INSTITUTE OF TERRESTRIAL ECOLOGY
(NATURAL ENVIRONMENT RESEARCH COUNCIL)
SNH (Southeast Region)/NERC CONTRACT 923/D2J/206/297
ITE PROJECT T08051l5 (h5?)

POPULATION MODELS OF HERRING AND LESSER BLACK-BACKED GULLS ON THE ISLE OF MAY NNR

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November 1994

RECOMMENDATIONS FOR THE MANAGEMENT OF GULLS ON THE ISLE OF MAY NNR

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1. There is no suggestion that current numbers of herring or lesser black-backed gulls are having a serious adverse effect on the other avifauna, vegetation or amenity value of the Isle of May. Therefore there is no justification for implementing an immediate cull of adult gulls.

2. We suggest that the "target" levels of gulls be raised to the levels predicted by our model, i.e. 2700 pairs of herring gulls and 1300 pairs of lesser black-backed gulls as long as

(a) The breeding populations of herring and lesser black-backed gulls continue to be censused on the Isle of May each year using the current methodology.

(b) Control measures are initiated to ensure that no young gulls are reared on the island. This will allow the predicted increases to be kept under some check. Elimination of output should be part of a warden's duties.

(c) A study on the damage caused to other birds by increasing numbers of gulls (doubtless exacerbated by the increasing numbers of human visitors) is initiated.

(d) Vegetation monitoring is given a high priority to assess the effects of increasing numbers of gulls, perhaps by employing a botanist as a summer warden.

(e) The gulls nesting on the other Firth of Forth islands are censused in 1999 or 2000.

These schemes should give adequate warning if gulls start to cause damage to the reserve or gull numbers decline.

3. SNH should decide how it wants the Isle of May NNR to develop. The conclusion of such deliberations may influence the "target" levels of gulls.

4. A political and public-relations debate should be initiated to prepare the ground in case culling of adults needs to be carried out in the future.

CONTENTS

SUMMARY

1. Numbers of both herring and lesser black-backed gulls are now increasing on the Isle of May following periods of decline during the 1980s.

2. Breeding success of the herring gull is high, that of the lesser black-backed gull is lower.

3. Adult survival is high (88% p.a. for herring gull, 91% for lesser black-backed gull), but slightly lower than that estimated in the 1970s.

4. A simple population model using an adult survival rate of 0.88, a survival rate from fledging to first breeding of *ca.* 0.40 and age of first breeding of 4 years provides a good description of changes in numbers of herring gulls between 1986 and 1994.

5. This model predicts that there will be 2716 pairs of herring gulls (95% CI 2186-3245 pairs) on the Isle of May by 1998.

6. The dynamics of the lesser black-backed gull population are more complex than those of the herring gull and a simple population model did not provide a good description of the observed changes between 1986 and 1994. The population appears to be subject to periodic bursts of immigration and emigration. This makes it difficult to predict future population changes with any confidence. Our best estimate is that there will be a minimum of 1343 nests in 1999 but we stress that the error about this figure will be large but unquantifiable.

7. The herring gull population in the Firth of Forth appears to be increasing slowly; that of the lesser black-backed more rapidly, possibly at 8% p.a.

8. No work is being carried out to assess the impact of herring and lesser black-backed gulls on the other avifauna, vegetation or amenity value of the Isle of May. There is no suggestion that current population levels of gulls are having a serious adverse effect on any aspect of the reserve. It is unknown whether the predicted increases in gull numbers will be large enough to cause any damage.

9. We consider there is no ecological evidence to justify implementing a cull of adult birds. However it may be prudent to adopt a precautionary approach. We recommend that (a) breeding output is severely reduced, (b) the population is monitored annually, (c) a study is made of the effect of increasing numbers of gulls on the seabirds, and (d) a serious attempt is made to monitor the vegetation of the island. SNH needs to decide on how the reserve should develop before it can set acceptable and justifiable upper limits on gull numbers.

1 BACKGROUND

In the late 1960s and early 1970s the rapidly expanding herring and lesser black-backed gull populations on the Isle of May were perceived as having a serious impact on the other bird species, the vegetation and the amenity value of the island. A major programme of control was implemented so that by the mid 1980s, total numbers had been reduced to 2,600 pairs, still well above the target population of 1000 pairs set by the initial (1972) review but in line with a decision made in 1976 to revise the target to 2-3,000 pairs. Since 1989 no control measures have been enforced, instead considerable time and effort has been directed towards obtaining demographic information. A sudden and marked increase of 50% in total numbers of both herring and lesser black-backed gulls was recorded between 1992 and 1993. This resulted in populations of both species being higher than those recommended in the current National Nature Reserve Management Plan. The plan is due to be reviewed in late 1994 and there is therefore an urgent need to evaluate current population trends and on the basis of the available demographic data predict future changes. In addition the impact of these current and projected gull populations on the other bird species, the vegetation and the amenity value of the island needs to be assessed.

2 OBJECTIVES

1. Review the accepted level for gull populations

In the past "target" gull populations have been set at levels which, it was assumed, would allow for the recovery of vegetation and would minimise the effect of gull predation on the breeding success of the key bird species. The NNR's current (4th) Management Plan allows for a maximum of 2,000 herring gull and 800 lesser black-backed gull nests. For the forthcoming Management Plan Review this figure needs to be re-evaluated to see whether or not in the light of current information it is set at the correct level.

2. Following past control measures, gulls have been prevented from recolonising certain areas of the island. These have included areas
(a) favoured by terns, (b) *Festuca/Armeria* grassland, (c) areas of serious soil disturbance and erosion. A review is required of this area based strategy.

3. Review Isle of May gull populations in the context of other gull colonies in the Firth of Forth. Make recommendations for further research work on the Firth of Forth populations.

4. Review previous ten year data sets on gull species for the Isle of May. Incorporate data into population models for both gull species.

5. Using population models, predict future population trends under different management options and assess their effectiveness e.g. culling of adults, control of breeding output.

3 POPULATION PARAMETERS: METHODS AND DATA

3.1 Population estimates

Each year since 1983 the numbers of gull nests have been counted during the last few days of May when peak numbers of birds had laid but before many clutches had hatched. Field trials indicated that this was the best time to assess the breeding population (Wanless & Harris 1984).

Each count (which included clutches, well-formed but empty nests and any broods of chicks) was made by a team of people systematically searching each of 35 sections of the island, in narrow strips delimited by bamboo canes. Up to 1988 all clutches (except those on The Maidens) were smashed and empty nests destroyed. In subsequent years eggs and nests were marked with a coloured spray. The efficiency of the count of each area was assessed by a single observer, usually one who had not taken part in the count, visiting the area immediately after the count had been made and recording the number of marked and unmarked (or destroyed and overlooked) nests and clutches. The normal counting efficiency was c. 85% and area counts were adjusted to allow for these missed nests.

The nests of the two gull species cannot be identified with any certainty. Therefore the proportions of herring and lesser black-backed gulls nesting in each area were assessed by counts of individual gulls, visible from vantage points after they had been disturbed. Normally 30-55% of the individual gulls estimated to be present on the island were checked. The estimated total of nests in each section was then assigned to the two species using the appropriate herring:lesser black-backed gull ratio. Annual nest totals for each species were then calculated.

Numbers of herring gulls declined steadily, at 6% p.a., from 2578 nests in 1983 to 1462 in 1992 but then increased by 41% to 2059 in 1993 (Table 1, Fig. 1). The 1994 count was 2122 nests.

The pattern of change was slightly different for lesser black-backed gulls where numbers declined by 35% p.a. from 1488 nests in 1984 to 534 in 1987 before increasing steadily but unspectacularly (+8% p.a.) until 1992 after which there was a large increase (+68%) between 1992 and 1993 which paralleled that of the herring gull. The 1994 count was 1270 nests.

3.2 Breeding success

Breeding success was assessed by ringing as many well-grown (i.e. specifically identifiable) chicks as possible and making a survey of large or recently fledged gulls in the first or second week of August to determine the proportion which were ringed. Very few young die after reaching ringable age. The sample survey usually consisted of 30-60% of the total young fledging. Knowing (a) the numbers of each species ringed, (b) the proportion ringed, and (c) the number of nests of each species, the average breeding output of each species was

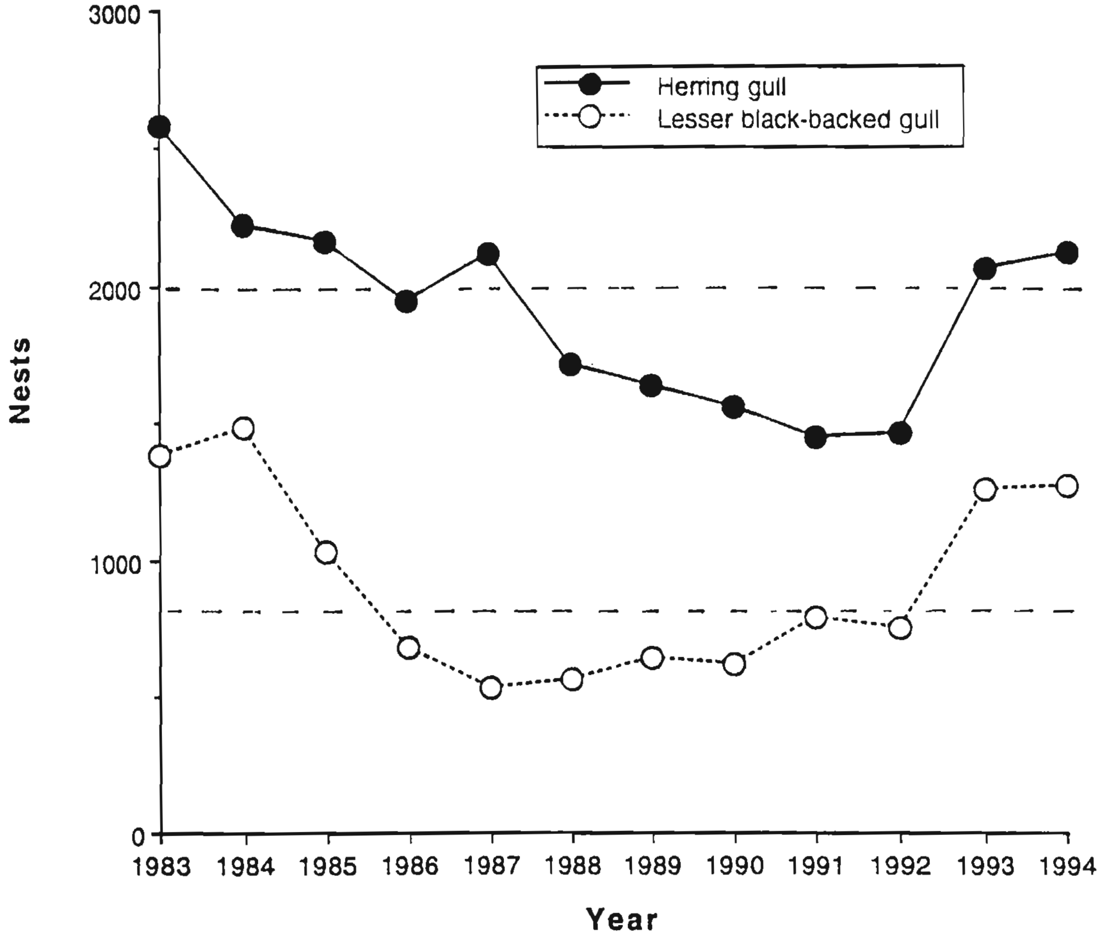


Figure 1. The numbers of gull nests on the Isle of May 1983-1994. The dotted lines are the relevant population levels set by the current management plan.

calculated, making allowances for areas where nests had been destroyed.

