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The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes

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Summary

1. Marine predators can be adversely affected by human activities in several potentially interacting ways. Industrial fisheries can affect predator populations adversely through competition for shared prey, and marine environmental change has also been implicated in population declines. In the North Sea, black-legged kittiwakes *Rissa tridactyla* have declined by > 50% since 1990, a period during which a lesser sandeel *Ammodytes marinus* fishery was active and profound oceanographic changes occurred. We studied the role of fisheries and oceanography in kittiwake declines on the Isle of May, south-east Scotland, where sandeels are the main prey.

2. Demographic data were collected from 1986 to 2002. We examined changes over time and correlations between population parameters, the local sandeel fishery and environmental factors, and incorporated the results in a deterministic and a stochastic matrix population model.

3. Breeding success and adult survival were low when the sandeel fishery was active (1991–98) and were also negatively correlated with winter sea temperature, with a 1-year lag for breeding success. Modelling showed that the observed changes in population parameters could explain the change in population growth rate from +8% year^{-1} in the late 1980s to −11% year^{-1} in the late 1990s. An observed improvement in breeding success from 2000 onwards has been insufficient to arrest the population decline. To stabilize the population, breeding success must increase to unprecedented levels or survival needs to increase substantially. Stochastic modelling indicated that the population was unlikely to increase if the fishery was active or sea temperature increased, and that the population was almost certain to decrease if both occurred.

4. Sandeel recruitment is reduced in warm winters, and we propose that this explains the temperature effects on kittiwake survival and breeding success. The fishery also had a strong effect on demographic performance, although the exact mechanism is unclear as kittiwakes and fishermen target different sandeel age groups.

5. *Synthesis and applications*. Poor breeding success of kittiwakes was associated with warm winters and the presence of a local sandeel fishery. Reversing the trend towards warmer winters may be impossible and, at best, would be a very slow process. Therefore, to safeguard kittiwake populations we recommend that the current closure of the commercial sandeel fishery remain in place indefinitely. This study shows that adequate monitoring of the effect of a fishery or of environmental change on seabird populations needs to include survival as well as breeding success.

Key-words: adult survival, *Ammodytes marinus*, breeding success, oceanography, population model, sandeels

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Introduction

One of the main issues in fisheries management is assessing and reducing fishery effects on other predators such as marine mammals and seabirds (Ormerod 2003). Such effects may be direct, as in by-catch mortality (Tuck *et al*. 2001), or indirect through reductions in food supplies. During the 20th century, many seabird species showed large increases in population size in the north-east Atlantic (Mitchell *et al*. 2004). For some, these increases were probably linked to growing and changing human fisheries (Montevecchi 2002), either through provisioning of extra food in the form of discards and offal (Garthe, Camphuysen & Furness 1996) or through high fishing pressure on large predatory fish leading to increased availability of the smaller fish that usually form the main prey of seabirds (Sherman *et al*. 1981; Furness 1982). However, towards the end of the last century, the development of industrial fisheries harvesting small forage fish has led to direct competition between humans and seabirds. Regional declines have become apparent in some seabird species (Anker-Nilssen, Barrett & Krasnov 1997; Heubeck *et al*. 1999) and some have been related to human fisheries (Anker-Nilssen, Barrett & Krasnov 1997). Overexploitation has been suggested as the cause of population crashes of some forage fish species and concomitant declines in seabird populations during the last 50 years (Newton 1998).

The largest single-species industrial fishery in the North Sea harvests the lesser sandeel *Ammodytes marinus* Raitt, up to a million tonnes of which are landed each year (ICES 2003). Lesser sandeels are an important prey for most species of seabirds around the North Sea during the breeding season (Monaghan 1992; Wanless, Harris & Greenstreet 1998). Among these is the black-legged kittiwake *Rissa tridactyla* (L.), which in this region feeds almost exclusively on lesser sandeels (Harris & Wanless 1997; Lewis *et al*. 2001). Adult kittiwakes eat mostly older (1+ year group) sandeels during April and May, but switch to juvenile (0 year group) sandeels for both themselves and their young in June and July (Harris & Wanless 1997; Lewis *et al*. 2001). The number of kittiwakes breeding along the British North Sea coast declined by 20–50% between *c*. 1986 and 2000, with even stronger declines in Shetland (Heubeck *et al*. 1999; Heubeck 2004). The cause and mechanism of these declines are unclear, although consistently low breeding success was observed in Shetland and south-east Scotland (Mavor *et al*. 2003). The underlying cause is likely to be low availability of sandeels, but in the absence of long-term sandeel monitoring outside Shetland correlations have to be sought between kittiwake performance and proxies thought to be affecting sandeel abundance.

In 1990, a summer industrial fishery for sandeels started around the Wee Bankie off the Firth of Forth, south-east Scotland. Landings from this fishery quickly grew to 100 000 tonnes in 1993 but then stabilized at a lower level (see Appendix 1). Subsequent research indicated that the Wee Bankie fishery almost certainly caused local depletion of sandeel numbers, which coincided with reduced breeding success of kittiwakes (Rindorf, Wanless & Harris 2000). In 2000, following advice from the International Council for the Exploration of the Sea (ICES) Advisory Committee on the Marine Environment, summer fishing for sandeels was banned in 20 000 km^2 of sea to the east of Scotland and north-east England, an area that included the Wee Bankie (Wright *et al*. 2002). A limited scientific fishery was maintained in the exclusion zone in 2000–01 (see Appendix 1).

