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# Fishing vs. natural recruitment variation in sandeels as a cause of seabird breeding failure at Shetland: a modelling approach

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Sandeels represent a major component in the diet of fish, bird, and mammal predators as well as supporting a large industrial fishery. The availability of young sandeels in coastal waters around Shetland is generally considered a key factor influencing the breeding success of many seabird species in the area, but the risk to the populations as a direct consequence of the fishery is unknown. Low exploitation rates coupled with high natural mortality rates make assessment of the Shetland sandeel stock problematic and safe biological limits have not yet been defined. We use stochastic models to evaluate the likely effect of varying fishing mortality on kittiwake breeding success. The models consider some main sources of uncertainty about natural processes, such as recruitment and natural mortality, which may affect the design of robust management strategies. The type of model tested had a stronger influence on sandeel recruitment than the level of fishing pressure. Even with low exploitation rates, poor years for seabird breeding were inevitable.

Keywords: kittiwake, sandeel, seabird breeding, Shetland.

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## Introduction

Sandeels (*Ammodytes* sp.) are small, shoaling fish that are ubiquitous throughout the North Sea, including shallow coastal waters over sandbanks (Macer, 1966; Reay, 1970). The industrial fishery for sandeels in the North Sea is the largest single-species fishery in this area. Sandeels are an important part of the marine foodweb, forming a major component in the diets of many fish, marine mammal, and seabird species (Furness, 1990; Hammond *et al.*, 1994; Tollit and Thompson, 1996; Wright and Tasker, 1996; Greenstreet *et al.*, 1998; Doyle and Greenstreet, 1999).

The availability of young sandeels in the coastal waters around Shetland appears to be a crucial factor influencing local breeding success of many seabirds such as the kittiwake *Rissa tridactyla* (Danchin, 1992; Hamer *et al.*, 1993), Arctic skua *Stercorarius parasiticus* (Phillips *et al.*, 1996) and Arctic tern *Sterna paradisea* (Monaghan *et al.*, 1989, 1992; Monaghan, 1992). The dependence of seabird breeding on sandeels has resulted in conflict between the fishing and environmental interests, most notably in the Shetland area in the 1990s.

Around Shetland, juvenile sandeels recruit to the fishery as 0-group fish (Wright, 1996). The fishing grounds are close inshore and often adjacent to major breeding seabird colonies (Monaghan, 1992). During the late 1980s, the breeding success of the local seabird populations declined concurrently with a decline in the sandeel population and landings. At the time, there was considerable controversy about the relationship between the fishery and the availability of sandeels to breeding birds. Environmental groups argued for a closure of the fishery as a precautionary measure. Subsequent research indicated that the decrease in the sandeel population was not caused by fishing but by environmentally induced fluctuations in recruitment (Kunzlik, 1989; Wright, 1996).

Compared with the total North Sea sandeel catch of 0.5 million to 1 million tonnes per year, the fishery around

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Shetland is very small, averaging approximately 20 000 tonnes annually before 1991 (ICES, 2000). Following a peak in 1982 (52 000 tonnes), landings and recruitment went into decline and the fishery was closed completely at the end of the fishing season in 1990. After several years of extremely low recruitment, the production of a large year class in 1991 induced a recovery of the stock and the fishery was reopened in 1995. Recruitment to the Shetland stock is highly variable from year to year (ICES, 2000), but the mechanisms behind recruitment variability are poorly understood.

At present, the fishery operates with an annual Total Allowable Catch (TAC) of 7000 tonnes and a closed season during June and July to avoid competition with seabirds during the chick-rearing season. However, landings since 1995 have been extremely low with only 1300 tonnes landed in 2001. The low exploitation rate coupled with high natural mortality makes stock assessment problematic and safe biological limits have not been defined for this stock. The ecological interactions between sandeels, their predators, and the fishery remain poorly understood.

Currently, the fishery is not regarded as a threat to breeding seabirds, but an increase in catch may reduce sandeel availability. It is assumed that high fishing activity would raise the risk of breeding failure for local seabirds. By constructing sandeel population models incorporating functional responses for seabird populations, it should be possible to quantify the risk of breeding failure under different exploitation rates and to design suitable fishery management regimes. However, the processes involved are highly uncertain and parameter estimates have to be based on assumptions that are difficult to verify. To address this problem, we developed a range of alternative population models to reflect the uncertainty about processes such as recruitment and natural mortality. The results of Monte Carlo simulations for different models were compared statistically. The performance of different management regimes was evaluated in terms of consequences for the sandeel stock, for the fishery, and for breeding seabirds.

## Sandeel population biology

Recruitment to the Shetland stock is variable and is positively autocorrelated ($n = 24$; $r_1 = 0.54$; $p < 0.05$) (ICES, 2000; Figure 1). In biological time-series, positive autocorrelations are considered indicative of environmental forcing (Steele, 1985; Petchey *et al.*, 1997). Trends in spawning-stock biomass tend to follow recruitment trends with a two-year lag (Wright, 1996).