The mean breeding output of the herring gull 1989-94 was 1.38±SE 0.12 chicks/nest counted whereas that of the lesser black-backed gull was significantly lower at 0.81±0.09 (paired t-test, t = 6.03, 5 d.f., P<0.002 (Table 1)).

Breeding success (young fledged per pair) of herring gulls varies considerably, e.g. it was 0.67-0.91 on the Isle of May when the colony was dense and undisturbed (Parsons 1975) whereas Monaghan (1979) found it to be near 2.0 for isolated pairs nesting in towns. The current high success on the Isle of May is probably due to gulls nesting at a low density. Between 1989 and 1994 there was an almost statistically significant negative relationship between breeding output and population size (R^2 = 61%, n = 6 years, P = 0.07).

There are few previous data for the lesser black-backed gull. Duncan (1981) estimated breeding success at 0.85 young per pair in 1975. There was no obvious relationship between the output of lesser black-backed gulls in 1989-94 and population size.

The breeding success of Isle of May gulls at present appears to be typical for the species in the UK.

3.3. Total young fledged

In 1984-87, attempts were made to prevent any production of chicks except on The Maidens. In 1988, all first clutches were destroyed but there was no destruction of relays. In 1989-93 only nests in specific areas (North Plateau south of Three Tarn Nick), South Plateau, East Braes) were destroyed. In 1994 nests on North Plateau, Colm Hole-Kirkhaven, Burrian and part of Tarbet were also destroyed. Thus, the totals of young reared each year has varied dramatically depending on the extent of nest-destruction with totals being very low 1984 to 1987 during which time the main production was 150-350 young herring gulls on The Maidens and about 50 young per year elsewhere on the island. These annual totals given in Table 1 are used in the later population models.

3.4 Adult survival

Changes in adult survival have a great effect on population change. Migot (1992) considered that the relative sensitivity of the annual rate of change of French herring gulls to adult survival was five times greater than to a parameter of fecundity. Therefore, considerable attention was given to obtaining an accurate and up-to-date assessment of survival. Starting in 1989 incubating adults were caught with walk-in traps. Birds were given a unique colour-combination which always included a green ring with a large engraved M (as a colony specific ring). Gulls were sexed from their overall head-and-bill length using the cumulative frequency distribution curve (see Coulson *et al.* 1983).

Each year, more adults were colour-ringed to maintain about 150 colour-ringed adults of each species in the population. Searches were made for these individually marked birds on the Isle of May throughout each subsequent season.

The data were analysed using the modified Cormack-Jolly-Seber method using the program SURGE (Lebreton *et al.* 1992). This method does not allow the calculation of the survival over the last winter (in this case 1993-94) as there is no way of assessing the "finding efficiency". In the following analysis "recapture" refers to the sighting of a marked individual.

Tables 2 & 3 show the basic capture-recapture data as input to SURGE. We calculated minimal survival estimates - 82.2% and 87.4% for male and female herring gulls respectively, and 88.2% and 88.1% for male and female lesser black-backed gulls - from resightings of those birds in a given year. As expected these estimates are lower than the SURGE values by the following amounts: 3.6% (herring gull males), 1.7% (herring gull females), 3.6% (lesser black-backed gull males) and 2.6% (lesser black-backed gull females). Table 4 shows estimated annual survival rates for males and females and both sexes combined, for the two species. The estimates are based on a model in which the recapture rate is allowed to vary between years. Although the differences between the basic and modelled survival rates are quite small, reflecting the high recapture rate (Table 5), they have important consequences for population projections.

SURGE can also be used to fit different models in which either survival or recapture rate is constant and by comparing the fit of different models we can test specified hypotheses For example, to test for annual variations in survival we compare the fit of a model in which both survival (s_t) and recapture (p_t) are time-dependent with a model in which survival (s) is constant and recapture rate (p_t) is time-dependent. Tables 6 & 7 show some results. In no case is a statistically significant difference in annual survival rates or recapture rates detected. This is not to say that there are not any differences, merely that the observed differences are consistent with the amount of sampling error in the estimates (see Table 4).

A single survival estimate for use in the population projection analysis can be calculated as the arithmetic mean or geometric mean of the annual estimates, as in Table 5, or we can use an estimate based on a model which assumes a constant survival. Table 8 shows estimates using the latter approach. Clearly, it does not make much difference which method is chosen and 88% for herring gull and 91% for lesser black-backed gulls were used for all models unless otherwise stated.

Table 8 also shows a comparison of the sexes using a model with constant survival. Estimated survival in the herring gull is about 4% higher in females but the difference is not statistically significant. For the lesser black-backed gull the difference is even smaller. We therefore use single estimates for the two species: 88% for herring gull, 91% for lesser black-backed gull.

There are few estimates of the annual survival of European herring gulls. Chabrzyk and Coulson (1976) indirectly estimated the survival of Isle of May adults as 93.5% and, a decade later, Coulson and Butterfield (1986) reported a survival of 91.7% for a small sample of colour-ringed birds at a small colony in NE England. A similar study at a French colony 1984-86 estimated survival at 89% (Migot 1992) but on Skomer, Dyfed the survival rate declined dramatically from 91.6% in 1978 to 70-80% 1989-92 (Perrins 1993).

There are even fewer published survival rates for the lesser black-backed gull but on Skomer it varied from 97.3% to 56.7% with a highly significant decline between 1976 and 1992 (Perrins 1993).

Given that there are considerable annual and regional differences in survival of these gulls (Monaghan 1993), we use only our own measured survival rates in the models.

3.5 Nonbreeding

In 1994, 60 out of 150 (40%) individually marked herring gulls probably did not breed as they were never observed attending eggs or young. The figure for lesser black-backed gulls was 71 out of 161 (44%). Comparable figures for 1993, were for herring gulls 33% (of 135 birds) and lesser black-backed gulls 33% (of 139 birds) (J. Calladine unpublished data).

Several other studies have reported considerable numbers of experienced adults failing to breed We have no information on (a) the annual variation in nonbreeding,or (b) whether these birds make nests but do not lay (and so could be included in the population estimates) so no allowance has been made for it in the model.

3.6 Age of first breeding

Previous studies have found that, although a very few gulls breed in their third year, in a stable population most do not start to breed before their fifth or sixth year. However, Coulson *et al.* (1982) documented how the age of first breeding in herring gulls on the Isle of May was reduced to 4 years (when at least 65% of birds returning had bred) as the population was reduced.

Survival to breeding age

Chabrzyk & Coulson (1976), using Isle of May demographic data, calculated that about 60% of young survived to breeding age. We use a range of values.

Searches for colour-ringed adults

Some colour-ringed adults were seen only very infrequently on the Isle of May.

To assess the possibility that some of these birds, and others which was never seen, were present in neighbouring colonies, J. Calladine checked adults in other colonies in and near the Firth of Forth for colour-rings in 1994: Inchcolm (8 May, 25 May, 10 July), Inchkeith (9 May, 26 May, 7 July), Fidra (11 May, 7 July), Craigleith (11 May, 27 May, 7 July), St Abb's Head (12 May, 6 July) and the inland colony at Coire Odhaine (10 May, 8 July).

Only two birds from the current colour-ringing scheme were seen - both lesser black-backed gulls on Craigleith on 7 July. Both had been seen regularly on the May during 1994, one had laid eggs (and subsequently failed), the other had not bred. We assume that once adults have bred they remain faithful to their chosen colony.

4 POPULATION MODELS

Before attempting to predict how gull populations might change on the Isle of May over the next 5 years, we tested how well a simple population model fitted the observed changes in numbers between 1987 and 1994, a period for which we had good demographic data. We used a difference equation model (Caswell 1989) which assumes a closed population and a 50:50 sex ratio in fledged chicks in which changes in population size are given by:

$$N_{t+1} = s_A N_t + s_{4R} p Y_{t-3}/2 + s_{5R}(1 - p) Y_{t-4}/2$$

where

N_t is the number of breeding females in year t (assumed to be equivalent to the number of breeding pairs).

Y_t is the total number of young fledged in year t.

p is the proportion of birds which breed for the first time aged 4 years.

s_{4R} and s_{5R} are the survival rates of fledged young to breeding ages 4 and 5 years respectively.

s_A is adult survival.

4.1 Herring gull

4.1.1 Estimation of model parameters

To estimate the model parameters, we fitted a model to the data for the number of breeding females and the total numbers of young fledged in each year. Parameter estimates were obtained by minimising the sum of the squares (ss) of the proportional errors of prediction, i.e. by minimising

$$SS = \sum \left(\frac{N_t - \hat{N}_t}{N_t}\right)^2$$

where $\hat{N}_t$ is the estimated population size in year t.

Fitting the full model to the data for herring gulls gave

$$\hat{N}_{t+1} = 0.916 N_t + 0.544 Y_{t-3}/2 - 0.234 Y_{t-4}/2$$

The negative term for birds first breeding at 5 years suggests that few birds breed at this age. Fitting a model with age of first breeding equal to 4 years gave

$$\hat{N}_{t+1} = 0.865N_t + 0.460Y_{t-3}/2$$

The estimated adult survival rate of 0.865 is close to the value of 0.88 obtained from the SURGE analysis of the captive-recapture data. However, the model based estimate has a relatively large standard error (s.e. = 0.041) and we therefore preferred to use the capture-recapture estimate.

Fitting a model with adult survival fixed at 0.88 gave

$$\hat{N}_{t+1} = 0.88N_t + 0.44Y_{t-3}/2$$

The estimated survival rate of fledged young to breeding age of 4 years was 0.44.

4.1.2 Checking the fit of the model

The fit of the model was examined using stepwise and free-running predictions. In the stepwise prediction method, population size in a given year is predicted from the observed population size in the previous year. This effectively highlights particular years in which predictions are poor and also provides a method for assessing errors of long-term prediction. A comparison of predicted numbers (assuming s_R of 0.40 and 0.44 respectively) and actual counts is shown in Figure 2.