Changes in oceanographic conditions can also exert a profound influence on ecosystem structure and hence top predator populations (Hunt *et al*. 2002). Physical and biological oceanographic conditions in the North Sea have changed markedly in recent decades (Beaugrand 2004), and high winter sea temperatures have been shown to reduce recruitment of sandeels, which spawn in winter (Arnott & Ruxton 2002). There is some evidence that seabird population dynamics in the region may be linked to ocean climate fluctuations (Thompson & Ollason 2001; Durant, Anker-Nilssen & Stenseth 2003). Previous studies of kittiwakes have shown a link between breeding success and prevailing weather patterns (Aebischer, Coulson & Colebrook 1990), but no study so far has investigated the combined effects of oceanography and fisheries on a North Sea seabird.

Since 1986, the Isle of May in the outer Firth of Forth has been part of the UK Joint Nature Conservation Committee (JNCC) seabird monitoring programme. Numbers, breeding success and adult survival of kittiwakes and other seabird species are monitored annually. Kittiwakes breeding on the Isle of May forage largely within the area targeted by the Wee Bankie sandeel fishery (Wanless, Harris & Greenstreet 1998; Daunt *et al*. 2002) and are thus potentially vulnerable to declines in sandeel abundance caused by the fishery. We used data collected between 1986 and 2002 to (i) estimate population parameters and model the growth of the Isle of May kittiwake population over this period; (ii) investigate to what extent the Wee Bankie sandeel fishery and oceanographic change are likely to have affected population growth; and (iii) predict future population growth under various scenarios of fishery and oceanographic conditions.

Methods

STUDY AREA AND FIELD METHODS

The Isle of May (56°11′N, 2°33′W) is one of the most important seabird colonies along the British North Sea coast. We have monitored population size, breeding success and adult survival of kittiwakes at the Isle of May since 1986. Single total counts of the number of completed kittiwake nests (Harris 1987) were carried out in late May or early June, when egg laying was completed, every year from 1986 to 2002. In 15 plots distributed to give a good geographical spread within the whole colony, active nests were identified and counted during early incubation, and several visits were made during the fledging period to determine the success of each nest. Plot limits have only been constant since 1992, so earlier plot counts of nests are not used here. The unit used for quantifying annual mean breeding success was the number of fledged chicks per completed nest (Harris 1987). Annual estimates presented are means [with 95% confidence limits (CL)] across plots, weighted by plot sample size. These means were then used in a multiple regression analysis (weighted by inverse standard error) to identify environmental covariates of breeding success (see below).

Breeding kittiwakes have been ringed with unique colour-ring combinations and metal rings every year since 1986. Initially, all birds were ringed in two study plots, but as the population declined it became difficult to maintain a satisfactory sample of marked birds, so from 1996 birds were also ringed in five other plots dispersed around the island. Searches for colour-ringed birds throughout the breeding season were concentrated in these areas, but regular searches have also been made elsewhere and some birds (maximum 15 year^{-1}) have been located as breeders elsewhere on the island. A total of 470 breeding adults was colour-ringed in 1986–2001; 69 of these had originally been ringed as chicks (1970–89) so were of known age. The total number of colour-ringed birds observed annually (including newly ringed birds) ranged from 129 to 181 (mean 148).

ADULT SURVIVAL ANALYSIS

We used MARK (White & Burnham 1999) to estimate annual probabilities of survival and resighting of breeding kittiwakes, and U-CARE (Choquet & Pradel 2002) to test goodness-of-fit of the initial model. Because birds were less likely to be seen if they moved outside the main study plots, at least until first detection at a new site, we expected to find evidence of 'trap-happiness' (i.e. higher resighting probability of birds seen the previous year). We therefore analysed capture histories using a recent multistate approach to modelling trap dependence (L. Crespin, personal communication). In this approach, two states were defined: 'seen' and 'not seen'. Resighting probabilities were then estimated as transition probabilities to the seen state, separately for birds seen and those not seen in the previous year, whereas the nominal resighting probabilities in MARK were fixed to 1 for the seen state and 0 for the not seen state (Frederiksen, Wanless & Harris 2004). In contrast to previous techniques for dealing with trap dependence (Pradel 1993), the multistate approach allows simultaneous modelling of age and trap dependence in survival and resighting probabilities.

We tested the effect of relative age (time since colour-ringing, hereafter referred to as 'age') and time on survival and resighting probabilities by fitting models including either constancy, categorical effects, linear or quadratic trends over 'age' or time. Model notation follows the principles of Lebreton *et al*. (1992): survival and resighting probabilities are denoted ϕ and p, respectively. Subscripts indicate predictors included in the model (see Appendix 2), with capital letters used for linear trends over 'age' or time. An asterisk between two terms indicates that an interaction term is included, and a plus sign indicates an additive model without interactions. Specific hypotheses about environmental effects on survival were tested, with models constraining variation over time to be a function of one or more covariates (see below). The most appropriate model to describe the data was selected using AIC$_c$, Akaike's information criterion adjusted for sample size (Burnham & Anderson 1998), and the importance of covariates was assessed as the proportion of between-year variation explained (analogous to R^2 in regression).

