) Population dynamics of Common Guillemots *Uria aalge* on Skomer Island, Wales. *Ornis Scandinavica*, **22**, 55–59.
- Hodgson, D.J. & Townley, S. (2004) Linking life history changes to population dynamic responses: the transfer function of a projection matrix perturbation. *Journal of Applied Ecology*, **41**, 1155–1161.

- Hooge, P.N. & Eichenlaub, B. (2000) *Animal movement extension to ARCVIEW, Ver. 2.0*. Alaska Science Center – Biological Science Office, US Geological Survey, Anchorage, AK, USA.
- Jeschke, J.M., Wanless, S., Harris, M.P. & Kokko, H. (2007) How partnerships end in guillemots, *Uria aalge*: chance events, adaptive change, or forced divorce? *Behavioural Ecology*, **18**, 460–466.
- Klomp, N.I. & Furness, R.W. (1992) Nonbreeders as a buffer against environmental stress: declines in the numbers of great skuas on Foula, Shetland and prediction of future recruitment. *Journal of Applied Ecology*, **29**, 341–348.
- Lebreton, J.-D. & Clobert, J. (1991) Bird population dynamics, management and conservation: the role of mathematical modelling. *Bird Population Studies: Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. Lebreton & G.J.M. Hiron), pp. 105–125. Oxford University Press, Oxford, UK.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Lebreton, J.-D., Hines, J.E., Pradel, R., Nichols, J.D. & Spendlow, J.A. (2003) Estimation by capture–recapture of recruitment and dispersal over several sites. *Oikos*, **101**, 253–264.
- Lee, D.E., Nur, N. & Sydeman, W.J. (2007) Climate and demography of the planktivorous Cassin's auklet *Ptychoramphus aleuticus* off northern California: implications for population change. *Journal of Animal Ecology*, **76**, 337–347.
- Nichols, J.D., Hines, J.E., Pollock, K.H., Hinz, R.L. & Link, W.A. (1994) Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. *Ecology*, **75**, 2052–2065.
- Peterson, C.H., Rice, S.D., Short, J.W. *et al.* (2003) Long-term ecosystem response to the *Exxon Valdez* oil spill. *Science*, **302**, 2082–2086.
- Phillips, R.A., Silk, J.R.D., Croxall, J.P. & Afanasyev, V. (2006) Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biological Conservation*, **129**, 336–347.
- Porter, J.M. & Coulson, J.C. (1987) Long-term changes in recruitment to the breeding group, and the quality of recruits at a Kittiwake *Rissa tridactyla* colony. *Journal of Animal Ecology*, **56**, 675–689.
- Potts, G.R., Coulson, J.C. & Deans, I.R. (1980) Population dynamics and breeding success of the shag *Phalacrocorax aristotelis* on the Farnes Islands, Northumberland. *Journal of Animal Ecology*, **49**, 465–484.
- Pradel, R. (1993) Flexibility in survival analysis from recapture data: handling trap-dependence. *Marked Individuals in the Study of Bird Population* (eds J.-D. Lebreton & P.M. North), pp. 29–37. Birkhäuser-Verlag, Basel, Switzerland.
- Pradel, R., Johnson, A.R., Viallefont, A., Nager, R. & Cézilly, F. (1997) Local recruitment in the Greater Flamingo: a new approach using capture–mark–recapture data. *Ecology*, **78**, 1431–1445.
- Pradel, R., Gimenez, O. & Lebreton, J.-D. (2005) Principles and interest of GOF tests for multistate capture–recapture models. *Animal Biodiversity and Conservation*, **28**, 189–204.
- Sandvik, H., Erikstad, K., Barrett, R. & Yoccoz, N.G. (2005) The effect of climate on adult survival of five species of North Atlantic seabirds. *Journal of Animal Ecology*, **74**, 817–831.
- Schwarz, C.J., Schweigert, J.F. & Arnason, A.N. (1993) Estimating migration rates using tag-recovery data. *Biometrics*, **49**, 177–193.
- Skalski, J.R., Hoffmann, A. & Smith, S.G. (1993) Testing the significance of individual- and cohort-level covariates in animal survival studies. *Marked Individuals in the Study of Bird Population* (eds J.-D. Lebreton & P.M. North), pp. 9–28. Birkhäuser-Verlag, Basel, Switzerland.
- Tavecchia, G., Pradel, R., Genovart, M. & Oro, D. (2007) Density-dependent parameters and demographic equilibrium in open populations. *Oikos*, **116**, 1481–1492.
- Thompson, P. & Ollason, J. (2001) Lagged effects of ocean climate change on fulmar population dynamics. *Nature*, **413**, 417–420.
- Velando, A., Munilla, I. & Leyenda, P.M. (2005) Short-term indirect effects of the Prestige oil spill on European shags at Illas Cies (Galicia, Spain): changes in prey availability. *Marine Ecology Progress in Series*, **302**, 263–274.
- Votier, S.C., Furness, R.W., Bearhop, S. *et al.* (2004) Changes in fisheries discard rates and seabird communities. *Nature*, **427**, 727–730.
- Votier, S.C., Hatchwell, B.J., Beckerman, A. *et al.* (2005) Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecological Letters*, **8**, 1157–1164.
- White, G.C. & Burnham, K.P. (1999) Programme MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (Suppl.), 120–139.
- Williams, B.K., Nichols, J.D. & Conroy, M.J. (2001) *Analysis and Management of Animal Populations*. Academic Press, London.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Number of common guillemots *Uria aalge* ringed in Britain and Ireland 1910–2005

Appendix S2. M-array for common guillemots marked as juveniles (state 1) and resighted as non-breeders (state 2)

Appendix S3. M-array for common guillemots recorded as non-breeders (state 2) and resighted as non-breeders (state 2)

Appendix S4. M-array for common guillemots marked as non-breeders (state 3) and re-sighted as breeders (state 3)

Appendix S5. Age at first re-sighting (years) in common guillemots ringed at Skomer, Wales

Appendix S6. Age at first-breeding (years) in common guillemots ringed at Skomer, Wales

Appendix S7. Model selection to estimate factors influencing non-breeder survival of common guillemots at Skomer

Appendix S8. Model selection to estimate factors influencing the second stage of recruitment (from non-breeder to breeder) in common guillemots at Skomer

Appendix S9. Estimating the number of juvenile guillemots reaching the age of first re-sighting from Skomer

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