The annual proportionate (%) errors of stepwise prediction $((N_t - \hat{N}_t)/N_t)$ for the two models shown in Figure 2 are given below:

Year	s_R **= 0.40**	s_R **= 0.44**
1987	-6.3%	-8.8%
1988	-10.6%	-10.8%
1989	5.3%	5.1%
1990	5.0%	4.7%
1991	0.3%	0.1%
1992	1.1%	-1.1%
1993	14.7%	12.4%
1994	-3.7%	-5.3%
Sum of squares	**4.4%**	**4.3%**

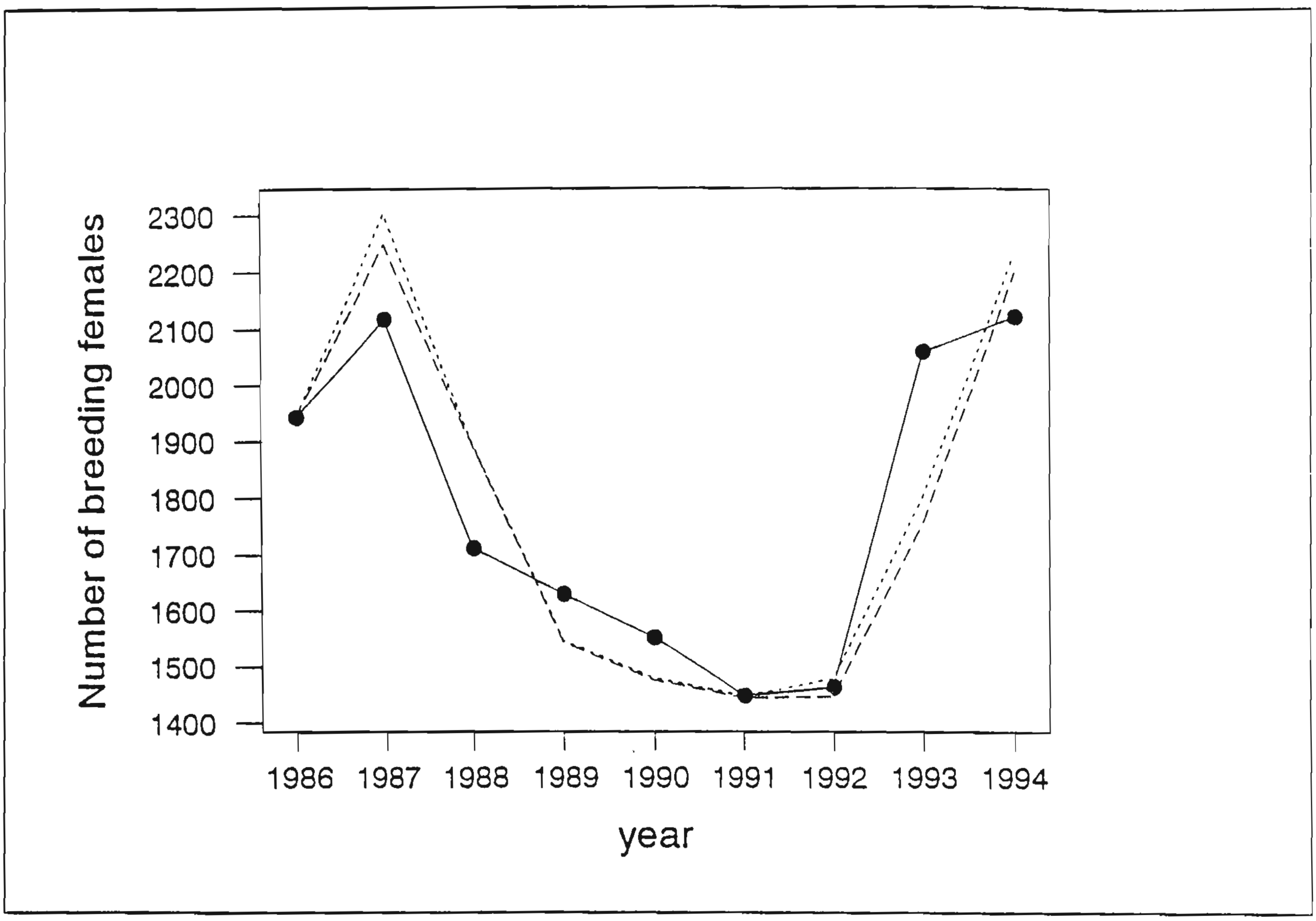


Figure 2. A comparison of observed numbers of herring gulls (solid dots and lines) and these predicted using the stepwise method 1986-94. Dotted and pecked lines use s_R = 0.44 and 0.40, respectively.

The fit of both models is very similar and for both predictions were poorest in 1988 and 1993 with numbers being overestimated in the former and underestimated in the latter.

The observed gradual decrease between 1987 and 1990 and the levelling off of numbers between 1990 and 1992 are consistent with the massive reduction in recruits from the colony due to the control of breeding output implemented between 1984 and 1988 (Table 1). The marked increase in 1993 coincides with the relaxation of these control measures in 1989. The observed count in 1993 exceeds both predicted values, possibly indicating a higher survival to breeding of the 1989 cohort and/or net immigration to the colony. However, counts for 1994 compare well with predicted values so there is little to suggest that a radical change in vital rates had occurred at the end of the period.

A simple graphical illustration of the fit of the observed counts to the model is obtained by plotting the annual change ($R_t = N_{t+1}/N_t$) against the chick production rate recruitment (Y_{t-3}/N_t). If the model holds this should be a straight line apart from random scatter. Figure 3 confirms this and shows the fitted line with $s_A = 0.88$, $s_R = 0.40$.

In the free-running prediction method, population size in a given year is predicted by repeatedly applying the model to the population size at the beginning of the series. This is the approach adopted for long-term prediction. However, with this method prediction errors are cumulative since errors for any year affect those in subsequent years. This feature makes it difficult to see where the model may be failing. Free-running predictions for the two models and actual counts of herring gulls are shown in Figure 4. As expected from the stepwise predictions there is little to chose between fitted models from their free-running predictions.

Proportionate (%) errors of free-running prediction were calculated in the same way as stepwise predictions. Errors for the two models shown in Figure 4 are given below:

Year	**$s_R = 0.40$**	**$s_R = 0.44$**
1987	-6.3%	-8.8%
1988	-17.5%	-20.4%
1989	-10.8%	-13.8%
1990	-5.0%	-8.0%
1991	-4.5%	-7.8%
1992	-2.8%	-7.0%
1993	14.4%	9.4%
1994	7.6%	1.4%
Sum of squares	**7.4%**	**9.2%**

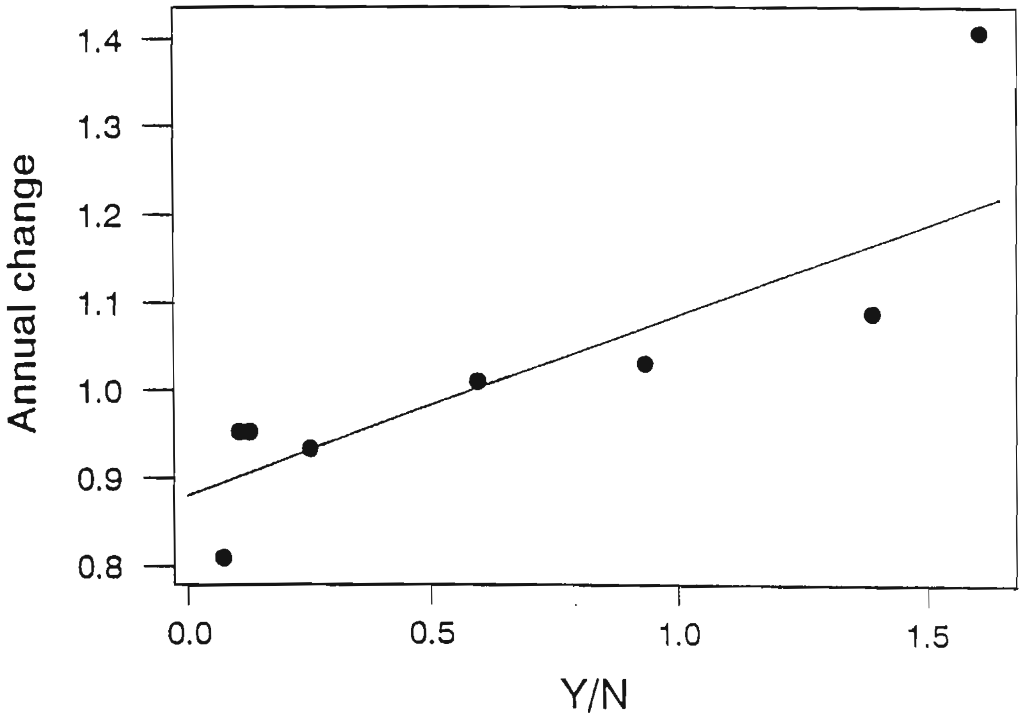


Figure 3. A graphic check of the fit of the stepwise prediction model for population changes in herring gulls on the Isle of May 1986-94. The annual change (R_t) is plotted against the chick production rate recruitment (Y_{t-3}/N_t). Also shown is the fitted line with $s_R = 0.88$, $s_R = 0.40$.

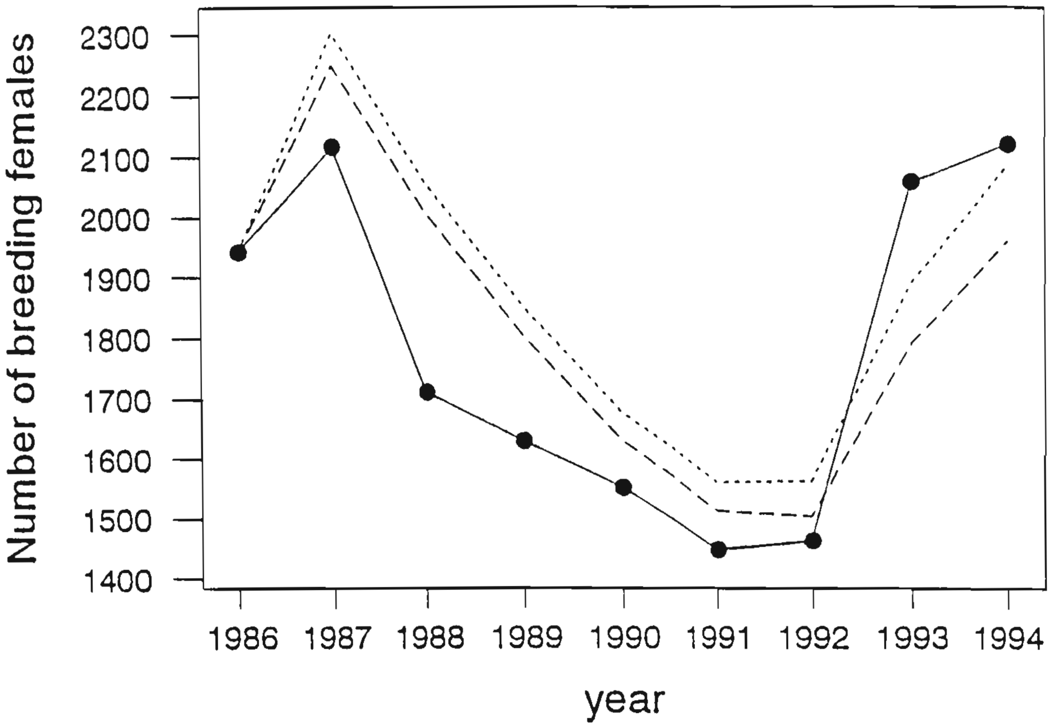


Figure 4. A comparison of observed numbers (solid dots and lines) and these predicted using the free-running prediction method for herring gulls on the Isle of May 1986-94. Dotted and pecked lines use s_R = 0.44 and 0.40 respectively.

However the observed pattern of errors is not easy to interpret because of the effect of serial correlation.

