

THE UK AND IRELAND SEABIRD MONITORING PROGRAMME – A HISTORY AND INTRODUCTION

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The intimate relationship of Britain and Ireland to their surrounding seas has meant that seabirds have long been a part of the culture of these islands. In historical times (and to a very limited extent in modern times) this relationship was one of exploitation by humans of seabirds as a source of food or feathers. As the necessity to use seabirds for these purposes declined in the 19th century, so the appreciation of their intrinsic value rose. Fears of over-exploitation, particularly as a source for feathers, coupled with evidence of decline at the massive colony of seabirds on Flamborough Head in north-east England, led both to the foundation of the organisation that is now the Royal Society for the Protection of Birds (RSPB) and to some of the first bird conservation legislation. The evidence of decline was based on diminishing harvest returns, and this might be argued as being the first evidence of seabird monitoring in the UK.

Some seabirds are comparatively easy to count at their colonies, and these started to attract the attention of biologists in the early part of the 20th century. Gurney (1913) published on the Northern Gannet *Morus bassanus* population, while Fisher (1952) compiled a massive work on the spread of the Northern Fulmar *Fulmarus glacialis*. Following these leads, Coulson (1963) organised a count of Kittiwake *Rissa tridactyla* colonies in 1959. Such population censuses were widened to include all seabirds in Operation Seafarer in 1969-70 (Cramp *et al.* 1974).

More frequent counts of seabird colonies, or studies of parameters other than population size began in the 1950s. Among the first of these studies was one started on Eynhallow, Orkney by George Dunnet and Robert Carrick of Aberdeen University, and continued by George Dunnet and co-workers (see Dunnet 1991, 1992). This study focussed on various aspects of population ecology including frequency of breeding, breeding success, age of first breeding and longevity. One striking feature of the study is the relative ease with which much of the data could be collected in one or two short trips to the island each year. The power of the data lies in its long-term nature, which reveals trends that are not detectable from short-term studies.

Following Operation Seafarer, it became obvious that Britain and Ireland had some internationally important seabird populations, and it was important to ensure that these populations were healthy. Thus in the early 1970s, a number of schemes to monitor numbers of some species at some colonies commenced. In Shetland, the Institute of Terrestrial Ecology (ITE) established a scheme that was subsequently adopted by Aberdeen University and in Orkney, the then Nature Conservancy Council (NCC) also initiated seabird monitoring. The RSPB established schemes to monitor numbers on some of their reserves and in other important colonies including some on the west coast of Ireland (see Stowe 1982a, b for a review). Most of these schemes produced annual reports and occasional synthesis papers (e.g. Harris & Murray 1981; Heubeck *et al.* 1986).

In the early 1980s, it became clear that a new baseline survey of seabird numbers was required. There was widespread evidence that seabird populations had changed, and in many areas no monitoring programme had been established. In those areas where monitoring had been carried out, there was a need to check that the results were representative of actual population change. Thus the Seabird Colony Register counts of the mid-1980s were initiated. At the same time it was realised that seabird monitoring in Britain and Ireland was not very well co-ordinated and could be better focussed. Thus the NCC, in partnership with other organisations launched a review of seabird monitoring.

An early question that was asked in this review was "Why monitor seabirds?" Four main reasons to monitor emerged:

- a) Intrinsic value of seabirds. Seabirds are now a valued feature of British and Irish coastlines. Members of the public are very concerned about their health as is demonstrated at every major oil spill or mortality incident. Answers are needed to questions on the current status and health of seabird populations; responses using data from counts made several years previously are not usually adequate;
- b) International significance and obligation. Several international conservation measures require that the UK and the Republic of Ireland report on the state of their seabird populations. Most notable among these are the EC Birds Directive (79/EEC/409) and the Ramsar convention;
- c) Impact of potential and real threats to seabirds. There is a need to understand the effects of threats; these might include oil pollution incidents, the arrival of mammalian predators on islands and the impact of local changes in fisheries; and
- d) Indicator of the state of the wider marine environment. Seabirds are one of the more visible components of our marine fauna. As direct monitoring of the state of our seas is difficult some parameters of seabird populations might act as sensitive and easily observed indicators of wider environmental conditions.

A scheme to provide some answers to these questions was required. Such a scheme would draw on current schemes, and in order to be sustainable into the future, should be relatively inexpensive. Expensive and elaborate schemes, being much more susceptible to budget cuts and to changing conservation fashions, should be avoided, and any programme of work that aimed to understand long-lived animals such as seabirds also needed to be long-term.

In order to bring together existing seabird schemes and make recommendations for the future, the ITE (Mike Harris) was commissioned to review the objectives and methods of current schemes. Broad recommendations of the review included:

- a) a switch to a monitoring scheme working at two levels: a set of four or five “key sites” spread geographically around Britain, complemented by a wider voluntary scheme at as many other colonies as possible. The key sites were Skomer (west Wales), the Isle of May (east Scotland), Fair Isle (Northern Isles) and Canna/Rum/St. Kilda (west Scotland). Owing to their tendency to change breeding locations between years, tern monitoring would aim to cover as many colonies as possible each year;
- b) a change in emphasis to monitoring breeding performance rather than numbers. Breeding performance is relatively easy to monitor in several species and is more likely to be responsive to immediate changes in the environment than are numbers of birds. This is due to the buffered nature of seabird populations, with long periods of immaturity and the capacity to refrain from breeding in some years;
- c) standardisation of methods, both of counting and of selection of plots (in order to achieve a more representative sample within colonies). The initial methods suggested by the ITE report were eventually revised and enlarged upon to eventually comprise a manual of standard monitoring methods (Walsh *et al.* 1995b); and
- d) greater co-ordination of activities. A post should be created (and subsequently was by the Joint Nature Conservation Committee, JNCC) to co-ordinate activities and produce an annual seabird monitoring report. This report should include in a standard format the monitoring work organised by RSPB, JNCC and the Shetland Oil Terminal Environmental Advisory Group.

The most visible output from the now well-established Seabird Monitoring Programme (SMP) has been the annual report (Walsh *et al.*, 1990, 1991, 1992, 1993, 1994, 1995a; Thompson *et al.* 1996, 1997, 1998, 1999; Upton *et al.* 2000). The current volume of papers illustrates some of the other products of the work. However, it is reasonable to ask whether we are now in a better position to answer the questions posed earlier. Information requests about seabird populations at colonies are received by the JNCC at a rate of about one per week. We could not have answered these as confidently without the SMP. We have been able to answer questions on the effects of major oil spills (most

notably the *Sea Empress* spill, and more recently that from the *Erika* off Brittany), and trends of seabird populations in areas affected by spills have been compared before and after the event. In an international context, we have been able to meet our reporting obligations, sometimes with acclamation from other nations. Finally, we have been able to identify adverse trends in seabird population parameters, and in some cases attempt to ensure, by managing human activities in the relevant areas, that such trends are not exacerbated. One such case has been off the east coast of Scotland where there have been a series of years of poor Kittiwake breeding success. The possibility that this was caused by reduced availability the birds' main food, sandeels *Ammodytes* spp., consequently prompted the closure by the European Union of the sandeel fishery near these colonies. Such management would not have been possible without the information generated by the SMP.

One of the more unexpected indicators of success is that the scheme (in particular the monitoring methods manual and the annual reports) is being copied elsewhere in the world. Examples include Alaska (Byrd *et al.* 1998), California, Seychelles and possibly in future the Gulf of Mexico.

ACKNOWLEDGEMENTS

The Joint Nature Conservation Committee works on behalf of, and is supported by, the Countryside Council for Wales, the Environment and Heritage Service in Northern Ireland, English Nature and Scottish Natural Heritage. Many other organisations, including Dúchas (the Heritage Service, National Parks and Wildlife, in the Republic of Ireland) and BirdWatch Ireland, have also contributed information to the Seabird Monitoring Programme that provides a wider perspective on the health of seabird populations in these islands.

The SMP owes a vast debt of gratitude to all of the volunteer counters who undertake the work at colonies across Britain and Ireland. All contributors are individually acknowledged in the annual reports. Paul Walsh and Kate Thompson have co-ordinated the programme for JNCC, Mark Avery, Jane Sears, Emma Brindley and Georgina Pickerell for the RSPB, and Martin Heubeck and his team have performed wonders in Shetland.

SAMENVATTING

HET BRITSE EN IERSE ZEEVOGEL MONITORINGPROGRAMMA: EEN INLEIDING MET EEN OVERZICHT VAN DE RECENTE HISTORIE

*Vanwege de relatieve eenvoud waarmee sommige zeevogels in kolonies zijn te tellen trokken ze de aandacht van biologen in het begin van de 20^e eeuw. Gurney (1913) publiceerde over de aantallen broedende Jan-van-genten *Morus bassanus* op de Britse Eilanden en Fisher (1952) stelde een uitgebreid overzicht samen van de zich rap uitbreidende populatie Noordse Stormvogels *Fulmarus glacialis* in het Noordoost-Atlantische gebied. In navolging daarop organiseerde Coulson (1963) een telling van alle kolonies Drieteenmeeuwen *Rissa tridactyla*. Het duurde vervolgens tot het einde van de jaren zestig (1969-70) voordat poging tot een integrale telling van alle zeevogelkolonies werd ondernomen (Operation Seafarer; Cramp *et al.* 1974). In de jaren vijftig werden ook de eerste programma's opgezet om naast het aantal broedvogels ook andere belangrijke variabelen te meten, zoals legselgrootte en broedsucces, jaarlijkse overleving, plaatstrouw en activiteit (bijvoorbeeld*

Dunnet 1991, 1992). Begin jaren tachtig groeide de overtuiging dat de Britse zeevogelpopulatie dringend aan een nieuwe inventarisatie toe was. Dit resulteerde in de oprichting van het Seabird Colony Register, waarbij delen van de populatie zodanig beschreven werden dat overgegaan kon worden tot een meer permanente monitoring en waarbij zg. study plots werden ingesteld.. De meest tastbare resultaten van het nieuwe zeevogelmonitoringsysteem zijn de jaarverslagen (Walsh et al., 1990, 1991, 1992, 1993, 1994, 1995a; Thompson et al. 1996, 1997, 1998, 1999; Upton et al. 2000), alsmede een aantal publicaties in de nu voorliggende bundel artikelen. Vergelijkbare programma's zijn inmiddels opgezet in Alaska, California, de Seychellen en misschien in de toekomst in de Golf van Mexico.

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POPULATION TRENDS AND BREEDING SUCCESS OF CLIFF-NESTING SEABIRDS IN ORKNEY, 1976-98

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Population trends of Northern Fulmars, Kittiwakes, Common Guillemots and Razorbills have been monitored in sample plots at five colonies in Orkney since 1976; several complete counts of these colonies were also made. Numbers of Fulmars, Guillemots and Razorbills attending the colonies in the breeding season increased from 1976 to 1997. However, for all three species, the overall increase was punctuated by a period of decline in the early 1980s; there was also some variation between colonies in population trends. In contrast to the other species, breeding numbers of Kittiwakes declined by an average of 2.5% per annum over the same period, the overall rate of decline being inversely related to colony size. Breeding success of Fulmars, Kittiwakes and Guillemots was monitored annually for varying periods from the mid 1980s to late 1990s. Breeding success of both Fulmars and Guillemots was close to or above national averages in most years. Kittiwake breeding success was generally very high in the past 10-15 years, so the declining population appears paradoxical. Large-scale mortality of fledglings in some years, particularly the late 1970s, may be partially responsible but the continuing decline of the Orkney Kittiwake population remains to be fully explained.

Thompson K.R. & Walsh P.M. 2000. Population trends and breeding success of cliff-nesting seabirds in Orkney, 1976-98. *Atlantic Seabirds* 2(3/4): 103-132.

INTRODUCTION

The Orkney Islands, off the north coast of Scotland, hold major concentrations of breeding seabirds. In the mid-1980s, when seabirds were last comprehensively censused in Britain and Ireland, Orkney held almost 400 000 pairs of 22 species, including 15% of the British breeding population of Northern Fulmars *Fulmarus glacialis*, 13% of Kittiwakes *Rissa tridactyla*, 17% of Common Guillemots *Uria aalge* and 7% of Razorbills *Alca torda* (Lloyd *et al.* 1991).

In 1976, in view of the vulnerability of these four species to oil spills and other environmental changes, the former Nature Conservancy Council (now Joint Nature Conservation Committee) established a programme to monitor changes in their numbers at five colonies on Mainland Orkney - at Row Head, Marwick Head and Costa Head on West Mainland, and at Gultak and Mull Head on East Mainland (Fig. 1). Results of this programme have been reported for

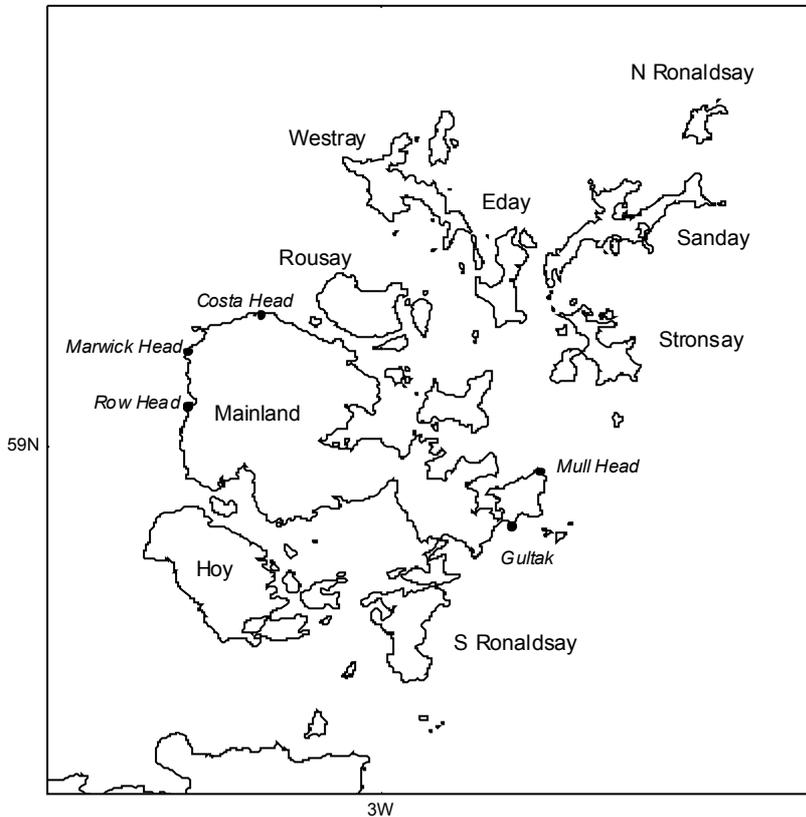


Figure 1. Map of Orkney showing location of study colonies.

1976-81 (Wanless *et al.* 1982ab) and 1976-85 (Benn *et al.* 1987). This paper updates information on population trends in sample plots at these colonies up to 1997 and also includes a summary of the results of various whole-colony counts made during the same period.