Sandeels are relatively short-lived fish (generally up to eight years) compared to most exploited North Sea fish species and become mature at two years (Macer, 1966; Gauld and Hutcheon, 1990). Adults are thought not to undertake extensive spawning migrations and during spawning attach their eggs to sand grains on the seabed (Reay, 1970; Warburton, 1982). At Shetland, larvae emerge during the early spring, when the North Sea circulation is largely wind-driven. Thus, larval transport by currents is likely to vary among years (Wright and Bailey, 1996; Proctor *et al.*, 1998). It has been suggested that the low recruitment around Shetland during the late 1980s was caused by a reduction in the passive transport of pre-recruit sandeels from spawning grounds elsewhere, such as Orkney (Proctor *et al.*, 1998). The size or frequency of potential influx of pre-recruits, or of losses owing to export, remains unquantified. Because fishing mortality is low ($\overline{F}_{(1-3)} < 0.3$) compared to natural mortality rates ($M_{(1)} = 1.2$, $M_{(2-7)} = 0.6$; ICES, 2000), fluctuations in stock size are driven primarily by natural processes.

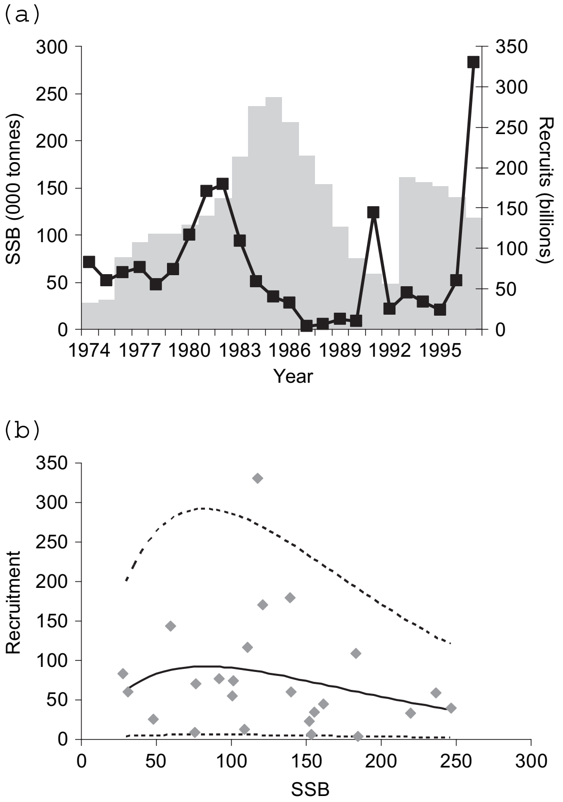

Figure 1. (a) Time-series of spawning-stock biomass (SSB) and recruitment and (b) stock-recruitment plot (drawn line: Ricker stock-recruitment model estimated from 10 000 bootstrap simulations; broken lines: 95% confidence interval) for sandeels at Shetland (data from ICES, 2000).

## Seabird breeding biology

Seabird populations can respond to food availability in various ways, including changes in adult survivorship, chick growth, fledging success, and colony attendance (Cairns, 1987). Each of these parameters may be sensitive to a particular range of prey availability values and integrates food availability over a specific time scale. Seabirds, being relatively long-lived, should be buffered against short sporadic periods of adverse environmental conditions such as low prey availability or bad weather by varying reproductive effort (Monaghan *et al.*, 1989, 1992; Phillips *et al.*, 1996).

At Shetland, the entire breeding season (arrival to departure) for small seabirds lasts from March to September (Furness, 1990) and overlaps with the sandeel fishery operating from April to September (except for the closure during June and July since 1995). Small surface feeding seabirds, such as kittiwakes (Harris and Wanless, 1990; Harris and Wanless, 1997; Rindorf *et al.*, 2000) and Arctic terns (Monaghan *et al.*, 1989, 1992), are considered particularly sensitive to fluctuations in prey availability (Furness and Tasker, 2000), and breeding success (number of chicks fledged per apparently occupied nest) of these may be regarded as a useful indicator of sandeel biomass over the breeding season. A relationship with sandeel abundance has been proposed before for kittiwakes in North Sea areas (Furness and Tasker, 1997, 2000).

Breeding success of kittiwakes for colonies around Shetland over 1986–1993 was taken from Dunnet and Heubeck (1995). Data for additional sites and years were supplied by Martin Heubeck, University of Aberdeen. Breeding success was plotted against four biomass measures of sandeel availability: 0-group, 0+1-group, 1-group, and 0 to 7-group (Figure 2). Biomass was calculated as a multiple of the number by age group and year estimated by stock assessment and mean weight-at-age (ICES, 2000). To take account of the influence of colony size on mean breeding success, a weighted mean breeding success was determined for each year and a logistic model was fitted through the data. Young kittiwakes at two colonies, Kettleness and Eshaness, have been subject to particularly high predation by great skuas (*Catharacta skua*), leading to very few chicks being fledged (Dunnet and Heubeck, 1995). All data for Kettleness and 1993–1996 data for Eshaness were excluded from analysis. Positive relationships between weighted mean breeding success and sandeel abundance were found for all four measures of biomass, but the relationship for 0+1-group was strongest.