4.1.3 Population predictions

The above model provides a reasonably good description of population changes for the herring gull on the Isle of May between 1986 and 1994. In contrast to previous conclusions of Coulson *et al.* (1982) that there was periodic net immigration into and net immigration away from the Isle of May colony, actual counts between 1986-94 conformed well with a simple model for a closed population. This agreement appeared to hold both in years when recruitment was normal and in seasons when few Isle of May recruits were available due to control of reproductive output. We therefore used the free-running prediction method to predict population changes over the period 1995-98 (Figure 5). Predicted numbers for 1998 are 2716 and 2860 breeding females with $s_R = 0.40$ and $s_R = 0.44$ respectively.

Clearly these predictions are sensitive to the values of s_A and s_R used. To assess how changes in these vital rates would alter the predicted numbers we reran the model using a realistic range of adult survival rates and recruitment rates (Table 10). Predictions for 1998 varied from 2635 breeding females ($s_A = 0.87$, $s_R = 0.40$) to 3169 breeding females ($s_A = 0.89$, $s_R = 0.50$).

4.1.4 Estimation of prediction errors

Errors in long-term predictions may be of four types:

(a) Systematic error due to errors in the estimates of adult survival and survival to breeding age.

(b) Random errors due to annual variation in the vital rates.

(c) Errors due to formulation of the model, e.g. the population might not be closed.

(d) Errors from future changes not accommodated by the model, e.g. systematic changes in the vital rates, increased immigration, etc.

For (d) we can only hope for the best!!

For (c) the observations appear to be consistent with the simple model.

For (a) we can make predictions using different combinations of vital rates, e.g. $s_R = 0.40$ and $s_R = 0.44$.

For (b) we can make a rough assessment based on the errors of prediction of the fitted model. Figure 6 shows the absolute proportionate errors plotted against observed population size from the model. This suggests that the

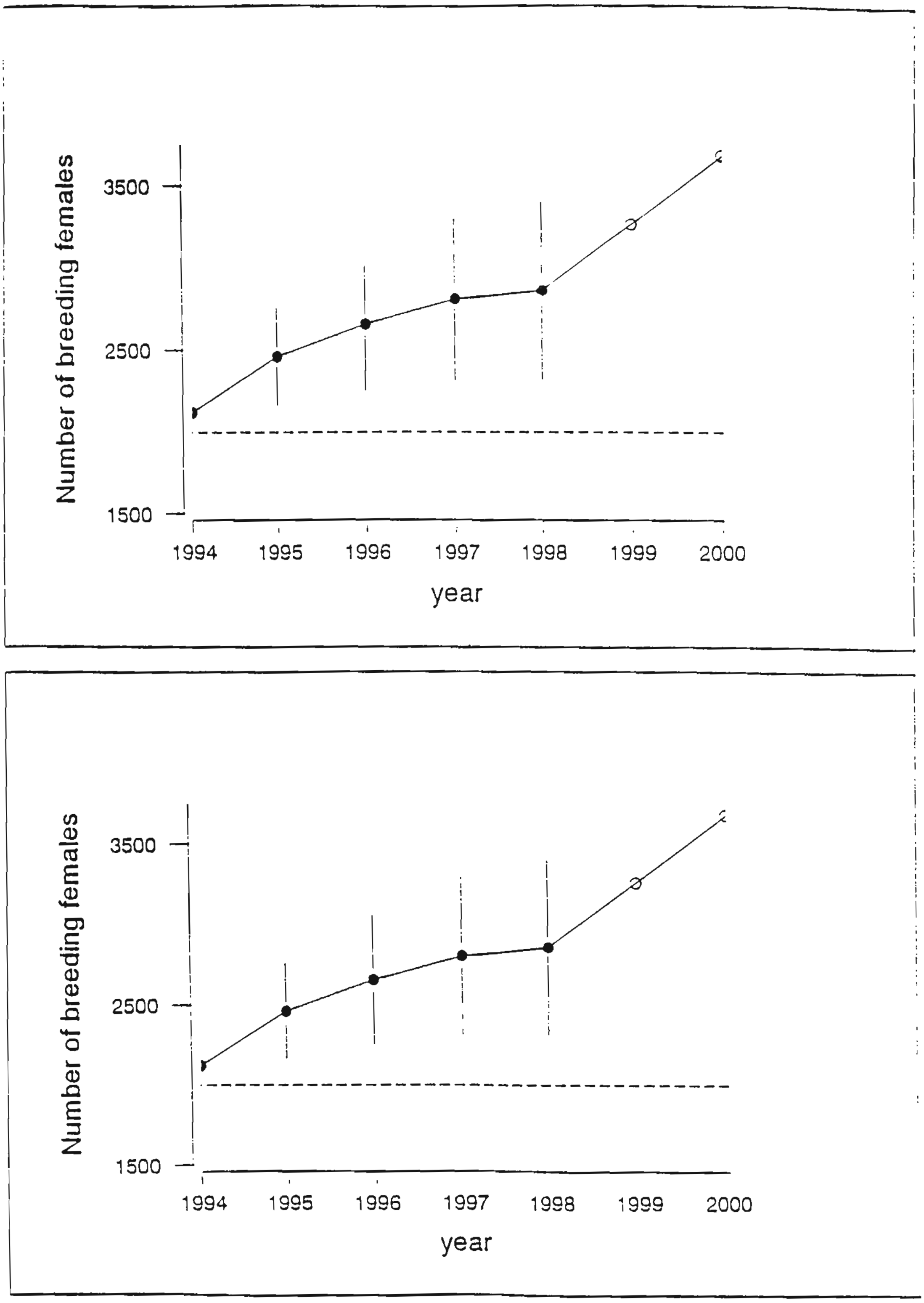


Figure 5. Predicted changes in numbers (and 95% confidence intervals) of herring gulls on the Isle of May 1994-2000. The solid symbols use past chick production figures, open symbols assume production at the past average level (and no CI is shown). The horizontal dashed line is the maximum population of 2000 pairs allowed under the current management plan. The upper graph uses $s_R = 0.40$, the lower uses $s_R = 0.44$.

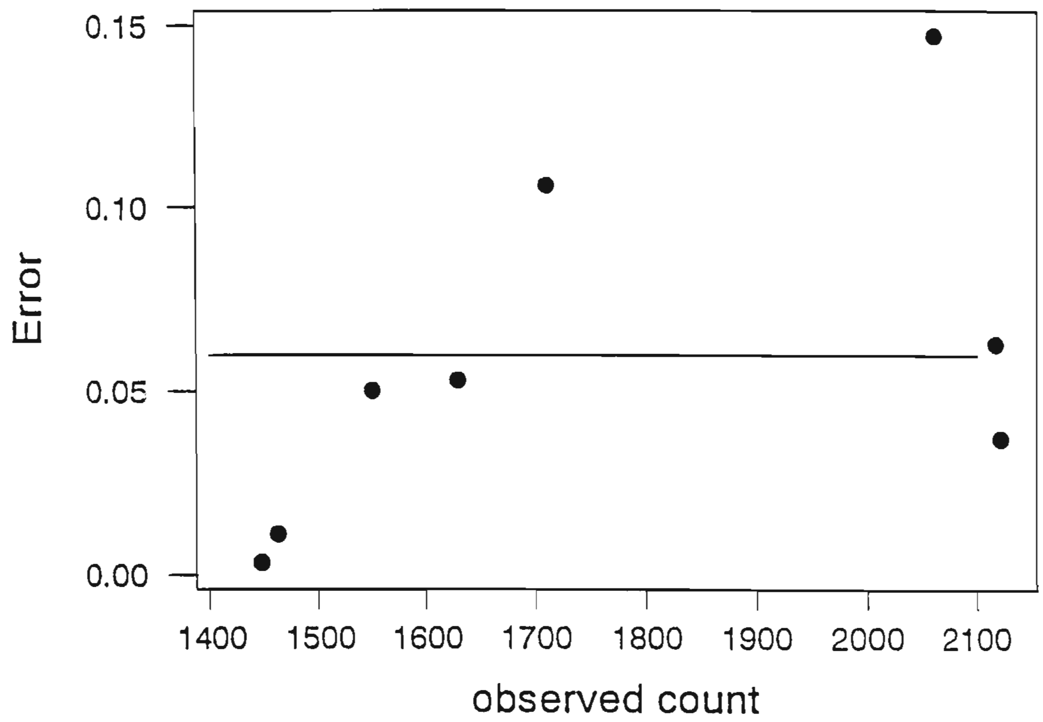


Figure 6. Absolute values of proportional errors using the model in Figure 2 to predict N. The horizontal line corresponds to an error of 6%.

random error in the stepwise prediction has a coefficient of variation (CV) of about 6%, i.e. given the population size in year *t* and chick production for year *t-3*, the estimate for year *t+1* has a CV of about 6%. More realistically, the random error is likely to depend on the number of adults in year *t*, the chick production in year *t-3*, and the random variation in the vital rates. However, over a fairly wide range a model with constant CV looks reasonable.

In free-running predictions random errors in predictions over one year are cumulative. Full details of the method used to calculated such errors are given as an Appendix to this report. In Figure 5 predicted numbers are shown with their 95% Confidence Interval. The size of the sampling errors indicate the limitation of the predictions. However, all the indications are that numbers will increase over the next few years. The predicted increase stems mainly from the fact that breeding output was not controlled between 1991 and 1993, the slight check predicted in 1998 results from the partial control of breeding output implemented in 1994.

4.1.5 Changes after 1998

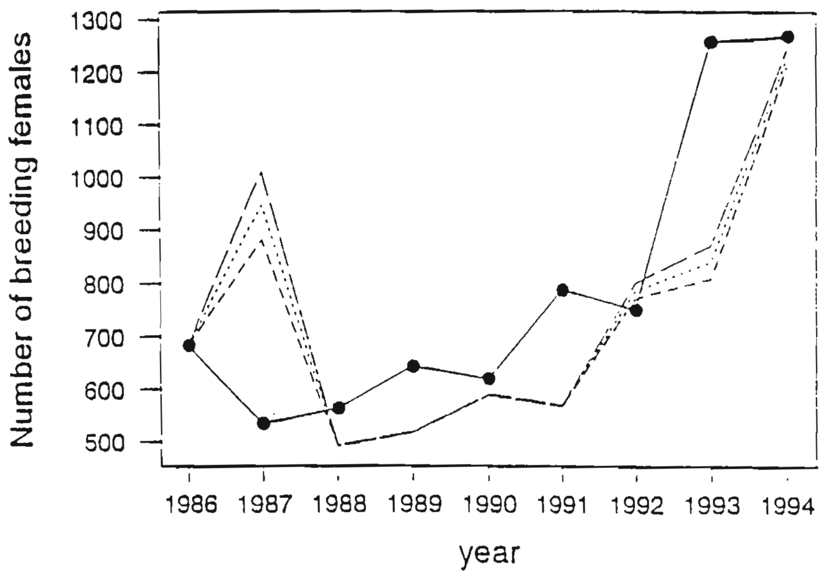
The difficulty of reliably predicting changes in numbers increases markedly after 1998 because the cohorts contributing to the population have yet to be produced . During the period between 1989-1994 when breeding success was not controlled, mean annual breeding success was 1.38 chicks/pair. We applied the average breeding output to the predicted populations in 1995 and 1996 respectively to estimate the number of young expected to be produced in each of these two seasons. Integrating these figures into the free-running prediction methods suggests totals of 3055 and 3396 breeding females in 1999 and 2000 (s_R = 0.4) and 3265 and 3680 breeding females (s_R = 0.44) (Figure 5). We emphasise that the errors associated with these estimates will be considerable.