ENVIRONMENTAL CORRELATES OF BREEDING SUCCESS AND SURVIVAL

To explore how kittiwake breeding success and survival was influenced by environmental factors, we tested for correlations with four covariates. (i) Kittiwakes winter throughout the North Atlantic (Coulson 2002), and survival as well as breeding success might be affected by winter weather conditions in the same or the previous year. We tested for a correlation with the winter North Atlantic Oscillation index (NAO; obtained from the US National Center for Atmospheric Research, http://www.cgd.ucar.edu/~jhurrell), a widely used summary measure of winter conditions throughout the kittiwake range (Drinkwater *et al*. 2003; Hurrell *et al*. 2003), for either the current or previous winter. (ii) Previous studies (Rindorf, Wanless & Harris 2000) found a correlation between kittiwake breeding success and the local abundance of sandeels in June, measured as catch per unit effort (CPUE), during the period when the fishery operated. CPUE data were only available for 1991–2001 (Wright *et al*. 2002), and for survival we used the mean of those years as the value for years without data; for breeding success, we report results restricting analysis to those years when CPUE data were available. (iii) The Wee Bankie sandeel fishery might affect kittiwake breeding success (Rindorf, Wanless & Harris 2000) or survival, either directly through food depletion or indirectly through disturbance, and we tested this hypothesis by including the presence or absence of a fishery in the models. We scored the fishery as present from 1991 to 1998, the period when landings were substantial (see Appendix 1). Despite some fishing taking place, 1990 and 1999 were scored as non-fishery years (but see the Results). (iv) Winter sea surface temperature (SST) has been found to affect sandeel recruitment (Arnott & Ruxton 2002), so we tested for correlations between breeding success and survival and inshore SST in February/March (obtained from the German Bundesamt für Seeschifffahrt und Hydrographie, http://www.bsh.de). A negative correlation with SST in the immediately preceding winter would indicate reliance on 0 group sandeels, whereas a negative correlation with SST 1 year earlier would imply that 1+ group sandeels were more important.

POPULATION MODELLING

A fully parameterized population model for Isle of May kittiwakes would need estimates of juvenile (first-year) survival, emigration and immigration (mostly by pre-breeders) and the age of recruitment to the breeding population. Our data were insufficient to estimate these parameters, but we had recorded emigration to, and immigration from, other colonies. Net recruitment (first-year survival corrected for net dispersal) was therefore estimated by fitting the model to the observed time series of population counts.

The first step was to develop a model to describe the growth of the kittiwake breeding population on the Isle of May 1986–2002 and assess whether the observed changes in growth rate could be explained by observed changes in breeding success and adult survival. We constructed a deterministic, time-specific matrix model (Caswell 2001) with 15 age classes. The initial age distribution was based on asymptotic properties of a model, with mean parameter values as observed from 1986 to 1989, when breeding success and survival were high (see the Results). The model was then parameterized with our annual estimates of breeding success and adult survival. A separate analysis of survival of the subsample of known-age birds indicated a strong quadratic relationship between true age, from age 2 onwards, and survival, with pronounced senescence (Frederiksen, Wanless & Harris 2004), and we used this relationship in the model rather than the observed relationship with 'age'. Age- and year-specific survival were thus modelled as a combination of results from the two analyses:

$$\text{logit}(\phi_{a,t}) = 1{\cdot}2 + 0{\cdot}334a - 0.020a^2 + (\beta_t - \bar{\beta})$$

where a indicates true age, t year, β_t annual effects on the logit scale from model ϕ_{A+t}, p_{t+m} (see the Results) and $\bar{\beta}$ the mean of annual effects from the same model. Under this model, mean survival increases from 0·86 at age 2 to 0·93 at age 7–10 years [we refer to this life stage, corresponding to the mean age at colour-ringing (8·3 years, $n = 69$) as prime age], and declines to 0·85 at age 15. Second-year survival (from age 1–2 years) was estimated by extrapolating this relationship. Previous studies have shown that most kittiwakes first breed when aged 3–5 years (Porter & Coulson 1987; Cam *et al.* 2002); we included this in the model by assuming that 25% of 3 year olds, 75% of 4 year olds and all birds 5 years or older are breeders. We then ran the model with varying values of first-year survival to (i) assess whether observed changes in adult survival and breeding success could explain population growth, or whether changes in recruitment also needed to be invoked, and (ii) find the value for net recruitment (first-year survival including net dispersal) that provided the best fit to the data.

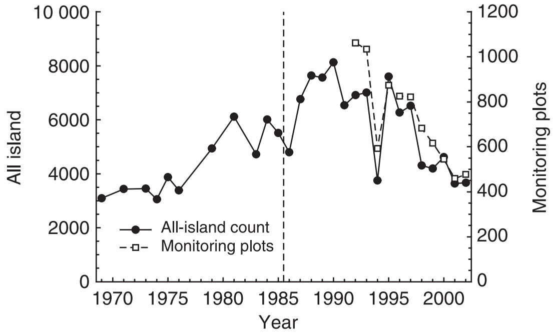

Fig. 1. The number of completed kittiwake nests counted on the Isle of May 1969–2002 (left axis), and in the 15 productivity monitoring plots 1992–2002 (right axis). The dashed line indicates the onset of annual monitoring of population size and parameters. Data from this study and Isle of May Bird Observatory and Scottish Natural Heritage records.