## Methods

We used an age-structured population model for sandeels linked to breeding success of kittiwakes being dependent on juvenile biomass. Effects of the fishery were simulated by changing fishing mortality on the sandeel stock. Uncertainty was addressed by examining three different recruitment models and two patterns of natural mortality.

### Population structure

The model time-step is one year. Eight age classes of sandeel were distinguished (0-group recruits through to 7+ fish). Individuals were transferred from one age class to the next in January (the last class being a cumulative one). The initial population (age 1 and older) conformed to the estimated stock numbers on 1 January 1981 (ICES, 2000; Table 1). Numbers of 0-group were calculated within the model using a stock-recruitment relationship. All sandeels $\geq$age 2 are assumed to be mature and all 0- and 1-group to be immature. Spawning-stock biomass (S) was calculated as the numbers of the mature part of the population multiplied by weight-at-age in the stock (Table 1).

### Mortality

Age-specific instantaneous fishing mortality rates (F) are available from stock assessment (ICES, 2000). F was decomposed into an age-specific selectivity effect ($s_a$) and a year-specific effect ($f_y$; Cook and Reeves, 1993):

$$F_{ay} = s_a f_y \tag{1}$$

Estimates of $s_a$ and $f_y$ and the associated covariance matrix were obtained by fitting a fully separable model (Cook and Reeves, 1993) over the years, 1981–1990 inclusive (Table 1). In the simulations, stochastic values for $s_a$ were selected from the covariance matrix using a multivariate correlation random number generator.

Models were tested with three levels of fishing mortality: $F_{low}$, $F_{med}$, and $F_{high}$ based on spawning-stock biomass per recruit values (Sissenwine and Shepherd, 1987; Jakobsen, 1992; Caddy and Mahon, 1995). $F_{med}$ corresponds to a mortality rate that on average balances recruitment. At $F_{high}$, recruitment is sufficient to replace losses in only 10% of the years, which may be regarded as a high-risk exploitation strategy. At $F_{low}$, recruitment exceeds the losses in 90% of the years, which is probably a safe exploitation strategy.

As for F, age-specific natural mortality rates (M) can also be decomposed into an age effect ($m_a$) and a year effect ($k_y$; Cook, 1993):

$$M_{ay} = m_a k_y \tag{2}$$

The $m_a$ are effectively the assumed age-specific natural mortality rates if $k = 1$ (ICES, 2002a; Table 1). In some simulations, interannual stochasticity was introduced into M assuming positive autocorrelation as a worst-case scenario. A first-order autoregressive model was used to generate autocorrelated $k_y$ values:

$$k_t = \phi_0 + \phi_1(k_{t-1} - \phi_0) + \varepsilon_t, \tag{3}$$

where $\phi_0$ is a constant equal to mean of $k_t$ (0.10), $\phi_1$ is the first-order autoregressive coefficient (+0.5), $k_t$ is the variable $k_y$ at time t, and $\varepsilon_a$ is a random variable drawn

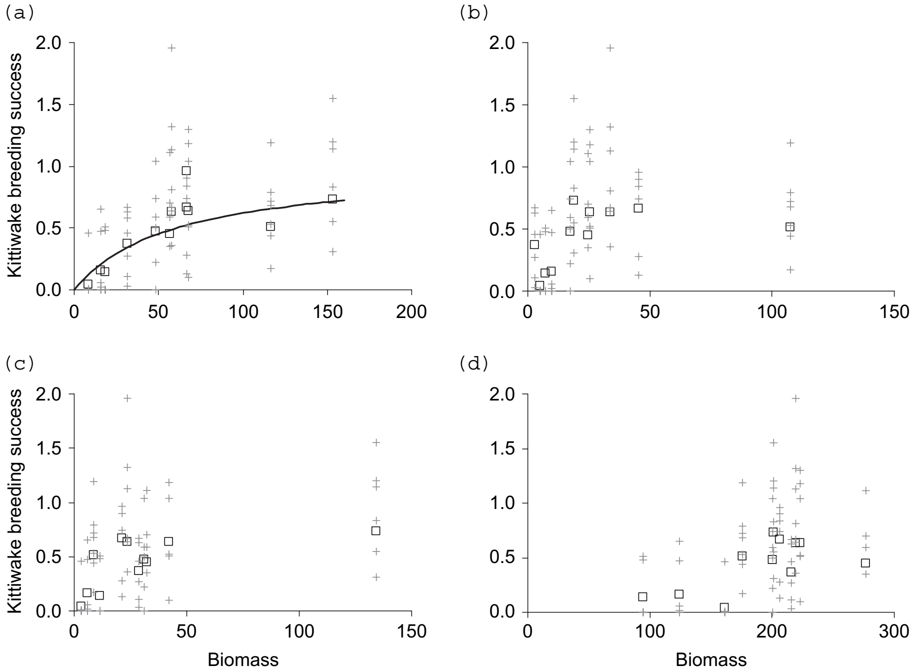

Figure 2. Kittiwake breeding success (young fledged per apparently occupied nest) at Shetland (1986–1993 from Dunnet and Heubeck, 1995; 1994–1996 from Heubeck, pers. comm.) against measures of sandeel biomass from ICES (2000): (a) 0+1-group with fitted logistic model; (b) 0-group; (c) 1-group; and (d) 0 to 7-group (+: mean breeding success estimated for individual colonies; □: weighted mean breeding success across all colonies per year).

from the normally distributed residual distribution with a mean of zero and standard deviation $\sigma_\varepsilon$ such that:

$$\sigma_\varepsilon = \sigma_k \sqrt{1 - \phi_1^2} \tag{4}$$

where $\sigma_k$ is standard deviation of the $m_a$ values (0.276).