4.2 Lesser black-backed gull

4.2.1 Estimation of model parameters

A similar approach was adopted for the lesser black-backed gull. However, in contrast to the herring gull, model predictions based on the observed s_A and s_R did not approximate closely to observed population changes, irrespective of the values of s_R or age of first breeding used (examples shown in Figures 7 and 8). Thus the relatively strong cohorts of chicks from 1982 and 1983 did not recruit into the breeding population in 1987-88, the population increased, albeit at a slow rate over a period when virtually no natal recruits were available (1989-92) and the observed increase in 1993 was greatly in excess of that expected from the chick production on the Isle of May in 1989-90. Proportionate errors given by both the stepwise and free running prediction methods were therefore markedly higher than comparable values for herring gulls (Table 9).

These result suggest that the dynamics of the lesser black-backed gull population are far more complex than those of the herring gull. In all probability



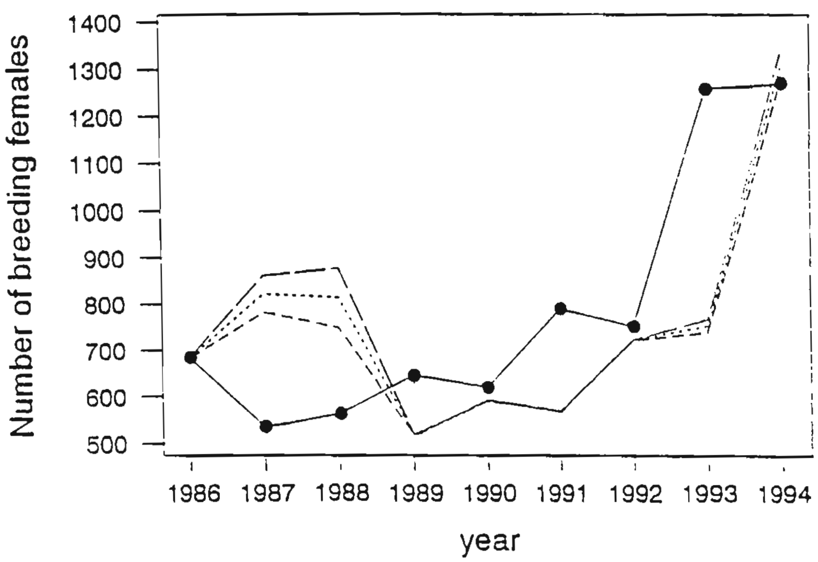
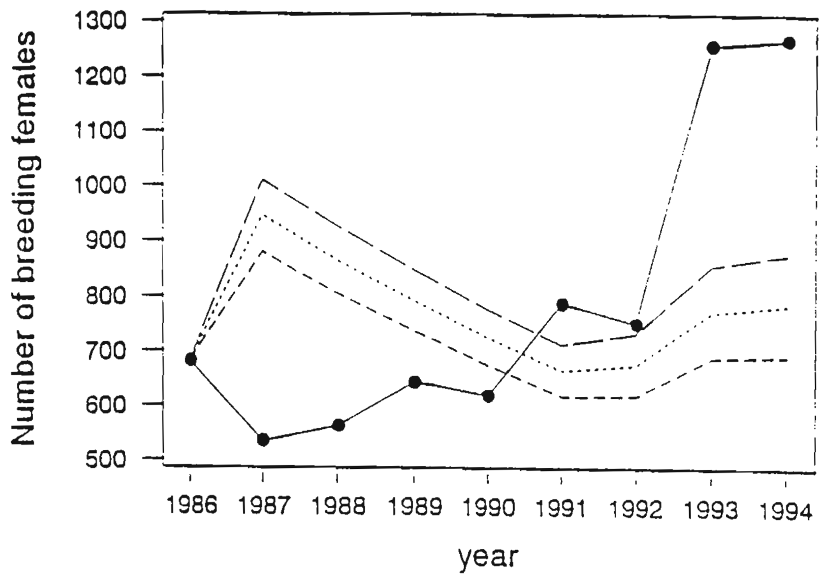


Figure 7. A comparison of observed numbers of lesser black-backed gulls (solid dots and lines) with those predicted using the stepwise method. Dashed, dotted and pecked lines use $s_R = 0.6$, $s_R = 0.5$ and $s_R = 0.4$, respectively. The upper graph uses an age of first breeding of 4 years, the lower an age of 5 years.



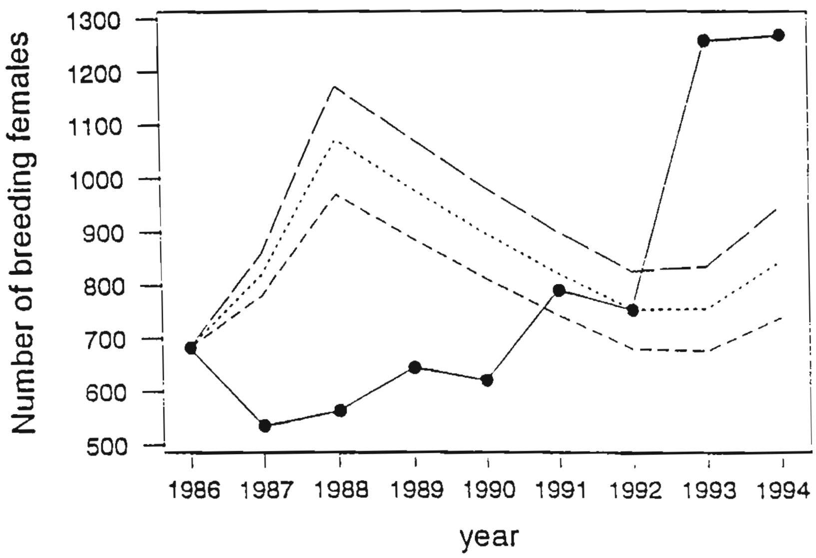


Figure 8. A comparison of observed numbers of lesser black-backed gulls (solid dots and lines) with those predicted using the free-running method. Conventions as in Figure 7.

the colony on the Isle of May is not a closed population and periodically exports recruits, as in the case of the 1982 and 1983 cohorts, or attracts recruits from other colonies, notably in 1991 and 1993.

4.2.2 Population predictions

A simple population model does not, therefore, provide a good description of the observed changes in numbers of lesser black-backed gulls between 1986-94 with the result that the free running prediction method cannot be used to predict future population trends with any confidence. Over the last few years observed numbers have typically been higher than those predicted by the model, assuming that this pattern continues, minimum population estimates can be predicted for the period 1995-99 (Figure 9). Thus the population will probably increase to 1343 nests in 1999. We emphasize that the errors about these estimates are likely to be extremely large and it would not be surprising if numbers in some years were much higher than predicted due to pulses of immigration.

4.3 The Isle of May gulls in a wider context

4.3.1 Herring gull

In 1994 a complete census of the gulls on the islands in the Firth of Forth was organised by J. Calladine (SNH) using the methods employed on the Isle of May. The estimated totals of nests and the percentage changes since the last similar census made in 1987 were:-

	Herring gull		**Lesser black-backed gull**	
	1994	**% change since 1987**	**1994**	**% change since 1987**
Isle of May	2122	+1	1270	+144
Craigleith	2385	+5	934	0
The Lamb	130	-41	55	+450
Fidra	1149	+180	492	+251
Eyebroughy	45	-74	0	0
Inchkeith	4977	+22	2607	+49
Inchmickery	108	+77	108	+77
Inchcolm	1615	+55	1669	+129
Carr Craig	38	{+93}	0	0
Haystack	16	{ }	0	0
Inchgarvie	210	+91	11	+10
Total	12795	+22	7146	+72

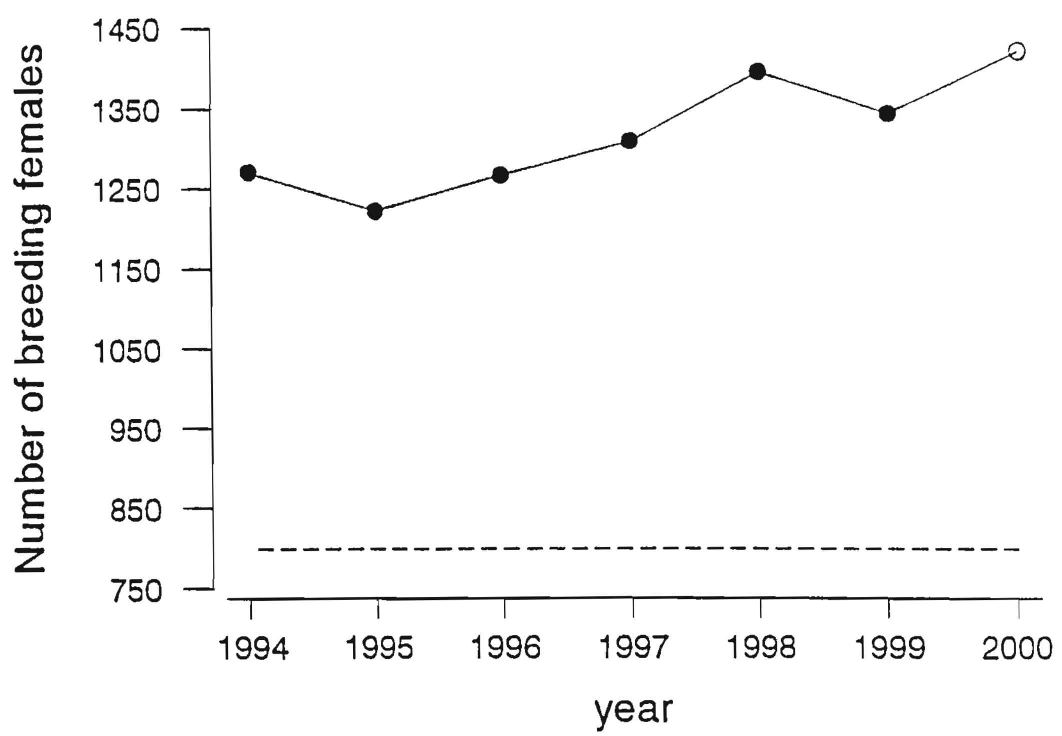


Figure 9. Predicted changes in numbers of lesser black-backed gulls on the Isle of May 1994-2000. The horizontal dashed line is the maximum population of 800 pairs allowed under the current management plan.

There are large colonies of herring gulls at Arbroath (363 + pairs in 1989) and at Rosyth Dockyard (600 pairs in 1989) but no recent counts are documented (Walsh & Gordon 1994).

The data are too fragmentary to even hazard a guess at the details of change in the Forth population, but if the increase had been expontential, the rate would have been 2-3% pa. The Isle of May has about 17% the population in the Firth of Forth, 11% of the population between Aberdeen and the English border.