As a second step, we modelled how the population might recover from the observed severe decline since 1995 (Fig. 1). We took the predicted age distribution from the first modelling exercise in 2000, i.e. after 10 bad breeding years, as a starting point and constructed a constant, deterministic model in ULM (Legendre & Clobert 1995). Within this model, we ran scenarios with varying values of breeding success, adult and first-year survival, in order to evaluate which improvements in these parameters would be necessary to induce stability in the population. Finally, we used a stochastic matrix model to predict population growth under various scenarios of fishery and oceanographic change (see Appendix 3).

Results

POPULATION SIZE

Continuing a trend observed since 1969, the number of completed kittiwake nests counted increased from 4801 in 1986 to a peak of 8129 in 1990; subsequently numbers declined to 3666 in 2002 (Fig. 1). The pronounced dip in 1994 corresponded to a documented non-breeding event; *c.* 40% of all birds attending the colony early in the season did not build nests. Both the all-island counts and the monitoring plots showed a decline of about 50% from 1995 to 2001 (Fig. 1), or approximately 11% year^{-1}.

BREEDING SUCCESS

Breeding success varied widely, from 1·24 fledged chicks per completed nest in 1986 to 0·02 in 1998. During 1986–89, breeding success was high, with a mean of 1·07 (95% CL 1·00–1·14; Fig. 2). The 10 subsequent seasons (1990–99), i.e. the period when the Wee Bankie sandeel fishery was active, were characterized by low and variable breeding success [mean 0·30 (0·26–0·34)], followed

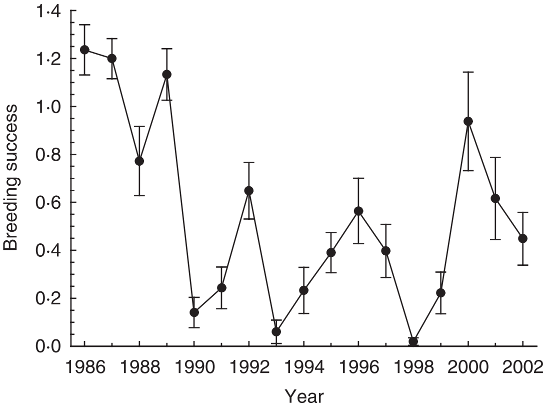

Fig. 2. Kittiwake breeding success on the Isle of May 1986–2002, expressed as the number of fledged chicks per completed nest. Weighted means and 95% confidence limits of 15 monitoring plots (10 in 1986) are shown.

Table 1. Percentages of the total between-year variation in breeding success and adult survival explained by linear and quadratic trends, as well as several environmental covariates. Values shown are R^2 for breeding success and proportion of deviance explained for survival. Results for survival are shown for models with 'age' dependence in either survival or resighting probability (see text). For breeding success, the amount of variation explained by CPUE refers to an analysis using only years when this covariate was available (1991–2001)

		Survival	
Covariate	Breeding success	'Age'-specific survival	'Age'-specific resighting
Year (linear trend)	33	30	28
Year (quadratic trend)	64	42	50
Fishery (1991–98)	40	14	24
NAO	0·6	0·1	0·2
NAO (lagged)	22	9	5
SST	22	14	26
SST (lagged)	45	6	12
CPUE	17	0·5	0
Fishery + SST	50	35	52
Fishery + SST (lagged)	81	21	35

by a partial recovery in 2000–02 after the closure of the fishery [mean 0·68 (0·57–0·79)]. When all fishery years (1990–99) were included, the presence or absence of a fishery explained 70% of the observed between-year variation in breeding success, but if fishery was only scored as present in 1991–98, i.e. when landings were substantially higher than in the scientific fishery 2000–02 (see Appendix 1), this proportion dropped to 40% (Table 1). Breeding success was also highly correlated with winter SST in the previous year, and together these two variables explained 81% of the variation (Table 1 and Fig. 3) (type III multiple regression: fishery $F_{1,14} = 26·6$, $P = 0·0001$; SST_{t-1} $F_{1,14} = 30·3$, $P < 0·0001$; interaction $F_{1,13} = 0·23$, $P > 0·5$). Other environmental covariates explained only minor proportions of the variation, whereas a quadratic trend summarized the data well (Table 1).

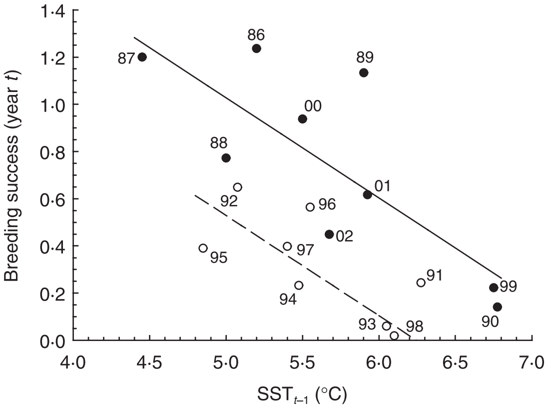

Fig. 3. Kittiwake breeding success as a function of local SST in February–March of the previous year and presence/absence of the Wee Bankie sandeel fishery. Data labels indicate current year. Regression lines estimated from weighted multiple regression (see text). Filled circles and solid line, non-fishery years; open symbols and dashed line, fishery years.