While information on population trends may indicate long-term effects of environmental change on seabirds, year-to-year variation in breeding success is potentially a more sensitive indicator of sudden environmental change. Annual monitoring of Common Guillemot breeding success was initiated in 1983 and Kittiwakes were included from the following year. In 1989, this aspect of the Orkney seabird monitoring programme was considerably expanded and Northern Fulmars were added. This work has since continued on an annual basis. The results obtained are examined here in relation both to population trends in

Orkney and to the breeding performance of the same species in other regions of Britain.

METHODS

Sample plot counts

At each of the five colonies selected for monitoring in 1976 (Fig. 1), the boundaries of between four and seven sample plots were marked onto photographic prints (Jones 1978). These plots were selected for ease and safety of counting and to include as wide a range of cliff types as possible rather than at random, as is now recommended for population monitoring (Walsh *et al.* 1995). Following the recommendations of Wanless *et al.* (1982a), counting was discontinued at several plots in 1982 and 1983 and new plots were added in 1983 and 1984; three auk monitoring plots at Costa Head and Marwick Head, in which count accuracy was poor, were replaced by four smaller plots typically holding 100-300 Common Guillemots (Wanless *et al.* 1983), and a plot at Marwick Head, where winter gales had caused substantial topographical changes, was replaced by several more plots (Tasker 1983; Griffiths 1984). These changes rendered the plot series more representative and improved count accuracy while retaining most of the original plots, thus enabling long-term comparisons to be made. The proportions of the total numbers of each species visible from land at each colony that were contained within the monitoring plots in 1985/86 are shown in Table 1. The same plots have been counted since 1985, with the exception of one plot at Marwick Head in which Kittiwakes were not counted in 1985. Counts were made annually up to and including 1988 and thereafter triennially (i.e. in 1991, 1994 and 1997). Full details of individual plots are given in Jones (1978), Wanless *et al.* (1982a) and Tasker (1983).

Count units used for the plots are individual birds for Guillemots, Razorbills and Fulmars (Wanless *et al.* 1982b) and apparently occupied nests for Kittiwakes. These count units are those generally adopted for counting these species in Britain and Ireland, with the exception of Fulmars where the recommended unit is apparently occupied sites (Walsh *et al.* 1995). Individual Fulmars were counted because of difficulty in identifying apparently occupied sites on Orkney cliffs; inter-observer variation in counts was found to be less for individual birds than for counts of apparently occupied sites (Wanless *et al.* 1982b). All counts used in the analyses reported here were made in June in winds of Beaufort force 4 or less and never in fog or heavy rain. Counts of auks were made between 06:00h and 15:30h GMT from 1-22 June, generally before the first chicks fledge. These restrictions on dates, times and weather conditions were adopted to minimise day to day variability in counts, particularly of auks (Walsh *et al.* 1995). Plots were normally counted a minimum of five times each year from fixed positions that ensured consistency in viewing angles. Where possible, counts at each colony were carried out at approximately the same time

of day in each year (Costa Head 06:00-10:00h, Gultak 10:30-14:30h, Marwick Head 11:00-15:00h, Mull Head 11:30-15:30h and Row Head 07:30-11:30h) in order to further minimise potential variability (Harris *et al.* 1983). There were some exceptions to this, particularly in 1986 and 1997 when some counts were carried out later at Costa Head and earlier at Gultak, Marwick Head, and Row Head. In addition, the Gultak plots were counted later in 1980 and one count at Row Head in 1997 was made in the afternoon.

Following the methods adopted by Benn *et al.* (1987), counts for each year and species were summed across the plots in each colony for those days in which all plots were counted and mean and standard deviations calculated. The statistical significance of changes between consecutive years was assessed using two-tailed *t*-tests applied only to those plots common to both years. In order to examine long-term trends, an index was established for each species at each colony using 1976 as the baseline (index value 100). Colony index values for subsequent years were calculated using the percentage change over all plots common to adjacent years. An overall index for Mainland Orkney was also calculated for each species, using all common plots between years, regardless of colony. The overall Mainland Orkney indices for the period 1976 to 1985 reported here are from Benn & Tasker (1985). Indices for individual colonies in this period, although not published, were also derived from Benn and Tasker (1985). Subsequent colony and combined indices were calculated as described above by comparison with the 1985 counts and indices. Average annual rates of population change were calculated by linear regression of the logarithms of index values on year. The regression slope is equivalent to the average annual rate of increase or decrease and its significance (i.e. probability of differing from zero) can be assessed using a *t*-test (Wilkinson 1990).

Whole-colony counts

In addition to the sample plot counts described above, a number of whole-colony counts have been undertaken at the five study colonies since 1976. All species were counted at Marwick Head in 1979 (Planterose 1979); all except Fulmar at all five colonies in 1981 (Wanless *et al.* 1982a); Kittiwakes at Marwick Head in 1983 (Tasker 1983); all species at all colonies in 1985 or 1986 (Benn & Tasker 1985, Beveridge 1986); all species at all colonies, except Fulmar and auks at Costa Head, in 1991 (JNCC unpublished data); and Kittiwakes at all colonies in both 1994 and 1997 (JNCC unpublished data). All of these, with the exception of the 1979 count at Marwick Head, were made from land only and so exclude sections of the colonies visible only from the sea. Most of these counts were made applying the same date, time and weather criteria as for the plot counts; notable exceptions are detailed in the Results.

Breeding success

Kittiwake Between 1986 and 1988, breeding success of Kittiwakes was estimated in the population monitoring plots by dividing the total number of chicks present in mid-July (prior to first fledging) by the peak count of apparently occupied nests in the plot in June. Such low intensity methods typically overestimate actual breeding success by *c.* 10-20% (Walsh *et al.* 1995).

More intensive monitoring, following the progress of individually identified nests recorded on photographs from early incubation to near fledging, was initiated in two study plots at Marwick Head in 1984. Up to 1986, those chicks known to have reached at least 30 days old when last observed were assumed to have fledged. This tends to overestimate breeding success as fledging does not occur until chicks are 35 or more days old (Walsh *et al.* 1995). From 1987 onwards, only chicks known to be over 35 days old, or assessed to be so on the basis of plumage characteristics (Walsh *et al.* 1995), were assumed to have fledged. Since 1989, a much larger-scale intensive monitoring scheme, using a total of 15 plots in the five colonies (with the exception of Costa Head from 1992 to 1997 inclusive), has been undertaken each year. Details of original plot selection are given in Ribbands (1990). Breeding success for each colony is herein expressed as the mean of the individual plot figures (Walsh *et al.* 1995).

Northern Fulmar Monitoring of Fulmar annual breeding success was initiated in 11 sample plots at Costa Head, Mull Head and Gultak in 1989 (Ribbonands 1990) using standard methods recommended by Walsh *et al.* (1995). In 1989 and 1991, a single plot was also monitored at Row Head. Two or three visits were made to each plot between late May and mid-June to identify apparently occupied breeding sites. These sites were checked again on one or more visits in August and for each plot breeding success was estimated as number of large young present per regularly occupied site. As with Kittiwakes, breeding success of the colony is expressed as the mean of all individual plots (Walsh *et al.* 1995).

Common Guillemot Guillemot breeding success has been monitored annually, with the exception of 1992, in single plots at Marwick Head since 1983 and at Mull Head since 1989. A single plot was also monitored at Row Head in 1989 and 1991. Monitoring breeding success of Guillemots is difficult as no nest is constructed and both eggs and chicks may be difficult to see. A minimum of three visits were made to each plot during the late incubation period to identify 'active' sites definitely occupied by breeding pairs, and additional 'regular' sites at which pairs may have failed earlier in the season (see Walsh *et al.* 1995 for definitions). These sites were then checked at intervals of no more than two days during the chick period. Average breeding success is defined as the number of

Table 1. Proportions of Orkney Common Guillemots, Razorbills, Northern Fulmars, and Kittiwakes visible from land that were within population monitoring plots in 1985 or 1986.

	Common Guillemot (ind)	Razorbill (ind)	Northern Fulmar (ind)	Kittiwake (nests)
Mull Head 1985				
count	1171	125	312	1066
% in plots	80.2	52.0	44.2	65.0
Gultak 1985				
count	1799	470	945	522
% in plots	15.1	39.8	27.2	34.3
Row Head 1985				
count	6103	142	256	2212
% in plots	12.6	10.6	12.5	16.4
Costa Head 1985				
count	7492	673	2548	1652
% in plots	22.7	19.4	7.8	13.7
Marwick Head 1986				
count	22 320	948	1045	3704
% in plots	8.5	9.1	2.1	14.8
All colonies 1985/86				
count	38 885	2358	5106	9156
% in plots	14.4	20.5	12.7	21.8

chicks reaching 15 or more days old when last seen per 'active' plus 'regular' site (Walsh *et al.* 1995).

RESULTS

Population trends in sample plots 1976-97 and comparisons with whole-colony counts

Common Guillemot Changes in Guillemot population indices in monitoring plots for all colonies combined are shown in Fig. 2. Between 1976 and 1981, numbers increased steadily at an average rate of 7.8% *per annum* ($t = 11.606$, $df = 4$, $P < 0.001$) before declining at 3.1% p.a. in the period to 1986 ($t = 4.343$, $df = 4$, $P < 0.05$). From 1986, numbers again increased, although with some fluctuation, at an average rate of 1.6% p.a. ($t = 5.213$, $df = 4$, $P < 0.01$); the index value in 1997 was slightly greater than 50% higher than in 1976.

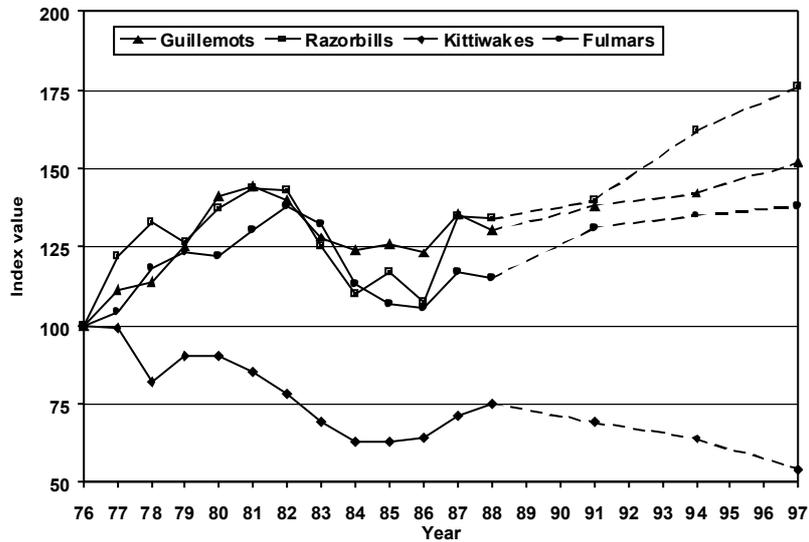


Figure 2. Population indices for individual Common Guillemots, Razorbills and Northern Fulmars and for Kittiwake nests in sample plots across all colonies combined, 1976–97. Broken lines indicate non-annual counts.

The pattern of changes in numbers of Guillemots in sample plots in individual colonies (Fig. 3) is broadly similar to that for all colonies combined. Numbers fell significantly at Row Head in 1984 and at Costa Head in 1986, in contrast to the remaining colonies where numbers were relatively stable between 1983 and 1986. More recently, in the ten years following 1988, numbers in plots at Marwick Head, by far the largest colony (Table 1), declined overall by 7.8% while those at Gultak fluctuated with an overall increase of just 8.6%. These figures compare with a combined increase of 32.2% at the other three colonies. The potentially large variations in numbers of Guillemots attending breeding colonies from day to day, in combination with the often very high densities of birds present, greatly affect the accuracy of the Guillemot population estimates based on single counts. Indeed, the use of multiple counts of sample plots, which enables measures of variability in attendance to be attached to sample population means, was devised specifically to overcome the inherent difficulties in quantifying Guillemot population trends (Harris *et al.* 1983). However, while plot counts are preferred to single whole-colony counts for year to year population monitoring, it is also recommended that whole-colony counts are undertaken periodically as a check on whether colonies appear to be expanding or contracting (Walsh *et al.* 1995).

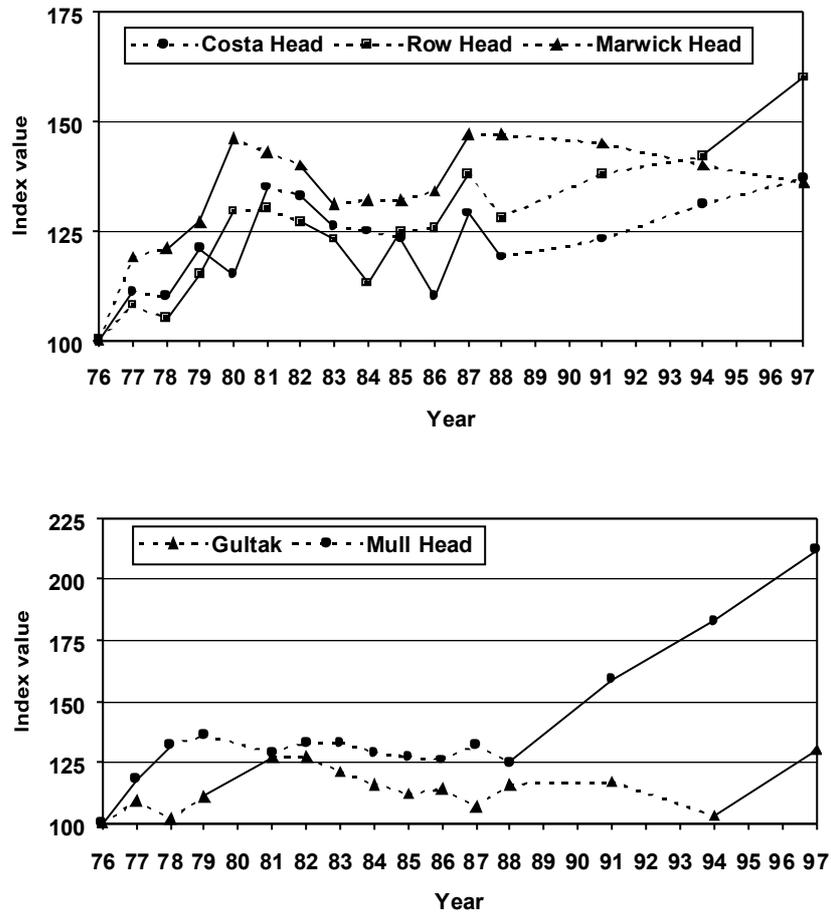


Figure 3. Colony population indices for individual Common Guillemots in sample plots, 1976-97. Solid lines indicate that mean numbers in all plots combined differed significantly ($P < 0.05$, two-tailed t -test) between the two linked counts and dotted lines indicate no significant change. In some instances counts were made at intervals of more than one year and that annual changes in the intervening period are unknown. a) West Mainland colonies; b) East Mainland colonies.

Table 2. Comparable land-based whole-colony counts for Orkney Common Guillemots (individual birds) and comparison of changes in whole colony counts (% WCC = % change from previous highest directly comparable count) and mean plot counts (% MPC = % change in plot counts over same period).