In a review of the UK herring gull population 1986-93, Walsh & Gordon (1994) considered that the Scottish population had decreased by 4% p.a. over the period. Their figures suggest a slowing down, or even a slight increase, between 1992 and 1993.

4.3.2 Lesser black-backed gull

Numbers on the Forth Islands had increased by 72% (if the increase was exponential, average = 8% p.a.) between 1987 and 1994. Not included in the totals are the colonies at Loch Leven, Rosyth Docks (865 pairs in 1990) and Dunbarton Warehouses (211 pairs in 1988). In 1987 the Isle of May had 12.5% of the Forth Islands total, in 1994 17.8%. The counts of the other islands are too fragmentary to allow a detailed analysis.

Walsh & Gordon's (1994) analysis indicated that the coastal population in the UK increased at an average of 6.3% p.a. between 1986 and 1993. The increase was even more marked in Scotland, averaging about 10% p.a.. Several populations increased markedly between 1992 and 1993. Flanders Moss (Stirling) had *ca* 8000 pairs in 1980 (Whitelaw 1987) but the colony has since disappeared while a nearby site, Meall a' Choire Odhair (Perth & Kinross) held 1200-1450 pairs in 1988-9 (Walsh & Gordon 1994).

All the evidence suggests that lesser black-backed gull populations are relatively mobile (Coulson 1991) and as such are very difficult to model and it may well be impossible to produce predictions for future changes at single colonies.

4.3.3 Conclusion

The Isle of May gull populations cannot be viewed in isolation. The effects of any control measures will influence other, perhaps distant, populations just as control measures at other colonies (e.g. Inchmickery, Rosyth, Arbroath, Farne Islands) are likely to have unquantifiable effects on the gulls breeding on the Isle of May (see Coulson 1991).

It is essential that an attempt be made to continue documenting gull numbers at all colonies in and near the Forth. At the very least, another complete census should be made in five years time. This would be convenient as there are plans being made to undertake a third complete census of UK seabirds at the turn of the century.

5 THE EFFECTS OF GULLS ON THE ISLE OF MAY NNR

5.1 Other seabirds

The populations of most other seabirds on the Isle of May have, in general, increased over the last few decades. No work has ever been undertaken to assess systematically the impact of herring and lesser black-backed gulls on these species. The following is, therefore, a rather general summary of largely opportunistic observations made over the past 20 years. It is, however, clear that (a) predation on other seabirds e.g. taking guillemot eggs, tern chicks, etc. is carried out a by a small number of individuals which specialise in these activities, and (b) the problem is exacerbated by human disturbance. It is not clear whether the numbers of seabird specialists increases as total gull numbers increase, nor is it known what effect changes in the availability of other sources of food have on the number of gulls specialising on seabirds.

Fulmar *Fulmarus glacialis*. Currently increasing at 6% p.a.. Little or no interaction with gulls unless disturbed off eggs.

Shag *Phalacrocorax aristotelis*. In 1994 the population crashed to its lowest level for 40 years. Gulls take a few eggs and chicks, usually after humans have disturbed nesting adults, but overall, gulls have a negligible effect.

Eider *Somateria mollisima*. The population is increasing at 9% p.a.. Substantial numbers of clutches are destroyed by gulls, most probably after birds have been disturbed by humans. The numbers of ducklings eaten by gulls is unknown.

Kittiwake *Rissa tridactyla*. The population is now more-or-less stable. In many recent years, adults have been neglecting their chicks, some of which are taken by specialist gulls. However, overall losses to gulls are probably of little consequence as most predated chicks were moribund.

Common/Arctic tern *Sterna hirundo/paradissea*. The population is either still increasing slowly or stable. One of the most "distressing" sights on the Isle of May is a gull being mobbed by a large group of terns after it has snatched an egg or chick. In some years gulls probably take the bulk of eggs and chicks and are certainly the proximate cause of breeding failure for terns. However, it may well be that low food availability is the ultimate factor and, if the food supply is good, the terns can cope with the gulls. The policy of smashing clutches laid by gulls in or near current or past tern nesting areas has been successful in preventing gulls from breeding in the tern colony and has probably reduced losses to gulls.

Guillemot *Uria aalge* and Razorbill *Alca torda*. Numbers of the former species are stable whereas numbers of the latter are increasing. At present gulls have no serious effect on breeding output, although they do regularly take eggs when incubating adults are disturbed.

Puffin *Fratercula arctica*. Herring and lesser black-backed gulls steal many fish from puffins which are feeding chicks and also kill substantial numbers of chicks near and at fledging. Great black-backed gulls *L. marinus* probably kill several hundred adult puffins each year but the population should be able to sustain this. Puffin numbers have been more or less stable since 1984 and there is no reason to suppose that cessation of population increase was linked to gulls.

If gulls are to have any impact on puffins it will be by the destruction of vegetation and later erosion of soil.

5.2 Other species

Oystercatcher *Haematopus ostralegus*. Numbers have increased substantially since gull numbers were reduced but breeding success remains so low that the population cannot sustain itself without substantial immigration. Gulls are the main cause of breeding failure. Any future increase in gull numbers will probably have an adverse effect on oystercatcher numbers.

5.3 Vegetation

The Isle of May Fourth Management Plan described the flora as follows:-
"The Isle of May supports a variety of vegetation types, including crevice communities, cliff grasslands, beach head saltings, clifftop flushes and pools and a range of bird-modified communities. The crevice communities hold a number of rare or local plants, including Puccinellia capillaris (Northern Salt-marsh Grass), Ligusticum scoticum (Lovage), Artemisia maritima (Sea Wormwood) and Catapodium marinum (Darnel Fescue). Maritime grasslands are generally of the Festuca-Armeria or Holcus-Armeria types, although there is local development of a rather unusual community which is floristically more akin to salt-marsh, with species such as Spergularia marina (Less Sandspurrey), Glaux maritima (Sea Milkwort) and Puccinellia capillaris (Phillipson 1980)."

"Much of the vegetation has been altered to a greater or lesser extent by the gull colonies (Sobey 1976, Sobey and Kenworthy 1979), and the extensive areas of Armeria-rich clifftop vegetation were replaced by bird modified communities dominated by Stellaria media (Chickweek), Holcus lanatus (Yorkshire Fog), Rumex acetosa (Sorrel), Silene maritima (Sea Campion), and Tripleurospermum maritimum (Scentless Mayweed). Recent, as yet unpublished, work by the NCC would seem to suggest that the ground area covered by the perennial species components of these communities is increasing at the expense of annual species cover and bare ground; most of the survey plots showing a remarkably consistent increase in the percentage cover of Silene maritima."

"The island has been noted for a number of interesting bryophyte and lichen communities including several rare or local species. The lichen flora was "in many respects comparable with that of upland regions of West Britain" (Sheard and Ferry 1967), and the bryophyte flora included western-oceanic species, notably Frullania

germana (Watson 1953, 1957 & 1959). It is considered, however that many of these species may have disappeared due to vegetation changes provoked by the increasing gull populations of the late 1950's and 1960's."

A major problem in assessing any long-term changes in the vegetation on the island regardless of gull numbers are the great annual differences. For instance one year chickweed covers large areas, the next year grasses appear dominant. As far we are aware there had been no systematic review of recent vegetation changes and the failure to monitor changes in vegetation precludes any assessment of the possible effects of the removal of gulls. However, it is obvious that the reduction in gull numbers since the early 1970s has resulted in the revegetation of many previously bare and heavily eroded areas. If any gull control measures are instigated these should concentrate on colonies on vegetated but potentially erodable areas, e.g. Burrian.

5.4 Gull free areas

Over the last 15 years attempts have been made to eliminate gulls from about half the island to allow the revegetation of bare areas by perennial species, protect the large central areas of maritime grassland from damage and protect tern nesting areas from disturbance (Figure 10). This policy has been well implemented and there are now very few gulls in the "gull free area". An area between Three Tarn Nick-Bishops Cove and the Lighthouse has also been cleared as this was the site of the main recolonisation of terns. As far as can be seen the aims have been attained and the policy should continue.

5.5 Humans

Humans are ambivalent concerning gulls. For instance, these birds are considered to be an essential part of the coastal environment, but only if they do not cause any problems, e.g. waking people at dawn, fouling intruders at breeding colonies (e.g. at Inchcolm).

Visitors to the Isle of May complained vociferously when there were *ca* 20 000 pairs of gulls, our present impression is that most people find the current numbers of gulls acceptable. The main adverse affect of gulls on humans is their tendency to make aerial attacks on people if they approach too close to the clutch/brood. As previously noted in relation to predation on other seabirds, such behaviour is confined to a small number of individuals. In many cases aggressive birds nest well away from areas visited by the public and problems arise only when such individuals breed next to the paths . At present there are probably <5 aggressive birds on the island. It is likely, but by no means certain, that the number of aggressive birds would increase if gull numbers expanded.

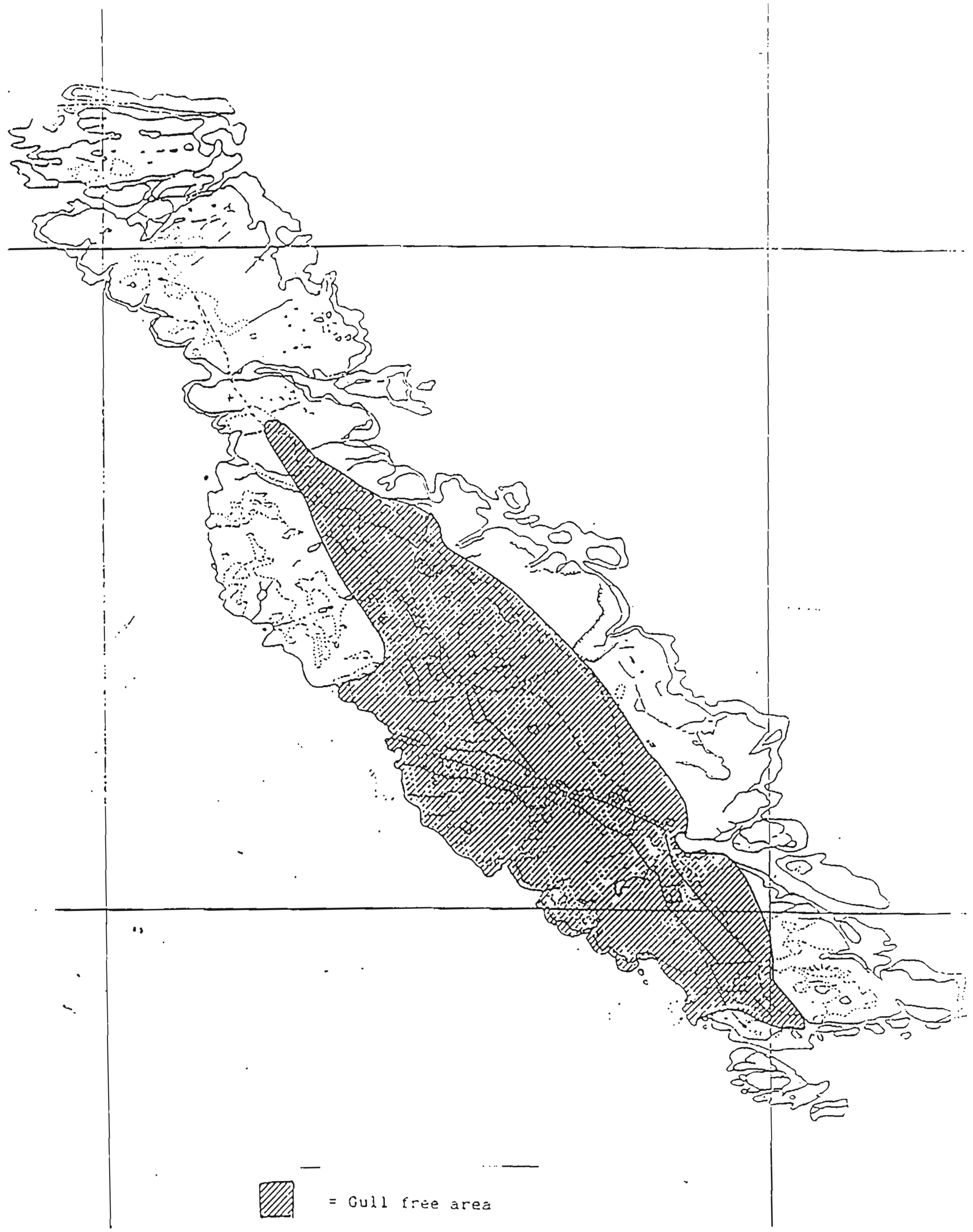


Figure 10. Gull free areas (from The Isle of May Fourth Management Plan 1990-1994).