Table 2. Model selection for the analysis of kittiwake adult survival. Models are ranked according to $\Delta\mathrm{AIC_c}$, i.e. the difference in $\mathrm{AIC_c}$ between the model in question and the best model. For explanation of model subscripts, see Appendix 2

	Model	Deviance	Number of parameters	$\Delta\mathrm{AIC_c}$
1	ϕ_{A+T2}, p_{t+m}	807·04	21	0
2	ϕ_{F+SST}, p_{A*m}	835·64	7	0·26
3	ϕ_{A+T}, p_{t+m}	810·05	20	0·97
4	ϕ_{T2}, p_{A*m}	836·42	7	1·03
5	$\phi_{A+F+SST}, p_{t+m}$	808·81	21	1·77
6	ϕ_{A+T2}, p_{t*m}	780·67	35	2·32
7	ϕ_{A+T2}, p_{A*m}	836·30	8	2·93
8	ϕ_{A+SST}, p_{t+m}	814·03	20	4·96
9	ϕ_{A+F}, p_{t+m}	814·16	20	5·09
10	$\phi_{A+F+SST-1}, p_{t+m}$	812·24	21	5·20
11	$\phi_{A+NAO-1}, p_{t+m}$	815·28	20	6·20
12	ϕ_{A}, p_{t+m}	817·69	19	6·58
13	$\phi_{A+SST-1}, p_{t+m}$	816·19	20	7·11
14	ϕ_{A+CPUE}, p_{t+m}	817·57	20	8·50
15	ϕ_{A+NAO}, p_{t+m}	817·65	20	8·58
16	ϕ_{A+t}, p_{t+m}	792·25	33	9·77
17	ϕ_{a+t}, p_{t+m}	776·23	47	22·73
18	ϕ_{t}, p_{t+m}	821·37	32	36·84
19	ϕ_{t}, p_{t*m}	795·54	45	37·88

ADULT SURVIVAL

Initial goodness-of-fit tests of model ϕ_t, p_t with time-dependence in survival and resighting probabilities showed a highly significant lack of fit in one component (directional test for trap-happiness: $z = -14·2$, $P \ll 0·001$), indicating capture heterogeneity in the form of immediate trap dependence (Pradel 1993). The remaining test components showed no evidence of lack of fit ($\chi^2 = 47·8$, d.f. = 43, $P = 0·28$), indicating satisfactory fit of model ϕ_t, p_{t*m} including trap dependence, which we therefore used as a starting point for the analysis. Table 2 illustrates the process of model selection for the survival analysis. Temporal variation in resighting

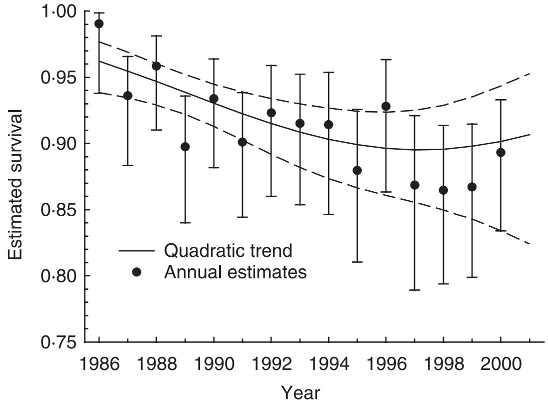

Fig. 4. Survival estimates of Isle of May kittiwakes (from model 1 in Table 2), with 95% confidence limits. The line shows a quadratic trend over time in survival during the year immediately after colour-ringing (prime-age survival). For comparison, annual estimates from the model with full variation over time (model 16 in Table 2) are also shown.

probability *p* was similar for individuals seen or not seen in the previous year (model 18 vs. model 19). The fit of the model was improved by the addition of a categorical 'age' effect in survival (model 17 vs. model 18), and the 'age' effect was well summarized by a linear trend (on the logit scale; model 16 vs. model 17). Between-year variation in survival was not pronounced (categorical year effect not needed; model 12 vs. model 16) but could be summarized by a quadratic trend (model 1 vs. model 12), explaining 42% of total between-year variation (Table 1). Environmental covariates were less successful at explaining between-year variation in survival (Table 1; models 8–15 in Table 2), although a model with fishery and SST was almost as good as the quadratic trend (model 5). An alternative parameterization, with 'age'-dependence in resighting probability rather than in survival, had a very similar AIC_c (Table 2, model 4); under this parameterization, 'age'-dependence in survival was not supported (model 7 vs. model 4). All environmental effects were more pronounced under this parameterization, i.e. they explained a larger proportion of the annual variation (Table 1; model 2 in Table 2, other results not shown). Prime age survival estimates from the highest ranked model showed a decline during the first 10 years of the study, from about 0·96 to 0·90, followed by stabilization or a slight improvement (Fig. 4). At the same time, survival declined with 'age' from about 0·9 to about 0·7 after 15 years. Both fishery and SST had negative effects on survival (Fig. 5; likelihood ratio test with 'age' dependence in survival: fishery $\chi_1^2 = 5{\cdot}23$, $P = 0{\cdot}022$; SST $\chi_1^2 = 5{\cdot}36$, $P = 0{\cdot}021$; interaction $\chi_1^2 = 1{\cdot}63$, $P = 0{\cdot}20$; both effects were more pronounced with 'age' dependence in resighting probability). As expected from their respective dependence on SST, survival was positively correlated with breeding success in the following year ($r = 0{\cdot}67$, $P = 0{\cdot}0042$; see Appendix 4). Resighting probabilities varied between years, but were generally high for birds seen in the previous year (weighted mean from model 1: 0·93) and much lower for those not seen in the previous year (weighted mean: 0·37).