	1979 ^a	1981 ^b	1985 ^d	1986 ^e	1991 ^f
Marwick Head					
All sections	27 715	-		22 320	30 854
Count positions 1-11 only	27 225	17 865		21 730	
% WCC		-34.4	-	+21.6	+38.2
% MPC (see note 1)		(+13)	-	(-6)	+8.0
Row Head (see note 2)					
	-	6921	6 103		8271
% WCC			-11.8		+35.5
% MPC (see note 1)			-6.0		+11.1
Costa Head (see note 3)					
		7504+	6857 - 7492		
% WCC			≥ -0.2 ≤ -8.6		
% MPC (see note 1)			-10.8		
Gultak					
			1799		2486
% WCC					+38.2
% MPC (see note 1)					+4.7
Mull Head					
	-	1390	1171	-	1593
% MPC (see note 1)			-3.6		+25.1

Notes to Tables 2-5

- (1) Changes in plot means for 1981-85 are those published in Benn *et al.* (1987); those for 1991-97 are JNCC (unpublished) and those in parentheses for other years are approximate, based on percentage changes in plot indices derived from Benn & Tasker 1985. Figures in italics indicate that the plots held 50 or fewer birds.
- (2) Some of the counts shown for Row Head in 1985 differ from those published in Benn & Tasker (1985) as examination of the original field data (held by JNCC) revealed some tallying errors.
- (3) The Costa Head count in 1981 (Wanless *et al.* 1982a) may have excluded some sections (First and Second Geos (Benn & Tasker 1985) at the west end of the colony that were counted in later years. Hence, the 1981 figures are minimum estimates while the 1985 figures are given as a range excluding and including the areas possibly missed in 1981.
- (4) Highest directly comparable counts at Marwick Head are sums of all actual land-based counts (i.e. excluding estimates for missed sections or sections not visible from land) that are directly comparable between 1991 and 1994 and between 1994 and 1997. These include sections of cliff visible from land that were not located in earlier counts (JNCC unpublished data).
- (5) Parts of Costa Head in 1997 were not counted until 4 July following a storm that destroyed some Kittiwake nests present in June. For these sections, a correction factor was applied based on percentage losses of nests in previously counted sections over the intervening period (JNCC unpublished data).

It should be further noted that the whole-colony counts shown in Tables 2-5 are not equivalent to actual numbers of birds as some sections of the cliffs are not visible from land. Sources: a) Planterose 1979; b) Wanless *et al.* 1982a; c) Tasker 1983; d) Benn & Tasker 1985 (and see note 2); e) Beveridge 1986; f) JNCC unpublished data.

There have been relatively few whole-colony counts of Guillemots at the Orkney Mainland study colonies since 1976 against which to compare the plot results. In addition, there is some uncertainty as to the coverage of the Costa Head and Gultak colonies in 1981: maps in Wanless *et al.* (1982a) indicate that some sections that were counted in later years (Benn & Tasker 1985) may have been excluded in 1981. This renders direct comparisons between the 1981 and 1985 counts at these colonies difficult. Those whole-colony counts that can be compared directly are summarised in Table 2, alongside changes in plot counts for the same periods. In most cases there is agreement as to the direction of changes in numbers as indicated by whole-colony versus sample plot counts, although the magnitude of changes in plot counts is generally less than that indicated by whole-colony comparisons. However, at Marwick Head, there is disagreement between the plot and whole colony counts as to the direction of population changes between 1979 and 1986. This may in part reflect the low proportion of the whole population contained within monitoring plots at this colony (Table 1), although even at Mull Head, where more than 80% of the population are contained within sample plots, there is incomplete agreement between plot and whole-colony counts. In addition, the 1981 counts at Marwick Head were carried out very rapidly (over just five hours on two days, compared with in excess of 20 hours over 11 days in 1979) and were not made on currently recommended dates and times for Guillemots (Wanless *et al.* 1982a, Planterose 1979).

Razorbill The overall pattern of change in Razorbill numbers in sample plots across all colonies combined is very similar to that observed for Guillemots (Fig. 2). Between 1976 and 1981, numbers increased at an average rate of 6.2% p.a. ($t = 3.754$, $df = 4$, $P < 0.05$), although there was an overall decrease between 1978 and 1979 that mainly reflected declines at the East Mainland colonies of Gultak and Mull Head (Fig. 4b). From 1981 to 1986, numbers declined at 6.1% p.a. ($t = 4.825$, $df = 4$, $P < 0.01$) but thereafter increased again, at an average annual rate of 3.8% ($t = 4.743$, $df = 4$, $P < 0.01$); the overall index value in 1997 was around 75% higher than the 1976 baseline.

The patterns of change in individual colonies (Fig. 4) are generally similar to that for all colonies combined. The overall increase between 1976 and 1997 was greater at the East Mainland colonies of Gultak and Mull Head (Fig. 4b), where index values more than doubled, than at the three West Mainland sites (Fig. 4a). The main exception to the overall trend was Row Head, where overall numbers declined since 1976. However, the very low numbers of Razorbills monitored at this small colony (Table 1) mean that minor variation in

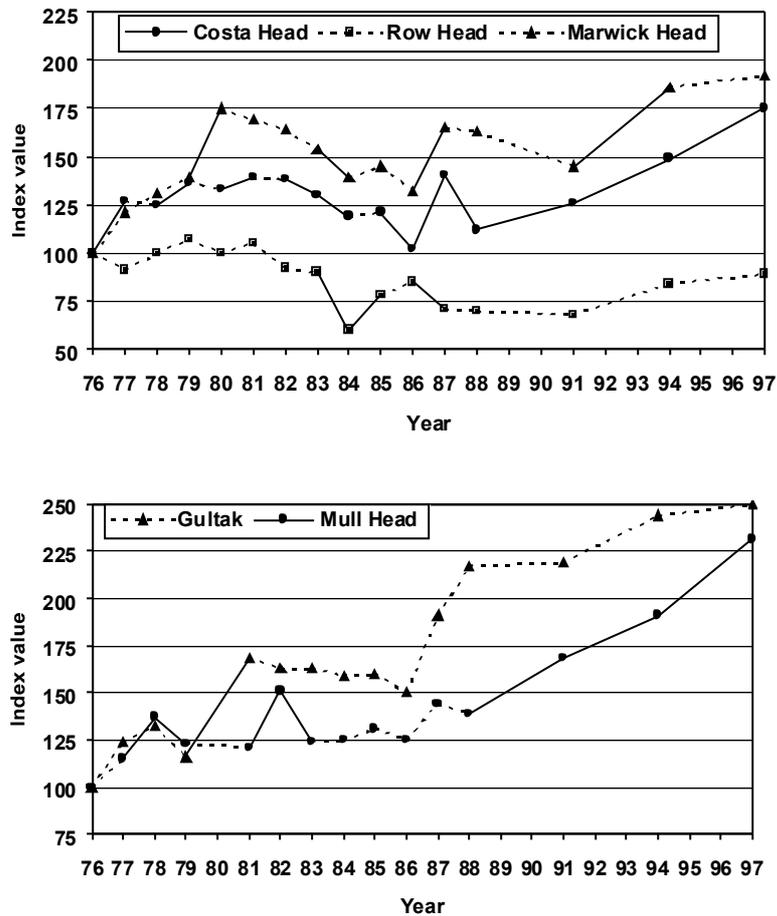


Figure 4. Colony population indices for individual Razorbills in sample plots, 1976-97. See Fig. 3 for conventions.

the numbers of birds attending the cliffs can have a marked effect on annual plot means.

Table 3 summarises directly comparable whole-colony counts for Razorbills and compares changes in these with those observed in sample plot counts over the same periods. No comprehensive counts of Razorbills were made at Marwick Head in either 1979 (Planterose 1979) or 1981 (Wanless *et al.*

1982a), thereby preventing comparison with later counts. Generally, plot counts and whole-colony counts are in broad agreement with respect to the direction and approximate magnitude of changes in numbers over comparable periods; an exception is Row Head, where plot counts indicate a decline between 1985 and 1991, while whole-colony counts increased, but this again could reflect the very small numbers of Razorbills in the sample plots at this colony.

Table 3. Comparable land-based whole-colony counts for Orkney Razorbills (individual birds) and comparison of changes in whole colony counts (% WCC) and mean plot counts (% MPC). See Table 2 for conventions.

Colony	1981 ^b	1985 ^d	1986 ^e	1991 ^f
Marwick Head			948	1,088
% WCC				+14.8
% MPC (see note 1)				+10.3
Row Head (see note 2)	189	142		162
% WCC		-24.9		+14.1
% MPC (see note 1)		-30.0		-12.8
Costa Head (see note 3)	771+	557 – 673		
% WCC		≥-12.7 - ≤-27.8		
% MPC (see note 1)		-20.0		
Gultak		470		760
% WCC				+61.7
% MPC (see note 1)				+37.0
Mull Head	84+(incompl)	125	-	141
% WCC		(≤ +48.8)		+12.8
% MPC (see note 1)		+13.2		+28.4

Northern Fulmar Numbers of Fulmars in sample plots also show three distinct phases of change (Fig. 2). From 1976 to 1982, numbers increased on average by 5.3% p.a. ($t = 7.979$, $df = 5$, $P < 0.001$), followed by a decline averaging 7.1% p.a. ($t = 5.424$, $df = 3$, $P < 0.05$) to 1986. From 1986-97 numbers again increased, by 2.3% p.a. ($t = 5.216$, $df = 4$, $P < 0.01$); the overall index value in 1997 was nearly 40% higher than the 1976 baseline.

Patterns of change at individual colonies (Fig. 5) have been rather more variable for Fulmars than for Guillemots and Razorbills (Figs. 3 and 4). At the largest colony, Costa Head, numbers in sample plots increased by only 5.5% overall from 1988-97, compared with 20.0% across all colonies combined in the same period and there was a significant decline between 1988 and 1991. At Row Head, a marked increase between 1985 and 1987 was followed by a decline to 1988, after which numbers stabilised. However, as with Razorbills, actual

numbers of Fulmars monitored at this colony are small (Table 1) and so counts are likely to fluctuate greatly from year to year. The same is also true of Marwick Head, the only colony at which Fulmar numbers in sample plots have declined overall since 1976.

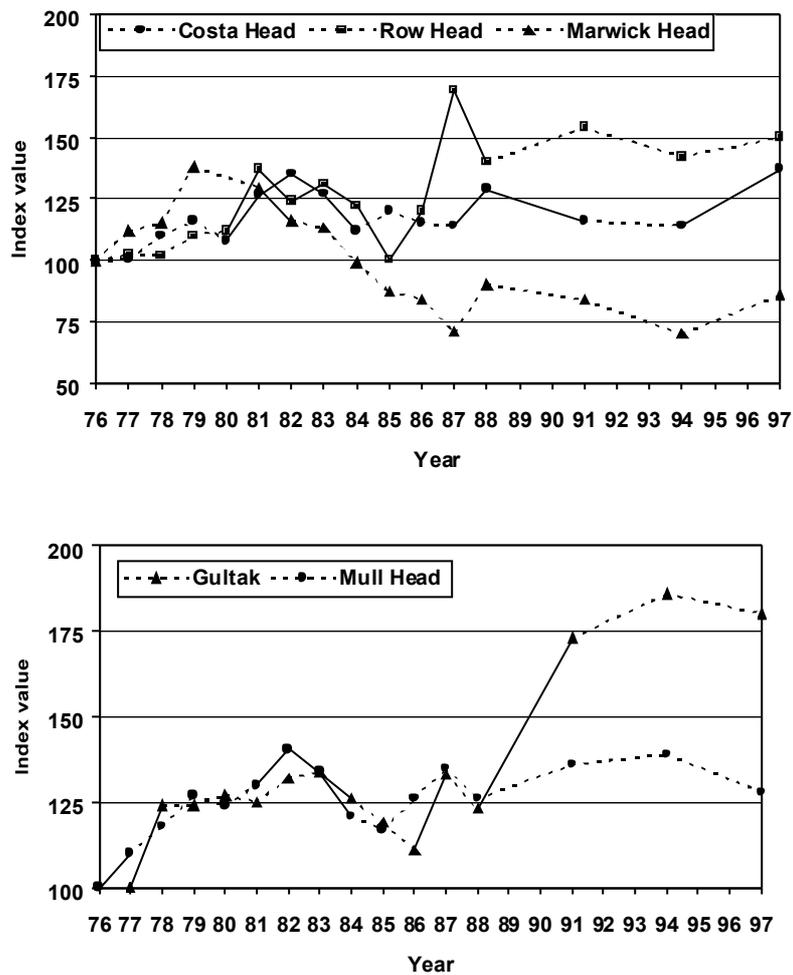


Figure 5. Colony population indices for individual Northern Fulmars in sample plots, 1976-97. See Fig. 3 for conventions.

Table 4. Comparable land-based whole-colony counts for Orkney Northern Fulmars (individual birds) and comparison of changes in whole colony counts (% WCC) and mean plot counts (% MPC). See Table 2 for conventions.

Colony	1985 ^d	1986 ^e	1991 ^f
Marwick Head		1045	977
% WCC			-6.5
% MPC (see note 1)			-0.8
Row Head (see note 2)	256		330
% WCC			+28.9
% MPC (see note 1)			+53.5
Gultak	945		1533
% WCC			+62.2
% MPC (see note 1)			+45.0
Mull Head	312	-	361
% WCC			+15.7
% MPC (see note 1)			+16.0

There are very few whole-colony counts of Fulmars available for comparison with the plot counts. Fulmars were not counted in 1981, and the 1991 counts did not include Costa Head. In addition, the 1979 count at Marwick Head was incomplete, with those birds interspersed with Kittiwakes on the lower ledges having been overlooked (Planterose 1979). However, where direct comparisons can be made, there is generally fairly good agreement as to the direction and approximate scale of change (Table 4).

Kittiwake The pattern of change observed in Kittiwake plot counts between 1976 and 1997 is very different from the other three species (Fig. 2). Numbers of apparently occupied nests declined on average by 2.5% p.a. ($t = 6.032$, $df = 14$, $P < 0.001$); the 1997 index value is slightly greater than 50% of the 1976 baseline. The same basic pattern was observed across all five colonies (Fig. 6); decline was proportionately greatest at Gultak (the smallest colony) and Row Head, and least at the north coast colonies of Costa Head and Mull Head. At Marwick Head, the largest colony, numbers apparently stabilised in the sample plots between 1987 and 1997 following a very rapid decline to 1986.