5.6 Conclusion

At present the gulls have no obvious adverse effects on the other bird populations on the NNR and there is no reason to suppose that, as long as there are adequate food supplies for the auks and terns, this should not continue. The lack of vegetation monitoring makes it impossible to assess what effect the gulls have had on the vegetation in recent years. Consideration should be given to studying the effects of gulls on (a) the seabirds and (b) the vegetation.

6 MANAGEMENT OPTIONS

The above analyses suggest strongly that the population of herring gulls will increase substantially over the next five years. The situation for the lesser black-backed gull is less clear but it too is likely to increase. Thus by the end of the century we expect that numbers of both sepcies will be well in excess of the current population targets. Because the herring gull population size in any given year appears to be largely dependent on the breeding population in the previous season and the number of young produced 3 years before, there is rather little scope for managing the herring gull population on the Isle of May over the next 4 seasons, without recourse to killing breeding adults. Given the current target population of 2000 pairs this would be a fairly minor undertaking at present and would only necessitate killing a few hundred birds per annum. However, if no action was taken, assuming that the expected population increase occurs, a larger scale cull of more than 1000 adults would be needed by the end of the century. The present number of lesser black-backed gulls already exceeds the target of 800 pairs by almost 1000 birds. Given the predicted increase coupled with the possibility of large scale immigration, it is likely that a major cull will be needed by the end of the century to bring numbers in line with the present prescribed level.

Whether such culling is deemed necessary depends upon the perceived damage suffered by other species on the Isle of May (including the amenity value of the reserve). It will be up to SNH to decide how the reserve should develop and set management priorities. For instance, should gulls be allowed to increase until they have a demonstrable adverse effect on the other seabirds or the vegetation, or should numbers be controlled when they start to annoy the increasing number of day-trippers? Realistic and justifiable upper limits to gull numbers could then be set. Our personal view is that the present gull numbers are acceptable. However a major difficulty arises in trying a) to assess the levels of damage/disturbance likely to be associated with the predicted populations by the end of the century, and b) to decide whether such levels would warrant the implementation of control measures on the gull populations.

A second management option is the control of breeding output by the large scale destruction of clutches and broods . In the past the effectiveness of this method has been questioned but results from the Isle of May indicate that intensive control, in which output was limited to <200 chicks, did indeed keep herring gull numbers down. Although the impact on lesser black-backed gulls was less clear the technique did appear to have some effect on this species. While we cannot rule out the possibility that other factors were responsible for the low populaiton levels of gulls on the Isle of May during the late 1980s, we feel that the results are sufficiently encouraging for the control of breeding output to be considered as a management tool.

As mentioned previously, the control of breeding output only becomes effective 4-5 years after it is carried out. Thus a decision to implement such control in

1995 and thereafter would only start to have an effect on the gull populations towards the end of this century.

In management terms this creates some problems because a decision to implement control measures needs to be taken before adverse effects are apparent. This could be considered to be a precautionary approach. If no action is taken until there is evidence of damage, then several years, during which the situation is likely to deteriorate further, will inevitably elapse before any reduction in gull numbers and hence improvement in the situation, can be expected. Given the past history of gull problems on the Isle of May, careful thought should be given to the precautionary approach.

We suggest the following:

SNH decides how it wants the reserve to develop and how many gulls it wants on the island. There is currently no obvious reason why both species should be allowed to increase at the predicted rate as long as:-

a) Starting in 1995, the gulls are prevented from rearing <u>any</u> young. In practice it will probably be difficult to reduce the output to less than 50 chicks. There seems no reason to exclude The Maidens from this. This should slow down the rate of increase in 1999 and later. This could be incorporated into a warden's work programme. If so, the possibility of having to kill gulls should be mentioned during any interview for a warden's appointment.

b). The gull population is monitored annually.

c) A study is initiated on the damage (if any) caused to the other bird populations by the gulls. This could replace the current monitoring of gull survival.

d) Vegetation monitoring should be carried out (maybe by a botanist being appointed as one of the summer wardens) to assess changes in vegetation.

e) The gulls nesting on the other Firth of Forth islands should be censused in 1999 or 2000.

f) A political and public-relations debate is initiated to prepare the ground in case culling needs to be carried out in near the future.

7 ACKNOWLEDGEMENTS

We thank previous Isle of May summer wardens and many other people who helped count and ring gulls over the years. We are especially grateful to John Calladine who carried out the bulk of the fieldwork during the last five years and also organized the 1994 census of Firth of Forth gull colonies. Pete Kinnear organized the previous Firth of Forth count and has given considerable support to the gull studies during the previous decade. Peter Rothery provided statistical advice and carried out the SURGE analysis. Much of the data used in this report was collected during contracts placed with ITE by NCC, NCCS and SNH.

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10 APPENDIX: Estimating accumulating random errors of prediction (by P. Rothery)

Random errors in prediction over one year accumulate in the free-running predictions. To estimate the effect we consider the following simple model in which population change in year t is given by.

$$N_{t+1} = s_A N_t + s_R Y_{t-3}/2 + \varepsilon_{t+1}$$

where N_t is the ***actual*** population size in year t and ε_t is a random component of change.

Applying the model from 1994 gives the following.

Actual population 1995:

$$N_{95} = s_A N_{94} + s_R Y_{91}/2 + \varepsilon_{95}$$

Estimated population 1995:

$$\hat{N}_{95} = s_A N_{94} + s_R Y_{91}/2$$

Estimation error for 1995:

$$N_{95} - \hat{N}_{95} = \varepsilon_{95}$$

Actual population 1996:

$$N_{96} = s_A N_{95} + s_R Y_{92}/2 + \varepsilon_{96}$$

Estimated population 1996:

$$\hat{N}_{96} = s_A \hat{N}_{95} + s_R Y_{92}/2$$

Estimation error for 1996:

$$\begin{aligned} N_{96} - \hat{N}_{96} &= s_A(N_{95} - \hat{N}_{95}) + \varepsilon_{96} \\ &= s_A \varepsilon_{95} + \varepsilon_{96} \end{aligned}$$

The prediction error from the previous year is accumulated with contribution multiplied by the adult survival rate. Carrying on in this way.

Actual population 1997:

$$N_{97} = s_A N_{96} + s_R Y_{93}/2 + \varepsilon_{97}$$

Estimated population 1997:

$$\hat{N}_{97} = s_A \hat{N}_{96} + s_R Y_{93}/2 \; .$$

Estimation error for 1997:

$$N_{97}-\hat{N}_{97} = s_A(N_{96}-\hat{N}_{96}) + \varepsilon_{97}$$

$$= s_A^2\varepsilon_{95} + s_A\varepsilon_{96} + \varepsilon_{97}$$

Prediction errors are now carried over from 1995 although the weight is reduced by a further factor of s_A.

If the variance of the random component of change from year t to year t+1 is denoted by V_{t+1} then the standard errors of free-running predictions up to 1998 are as follows.

$$se[\hat{N}_{95}] = \sqrt{V_{95}}$$

$$se[\hat{N}_{96}] = \sqrt{s_A^2V_{95}+V_{96}}$$

$$se[\hat{N}_{97}] = \sqrt{s_A^4V_{95}+s_A^2V_{96}+V_{97}}$$

$$se[\hat{N}_{98}] = \sqrt{s_A^6V_{95}+s_A^4V_{96}+s_A^2V_{97}+V_{98}}$$

The analysis of the fitted model suggests a random component with constant coefficient of variation of approximately 6% i.e. $V_t = 0.0036N_t^2$. In practice, this is estimated by $V_t = 0.0036\hat{N}_t^2$.

Figure 1. The numbers of gull nests on the Isle of May 1983-1994. The dotted lines are the relevant population levels set by the current management plan.

Figure 2. A comparison of observed numbers of herring gulls (solid dots and lines) and these predicted using the stepwise method 1986-94. Dotted and pecked lines use $s_R = 0.44$ and 0.40, respectively.

Figure 3. A graphic check of the fit of the stepwise prediction model for population changes in herring gulls on the Isle of May 1986-94. The annual change (R_t) is plotted against the chick production rate recruitment (Y_{t-3}/N_t). Also shown is the fitted line with $s_R = 0.88$, $s_R = 0.40$.

Figure 4. A comparison of observed numbers (solid dots and lines) and these predicted using the free-running prediction method for herring gulls on the Isle of May 1986-94. Dotted and pecked lines use $s_R = 0.44$ and 0.40 respectively.

Figure 5. Predicted changes in numbers (and 95% confidence intervals) of herring gulls on the Isle of May 1994-2000. The solid symbols use past chick production figures, open symbols assume production at the past average level (and no CI is shown). The horizontal dashed line is the maximum population of 2000 pairs allowed under the current management plan. The upper graph uses $s_R = 0.40$, the lower uses $s_R = 0.44$.

Figure 6. Absolute values of proportional errors using the model in Figure 2 to predict N. The horizontal line corresponds to an error of 6%.

Figure 7. A comparison of observed numbers of lesser black-backed gulls (solid dots and lines) with those predicted using the stepwise method. Dashed, dotted and pecked lines use $s_R = 0.6$, $s_R = 0.5$ and $s_R = 0.4$, respectively. The upper graph uses an age of first breeding of 4 years, the lower an age of 5 years.

Figure 8. A comparison of observed numbers of lesser black-backed gulls (solid dots and lines) with those predicted using the free-running method. Conventions as in Figure 7.

Figure 9. Predicted changes in numbers of lesser black-backed gulls on the Isle of May 1994-2000. The horizontal dashed line is the maximum population of 800 pairs allowed under the current management plan.

Figure 10. Gull free areas (from The Isle of May Fourth Management Plan 1990-1994).

Table 1. Population estimates and chick production for the Isle of May 1982-94.