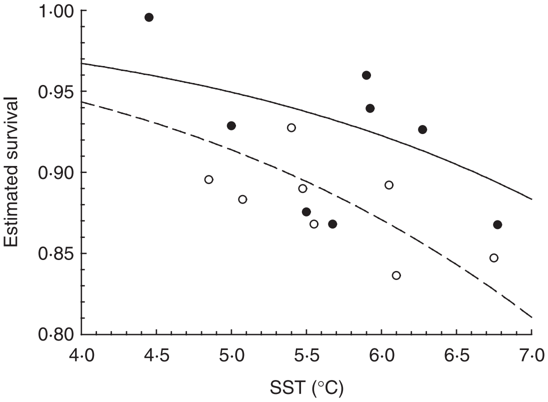

Fig. 5. Kittiwake survival from year *t* to *t* + 1 as a function of local SST in February–March of year *t* and presence/absence of the Wee Bankie sandeel fishery. Regression lines are estimated from a statistical model and are parallel on a logit scale. For clarity, results are shown from a model with 'age'-dependence in resighting probability rather than survival (model 2 in Table 2). Also shown are point estimates from the equivalent model with full variation over time. Filled circles and solid line, non-fishery years; open symbols and dashed line, fishery years.

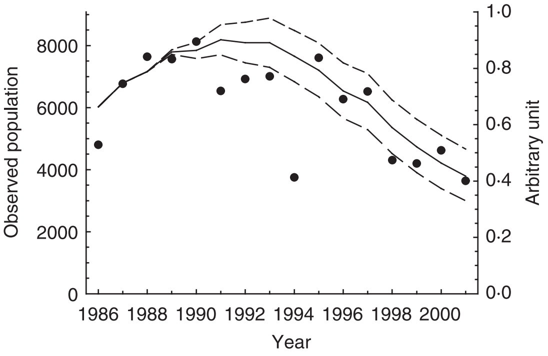

Fig. 6. Observed (symbols) and modelled (lines) size of the kittiwake breeding population. Model results are shown for three values of first-year survival (from the top 0·5, 0·4 and 0·3) and are scaled to be comparable with the counts.

POPULATION MODELLING

The starting age distribution of the simulation model was obtained from the asymptotic properties of a model using mean parameter values 1986–89 and a first-year survival of 0·4 (see below); the asymptotic population multiplication rate λ predicted from this model was 1·076. Using annual estimates of breeding success and survival, we attempted to find the value of first-year survival that would provide the best agreement between the observed and modelled size of the breeding population. A good fit was obtained for a value of 0·4 (Fig. 6); taking this value as constant, the model described well both the population increase during the late 1980s and the subsequent decline (Fig. 6). As expected from the observed high incidence of

Table 3. Improvements in mean population performance needed to stabilize the Isle of May kittiwake population, according to a deterministic matrix model. Basic population parameters were: breeding success, 0·68; age-dependent survival with prime age adult survival, 0·908; first-year survival, 0·4. Also shown is the initial decline expected from the 2000 population size (see also Appendix 5)

Parameter	Value needed	Improvement needed (%)	Initial decline (first 10 years) (%)
Breeding success (BS)	1·17	72	31
Prime-age survival (ϕ_{ad})	0·941	3·6 (36% decline in mortality)	19
First-year survival	0·688	72	31
Improvement in several parameters (for example)	*BS* 0·9 ϕ_{ad} 0·925	32 1·9 (18% decline in mortality)	25

non-breeding in 1994, the count for that year was much lower than predicted by the model. In 2000, after 10 bad breeding years (Fig. 2), the modelled age structure of the population had changed considerably; the proportion of the population more than 10 years old was predicted to be 61%, in contrast to 25% in the starting age distribution.

To investigate whether the change in population growth rate was linked to changes in survival and/or breeding success, we ran the model with one or both of these sets of parameters fixed at the observed mean for 1986–89. Predicted breeding population size in 2001 was 2·43 times as high as under the best-fit model if no change in survival was assumed, 2·03 times as high if no change in breeding success was assumed, and 4·85 times as high if both survival and breeding success were assumed to have remained at the favourable levels recorded during the early years of the study.

In the next step, we used the predicted age distribution in 2000 as a starting point for prospective modelling, aiming to investigate how likely the population would be to stabilize and recover. The growth of the population was simulated under several scenarios for improvement in various population parameters, starting in 2000. The basic model, using the observed mean breeding success 1990–99 (0·30 fledged chicks pair^{-1}) and a prime age survival as observed in the late 1990s (0·908), predicted a λ of 0·894, i.e. close to the observed 11% decline per year. Incorporating the observed improvement in breeding success 2000–02 (0·68) changed λ to 0·950 and was thus not sufficient to stabilize the population. Table 3 lists the improvements needed to achieve $\lambda = 1$, i.e. asymptotic population stability, as well as the initial decline due to the unbalanced age structure (assuming improvements take effect from 2000). All scenarios predicted that even if further improvements took effect from 2000, a decline of 19–31% would still be expected over the first few years; this accords well with population counts 2000–03 (see Appendix 5).