## Recruitment

Because of uncertainty about the underlying mechanisms, three stock-recruitment models were applied. The base case was a Ricker (1954, 1975) model with gamma-distributed error terms. Secondly, a Ricker model with autocorrelated error terms was used to simulate environmental forcing on recruitment variability. The last case considered was a Ricker model with weak curvature near the origin as a "worst-case" scenario. The stock-recruit data contain few observations in the range of low stock sizes and therefore the shape of the relationship near the origin cannot be reliably determined. However, if the curvature near the origin had been overestimated in the base case, the model population would appear more resilient to high exploitation rates than the population in the real world would be. Recruitment variability caused by emigration and immigration was assumed to be incorporated in the residuals of the stock-recruit models.

Table 1. Input parameters for sandeel population model (based on ICES, 2000; $P_{in}$: initial population size in millions; ma: proportion mature; $w_a$: weight-at-age in grams; $s_a$, $m_a$: ln age-specific selectivity effect of fishing and natural mortality, respectively).

| Age | $P_{in}$ | ma | $W_a$ | $s_a$ | $\sigma(s_a)$ | $m_a$ |
|---|---|---|---|---|---|---|
| 0 | – | 0 | 0.746 | −2.4599 | 2.7371 | 0.8 |
| 1 | 23 279 | 0 | 3.095 | −2.1144 | 2.3163 | 1.2 |
| 2 | 8 328 | 1 | 5.409 | −2.0847 | 2.3905 | 0.6 |
| 3 | 3 637 | 1 | 8.585 | −1.8717 | 2.4813 | 0.6 |
| 4 | 1 543 | 1 | 11.143 | −2.0775 | 2.2935 | 0.6 |
| 5 | 747 | 1 | 13.705 | −2.1885 | 2.6955 | 0.6 |
| 6 | 380 | 1 | 15.605 | −2.4615 | 3.2034 | 0.6 |
| 7+ | 517 | 1 | 21.254 | −2.1885 | 2.6955 | 0.6 |

### *Case 1*

The Ricker stock-recruit model is widely used in fishery science and is simple and robust:

$$R = aS\, e^{-bS}, \tag{5}$$

where R is recruitment, S is spawning-stock biomass, and a and b are constants. The model is dome-shaped, implying that density-dependent processes tend to dominate at high values of spawning-stock biomass.

We assumed that the variability around the functional relationship followed a gamma-distribution function instead of the more commonly used lognormal distribution, because the latter may result in bias if the assumption is not exactly met or sample size is small (MacCall and Ralston, 2002).

The stock-recruit model assuming gamma-distributed error terms (residuals distributed randomly and independently − white noise) was fitted by minimizing the sum of the deviances:

$$\mathrm{Dev} = \sum_{i=1}^{n} -\ln\left(\frac{R_i}{\hat{R}_i}\right) + \left(\frac{R_i - \hat{R}}{\hat{R}_i}\right), \tag{6}$$

where $R_i$ is observed recruitment (billions) for a specific $S_i$, $\hat{R}_i$ is predicted recruitment (billions) for the same $S_i$, and n is the number of observations i. The best-fit Ricker model with 95% confidence intervals estimated from 10 000 bootstrap simulations is shown in Figure 1b.

In the stochastic version, a bootstrap stock-recruit data set was generated for each simulation of n years. Parameters and residuals of the fitted Ricker model were recorded and used to calculate recruitment in each model year. Recruitment variability was generated by randomly selecting a residual from the bootstrapped data set with replacement to preserve the parameter covariance matrix.

### *Case 2*

As before, the parameters of the Ricker model and associated residuals were determined by 10 000 bootstrap simulations. Autocorrelation was introduced into the residual sets by a two-stage process. Firstly, a first-order autoregressive model was used to generate a random autocorrelated series with a mean of 0 and standard deviation of 1 for each population simulation of n years:

$$y_t = \beta_1 y_{t-1}, \tag{7}$$

where $y_t$ is the observation at time t and $\beta_1$ is the autocorrelation coefficient.

The log-transformed historical recruit time-series for the Shetland sandeel stock was positively and strongly ($\beta_1 = 0.6$) autocorrelated (red noise) at a lag of one year. This value was selected here as representing strong forcing on the time-series. Secondly, the bootstrap data sets were ranked in ascending order. Values in each generated autocorrelated series were assigned a rank position (ascending order) without re-arranging the series. These were then used to re-order the bootstrap sets so following the pattern in the autocorrelated series.

### *Case 3*

Bootstrap output for the model parameters and residuals were generated as described for Case 1. A subset was then selected from this output in which parameter a fell in the lower quartile of the range of estimates. Recruitment variability was generated by randomly selecting a residual from the bootstrap data set.