Year	Counts (nests)		Productivity (young/pair)		Total young reared	
	Herring gull	Lesser black-backed-gull	Herring gull	Lesser black-backed gull	Herring gull	Lesser black-backed gull
1982	2300	c. 550	No data		2400	800
1983	2578	1385	No data		2700	1300
1984	2230	1488	Controlled		150	20
1985	2165	1033	Controlled		180	20
1986	1943	682	Controlled		205	15
1987	2117	534	Controlled		390	20
1988	1711	563	Controlled (first clutches)		861	281
1989	1629	643	1.44	0.98	2350	630
1990	1551	618	1.23	0.54	1917	331
1991	1447	788	1.88	0.98	2709	776
1992	1462	751	1.52	1.04	2222	779
1993	2059	1259	1.04	0.81	2134	1018
1994	2122	1270	1.16	0.53	1775	369

Note: Productivity figures refer only to areas where no nest destruction occurred.

Table 2. Herring gull data input for survival analysis using SURGE.

		♂						♀					
		89	**90**	**91**	**92**	**93**	**94**	**89**	**90**	**91**	**92**	**93**	**94**
New releases	b_i	80	21	6	16	10	-	78	15	14	13	15	-
Recaptures for each cohort	a_{ij}		62	55	37	29	26		67	50	43	41	41
				17	15	12	11			13	12	12	8
					6	6	5				14	13	12
						16	13					12	11
							9						11
Seen for last time	c_{ij}	11	6	16	13	8	26	4	13	8	7	5	41
			2	1	4	3	11		1	1	1	4	8
				0	0	1	5			0	1	1	12
					0	3	13				1	1	11
						1	9					4	11
Releases + Recaptures		80	83	78	74	73		78	82	77	82	93	
R & R seen for last time		11	8	17	17	16		4	14	9	10	15	
Minimal survival (%)		86.3	90.4	78.2	77.0	78.1		94.9	82.9	88.8	87.8	83.9	

Overall minimal survival: ♂ $\frac{319}{388} = 82.2\ \%$; ♀ $\frac{360}{412} = 87.4\ \%$

Table 3. Lesser black-backed gull data input for survival analysis using SURGE.

	♂						♀					
	89	**90**	**91**	**92**	**93**	**94**	**89**	**90**	**91**	**92**	**93**	**94**
New releases year i b_{tr}	55	29	9	16	14	-	49	28	19	11	13	-
Recaptures for each cohort a_{ij}		44	41	38	37	31		40	38	31	28	25
			23	17	21	17			23	19	17	16
				8	8	6				18	16	16
					13	11					10	9
						14						11
Seen for last time c_{ij}	6	4	2	4	8	31	2	4	5	6	7	25
		4	2	1	5	17		3	3	3	3	16
			0	1	2	6			1	2	0	16
				2	3	11				1	1	9
					0	14					2	11
Releases + recaptures cij	55	73	73	79	93		49	68	80	79	84	
R & R seen for last time yri	6	8	4	8	18		2	7	9	12	13	
Minimal survival yri	89.1	89.0	94.5	89.9	80.6		95.9	89.7	88.8	84.8	84.5	

Overall minimal survival $\frac{329}{373} = 88.2$ % $\qquad \frac{317}{360} = 88.2$ %

Table 4. Estimated annual survival rates from SURGE allowing time-dependent recapture rates , AM = arithmetic mean; GM - geometric mean

	Estimated annual survival (s.e.)					
	Herring gull			Lesser black-backed gull		
Year	♂	♀	♂+♀	♂	♀	♂+♀
1989	87.2(4.0)	96.7(2.7)	91.9(2.4)	90.2(4.3)	97.6(3.0)	93.7(2.7)
1990	93.4(3.5)	84.7(4.3)	89.1(2.9)	89.4(3.7)	90.9(3.8)	90.1(2.6)
1991	82.5(5.2)	90.0(3.9)	86.0(3.2)	96.2(2.9)	90.8(3.7)	93.4(2.4)
1992	79.2(5.1)	88.8(3.7)	84.2(3.2)	90.9(3.5)	86.0(4.2)	88.5(2.7)
AM	85.6	90.1	87.8	91.7	91.3	91.4
GM	85.4	89.9	87.8	91.6	91.2	91.4

Table 5. Estimates of recapture rates for time-dependent survival rate.

	Estimated recapture rate (s.e.)					
	Herring gull			Lesser black-backed gull		
Year	♂	♀	♂+♀	♂	♀	♂+♀
1989	88.9(4.0)	88.8(4.0)	88.9(2.8)	88.7(4.8)	83.7(5.6)	86.2(3.7)
1990	84.9(4.5)	82.3(4.7)	83.6(3.2)	91.0(3.5)	88.6(4.1)	89.8(2.7)
1991	77.5(5.4)	84.6(4.3)	81.4(3.5)	82.5(4.6)	85.2(4.3)	83.9(3.2)
1992	87.5(4.4)	92.9(3.2)	90.5(2.6)	94.1(2.9)	90.9(3.5)	92.5(2.3)
AM	84.7	87.2	86.1	89.1	87.1	88.1

Table 6. Goodness of fit of different SURGE models allowing for constant and time-dependent rates for herring gull.

Model		No. of	Deviance		
Survival	Recapture	Parameters	♂	♀	♂+♀
1 Variable, s_t	Variable, p_t	9	574.25	519.17	1107.81
2 Constant, s	Variable, p_t	6	580.47	524.60	1112.53
3 Variable, s_t	Constant p	6	577.66	523.47	1113.83
4 Constant, s	Constant p	2	583.96	530.63	1119.57

Comparion of Models	d.f.	Deviance			Chi-squared % Points 10%	5%	1%
1 vs 2 H_o: survival constant	3	6.22	5.43	4.72	6.25	7.82	11.34
1 vs 3 H_o: recapture constant	3	3.41	4.30	6.02			
2 vs 4 H_o: recapture constant	4	3.49	6.03	7.04	7.78	9.49	13.28
3 vs 4 H_o: survival constant	4	6.30	7.16	5.74			

Table 7. Goodnes of fit of different SURGE models allowing for constant and time-dependent rates for lesser black-backed gull.

Model		No. of	Deviance		
Survival	Recaptue	parameters	♂	♀	♂+♀
1 Variable, s_t	Variable, p_t	9	433.83	444.29	884.52
2 Constant, s	Variable, p_t	6	436.11	448.78	886.95
3 Variable, s_t	Constant p	6	438.80	445.96	890.12
4 Constant, s	Constant p	2	440.79	450.51	891.48

Comparison of models		d.f.	Deviance		
1 vs 2	H_o: survival constant	3	2.28	4.49	2.43
1 vs 3	H_o: recapture constant	3	4.97	1.67	5.60
2 vs 4	H_o: recapture constant	4	4.68	1.73	4.53
3 vs 4	H_o: survival constant	4	1.99	4.55	1.36

Table 8. Estimates of survival rate assuming constant survival during 1989-93.

Model		Estimated annual survival (s.e.)					
		Herring gull			Lesser black-backed gull		
Survival	Recapture	♂	♀	♂+♀	♂	♀	♂+♀
2 Constant	Variable	85.8(2.0)	89.8(1.7)	87.7(1.3)	91.8(1.6)	90.7(1.8)	91.2(1.2)
4 Constant	Constant	86.3(1.8)	90.5(1.5)	88.5(1.2)	91.8(1.5)	91.3(1.6)	91.6(1.1)

Comparison of sexes

Herring gull

model 2 : ♀ - ♂ = 4.0 (s.e. = 2.63, z = 1.52)
model 4 : ♀ - ♂ = 4.2 (s.e. = 2.34, z = 1.86)

Lesser-black backed gull

model 2 : ♀ - ♂ = -1.1 (s.e. = 2.41, z = -0.46)
model 4 : ♀ - ♂ = -0.5 (s.e. = 2.19, z = -0.23)

Table 9. Proportionate errors of stepwise and free-running predictions $((N_t-\hat{N})/N_t)$ for fitted models for lesser black-backed gulls with age of first breeding of 4 and 5 years and s_R of 0.4, 0.5 and 0.6 respectively.

	Stepwise Age of first breeding (years)						**Free-running Age of first breeding (years)**					
	4			**5**			**4**			**5**		
Year	**s_R=0.4**	**s_R=0.5**	**s_R=0.6**	**s_R=0.4**	**s_R=0.5**	**s_R=0.6**	**s_R=0.4**	**s_R=0.5**	**s_R=0.6**	**s_R=0.4**	**s_R=05**	**s_R=0.6**
1987	-0.648	-0.772	-0.891	-0.461	-0.536	-0.610	-0.648	-0.772	-0.891	-0.461	-0.536	-0.610
1988	0.130	0.128	0.126	-0.325	-0.440	-0.556	-0.430	-0.536	-0.645	-0.723	-0.904	-1.083
1989	0.196	0.194	0.194	0.198	0.194	0.194	-0.146	-0.232	-0.319	-0.379	-0.524	-0.670
1990	0.048	0.047	0.045	0.047	0.045	0.044	-0.091	-0.173	-0.256	-0.312	-0.451	-0.591
1991	0.282	0.279	0.279	0.282	0.282	0.280	0.217	0.156	0.096	0.060	-0.041	-0.141
1992	-0.029	-0.048	-0.068	0.040	0.039	0.037	0.177	0.101	0.024	0.097	-0.001	-0.097
1993	0.357	0.332	0.307	0.412	0.401	0.390	0.454	0.387	0.320	0.465	0.401	0.338
1994	0.046	0.033	0.020	-0.002	-0.026	-0.050	0.455	0.381	0.309	0.419	0.335	0.254
Sum of squares	**0.687**	**0.863**	**1.026**	**0.610**	**0.763**	**0.955**	**1.126**	**1.2965**	**1.585**	**1.381**	**1.857**	**2.551**

Table 10. Free-running predictions of future herring numbers using different combinations of s_A and s_R.

		$s_R = 0.40$			$s_R = 0.44$			$s_R = 0.50$		
s_A	**Year**	**Adults**	**Recruits**	**Total**	**Adults**	**Recruits**	**Total**	**Adults**	**Recruits**	**Total**
	1994	-	-	2122	-	-	2122	-	-	2122
	1995	1846	542	2388	1846	596	2442	1846	677	2523
0.87	1996	2078	444	2522	2125	489	2614	2195	556	2751
	1997	2194	427	2621	2274	469	2743	2393	534	2927
	1998	2280	355	2635	2387	391	2778	2547	444	2991
	1994	-	-	2122	-	-	2122	-	-	2122
	1995	1867	542	2409	1867	596	2463	1867	677	2544
0.88	1996	2120	444	2564	2167	489	2656	2239	556	2795
	1997	2256	427	2683	2337	469	2806	2460	534	2994
	1998	2361	355	2716	2469	391	2860	2635	444	3079
	1994	-	-	2122	-	-	2122	-	-	2122
	1995	1886	542	2430	1889	596	2485	1889	677	2566
0.89	1996	2163	444	2607	2212	489	2701	2284	556	2840
	1997	2320	427	2747	2404	469	2873	2528	534	3062
	1998	2445	355	2798	2556	391	2948	2725	444	3169