Changes in Kittiwake plot counts and whole-colony counts are shown in Table 5. Generally, there is good agreement between these counts in the direction and scale of changes in numbers of Kittiwake nests at the five colonies. Closest

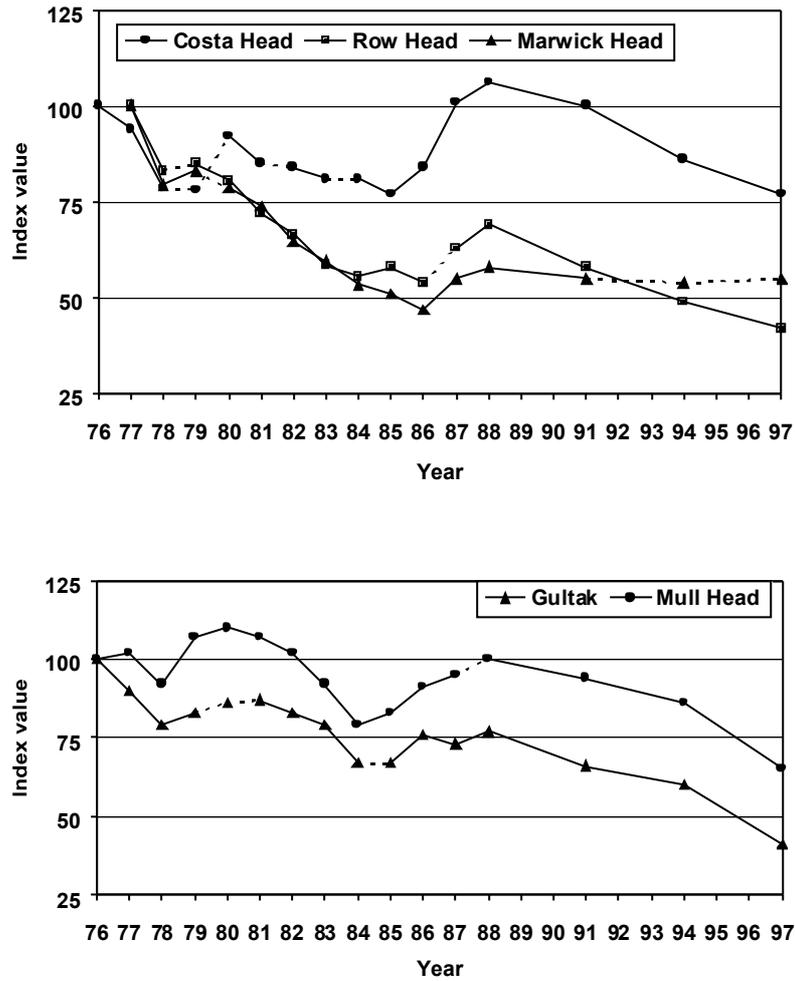


Figure 6. Colony population indices for individual Kittiwakes in sample plots, 1976-97. See Fig. 3 for conventions.

Table 5. Comparable land-based whole-colony counts for Kittiwakes (apparently occupied nests) and comparison of changes in whole colony counts (% WCC) and mean plot counts (% MPC). See Table 2 for conventions.

Colony	1979 ^a	1981 ^b	1983 ^c	1985 ^d	1986 ^e	1991 ^f	1994 ^f	1997 ^f
Marwick Head								
all sections	6945	-	4398		3704	5252	4589	4543
count positions 1-11 only	6436	3313	4113					
highest directly comparable (see note 4)						5698	5004	
highest directly comparable (see note 4)							4873	5102
% WCC		-48.5	+24.1		-15.8	+41.8	-12.2	+4.7
% MPC (see note 1)		(-11)	(-20)		(-20)	+16.7	-1.2	+0.9
Row Head (see note 2)								
	-	2549		2212		2606	2350	2099
% WCC				-13.2		+17.8	-9.8	-10.7
% MPC (see note 1)				-15.2		-0.7	-15.5	-13.8
Costa Head (see notes 3 & 5)								
		1796+		1501-1652		2656	2274	c. 2038
% WCC				≥ -8.0 - ≤ -16.4		+60.8	-14.4	- c. 10
% MPC (see note 1)				-2.0		+30.4	-14.5	-9.9
Gultak								
				522		599	662	415
% WCC						+14.8	+10.5	-37.3
% MPC (see note 1)						-1.5	-9.3	-32.3
Mull Head								
	-	1392	-	1066	-	1283	1129	791
% WCC				-23.4		+20.4	-12.0	-29.9
% MPC (see note 1)				-26.0		+13.6	-8.3	-24.7

agreement is at Mull Head, where 65% of the total population is included in sample plots (Table 1), but notable exceptions occur at Marwick Head, where plot counts declined significantly between 1981 and 1983 by around 20% (Fig. 6), while whole-colony counts indicated a 24% increase. Similarly, whole-colony counts increased between 1985 and 1991 at Gultak and Row Head, and between 1991 and 1994 at Gultak, while plot counts declined in these periods. Overall, both whole-colony and sample plot counts indicate that there was a substantial decline in the Mainland Orkney Kittiwake breeding population in the 1980s and 1990s. In the period 1991 to 1997, for which the most comprehensive data are available, whole-colony counts indicate a decline of 20.2% and mean plot counts a decline of 21.2% across all five colonies combined.

Breeding success

Common Guillemot Guillemot breeding success data are summarised in Fig. 7. Between 1983 and 1989, monitoring at the Marwick Head plot was very intensive, checks being made daily (Tasker 1983; Griffiths 1994; Benn 1985; Beveridge 1986; Ward 1987; Thomas 1988) or at most every two days (Ribbands 1990) from late May to the end of the fledging period. Thus, the majority of those pairs that laid eggs were probably detected and the data (shown as Marwick Head A, Fig. 7), are roughly equivalent to chicks fledged per 'active' plus 'regular' site (see Methods) in subsequent years.

At Mull Head and Row Head in 1989 and at all colonies in all years from 1990, increased work on other species led to less intensive monitoring of Guillemots, particularly during the early breeding season. In most years, plots were checked only three times in early June to identify 'active' and 'regular' sites. However, in 1991, 1994 and 1997, more visits were made and larger numbers of 'regular' sites were identified, particularly at Mull Head. Consequently, estimates of breeding success per 'active' plus 'regular' site are probably proportionately lower than those for 'active' only sites in these years.

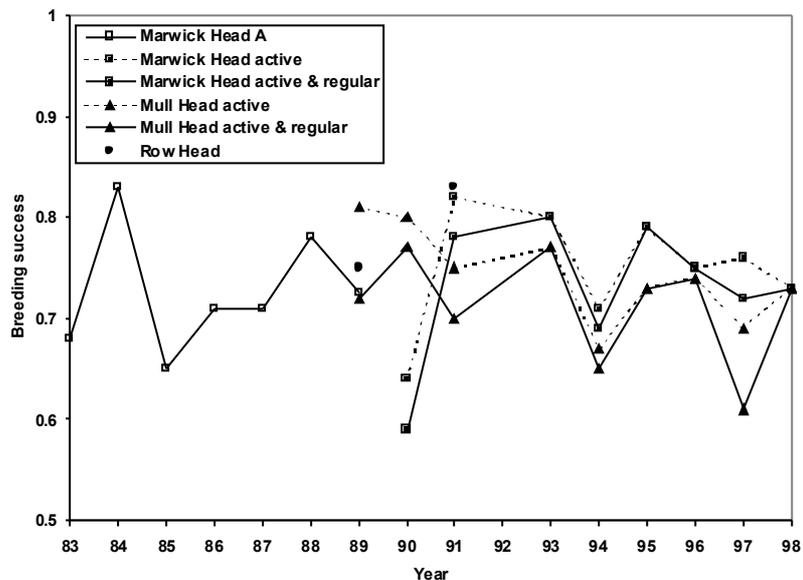


Figure 7. Common Guillemot breeding success (chicks fledged per 'active' plus 'regular' site), 1983-98. See text for explanation of the various data series.

Breeding success of Guillemots typically fluctuated between 0.7 and 0.8 chicks fledged per 'active' plus 'regular' site and in most years was apparently slightly higher at Marwick Head than at Mull Head. There were no apparent trends over time at either site. Mean breeding success was 0.73 ± 0.02 SE at Marwick Head for the period 1983-98 (series A to 1989, 'active' plus 'regular' sites from 1990) and 0.71 ± 0.02 per 'active' plus 'regular' site at Mull Head for the period 1989-98. These figures are similar to an average of 0.74 ± 0.01 measured for between three and 14 colonies in Britain annually between 1986 and 1997 (Thompson *et al.* 1999).

The exceptionally low breeding success recorded at Marwick Head in 1990 (0.59 chicks per 'active' plus 'regular' site) was associated with an unusually late median fledging date and a prolonged spell of strong, mainly westerly winds from late June to mid-July (Crossley 1990). Lower than usual breeding success (as measured both per 'active' and per 'active' plus 'regular' site) was also associated with a late breeding season in 1994 (JNCC, unpublished data). Breeding success was also low at Mull Head in 1997, although the effect was much less marked when 'active' sites only were considered, and may in part be an artefact associated with more frequent checks early in the breeding season (see above).

Northern Fulmar Fulmar breeding success data for the period 1989 to 1998 are summarised in Fig. 8. The 1989 data are not directly comparable with those for subsequent years, as preliminary checks to identify occupied sites were not made until mid-June. Fulmar breeding success in Orkney typically ranged between 0.4 and 0.6 chicks fledged per apparently occupied site and there were no apparent trends over time. In most years, breeding success was highest at Costa Head, the largest colony (1990-98 mean = 0.52 ± 0.02) and lowest at Mull Head (1990-98 mean = 0.43 ± 0.01) with Gultak being intermediate (1990-98 mean = 0.44 ± 0.04). These figures are similar to or greater than the average for 1986-97 of 0.43 ± 0.01 as recorded in between 13 and 41 colonies in Britain annually (Thompson *et al.* 1999). The exceptionally low breeding performance at Gultak in 1997 (0.19 chicks per site) was probably due to predation of chicks on the upper grassy slopes by feral cats (K. Thompson, pers. obs.). Mammalian predators may have contributed to low productivity at some of the Mull Head plots in 1994 (JNCC, unpublished data). Breeding success of 0.72 chicks fledged per apparently occupied site at a single small plot at Row Head in 1992 was exceptionally high for this species.

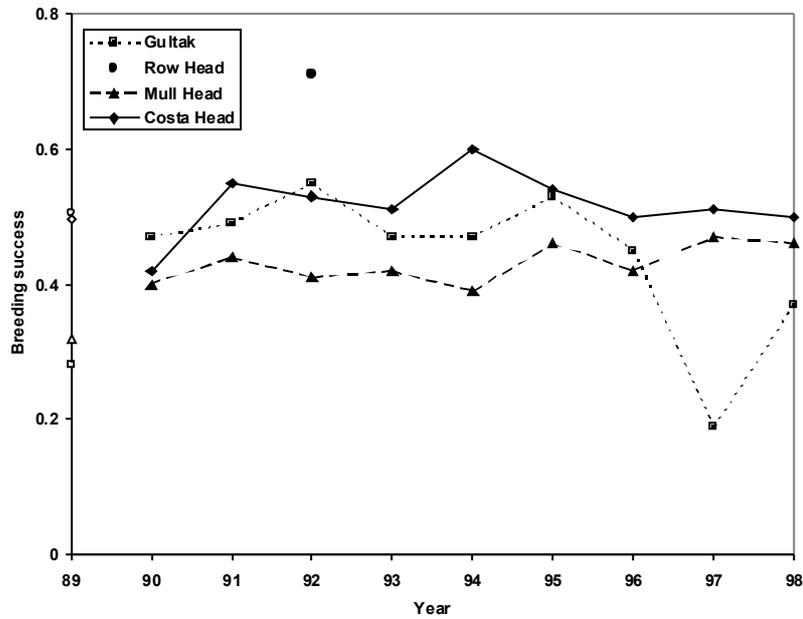


Figure 8. Northern Fulmar breeding success (chicks fledged per apparently occupied site), 1989-98.

Kittiwake Kittiwake breeding success for the period 1984 to 1998 is summarised in Fig. 9. Kittiwakes in Mainland Orkney typically produced about one chick per breeding pair *per annum*, although there is considerable variation in productivity between years and breeding success is generally lower in smaller colonies. Mean productivity for the four colonies monitored regularly by intensive methods, in descending order of colony size are: 1.15 ± 0.06 (Marwick Head, 1984-98), 1.13 ± 0.05 (Row Head, 1989-98), 1.09 ± 0.06 (Mull Head, 1989-98) and 0.88 ± 0.08 (Gultak, 1989-98). These figures compare with a Britain and Ireland annual average of 0.73 ± 0.03 for the period 1986-97 in 30 to 61 colonies. Breeding success at colonies on Mainland Orkney is consistently among the highest recorded throughout Britain and Ireland (Thompson et al. 1999).

Estimated breeding success apparently fluctuated between 1984 and 1986 at the two plots monitored intensively at Marwick Head, but late chick mortality was more likely to be detected in 1984 and 1986 when checks continued until most chicks had fledged. Similarly, the low breeding success in intensively monitored plots at Marwick Head in 1988 reflected late mortality of

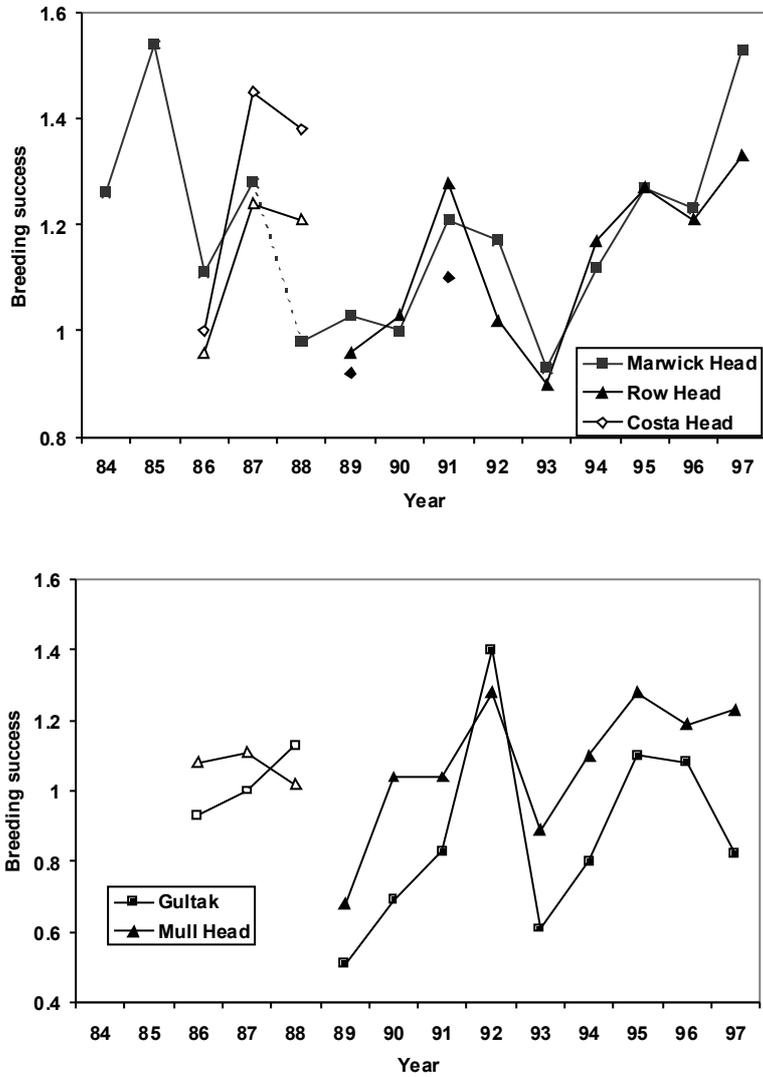


Figure 9. Kittiwake breeding success (chicks fledged per apparently occupied nest), 1984-98. Solid symbols indicate intensive monitoring methods and open symbols indicate low intensity monitoring methods. These two types of data are not directly comparable (see text). a) West Mainland colonies; b) East Mainland colonies.