## Seabird breeding success

The fitted logistic model (Figure 2a) was used to identify a range of sandeel biomasses at which kittiwake breeding success may be poor, not to produce actual predictions of breeding success. Management of the sandeel stock in the North Sea applies a decision rule stating that all sandeel fishing within 50 km of the UK coast is halted if the breeding success of kittiwakes drops below 0.5 chicks per apparently occupied nest for three consecutive years (ICES, 2002b). In the logistic model fitted to kittiwake breeding success against 0+1-group sandeel biomass (Figure 1d), a breeding success ≥0.5 was obtained when biomass was ≥60 000 tonnes and this value was selected as the "threshold" biomass to indicate failure of kittiwake breeding. In the historical data set, the biomass of 0+1-group dropped below this value in 7 out of 24 years (1986−1990 inclusive, 1993 and 1995; ICES, 2000).

## Output statistics and simulations

The selected summary statistics to compare model output were mean annual recruitment and SSB to describe the sandeel population status, and mean catch to describe fishery performance. In addition, two output statistics were calculated for potential effects on seabird populations: the number of years in a simulation with 0+1-group biomass below the threshold and the percentage of simulations producing series of three or more consecutive years with 0+1-group biomass below the threshold.

Simulations were run with a burn in a period of 100 years, without stochasticity, to reach equilibrium. Thereafter, stochasticity was switched on and a further 20 years were simulated. Output statistics were calculated from the stochastic period. To determine necessary sample size to infer stability in results, the running total mean (mean of the simulation means) for each output statistic was calculated during 5000 consecutive simulations. Because these means stabilized rapidly after about 1000 runs, we inferred that 5000 simulations was an adequate number. Simulations with and without stochasticity in natural mortality were carried out for each of the three levels of fishing mortality and for each of the three recruitment models (18 trials).

# Results

The mean output statistics from the 18 sets of simulations are shown in Table 2. The sandeel population was considered to have "crashed" if recruitment, and thus SSB, dropped to (near) zero for a number of consecutive years and showed no indication of increasing again. The incidence of crashing varied among F levels, being highest at $F_{high}$ (17−20%), and was slightly higher among recruitment models with low curvature near the origin (Case 3). Even for $F_{low}$, simulations still crashed in 1−3%

Table 2. Summary statistics from stochastic simulations of the Shetland sandeel stock for 18 different models: Cases 1, 2, and 3: recruitment (R) models with random gamma-distributed error terms, autocorrelated error terms, and weak curvature at the origin, respectively; Ct, A: constant and autocorrelated natural mortality (M); Med, High, and Low: instantaneous fishing mortality rates (F); %cr: percentage simulations where the population "crashed" (see text); R, SSB, C: mean values for recruitment (billions), spawning-stock biomass ($\times 10^3$ tonnes), catch ($\times 10^3$ tonnes), respectively (means for 20-year simulations, excluding crashed populations); y, %3y: mean number of years per 20-year simulation, and percentage of simulations with $\geq 3$ consecutive years, having juvenile sandeel biomass below threshold value, respectively (bold: baseline).

| Model specification | | | Output statistics | | | | | |
|---|---|---|---|---|---|---|---|---|
| R | M | F | %cr | R | SSB | C | y | %3y |
| **Case 1** | **C** | **Med** | **6** | **73 ± 18** | **134 ± 45** | **18 ± 16** | **3.4** | **22** |
| | | High | 17 | 74 ± 22 | 115 ± 50 | 25 ± 17 | 3.9 | 27 |
| | | Low | 1 | 71 ± 14 | 150 ± 37 | 11 ± 12 | 3.3 | 22 |
| | A | Med | 7 | 68 ± 19 | 146 ± 59 | 19 ± 17 | 4.5 | 42 |
| | | High | 17 | 69 ± 22 | 124 ± 61 | 26 ± 19 | 4.6 | 40 |
| | | Low | 2 | 66 ± 17 | 162 ± 55 | 11 ± 14 | 4.5 | 44 |
| Case 2 | C | Med | 6 | 70 ± 16 | 130 ± 44 | 17 ± 15 | 4.7 | 54 |
| | | High | 17 | 71 ± 19 | 113 ± 47 | 24 ± 17 | 4.9 | 55 |
| | | Low | 1 | 69 ± 13 | 146 ± 37 | 11 ± 13 | 4.4 | 53 |
| | A | Med | 7 | 66 ± 17 | 142 ± 59 | 18 ± 16 | 5.6 | 67 |
| | | High | 17 | 66 ± 20 | 121 ± 59 | 25 ± 18 | 5.9 | 66 |
| | | Low | 3 | 65 ± 16 | 160 ± 55 | 11 ± 13 | 5.5 | 67 |
| Case 3 | C | Med | 8 | 65 ± 18 | 125 ± 47 | 20 ± 12 | 4.0 | 28 |
| | | High | 20 | 63 ± 20 | 106 ± 63 | 20 ± 13 | 4.6 | 34 |
| | | Low | 2 | 66 ± 16 | 141 ± 49 | 10 ± 10 | 3.5 | 23 |
| | A | Med | 8 | 60 ± 18 | 136 ± 63 | 15 ± 13 | 5.0 | 45 |
| | | High | 20 | 58 ± 19 | 116 ± 41 | 21 ± 14 | 5.5 | 46 |
| | | Low | 2 | 60 ± 16 | 154 ± 59 | 10 ± 11 | 4.6 | 42 |

of trials. In calculating output statistics, simulations with population crashes were excluded.