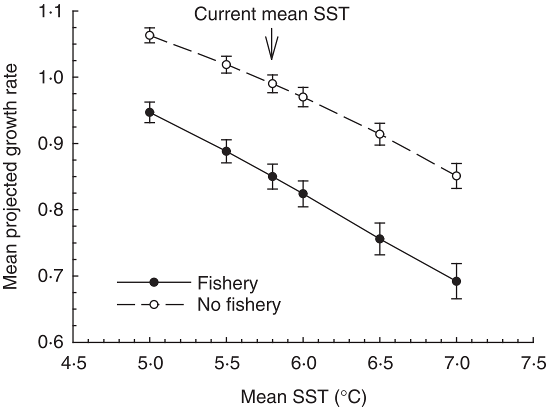

Fig. 7. Mean projected growth rate λ (± 2 SD) of the Isle of May kittiwake population from a stochastic matrix model (see Appendix 3 for details), as a function of mean winter SST and the presence/absence of the Wee Bankie sandeel fishery. $\lambda = 1$ indicates population stability.

The stochastic model indicated that the projected mean growth rate was strongly dependent both on SST and on whether a fishery was operating (Fig. 7). In the presence of the fishery, population increase was unlikely even if SST was substantially lower than today. It was also apparent that a continued decline in the kittiwake population was likely if winter sea temperatures in the North Sea increased in the future, even if there was no fishery. If the fishery was active and SST increased, a catastrophic decline of 25% year^{-1} or more was predicted (Fig. 7).

Discussion

CAUSES OF LOW BREEDING SUCCESS AND SURVIVAL

Breeding success at the Isle of May was high during the late 1980s, very low during the 1990s and showed a partial recovery 2000–02 (Fig. 2). Very similar patterns occurred at many British kittiwake colonies along the North Sea during this period (Mavor *et al*. 2003). The high breeding success observed during 1986–89 was comparable with the long-term mean at the very productive North Shields colony in north-east England (Thomas & Coulson 1988), whereas the worst years during the 1990s were similar to observed values in Alaska (Dragoo, Byrd & Irons 2001). The range observed over our 17-year study was thus comparable with that found for the species over its entire range. The period of low breeding success coincided with the activity of the Wee Bankie sandeel fishery (compare Appendix 1 and Fig. 2), but when the 2 years with very low catches (1990 and 1999) were excluded the correlation was less strong (Table 1). However, when winter SST during the previous year was included in the model, a very large part of the variation was explained (Table 1 and Fig. 3).

The highest ranked models for adult survival all included a decline with ‘age’ in either survival or resighting probabilities (Table 2). This could indicate senescence of either birds or colour-rings. However, an analysis of the subset of known-age birds provided strong evidence in favour of a quadratic trend in survival with true age rather than any effect of the age of the colour-ring (Frederiksen, Wanless & Harris 2004), and we used this result in conjunction with year-specific estimates from the model presented here as input for the population model. Adult survival declined substantially from the high values observed early in the study and subsequently stabilized (Fig. 4). The decline was less pronounced than in a previous analysis where the effect of 'age' was not taken into account (Harris, Wanless & Rothery 2000) but nevertheless substantial. The population model provided an estimate of the mean survival of all adults (aged ≥ 2 years) in the population, ranging from 0·98 in 1986–87 to 0·82 in 1998–99. Again, this range contains most estimates of kittiwake survival from other populations, from very high in Alaska (Hatch, Roberts & Fadely 1993; Golet, Irons & Estes 1998) to low in Brittany (Danchin & Monnat 1992) and at North Shields (Aebischer & Coulson 1990). Survival was low when the Wee Bankie fishery was active and when breeding success was also low (compare Appendix 1 and Figs 2 and 4), and when the previous winter's SST was included in the model a high proportion of the variation was explained (Table 1 and Fig. 5). Furthermore, there was a strong correlation between survival and breeding success in the following season (see Appendix 4).

It seems clear that the effect of SST on kittiwake breeding success and survival must be mediated through sandeel availability, and the changing importance of sandeel age classes to kittiwakes through the breeding season provides a clue to the mechanism. We propose the following scenario: warm winters lead to low sandeel recruitment, perhaps by reducing the food supplies available to larval sandeels (Arnott & Ruxton 2002). Kittiwakes start feeding on this weak year class of 0 group sandeel during chick rearing in June. This is too late to have a major effect on breeding success in the current year, but adults (and presumably fledglings) are in poor condition at the end of the breeding season and overwinter survival is correspondingly low. Next spring, breeding adults again feed mainly on the same weak year class in the early part of the breeding season (sandeels older than 1 group constitute a small proportion of kittiwake diet; Lewis *et al*. 2001) and their poor condition leads to low reproductive investment and correspondingly low breeding success. After a cold winter, the opposite situation occurs. The observed correlation between independent estimates of survival and breeding success in the following season ($r = 0{\cdot}67$; see Appendix 4) was sufficiently strong to lend some credence to this hypothesis. The sharp decline in breeding success in 1990 occurred soon after a 'regime shift' in the North Sea, when an increased influx of warm Atlantic water had major ecological consequences, including a change in plankton community composition (Beaugrand 2004). Sandeel size and quality declined markedly over the study period (Wanless *et al*. 2004), perhaps as a response to changes in ocean climate, and this may also have affected kittiwakes adversely.