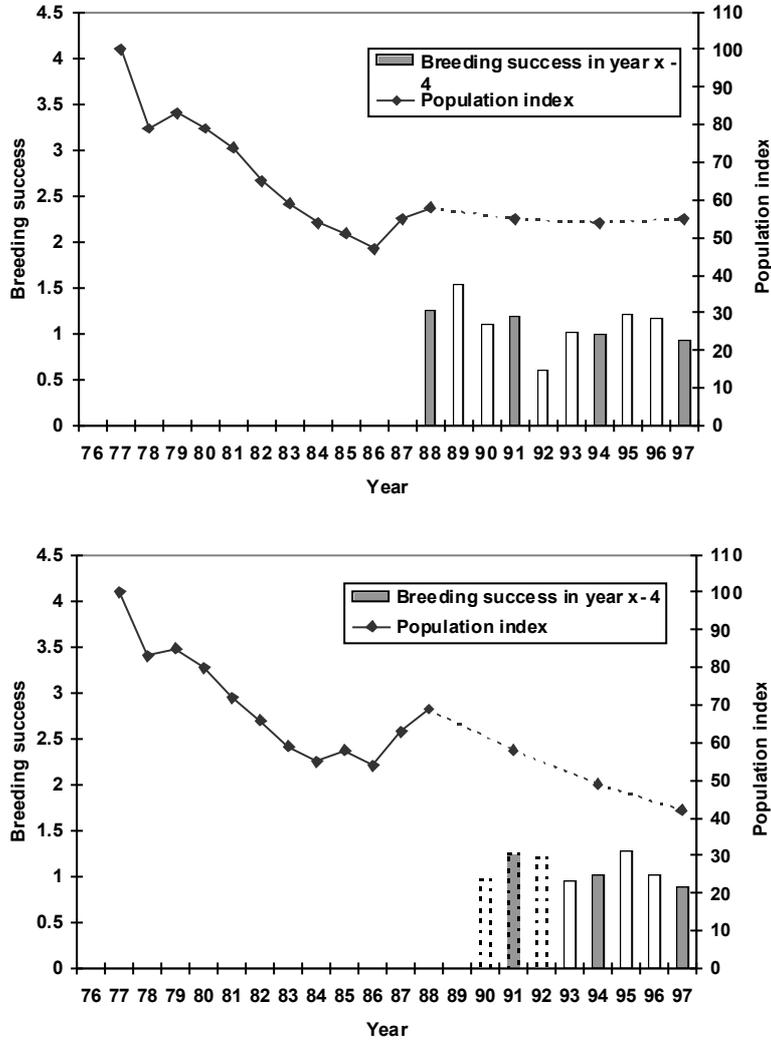


Figure 10 a-b. Kittiwake breeding success in relation to population trends. Bars with solid borders indicate breeding success measured by high intensity methods and bars with broken borders indicate breeding success measured by low intensity methods (which could overestimate success by 10- 20%). Shaded bars indicate breeding success four years prior to years for which population data are available and unshaded bars indicate breeding success for intervening years. a) Marwick Head; b) Row Head.

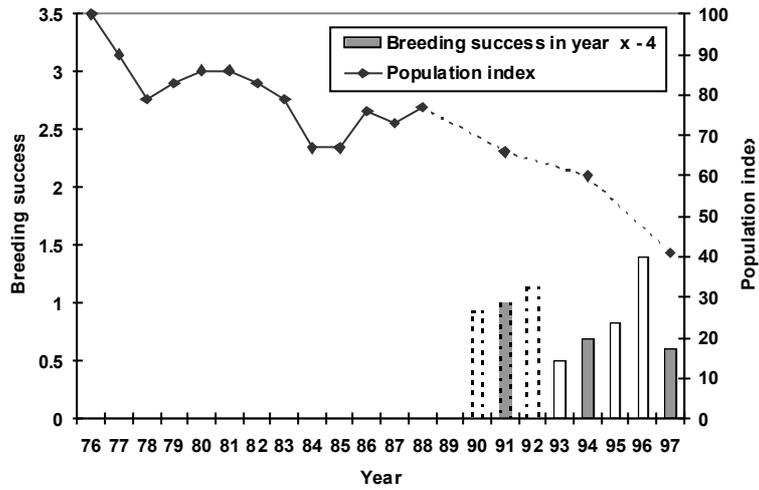
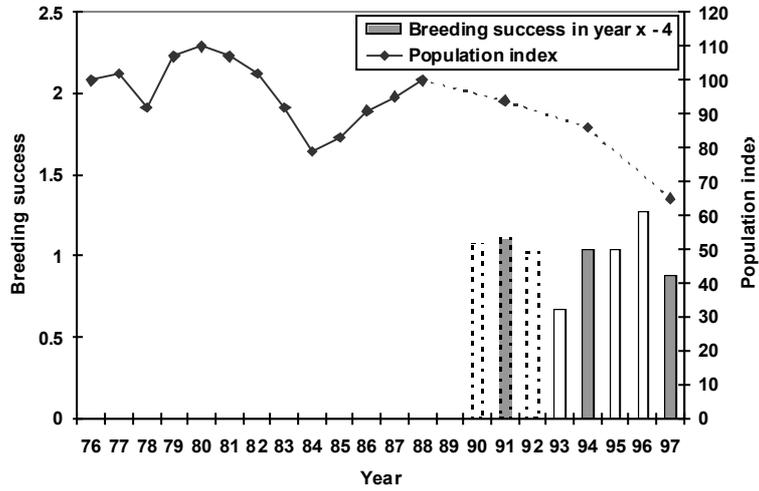


Figure 10 c-d. Kittiwake breeding success in relation to population trends. Bars with solid borders indicate breeding success measured by high intensity methods and bars with broken borders indicate breeding success measured by low intensity methods (which could overestimate success by 10- 20%). Shaded bars indicate breeding success four years prior to years for which population data are available and unshaded bars indicate breeding success for intervening years. c) Mull Head; d) Gultak

well-grown chicks that would not have been detected by the less intensive monitoring method used at the other colonies that year. Indeed, at Marwick Head itself in 1988, comparison of counts of chicks in mid-July with peak June nest counts in the population monitoring plots suggested mean breeding success of 1.17 chicks fledged per pair, nearly twice that estimated in the intensively monitored plots. The reason for the very low breeding success at East Mainland colonies (Mull Head and Gultak) in 1989 is not known. Poor breeding performance at all colonies in 1993 was caused by strong winds and heavy rain in late June and early July leading to high mortality among early hatched chicks (Paice 1993).

Given the generally high level of Kittiwake breeding success at Mainland Orkney colonies, the observed decline in Kittiwake populations at these sites is unexpected. Kittiwakes typically first breed at four or five years old (Wooler & Coulson 1977), so it might be expected that any trends in breeding success would be reflected in the size of the breeding population four or more years later. Fig. 10 shows population indices in relation to breeding success four years earlier. Data available for direct comparisons are limited as population monitoring took place only every three years between 1988 and 1997, while productivity monitoring at most colonies began only in 1986. Also, prior to 1989 (shown against 1993 in Fig. 10), monitoring of breeding success at most colonies was by low-intensity methods that are not directly comparable with later years, and which tend to miss any late season mortality, such as observed at Marwick Head in 1988.

However, as illustrated in Figs. 10b-d, there is an indication that falling population indices between 1991, 1994 and 1997 at Row Head, Mull Head and Gultak do reflect declines in breeding success in 1987, 1990 and 1993; no such relationship is apparent for Marwick Head (Fig. 10a). More importantly, it would be expected that a consistent downward trend in breeding success would be needed to drive a population decline, whereas it can be seen that breeding success fluctuated in intervening years.

DISCUSSION

Observed coefficients of variation in plot counts for the period 1976 to 1980 led Wanless *et al.* (1982b) to conclude that, depending on the number of counts made each year, the population monitoring scheme on Mainland Orkney should enable annual changes in numbers of the order of 10-20% for Guillemots, 30-50% for Razorbills, 20-30% for Fulmars and 5-10% for Kittiwakes to be detected. It can be seen in Figs. 3-6 that, indeed, with the exception of the Kittiwake, relatively few year to year changes are statistically significant. However, despite the inherent difficulties in detecting relatively small short-term

changes in auk and Fulmar populations, and the possible limitations imposed by non-random selection of plots (discussed in Benn *et al.* 1987) the Orkney monitoring scheme has proved valuable in detecting longer-term trends in seabird populations. Given the long lifespans and deferred sexual maturity of these species, such long-term monitoring is essential for the detection of trends at time-scales appropriate to their population dynamics.

Common Guillemot The overall increase in Guillemot numbers in the Orkney plots between 1976 and 1997 is in line with data from other parts of Britain. Numbers in Britain and Ireland more than doubled between 1969/70 and 1985-87 (Lloyd *et al.* 1991) and since 1986 there have been further highly significant increases in Guillemot numbers in monitoring plots at colonies in a number of regions, including eastern Scotland and Wales (Thompson *et al.* 1999).

This overall increase in numbers in the Orkney plots masks the period of stability or decline recorded at the five colonies in the early 1980s. A similar pattern was observed at a number of other monitored colonies in Scotland at this time (e.g. Isle of May, Canna and Troup Head), although the initial period of increase at these colonies halted one or two years later than observed in Orkney (Lloyd *et al.* 1991). However, at various other colonies throughout Britain (e.g. St Abb's Head, Farn Islands, Berry Head, Skomer and Bardsey) numbers steadily increased during the 1980s (Lloyd *et al.* 1991). In Shetland, where a population monitoring scheme similar to that in Orkney has been running since 1978, an initial increase to a peak in 1982 was followed by a decline to 1990, with particularly steep annual decreases from 1984 to 1985 and from 1989 to 1990. Although numbers recovered somewhat to the late 1990s, the increase was sufficient only to return populations to 1978 baseline levels (Heubeck 1998).

In Orkney, numbers of Guillemots counted in plots have varied considerably between colonies since the last population census in 1985/86 (Lloyd *et al.* 1991). In particular, at the Marwick Head colony, which alone holds over half of the Guillemots in the five monitored colonies, numbers in plots have remained fairly level. If the overall changes in plot indices for individual colonies between 1986 and 1997 are applied to the 1985/86 land-based counts, the results suggest an overall population increase of 10% to 1997, compared with a 22% increase across all plots combined.

Breeding success of Guillemots in Orkney from 1989-97 was generally similar to the average for this species in Britain, but there have been a few seasons with much lower than usual chick production. Given an average age of first breeding of six or seven years (Harris *et al.* 1994), it is not yet possible to determine if reduced breeding success in some years of this study will eventually be reflected in breeding numbers.

Razorbill The overall change in Razorbill numbers in the Orkney plots has been similar to, but even more pronounced than that observed in Guillemots, with major increases indicated at all but Row Head, where monitoring effort might be inadequate to detect actual population change. As with Guillemots, the apparent increase in Razorbill populations, particularly in the 1990s, is mirrored in several other regions, including south-east Scotland and Wales (Thompson *et al.* 1999).

The decline in Razorbill numbers in Orkney in the early 1980s and in particular the very marked decreases from 1982 to 1984, may perhaps be associated with a large wreck of this species on Orkney and North Sea coasts in February 1983 (Heubeck *et al.* 1992). However, in this context it should be noted that Guillemot numbers remained fairly stable following a similar scale wreck in Orkney in the winter of 1984/85. In Shetland, Razorbill population trends have been similar to those observed for Guillemots, with a fluctuating decline during the 1980s to around 50% of 1978 baseline levels, thereafter followed by a partial recovery (Heubeck 1998).

Northern Fulmar The general increase in Fulmar numbers in the Mainland Orkney plots accords with trends observed throughout Britain and Ireland between 1969/70 and 1985-87 (Lloyd *et al.* 1991) and subsequently in various regions, including south-east Scotland, north-east England and Wales (Thompson *et al.* 1999). In contrast to Guillemots and Razorbills however, Fulmars have also increased significantly in Shetland since the late 1970s (Heubeck 1998). In Shetland, there are disparities between trends in numbers of individual Fulmars and of apparently occupied sites at annually monitored sites. There is also some evidence to suggest that the numbers of loafing Fulmars attending colonies may be related to food supply (Shetland Oil Terminal Environmental Advisory Group, unpublished data). In the early years of the Orkney monitoring scheme, large discrepancies were noted in the apparent population trends indicated when both individual Fulmars and apparently occupied sites were counted (Wanless *et al.* 1982b). Thus, the decline in counts of individual birds in Orkney in the early 1980s, may not accurately reflect changes in the breeding population. The extent to which the presence of varying proportions of non-breeding adults in colonies may also have influenced the very similar apparent population trends recorded for Guillemots and Razorbills in Orkney is unknown.

Trends in Fulmar population plots, like those of Guillemots, have varied considerably between colonies in Orkney, and caution must be applied when extrapolating from changes in the combined colony index to the population as a whole. If the changes in individual colony indices in the period 1985/86 to 1997 are applied to the 1985/86 land-based counts, an overall population increase of 20% is suggested, in contrast to a 30% increase in the overall index value in the

same period. However, monitoring effort at both Row and Marwick Heads may be too low to allow detection of actual change at these colonies.

Fulmar breeding success in Orkney since 1989 has been comparable to or above the mean for Britain as a whole, with localised predation being responsible for the only notable instance of markedly reduced chick production. The species, therefore, appears capable of sustaining its expansion in Orkney.

Kittiwake Both plot counts and whole-colony counts indicate that, in marked contrast to the other three species monitored, Kittiwakes have declined substantially at Mainland Orkney colonies over the past two decades. This decline apparently continues at all colonies, with the possible exception of Marwick Head.

Kittiwake numbers increased in Britain and Ireland from around the beginning of the 20th century to at least 1985-87. There was an overall increase of 22% between 1969/70 and 1985-87 but an estimated 40% decrease in the total Orkney population over the same period (Lloyd *et al.* 1991). Since 1986, trends at regularly monitored colonies in Britain and Ireland have varied considerably between regions and over time (Thompson *et al.* 1999) but overall trends since the mid 1980s are unknown. However, in Shetland, the Kittiwake population decreased by about 50% between 1981 and 1997, with a particularly rapid rate of decline from the late 1980s to mid-1990s. This was attributed to a combination of a series of poor breeding seasons in the late 1980s, affecting subsequent recruitment to the breeding population, and a marked increase in Great Skua *Catharacta skua* predation of both adults and chicks (Heubeck *et al.* 1999).