Taking the output of the model with stochastic recruitment (Case 1), $F_{med}$, and constant M as the baseline, the percentage change in sandeel summary statistics for the other models was calculated relative to the baseline values (Figure 3). Introducing autocorrelation in the recruitment residuals (Case 2), using stock-recruit models with low curvature near the origin (Case 3) or autocorrelating M values all decreased mean recruitment. The largest declines in mean recruitment, at all levels of F tested, occurred in Case 3 and with autocorrelated M. Spawning-stock biomass (SSB) decreased at $F_{high}$ and increased at $F_{low}$. At $F_{high}$, SSB was more affected by autocorrelated M than by constant M while the reverse was true for $F_{low}$.

Mean catch increased with increased F by 33−41% in all models except in Case 3, where the increase was only 8−13%. In Case 3 and with constant M, $F_{med}$ actually resulted in a larger average catch than $F_{high}$. Reducing fishing pressure decreased mean catch by 38−47% in all models (Figure 3).

All models showed a high incidence of years with juvenile sandeel biomass below the threshold for successful seabird breeding. This happened on average during 3.3−5.9 years out of the 20 years simulated (Table 2). The recruitment model with autocorrelated residuals (Case 2) tended to produce runs with a higher incidence of years below the threshold and this is also the case for incorporating autocorrelation in M (Figure 4).

For all models, at least 22% of simulations (excluding crashed simulations) contained at least one period of three or more consecutive years below the threshold. Values were highest for models with autocorrelated recruitment residuals at all three levels of F. Introducing autocorrelation in M also greatly increased the incidence of such events for all recruitment models at all F.

## Discussion

One of the main concerns in managing the Shetland sandeel fishery is the potential impact on breeding birds. The simulations suggest that even with the most benign sandeel population dynamics model and low F, the probability of poor seabird breeding success would be once every six years (3.4 years in a 20-year period). Using conventional criteria used in management elsewhere in the North Sea, the fishery would have to be closed during a 20-year period in 22% of runs for the most optimistic model. What is of particular relevance, therefore, is the marginal increase in the need to close the fishery as F increases. The simulations indicate that for any of the stock-recruitment and natural mortality models considered, events requiring fishery closures increase marginally as F increases from $F_{low}$ to $F_{high}$, but that the probability of the sandeel stock collapsing rises sharply (Table 2). This result would suggest that the need to protect the sandeel stock from collapse would occur before the threat to seabird breeding was itself elevated.

Our results illustrate the importance of understanding the mechanisms driving recruitment for managing the sandeel fishery. Models of recruitment processes are based on our perceptions of underlying mechanisms, and the type of model chosen strongly influences predictions of population fluctuations and persistence. Generally, stock-recruit models incorporate random variation such that each randomized value is assumed to be independent of other values. However, this is rarely the case in biological systems as the effects of environmental stochasticity may persist longer than one season or one year (Moran, 1953; Grenfell *et al.*, 1998; Thompson and Ollason, 2001).

Positive autocorrelation noise in a single-species population model has been shown to decrease extinction risk because a random value at time t is likely to be similar to the value drawn at $t - 1$ (Ripa and Lundberg, 1996). However, autocorrelating the residuals around the stock-recruit curve (Case 2) seemed to have little influence on the