The Wee Bankie sandeel fishery also appears to have had a large effect on kittiwake performance (Figs 3 and 5). The exact mechanism is unclear, because the fishery is only likely to have had a strong direct effect on sandeel abundance in 1993, the peak year (Rindorf, Wanless & Harris 2000). Also, the fishery mainly took 1+ group sandeel in June and July, i.e. after the kittiwakes had switched to 0 group as their main prey (Lewis *et al*. 2001). However, it is possible that the fishery affected the behaviour of all sandeel age classes, so that they spent less time near the surface and thus became less available for surface feeders such as kittiwakes. Clearly, detailed studies of the behavioural responses of sandeels to fishing activity are required to elucidate the precise mechanism.

Kittiwake performance and population size declined at the same time as other sandeel-dependent seabirds were more successful on the Isle of May. As an extreme example, numbers of Atlantic puffins *Fratercula arctica* (L.), which to a large extent also feed their young on 0 group sandeels, increased by about 10% year^{-1} during the 1990s (Wanless *et al*. 2003). However, kittiwakes appear more sensitive to food shortages than many seabirds (Furness & Tasker 2000).

At Foula in Shetland, Oro & Furness (2002) found that kittiwake survival was associated with sandeel abundance, kittiwake body condition and breeding success of great skuas *Catharacta skua* Brünnich, an important predator of kittiwakes. The two first findings are consistent with our results, but great skuas are absent from the Isle of May and predation by great black-backed gulls *Larus marinus* L., for example, is rare. At the same time, kittiwake survival may also be affected by factors operating outside the breeding season. Identifying such factors is problematic, because only fragmentary data exist about the wintering areas of British kittiwakes: some individuals winter in the North Sea while others are dispersed in the North Atlantic (Coulson 2002). We found practically no correlation between adult survival and the winter NAO index (Table 1), a widely used indicator of winter conditions in the North Atlantic (Hurrell *et al*. 2003). In the future, application of lightweight data loggers (Wilson *et al*. 2002) may allow us to identify wintering areas more precisely and test whether survival is correlated with environmental conditions in these areas.

PREDICTIONS OF FUTURE POPULATION GROWTH

The dynamics of the Isle of May kittiwake population have changed dramatically over the study period, from an approximately 8% increase year^{-1} in the late 1980s to a 11% decline year^{-1} in the late 1990s (Fig. 1). Our model showed that this change could be explained by the observed declines in adult survival and breeding success (Fig. 6), and that both factors were important. There was no need to invoke changes in net recruitment, i.e. juvenile survival including emigration/immigration, as the model was rather insensitive to variation in this parameter (Fig. 6). Large changes in emigration or immigration also seem unlikely if kittiwakes, as evidence from other studies suggest, preferentially recruit to successful colonies (Danchin, Boulinier & Massot 1998): breeding success for all major colonies within approximately 150 km of the Isle of May was closely correlated with our study colony (Harris & Wanless 1997), and these colonies have also shown similar declining trends (Heubeck 2004). Both the deterministic and stochastic models also indicated that the kittiwake population was unlikely to increase under current environmental conditions, and that a reopening of the Wee Bankie fishery would probably lead to a marked decline in numbers (see Appendix 5 and Fig. 7). Furthermore, if climate change, as predicted by climate models, should lead to increases in North Sea temperatures in winter, this is predicted to exacerbate the already critical situation for kittiwakes, particularly if the fishery is active.

IMPLICATIONS FOR MANAGEMENT

In the North Sea, kittiwakes are almost completely dependent on sandeels during the breeding season. Therefore, any factor reducing the abundance or availability of sandeels is likely to have a negative effect and lead to population declines. We have identified two factors associated with low performance in kittiwakes at the Isle of May: high winter sea temperatures and an industrial sandeel fishery. It is unclear exactly how the fishery would affect the availability of sandeels to kittiwakes. Nevertheless, in a situation where kittiwakes are declining not only in the North Sea but throughout most of their range (Hatch, Roberts & Fadely 1993; Barrett 2001), any activities that endanger their main food supply should be avoided. Although sea temperatures are also to some extent within human control, any policy changes aimed at reversing the warming trend will be very slow to take effect. Thus, it seems prudent and in accordance with the precautionary principle to extend indefinitely the closure of sandeel fisheries within the feeding range of kittiwake colonies in the western North Sea.

Our results suggest that kittiwake performance is strongly dependent on sandeel availability, and therefore reflects the general health of marine ecosystems in terms of their ability to produce sufficient amounts of forage fish to sustain thriving populations of top predators. Monitoring kittiwake performance (breeding success and survival) could therefore be an efficient way of monitoring marine ecosystem health. Furthermore, intensive long-term studies remain the only source of consistent data allowing evaluation of both population trends and extensive monitoring programmes, and maintaining such studies should be a high priority for research and management.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE966/JPE966sm.htm.

Appendix S1. Annual sandeel landings from the industrial fishery in ICES squares 41E7 and 41E8.

Appendix S2. List of factors and covariates used as predictors in the analysis of survival and resighting probabilities, and the subscripts used to identify them.

Appendix S3. Details of the stochastic matrix model.

Appendix S4. The correlation between kittiwake survival and breeding success in the following season.

Appendix S5. Predicted population growth of Isle of May kittiwakes 2000–2010 under various scenarios.

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