Great Skuas have been recorded taking Kittiwake eggs, chicks, and juveniles at Orkney colonies (Ward 1987; Ribbands 1990; K. Thompson pers. obs.). However, there is no evidence to suggest a recent marked increase in Great Skua predation on Orkney seabirds, which in Shetland appeared to be prompted by a reduction in sandeel availability in the mid-1980s (Hamer *et al.* 1991). In addition, in contrast to the major concentrations of many hundreds of pairs of breeding Great Skuas found immediately adjacent to some Kittiwake colonies in Shetland (Heubeck *et al.* 1997), a total of only 25 pairs bred on Mainland Orkney at the last census in 1992 (Meek *et al.* 1994). Of these, only three (two at Mull Head and one at Gultak) were close to the Kittiwake colonies (RSPB, unpublished data). It seems highly unlikely, then, that predation by Great Skuas was responsible for the observed decline of the Kittiwake population on Orkney Mainland.

At the Orkney Mainland colonies, Kittiwake breeding success has been higher than the average for Britain and Ireland in all years since intensive monitoring began in the mid-1980s (Thompson *et al.* 1999). The most recent phase of the population decline in Orkney is not associated with any overall

falling trend in breeding success, as has been documented for the Isle of May and other colonies along the coast of south-east Scotland and north-east England since 1986 (Harris & Wanless 1997). The complete breeding failures in Shetland in the late 1980s and early 1990s, linked to reduced availability of sandeels (Hamer *et al.* 1993), and the more recent poor breeding seasons in Shetland (Thompson *et al.* 1999) have also not been paralleled at the Orkney colonies. However, while Kittiwake breeding success as indicated by fledging is generally high at the Orkney Mainland colonies, beached bird surveys indicate that in some years large numbers of young Kittiwakes die shortly after fledging (RSPB 1978-98). Exceptionally high levels of post-fledging mortality appeared to occur in 1976 and 1977; the number of dead juveniles found along West Mainland beaches being equivalent to between 6% and 7% of the combined breeding populations at Marwick Head and Row Head (Planterose 1979; Wanless *et al.* 1982a). In addition, higher than average densities were also found in 1978 (no data are available for 1979). It is difficult to assess the actual impact of post-fledging mortality on the Orkney Mainland Kittiwake population because the proportion of juvenile Kittiwakes that die and are subsequently detected on beached bird surveys is unknown and is potentially highly variable. However, it is noteworthy that the sharp decline in the Kittiwake breeding population between 1980 and 1984 occurred at the time when the mid to late 1970s cohorts would have been reaching maturity.

Since 1980, incidences of exceptional post-fledging mortality, as indicated by the beached bird survey data, have been sporadic and apparently less severe than those observed in the late 1970s. Given the consistently high average breeding success recorded since monitoring began in 1984, it seems unlikely that such mortality alone could explain the further decline in the Kittiwake population observed since 1988. The disparity between observed population trends and breeding success suggests either that adult or immature survival rates are lower than required to sustain the population, even at the high breeding success recorded, and/or that there is net emigration of Kittiwakes from Orkney Mainland to other colonies.

No data are available on winter survival rates of adults or on recruitment rates of Kittiwakes in Orkney; measurement of these parameters requires very intensive annual monitoring of individually colour-ringed birds (Harris & Calladine 1993). Heubeck *et al.* (1999) noted the contrasting population trends among Kittiwakes in the late 1980s, when a period of population growth in Orkney (Fig. 2) coincided with rapidly decreasing populations in Shetland and suggested that birds might have emigrated from Shetland to Orkney. However, given the more recent decline in the Orkney Kittiwake population despite high breeding success, the possibility also exists of movements in the opposite direction. Recoveries of ringed Kittiwakes from

colonies in eastern Britain have shown that while adults are generally faithful to their breeding colony, there is considerable emigration of young birds away from their natal colonies, including one recovery as an adult in Shetland of a bird fledged from the Isle of May. Fewer than 40% of young Kittiwakes eventually return to breed at their natal colony and some 20% may eventually breed in colonies over 400 km distant (Coulson & Nève de Mévergnies 1992). Hence, emigration of Orkney fledglings to Shetland might occur and in this context the observation of an apparent influx of over 1000 juvenile Kittiwakes into Yell in Shetland in August 1997 (Scalter 1998), following a very poor breeding season in Shetland itself, is of interest. A ringing study designed to assess the scale of any movement of Kittiwakes away from Orkney would be valuable, as would the inclusion in the Orkney monitoring programme of rigorous assessments of post-fledging Kittiwake mortality and the effect of Great Skua predation on Kittiwake numbers.

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SAMENVATTING

POPULATIEONTWIKKELINGEN EN BROEDSUCCES VAN ZEEVOGELS NESTELEND OP DE ORKNEYEILANDEN, 1976-98

Op de Orkney Eilanden worden populatieontwikkelingen van de Noordse Stormvogel Fulmarus glacialis, de Drieteenmeeuw Rissa tridactyla, Zeekoeten Uria aalge en Alken Alca torda sinds 1976 in vijf kolonies in zogenaamde 'study plots' gevolgd. Daarnaast werden deze kolonies ook af en toe integraal geteld. De aantallen Noordse Stormvogels, Zeekoeten en Alken die in de broedtijd in deze kolonies aanwezig waren, zijn tussen 1976 en 1997 toegenomen. Toch werd voor elk van deze soorten in het begin van de jaren tachtig een periode van neergang geconstateerd en werden verschillen gevonden in de mate van toename (of zelfs afname) tussen verschillende delen van de kolonies. In tegenstelling tot deze drie succesvolle soorten is de populatie Drieteenmeeuwen gemiddeld met 2.5% per jaar afgenomen, waarbij de mate van afname omgekeerd evenredig was aan de koloniegrootte. Het broedsucces van de Noordse Stormvogel, de Drieteenmeeuw en de Zeekoet werd gevolgd vanaf het midden van de jaren tachtig. Het broedsucces van Noordse Stormvogel en Zeekoet was in de meeste jaren vrijwel net zo hoog, of zelfs iets hoger dan het nationale gemiddelde. Paradoxaal genoeg was ook het broedsucces van de Drieteenmeeuw de laatste 10-15 jaar over het algemeen zeer hoog. Aangenomen wordt dat grote sterfte na het uitvliegen, zoals dat ook wel is gezien aan het eind van de jaren zeventig, deze paradox deels verklaart. In het stuk wordt echter geen eenduidige verklaring gegeven voor de gestage afname van de populatie op de Orkney Eilanden.

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ADULT SURVIVAL RATES OF SHAG
PHALACROCORAX ARISTOTELIS, COMMON
GUILLEMOT *URIA AALGE*, RAZORBILL *ALCA*
TORDA, PUFFIN *FRATERCULA ARCTICA* AND
KITTIWAKE *RISSA TRIDACTYLA*
ON THE ISLE OF MAY 1986-96

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On the Isle of May between 1986 and 1996, the average adult survival of Shags Phalacrocorax aristotelis was 82.1%, Common Guillemots Uria aalge 95.2%, Razorbills Alca torda 90.5%, Puffins Fratercula arctica 91.6% and Kittiwakes Rissa tridactyla 88.2%. Shags, Razorbills and Puffins all had a single year of exceptionally low survival but these years did not coincide. In contrast, Kittiwake survival declined significantly over the period and there was evidence that substantial non-breeding occurred in several years. Breeding success of Kittiwakes also declined, which gives rise to concern for its future status. Given a high enough level of resighting, return rates (the proportion of birds known to be alive one year that were seen the next year) on a year-by-year basis provide a reasonable indication of relative changes in adult survival.

Harris MP., S. Wanless & P. Rothery 2000. Adult survival rates of Shag *Phalacrocorax aristotelis*, Common Guillemot *Uria aalge*, Razorbill *Alca torda*, Puffin *Fratercula arctica* and Kittiwake *Rissa tridactyla* on the Isle of May 1986-96. *Atlantic Seabirds* 2(3/4): 133-150.

INTRODUCTION

Seabirds are a conspicuous component of marine and coastal ecosystems and Britain holds internationally important populations of several species. Typically seabirds exhibit deferred maturity, high adult survival and low reproductive rates, and consequently their populations sizes tend to be relatively stable (Lack 1966). Simple models demonstrate that with this suite of demographic parameters, declines in population size are more sensitive to reductions in adult survival than to either juvenile survival or breeding success (e.g. Croxall & Rothery 1991). The effect is more pronounced in those species with the highest adult survival rates and lowest reproductive rates (in a North Atlantic context this includes the auks and Procellariiformes) compared with those having lower

adult survival rates and higher reproductive rates (e.g. gulls and cormorants). There is additional value in monitoring seabird survival since, as Cairns (1987) pointed out, relationships between seabird population parameters and the marine environment are likely to be logistic. Adult survival is least sensitive to perturbations in the environment and as such may serve to monitor changes over ranges where other parameters, such as productivity, have 'bottomed-out' at zero. For many species, adult survival also provides an opportunity to monitor changes occurring in the wintering areas whereas productivity monitors only factors acting during the summer; from a conservation perspective, adult survival rate is clearly a key parameter to measure. Thus, an aim of the UK Joint Nature Conservation Committee's (JNCC) Seabird Monitoring Programme, established in 1986, was (and is) to obtain estimates of adult survival for a range of seabirds representing different life history and foraging strategies.

Adult survival estimates can be obtained from analysis of records of birds that have been ringed as chicks with conventional metal rings and subsequently been retrapped and/or recovered (e.g. Harris *et al.* 1994). However most colony-specific survival rates (including those described in this paper) are derived from birds that are individually colour-ringed as adults and then recorded as being present or absent in each successive season. This approach is only possible at colonies where adults are accessible for ringing and can easily be visually checked. Thus, the number of sites in the UK where survival data are collected is much lower than the number where reproductive output is monitored. Moreover, in general, obtaining adult survival rates requires a considerable commitment both within and between seasons, so survival monitoring has largely been restricted to the main JNCC sites. This paper presents a detailed analysis of adult survival rates of Shag *Phalacrocorax aristotelis*, Common Guillemot *Uria aalge*, Razorbill *Alca torda*, Puffin *Fratercula arctica* and Kittiwake *Rissa tridactyla* at one of these sites, the Isle of May, between 1986 and 1996.

METHODS

The Isle of May National Nature Reserve, Firth of Forth (56°11'N, 2°33'W), is one of the largest seabird colonies in east Scotland. In 1992, half-way through this study, there were 1600 pairs of Shags, 11,500 pairs of Guillemots, 1900 pairs of Razorbills, 21,000 pairs of Puffins and 6900 pairs of Kittiwakes on the island. Each summer, starting in 1986, breeding adults of all five species were caught and individually colour-ringed. Our aim was to have at least 120-150 marked individuals of each species present in the populations at the end of each summer. This target was exceeded in all species except the Razorbill. The mean annual totals of colour-ringed individuals alive in the population were 149

Shags, 390 Guillemots, 61 Razorbills, 163 Puffins and 153 Kittiwakes. The total numbers of birds included in the analyses were: Shag (246 males, 238 females, 3 unsexed), Guillemot (302, 269, 28), Razorbill (56, 44, 20), Puffin (129, 118, 127) and Kittiwake (122, 126, 111).

Many individuals were sexed by bill or head+bill measurements (Puffin, Harris 1979; Kittiwake, Coulson *et al.* 1983), size and vocalisations (Shag, Snow 1963), pairings with birds of known sex or, in a minority of cases, by direct observations of mating birds (Guillemot and Razorbill and some individuals of other species). From 1987 onwards, thorough and widespread searches for these marked individuals were carried out on the island.

Annual survival and resighting probabilities were estimated using Cormack-Jolly-Seber models running in the program SURGE 4.2 (Pradel & Lebreton 1993). The analysis cannot separate survival and permanent emigration. However, all these species exhibit high colony fidelity once individuals have recruited into the breeding population (Lloyd & Perrins 1977; Aebischer 1995; Fairweather & Coulson 1995; Harris *et al.* 1996). The approach follows Lebreton *et al.* (1992) in fitting models to allow examination of effects of year and differences between sexes. These models increased in complexity from the simple case of constant survival and resighting probability to the most general model, which allowed identification of separate patterns of annual variation in survival and resighting for males and females (Appendix I). The goodness-of-fit of each model was measured by the Akaike Information Criterion (AIC), i.e. minus twice the log likelihood plus twice the number of estimated parameters. Low values of AIC indicate parsimonious models and provide a basis for model selection. Likelihood ratio tests were used to calculate the statistical significance of differences between years and sexes in survival and resighting probabilities.

The goodness-of-fit of the Cormack-Jolly-Seber model was examined using TESTS 2 and 3 of the program RELEASE. However, for each species the resighting rate was very high so that most of the birds were resighted in the first year after release. In this case, the component 3.Sm of TEST 3 and TEST 2 are not informative, and most of the information relating to goodness-of-fit resides in TEST 3.SR (Lebreton *et al.* 1992). The corresponding values for the five species were: Shag: $\chi^2 = 8.97$, $df = 10$, $P = 0.53$; Guillemot: $\chi^2 = 7.27$, $df = 11$, $P = 0.78$; Razorbill: $\chi^2 = 5.51$, $df = 10$, $P = 0.86$; Puffin: $\chi^2 = 12.6$, $df = 11$, $P = 0.32$; Kittiwake: $\chi^2 = 11.87$, $df = 11$, $P = 0.37$. Thus, there was no evidence that subsequent resighting depended on whether the bird had been previously resighted. Furthermore, the high resighting rate suggests that the survival estimates should be robust to heterogeneity in resighting.

Tests for trends in annual survival used a random effects model (Burnham *in press*) with a linear trend on a logistic scale plus a random year

effect, i.e. $\log [S_t/(1 - S_t)] = a + bt + \varepsilon_t$, where S_t is the actual survival for year t . The null hypothesis of no trend ($b = 0$) corresponds to a random series. This is more realistic and less restrictive than the null hypothesis of constant survival, which is actually tested by comparing models using SURGE. The variance of the random year effect is obtained from the variation in the annual survival estimates after allowing for the effect of their sampling variances and covariances. The slope (b) is estimated by generalised least squares (Burnham *in press*).

We used the samples of sexed birds to examine sex differences in survival. As in some earlier analyses (Harris & Wanless 1995, Harris *et al.* 1997), the survival of sexed individuals appeared to be consistently higher than the survival of unsexed birds, probably due to the chances of a bird being sexed increasing with the number of years that it is recorded. Consequently, in population terms we consider that the best estimates of survival are those for all individuals rather than the subset of sexed birds.

Survival between two years is referred to by the former year, i.e. 1995 refers to survival between the 1995 and 1996 breeding seasons.

RESULTS

Survival Annual survival estimates for males, females and all individuals are given in Appendix IV. Sex differences in survival were not statistically significant (Appendix III), but this says little about the possible magnitude of the effect. Estimated mean differences (males – females) over the 11 years are (95% confidence interval): Shag -0.6% (-4.2%, 3.0%), Guillemot 0.2% (-1.4%, 1.8%), Razorbill -3.0% (-7.0%, 1.0%), Puffin -0.02% (-2.4%, 2.4%) and Kittiwake -0.6% (-3.4%, 2.2%). Temporal changes in the overall estimates are shown in Figure 1. In all species, a model with annual variation in survival was among the three most parsimonious models having low AIC values (Appendix II), and differences between years were highly statistically significant (Appendix III).