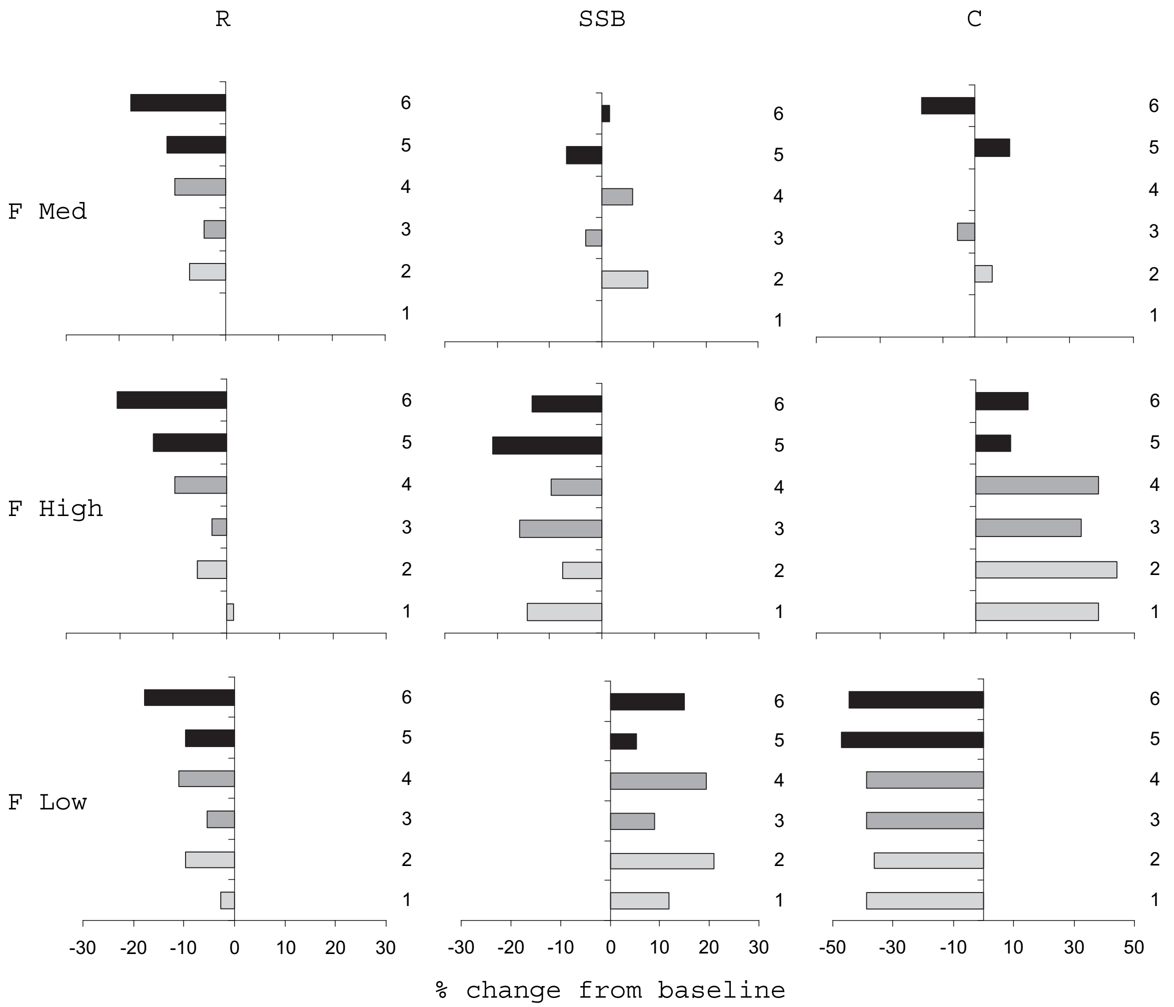

Figure 3. Percentage change in sandeel summary statistics (R: recruitment; SSB: spawning-stock biomass; and C: catch) from baseline model for three recruitment models (Case 1: 1/2; Case 2: 3/4; Case 3: 5/6) and two natural mortality models (constant M: 1/3/5; autocorrelated M: 2/4/6) at three levels of fishing mortality ($F_{med}$, $F_{high}$, and $F_{low}$).

number of simulations considered to have crashed (become extinct) or on the simulated population parameters compared to the base case. This does have strong implications for breeding seabirds. The frequency of years of juvenile sandeel biomass below the threshold set for "sufficient" seabird breeding success increased when the residuals around the stock-recruit curve were positively autocorrelated. As residuals below the curve are likely to occur in sequence, this produces a series of years of low recruitment to the sandeel population. This explains why more trials met closure conditions in stochastic simulations of 20 years. Similarly, introducing positive autocorrelation in natural mortality rates increased the frequency of years with conditions for poor seabird breeding success.

Evidence suggests that recruitment to the Shetland sandeel stock may be largely driven by hydroclimatic factors. Wright (1996) suggested that the poor recruitment during the late 1980s may have been caused by unfavourable oceanic currents reducing larval advection to Shetland. Analysis of North Sea data from the Continuous Plankton Recorder indicated a large anomalous period during these years, signifying unusual ocean-climate conditions (Edwards *et al.*, 2002). Furthermore, Arnott and Ruxton (2002) showed a relationship between recruitment to North Sea sandeels and the winter index of the North Atlantic Oscillation (NAO).

Fluctuations in large-scale climatic phenomena, such as NAO, tend to persist over long time scales (decades or more). Fluctuations in the NAO have been linked with timing of biological events and/or population dynamics in marine (Planque and Taylor, 1998; Sims *et al.*, 2001; Attrill and Power, 2002), freshwater (Straile, 2000; Gerten and Adrian, 2001), and terrestrial (Post and Forchhammer, 2002; Huppop