Guillemot survival appeared fairly stable, varying between 92% and 99% over the study period. Shag survival was extremely low in 1993 (15% compared with an average of 89% for the other 10 years). Puffin survival was poor in 1990 using both sexes combined (79%), although the effect was less in the separate analyses for males (88%) and females (85%). Also, over the 11 years mean survival was lower in the total group than in either sex. This might be due to a bias arising from sexing birds, i.e. those birds that survive are more likely to be sexed by observations of mating, combined with the high proportion of unsexed birds. However, the results for Kittiwake, which also included many unsexed birds, revealed very similar estimates in all three analyses. Razorbill

survival was relatively low in 1995 (73% compared with a long-term average of 91%).

Figure 1. Annual estimates of the survival of adult Shag, Common Guillemot, Razorbill, Puffin and Kittiwake on the Isle of May 1986-96. For details see Appendix IV.

In contrast to the other species, survival in the Kittiwake declined significantly during the period from 99% in 1986 to 83% in 1996 (Burnham's test for trend with random year effect: $b = -0.13$, $SE = 0.036$, $t_0 = -3.64$, $P < 0.01$, SD [random effect] = 0.22). There was a suggestion that survival rates in the Razorbill and Guillemot were correlated ($r = 0.58$, $n = 11$, $P = 0.06$), but no other pairwise correlations approached statistical significance.

In all species, the survival calculated for any given year was significantly correlated with the return rate the following year, i.e. number of birds seen in the second year / number of birds seen in the first year (all $r > 0.78$, $P < 0.005$), indicating that the return rate in any year was a good indicator of survival from the previous season. The average difference between the two estimates was 1.8% ($SE = 0.7$) in the Guillemot, 4.8% ($SE = 1.5$) in the Shag, 6.0% ($SE = 0.7$) in the Kittiwake, 6.7% ($SE = 1.4$) in the Razorbill and 8.4% ($SE = 1.9$) in the Puffin.

Resighting probability Estimated resighting probabilities for males, females and all birds are given in Appendix V. Average values for all five species were high: Shag (92%), Guillemot (98%), Razorbill (91%), Puffin (88%) and Kittiwake (90%). For each species, time-dependent resighting rates and sex effects occurred in one or more of the three most parsimonious models selected by AIC. The year effect was highly statistically significant in all species except Guillemot, but differences between sexes were not statistically significant for any species (Appendix III).

DISCUSSION

Comparisons of survival rates of the various seabird species monitored on the Isle of May with those obtained elsewhere in Europe, indicated broadly similar overall values (Table 1). The Isle of May data illustrate clearly that over an 11-year period species showed very different temporal patterns in survival and, in particular, highlight the lack of interspecific concordance in years of exceptionally low survival. Hence, conditions which culminated in high mortality appeared to be species specific, so from a conservation point of view, monitoring adult survival of one species cannot be used as a proxy for other species at a particular colony, even if they are closely related and/or apparently have similar life history or feeding strategies.

Table 1. Some estimates of the long-term survival (%) of adult Shag, Guillemot, Razorbill, Puffin and Kittiwake in Europe.

Place	Years	Adult survival	Source
Shag			
Isle of May, Scotland	1986-96	82.1	This study
Isle of May, Scotland	1967-92	87.8*	Harris <i>et al.</i> 1994
Farne Islands, England	1962-70	82.8	Potts <i>et al.</i> 1980
Guillemot			
Isle of May, Scotland	1986-96	95.2	This study
Isle of May, Scotland	1982-95	94.8*	Harris <i>et al.</i> 2000
Canna, Scotland	1983-95	92.4	Harris <i>et al.</i> 2000
Colonsay, Scotland	1984-95	96.7	Harris <i>et al.</i> 2000
Hornøya, Norway	1989-96	95.8	Erikstad <i>et al.</i> 1998
Razorbill			
Isle of May, Scotland	1986-96	90.5	This study
Skomer, Wales	1972-94	90.1	Poole <i>et al.</i> 1998
Puffin			
Isle of May, Scotland	1986-96	91.6	This study
Isle of May, Scotland	1973-92	93.6*	Harris <i>et al.</i> 1997
Skomer, Wales	1972-94	91.3	Poole <i>et al.</i> 1998
Røst, Norway	1990-96	92.7	Erikstad <i>et al.</i> 1998
Hornøya, Norway	1991-96	86.0	Erikstad <i>et al.</i> 1998
Kittiwake			
Isle of May, Scotland	1986-96	88.2	This study
North Shields, England	1954-84	80.1	Aebischer & Coulson 1990
North Shields, England	1987-92	79.0	Fairweather & Coulson 1995
Skomer, Wales	1978-94	87.2	Poole <i>et al.</i> 1998
Brittany, France	1980-85	80.8	Danchin & Monnat 1992
Hornøya, Norway	1990-95	80.3	Erikstad <i>et al.</i> 1998

* Includes some of the data incorporated in the current study.

Comparison of our colony-based adult survival estimates with records of birds washed up on beaches shows that low survival years for Shags (1993), Razorbills (1995) and Puffins (1990) on the Isle of May all coincided with years when winter wrecks of these species were recorded in north and east Scotland (Harris *et al.* 1991; Bourne 1996; Swann & Butterfield 1996; Harris & Wanless 1996). Exceptionally high numbers of Guillemots were also washed up on beaches during February and March 1994 (Bourne 1994; Brindley 1994). However, most of the birds involved appeared to be immatures and survival rates of adults on the Isle of May between 1993 and 1994 did not indicate any substantial increase in mortality (Fig. 1). Guillemots were also involved in the

Razorbill wreck in the 1995-96 winter. In this case no detailed information on the age of birds found dead is available. However, judging from our survival estimates, the lowest recorded during the study, and also the fact that ten Guillemots ringed on the Isle of May that were old enough to breed were reported dead, some adults probably were involved. The magnitude of the reduction in survival of Guillemots (91.6% compared with the 11-year average of 95.2%) was, however, much less than for Razorbills (73.0% compared with 90.5%).

In a 34-year study of Kittiwakes at North Shields, Aebischer & Coulson (1990) found significantly higher survival in females (81.8%, 95% confidence interval: 80.1% - 83.4%), than in males (78.3%, 95% confidence interval: 76.4% - 80.0%). However, this difference of 3.5% is not significantly different from the Isle of May difference of 0.6% after allowing for errors in both estimates. No sex differences in survival were reported by Golet *et al.* (1998) for Kittiwakes in Alaska whereas in northern Norway Erikstad *et al.* (1998) found that, in general, males survived better than females.

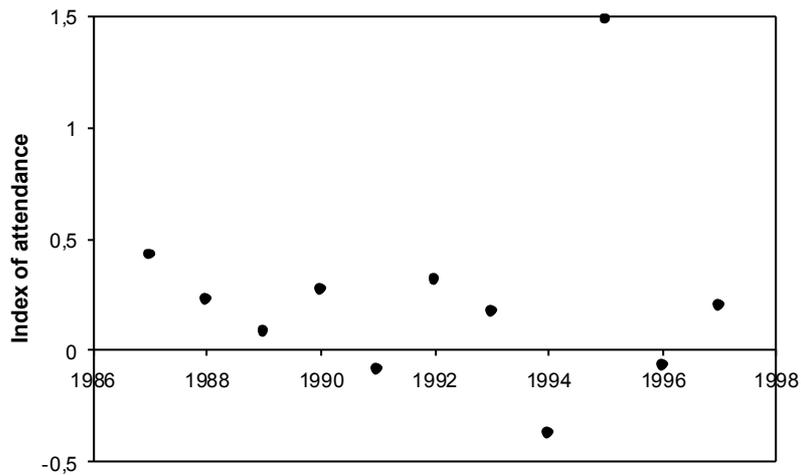


Figure 2. Annual indices of attendance of adult Kittiwakes on the Isle of May. Negative values suggest a considerable amount of non-breeding.

While results for Razorbill, Puffin, Guillemot and Shag indicate that survival rates were generally high and that poor survival years occurred only infrequently, a radically different pattern was shown by Kittiwake, survival of which declined significantly during the study. This downward trend is of particular concern because reproductive output of this species has also declined on the Isle of May over this period (Harris & Wanless 1997; personal data). The consequences of this reduction in adult survival were investigated in more detail following the approach of Ollason & Dunnet (1978). Thus an annual 'Index of Attendance' was obtained by multiplying the number of breeding pairs in one year (personal records) by the year-specific survival rate to give an expected number of pairs surviving to the next year. The difference between this value and the number of nests actually counted in June was expressed as a proportion of the counted nests to give an index which measured the attendance at the colony of first-time and experienced breeders (Figure 2). The index took positive values if the number of pairs recorded exceeded the predicted number of survivors, while negative indices indicated that observed numbers fell below the number predicted. During the study period negative values were recorded in three years (1991, 1994, and 1996), suggesting that not only did no Kittiwakes recruit to the breeding population in these seasons, but that some birds with previous breeding experience did not breed. The results of ongoing modelling studies using empirical productivity measurements confirm that substantial non-breeding by experienced adults probably occurred in these three years. It is striking that these three seasons followed winters in which one of the other seabird species had been involved in a wreck. If the non-breeding years occurred at random during 1990-96, the probability that each followed a wreck year is 0.029. However, this does not allow for the *post hoc* selection of the coincidence and suggests that non-breeding may be linked to adverse conditions occurring much earlier in the year.

In this study a very high level of effort was put into finding marked birds and this commitment was reflected in very high resighting rates for all the species. Consequently estimates of return rate i.e. the proportion of birds known to be alive in year t that were actually seen in year $t + 1$, were only slightly below the calculated survival rate which had been adjusted for resighting effort. In the context of obtaining a simple and rapid measure of annual survival, simple return rates provided a reasonable indication of relative changes in adult survival and a rapid means of identifying any serious problems.

The overall aim of the JNCC's Seabird Monitoring Programme, is to ensure that sufficient high quality data are collected, both regionally and nationally to 1) enable the conservation status of seabirds to be assessed; 2) monitor aspects of the health of the wider marine environment; and 3) provide sound advice relevant to the conservation needs of breeding seabirds. In this

context the estimation of adult survival rates is a key objective because population changes of seabirds are more sensitive to variations in this parameter than either juvenile survival or breeding success. In addition, reductions in adult survival are predicted to occur only when conditions have deteriorated markedly (Cairns 1987). The results presented in this paper for five species of seabirds breeding on the Isle of May provide evidence both of marked reductions in annual survival, presumably associated with adverse conditions during the winter, and of a sustained decline in Kittiwake survival. At present the reason for this decline is completely unknown. However, given the current concern about the potential impact of the industrial sandeel fishery on the North Sea ecosystem, particularly for small surface-feeding seabirds like Kittiwakes, in areas such as south-east Scotland where there is a large inshore fishery, establishing the cause of the decrease should be high on the conservation agenda.

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SAMENVATTING

OVERLEVING VAN VOLWASSEN KUIFAALSCHOLVER, ZEEKOET, ALK, PAPEGAADUIKER EN DRIETEENMEEUW OP ISLE OF MAY, 1986-96

Op Isle of May bedroeg de jaarlijkse overleving van volwassen vogels tussen 1986 en 1996 82.1% voor Kuifaalscholver Stictocorax [Phalacrocorax] aristotelis, 95.2% voor Zeekoet Uria aalge, 90.5% voor Alk Alca torda, 91.6% voor Papegaaiduiker Fratercula arctica en 88.2% voor Drieteenmeeuw Rissa tridactyla. Kuifaalscholvers, Alken en Papegaaiduikers kenden ieder een enkel jaar met buitengewoon hoge sterfte, maar deze jaren vielen niet samen. In tegenstelling tot deze soorten nam de jaarlijkse overleving van Drieteenmeeuwen significant af in de tijd en er waren aanwijzingen dat in sommige jaren een groot deel van de populatie geheel van broeden afzag. Ook het gemiddelde broedsucces van Drieteenmeeuwen nam af in de tijd, hetgeen aanleiding gaf tot grote zorg voor de toekomst. Het stuk gaat verder in op methodische aspecten, zoals dat bij een voldoende groot aantal ringaflezingen, de jaarlijkse terugkeer op de kolonie (het percentage vogels waarvan dus vaststaat dat ze na een jaar nog in leven zijn) op jaarbasis een goede indicatie kan geven van de adulte overleving.

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Shags (photo C.J. Camphuysen).

Appendix I. Summary of models fitted to capture-resighting data using SURGE 4.2. The Sex effect is additive on a logistic scale. A Year x Sex interaction implies a different pattern of annual survival for males and females, i.e. non-parallel changes on a logistic scale. n_p denotes the number of parameters that can be estimated.

Model notation	n_p	Model description	
		Survival	Resighting
1. (ϕ_{s^*t}, p_{s^*t})	46	Year, Sex, Year x Sex interaction	Year, Sex, Year x Sex interaction
2. (ϕ_{s+t}, p_{s^*t})	36	Year, Sex	Year, Sex, Year x Sex interaction
3. (ϕ_{s^*t}, p_{s+t})	36	Year, Sex, Year x Sex interaction	Year, Sex
4. (ϕ, p_{s^*t})	35	Year	Year, Sex, Year x Sex interaction
5. (ϕ_{s^*t}, p_t)	35	Year, Sex, Year x Sex interaction	Year
6. (ϕ_s, p_{s^*t})	26	Sex	Year, Sex, Year x Sex interaction
7. (ϕ_{s^*t}, p_s)	26	Year, Sex, Year x Sex interaction	Sex
8. (ϕ_{s+t}, p_t)	24	Year, Sex	Year
9. (ϕ, p_{s+t})	24	Year	Year, Sex
10. (ϕ, p_t)	23	Year	Year
11. (ϕ_s, p_t)	14	Sex	Year
12. (ϕ, p_s)	14	Year	Sex
13. (ϕ, p_t)	13	Constant	Year
14. (ϕ, p)	13	Year	Constant
15. (ϕ, p)	2	Constant	Constant

Appendix II. The three most parsimonious models with lowest values of the Akaike Information Criterion (AIC). Model numbering and description as in Appendix I.