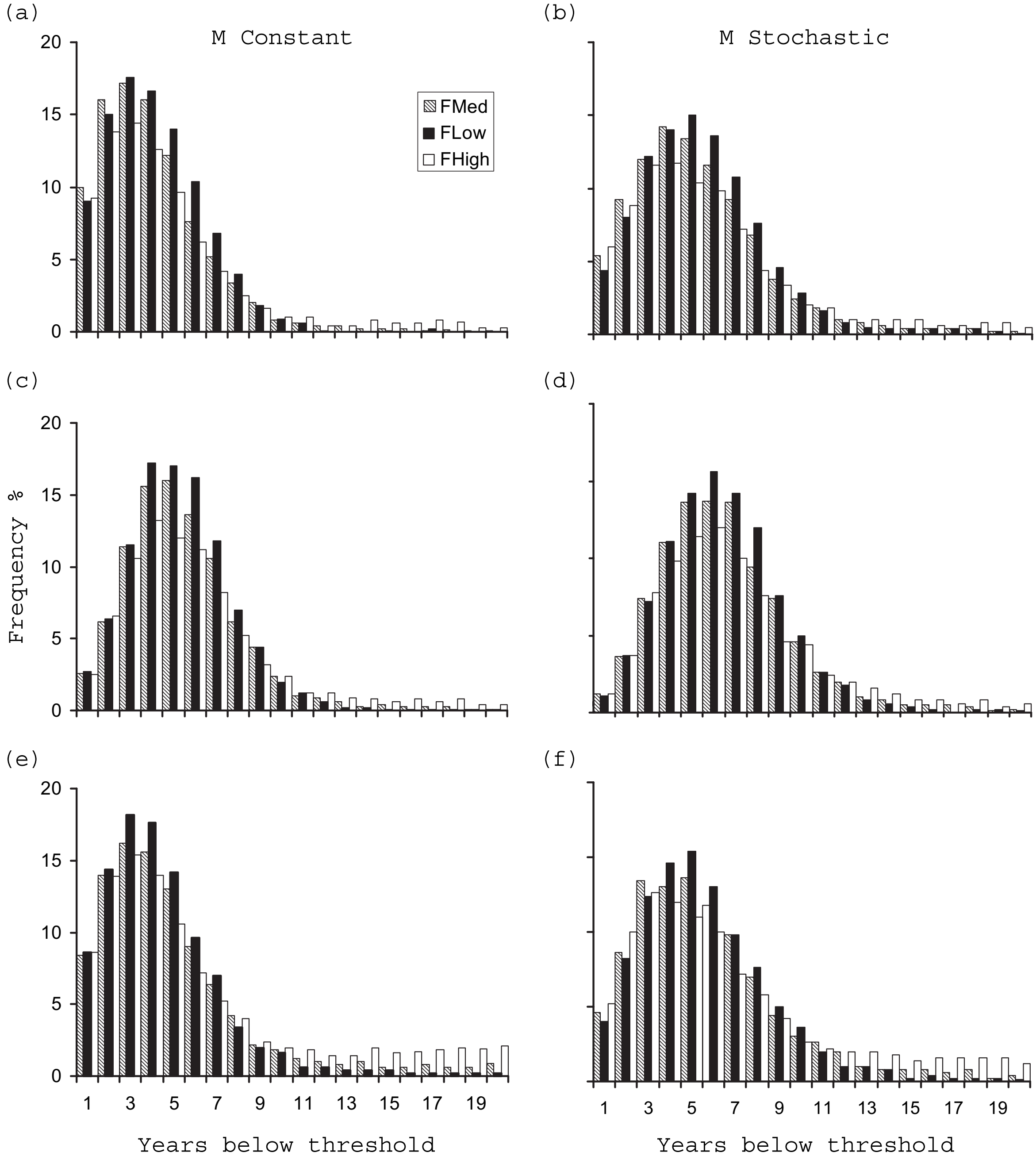

Figure 4. Frequency distribution of simulations with 1—20 years of juvenile sandeel biomass below the threshold value for three recruitment models (Case 1: 1/2; Case 2: 3/4; Case 3: 5/6) and two natural mortality models (constant M: 1/3/5; autocorrelated M: 2/4/6) at three levels of fishing mortality ($F_{med}$, $F_{high}$, and $F_{low}$), excluding simulations where sandeel populations crashed.

and Huppop, 2003; Post, 2003) systems. The positive autocorrelation in the Shetland sandeel recruit time-series and apparent synchrony in recruitment across Shetland fishing grounds suggests that environmental forcing may be strong (Poloczanska, 2001).

The set of recruitment models with low curvature near the origin (Case 3) had the highest rates of population crashes, as the incidence of high recruitment was reduced for any given SSB. Determining a realistic stock-recruit relationship is impossible with a limited data set over a restricted SSB range. Choosing a wrong model may overpredict the range of potential recruitment for any given SSB and might make the simulated population appear more resilient to exploitation. However, our results show that allowing for autocorrelation in the recruitment residuals has much more impact on most summary statistics than changing the curvature parameter (Case 2; Table 2).

If fluctuations in the sandeel stock at Shetland are driven largely by extraneous factors, this has important implications for fishery management. Even if exploitation rates are kept low, the risk of population crash exists. The risk increases with exploitation pressure. Of the simulations that did not crash, the type of model selected had stronger influence on sandeel recruitment and, as a derivative, seabird breeding success than fishing pressure. The frequency of years with sandeel biomass below the threshold increased with exploitation rate, but the occurrence of a series of three consecutive low years did not necessarily increase. Thus, the management system evaluated here would not seem to require additional measures on controlling fishing pressure to limit future closures to the fisheries. Poor breeding years for seabirds are inevitable, even with a greatly reduced fishery. It is up to seabird ecologists to understand the implications of breeding failure years on the long-term dynamics of seabird populations.

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