Species	Model	n_p	AIC
Shag	9. (ϕ_t, p_{s+i})	24	1962.98
	10. (ϕ_t, p_t)	23	1963.23
	8. (ϕ_{s+t}, p_s)	24	1963.56
Guillemot	14. (ϕ_t, p)	13	2382.70
	12. (ϕ_t, p_s)	14	2384.40
	10. (ϕ_t, p_t)	23	2390.22
Razorbill	12. (ϕ_t, p_s)	14	724.38
	14. (ϕ_t, p)	13	725.00
	5. (ϕ_{s+t}, p_t)	35	729.08
Puffin	9. (ϕ_t, p_{s+i})	24	1191.27
	10. (ϕ_t, p_t)	23	1192.05
	8. (ϕ_{s+t}, p_s)	24	1193.49
Kittiwake	10. (ϕ_t, p_t)	23	1616.00
	9. (ϕ_t, p_{s+i})	24	1617.29
	8. (ϕ_{s+t}, p_t)	24	1617.74

*Appendix III. Summary of likelihood ratio tests for differences in survival and resighting probabilities based on comparison of models for the null hypothesis (H_0) and an alternative hypothesis (H_A). Year effects tested after allowing for a sex effect and sex effects tested after allowing for year effects. Corresponding tests ignoring year and sex effects give very similar results. See Appendix I for model description. Statistical significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, based on the chi-squared distribution with 1 and 10 degrees of freedom for sex and year effects.*

Species	Survival		Resighting	
	Year effects	Sex effects	Year effects	Sex effects
	H_0 : Model 6 vs. H_A : Model 2	H_0 : Model 4 vs. H_A : Model 2	H_0 : Model 7 vs. H_A : Model 3	H_0 : Model 5 vs. H_A : Model 3
Shag	318.22 ***	0.20	52.39 ***	0.77
Guillemot	37.02 ***	0.12	12.71	0.14
Razorbill	27.54 **	0.20	52.39 ***	0.77
Puffin	22.92 *	0.54	65.95 ***	2.79
Kittiwake	34.16 ***	0.15	25.87 **	0.51

Appendix IV Estimates of annual survival (%) based on a model with time-dependent survival and resighting probabilities. Out-of-range estimates are set to 100%. All birds includes unsexed individuals.

Shag	Estimated survival % (SE)		
	Year	Males	Females
1986	92.7 (3.0)	93.1 (2.9)	92.9 (2.1)
1987	88.3 (3.9)	86.1 (3.9)	87.2 (2.8)
1988	85.8 (4.2)	93.2 (3.6)	89.5 (2.7)
1989	92.6 (3.2)	86.0 (4.2)	88.7 (2.7)
1990	90.1 (3.7)	85.5 (4.2)	88.0 (2.7)
1991	81.9 (4.3)	83.6 (3.9)	82.5 (3.0)
1992	80.8 (4.6)	77.4 (4.8)	79.0 (3.4)
1993	14.7 (3.9)	15.1 (4.9)	14.9 (2.7)
1994	84.6 (1.0)	100.0 (-)	92.8 (5.3)
1995	96.2 (2.3)	95.4 (2.7)	95.7 (1.8)
1996	92.1 (2.8)	91.3 (2.7)	91.8 (2.2)
Mean	81.8 (6.9)	82.4 (7.0)	82.1 (6.9)

Guillemot	Estimated survival % (SE)		
	Year	Males	Females
1986	100.0 (-)	98.4 (1.1)	99.4 (0.6)
1987	92.7 (1.9)	94.0 (1.9)	92.7 (1.4)
1988	94.6 (1.7)	98.7 (0.9)	96.5 (1.0)
1989	96.4 (1.4)	97.0 (1.4)	96.7 (1.0)
1990	90.6 (2.2)	94.4 (1.8)	92.1 (1.4)
1991	96.9 (1.3)	94.3 (1.8)	95.7 (1.1)
1992	98.4 (0.8)	95.5 (1.6)	97.1 (0.9)
1993	95.7 (1.4)	93.5 (1.8)	94.8 (1.1)
1994	95.5 (1.4)	95.4 (1.5)	95.4 (1.1)
1995	92.0 (1.9)	92.6 (1.9)	91.6 (1.4)
1996	97.1 (1.3)	94.0 (1.8)	95.0 (1.1)
Mean	95.4(0.9)	95.3 (0.6)	95.2 (0.7)

Razorbill			
Year	Estimated survival % (SE)		
	Males	Females	All birds
1986	93.7 (4.8)	100 (-)	96.8 (3.1)
1987	92.1 (4.4)	93.1 (4.6)	90.4 (3.5)
1988	92.6 (4.4)	100 (-)	94.9 (2.9)
1989	79.4 (6.6)	87.1 (6.0)	82.6 (5.0)
1990	86.2 (6.3)	96.5 (3.7)	89.5 (4.3)
1991	100 (-)	93.6 (4.6)	96.0 (2.7)
1992	91.0 (5.1)	96.8 (3.2)	94.2 (3.8)
1993	90.5 (5.9)	98.1 (3.3)	93.8 (4.2)
1994	85.7 (7.3)	93.1 (6.4)	92.1 (5.5)
1995	76.4 (8.6)	69.8 (9.2)	73.0 (6.4)
1996	96.6 (4.7)	88.5 (8.4)	92.4 (6.1)
Mean	89.5 (2.1)	92.4 (2.6)	90.5 (2.1)

Puffin			
Year	Estimated survival % (SE)		
	Males	Females	All birds
1986	91.4 (5.2)	100 (-)	91.8 (3.6)
1987	98.0 (3.8)	95.3 (4.5)	92.8 (3.8)
1988	92.0 (6.6)	95.3 (4.6)	93.2 (4.2)
1989	91.0 (7.7)	91.7 (0.7)	85.3 (5.8)
1990	88.3 (4.5)	84.9 (1.6)	79.0 (3.3)
1991	95.7 (2.0)	97.7 (1.7)	96.0 (1.4)
1992	97.1 (1.6)	95.8 (2.0)	93.2 (1.7)
1993	99.1 (0.9)	98.3 (1.5)	96.4 (1.3)
1994	97.5 (1.6)	91.8 (2.8)	93.5 (1.7)
1995	93.9 (2.3)	95.7 (2.3)	93.2 (1.8)
1996	95.7 (2.1)	93.3 (2.9)	93.2 (1.8)
Mean	94.5 (1.0)	94.5 (1.2)	91.6 (1.5)

Kittiwake			
Year	Estimates survival % (SE)		
	Males	Females	All birds
1986	98.7 (1.2)	98.5 (1.4)	98.9 (0.9)
1987	90.9 (3.2)	93.3 (3.5)	91.8 (2.2)
1988	94.9 (2.7)	92.5 (3.9)	95.4 (1.8)
1989	89.1 (4.1)	85.1 (5.3)	86.3 (2.7)
1990	92.2 (4.0)	90.2 (4.9)	90.5 (2.6)
1991	90.3 (4.5)	81.8 (5.8)	85.6 (2.9)
1992	85.6 (5.2)	88.4 (4.9)	86.5 (3.0)
1993	85.3 (5.3)	89.2 (4.3)	86.8 (3.1)
1994	80.7 (6.4)	83.5 (5.0)	84.2 (3.6)
1995	79.8 (6.3)	87.4 (4.8)	80.7 (3.7)
1996	83.7 (5.5)	88.2 (4.9)	83.0 (3.6)
Mean	88.3 (1.8)	88.9 (1.4)	88.2 (1.7)

Appendix V Estimates of annual resighting probability (%) based on a model with time-dependent survival and resighting probabilities. All birds includes unsexed individuals.

Shag	Estimated resighting % (SE)			
	Year	Males	Females	All birds
1986	-	-	-	-
1987	96.8 (2.0)	95.1 (2.4)	96.0 (1.6)	96.0 (1.6)
1988	87.3 (4.2)	85.6 (4.2)	86.6 (2.9)	86.6 (2.9)
1989	89.1 (3.9)	83.3 (4.6)	86.2 (3.0)	86.2 (3.0)
1990	85.9 (4.1)	78.5 (4.8)	81.7 (3.2)	81.7 (3.2)
1991	90.7 (3.6)	94.2 (2.8)	91.8 (2.2)	91.8 (2.2)
1992	89.3 (3.7)	96.9 (2.1)	92.3 (2.1)	92.3 (2.1)
1993	100 (-)	100 (-)	100 (-)	100 (-)
1994	100 (-)	81.7 (11.8)	90.2 (6.9)	90.2 (6.9)
1995	100 (-)	79.8 (10.2)	87.9 (6.8)	87.9 (6.8)
1996	96.9 (2.1)	96.9 (2.6)	96.7 (1.5)	96.7 (1.5)
1997	98.7(1.3)	100 (-)	99.3 (0.8)	99.3 (0.8)
Mean	94.1 (1.7)	90.1 (2.5)	91.8 (1.8)	91.8 (1.8)

Guillemot	Estimated resighting % (SE)			
	Year	Males	Females	All birds
1986	-	-	-	-
1987	99.4 (0.6)	99.1 (0.8)	99.2 (0.7)	99.2 (0.7)
1988	100 (-)	98.6 (0.9)	99.3 (0.5)	99.3 (0.5)
1989	97.0 (1.3)	97.9 (1.1)	97.4 (0.9)	97.4 (0.9)
1990	98.2 (1.0)	97.3 (1.3)	97.8 (0.8)	97.8 (0.8)
1991	98.8 (0.8)	98.6 (0.9)	98.7 (0.6)	98.7 (0.6)
1992	97.8 (1.1)	97.4 (1.1)	97.7 (0.8)	97.7 (0.8)
1993	99.5 (0.6)	97.5 (1.2)	98.3 (0.7)	98.3 (0.7)
1994	98.9 (0.7)	98.8 (0.8)	98.9 (0.5)	98.9 (0.5)
1995	97.4 (1.1)	97.6 (1.1)	97.0 (0.8)	97.0 (0.8)
1996	96.3 (1.3)	98.2 (1.0)	97.3 (0.8)	97.3 (0.8)
1997	97.2 (1.2)	97.4 (1.2)	97.4 (0.8)	97.4 (0.8)
Mean	98.3 (0.4)	98.0 (0.2)	98.0 (0.2)	98.0 (0.2)

Razorbill	Estimated resighting % (SE)			
	Year	Males	Females	All birds
1986	-	-	-	-
1987	92.0 (5.3)	100 (-)	95.9 (3.9)	95.9 (3.9)
1988	97.0 (2.9)	96.2 (3.6)	96.8 (3.0)	96.8 (3.0)
1989	96.4 (3.4)	96.7 (3.2)	96.4 (2.6)	96.4 (2.6)
1990	100 (-)	88.0 (6.2)	94.1 (3.3)	94.1 (3.3)

Year	Estimated resighting % (SE)		
	Males	Females	All birds
1991	92.0 (5.3)	87.2 (6.6)	89.9 (4.3)
1992	96.9 (3.1)	86.2 (6.4)	90.6 (3.7)
1993	96.2 (3.7)	90.0 (5.2)	93.5 (3.7)
1994	91.0 (5.9)	85.7 (6.5)	86.4 (4.5)
1995	94.6 (5.1)	85.2 (7.4)	87.5 (5.6)
1996	89.5 (6.8)	94.5 (5.2)	90.9 (4.4)
1997	87.5 (8.1)	86.7 (8.8)	81.8 (6.8)
Mean	93.9 (1.1)	90.6 (1.6)	91.3 (1.4)

Year	Estimated resighting % (SE)		
	Males	Females	All birds
1986	-	-	-
1987	74.1 (8.3)	100 (-)	83.5 (4.7)
1988	73.1 (8.2)	88.3 (7.4)	76.1 (5.4)
1989	87.0 (6.8)	94.5 (5.2)	84.3 (4.8)
1990	62.3 (10.3)	87.8 (7.7)	65.5 (6.6)
1991	98.0 (1.9)	100 (-)	92.1 (2.4)
1992	100 (-)	98.7 (1.3)	95.4 (1.5)
1993	96.9 (1.5)	98.9 (1.1)	93.9 (1.6)
1994	99.0 (1.0)	96.7 (1.8)	95.4 (1.4)
1995	94.8 (2.1)	95.3 (2.2)	92.8 (1.8)
1996	98.9 (1.1)	95.0 (2.4)	96.5 (1.3)
1997	94.8 (2.5)	95.6 (2.3)	95.0 (1.6)
Mean	89.0 (4.0)	95.5 (1.3)	88.0 (3.0)

Year	Estimated resighting % (SE)		
	Males	Females	All birds
1986	-	-	-
1987	100 (-)	96.2 (2.5)	97.8 (1.2)
1988	96.9 (2.0)	89.6 (4.3)	93.8 (2.0)
1989	95.0 (2.7)	95.3 (3.5)	93.6 (2.1)
1990	85.7 (4.6)	87.5 (5.2)	87.1 (2.8)
1991	84.2 (5.1)	96.9 (3.0)	89.4 (2.6)
1992	89.3 (4.5)	100 (-)	91.5 (2.5)
1993	86.2 (5.2)	89.1 (4.9)	85.3 (3.2)
1994	90.0 (4.6)	93.5 (3.6)	86.2 (3.1)
1995	77.9 (6.8)	87.0 (4.9)	80.0 (3.8)
1996	91.3 (4.6)	87.2 (4.8)	88.2 (3.2)
1997	96.7 (3.1)	90.0 (4.7)	92.6 (2.9)
Mean	90.3 (2.0)	92.0 (1.4)	89.6 (1.5)

INTEGRATED SEABIRD MONITORING STUDIES ON THE ISLE OF CANNA, SCOTLAND 1969-99

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*An annual survey of breeding seabird numbers on the Isle of Canna, western Scotland, was established in 1969; the breeding productivity of several species is also monitored each year. Over 53 000 seabirds have been ringed since the study started and the subsequent recoveries and recaptures have been used to assess changes in survival rates and return rates to the island. Northern Fulmars *Fulmarus glacialis* have shown great fluctuations in numbers since 1973 and from 1996-99 there has been a noticeable decline accompanied by a decrease in breeding output. The percentage of study burrows occupied by Manx Shearwaters *Puffinus puffinus* began to decline in the late 1980s and breeding success has also declined; the species is now close to extinction on the island. Shags *Phalacrocorax aristotelis*, Kittiwakes *Rissa tridactyla* and Common Guillemots *Uria aalge* all showed a steady increase in numbers up to the mid 1980s, after which numbers declined or, in the case of Guillemots, stabilised until the early 1990s when further increases took place. During the periods of population growth return rates of young Shags and Guillemots were high but they subsequently declined during the period of population decline/stability and in the case of Guillemot this was linked to a significant increase in first-year recovery rates. The period of decline was also associated with a drop in Shag and Kittiwake breeding output. These changes were probably driven by fluctuations in the food supply, although increased predation might have affected Fulmar and Manx Shearwater numbers.*

Swann R.L. 2000. Integrated seabird monitoring studies on the Isle of Canna, Scotland 1969-99. *Atlantic Seabirds* 2(3/4): 151-164.

INTRODUCTION

Canna, one of the Small Isles, is situated south of Skye at the southern end of the Minch off north-west Scotland (Fig. 1). It was recently declared a Special Protection Area under the EC Birds Directive for its nationally important concentrations of breeding seabirds. Seabird monitoring began here in 1969 as part of Operation Seafarer, the first complete census of all seabird colonies in Britain and Ireland. The island has been visited every year since 1969, rendering it one of the longest continuously running seabird monitoring sites in the British Isles (Swann & Ramsay 1984). In 1986 it was adopted as one of the core monitoring sites in the UK Government's Joint Nature Conservation Committee Seabird Monitoring Programme. The aim of this paper is to describe the long-term population trends of five breeding seabird species on the island and to explore the possible causes of the observed trends.

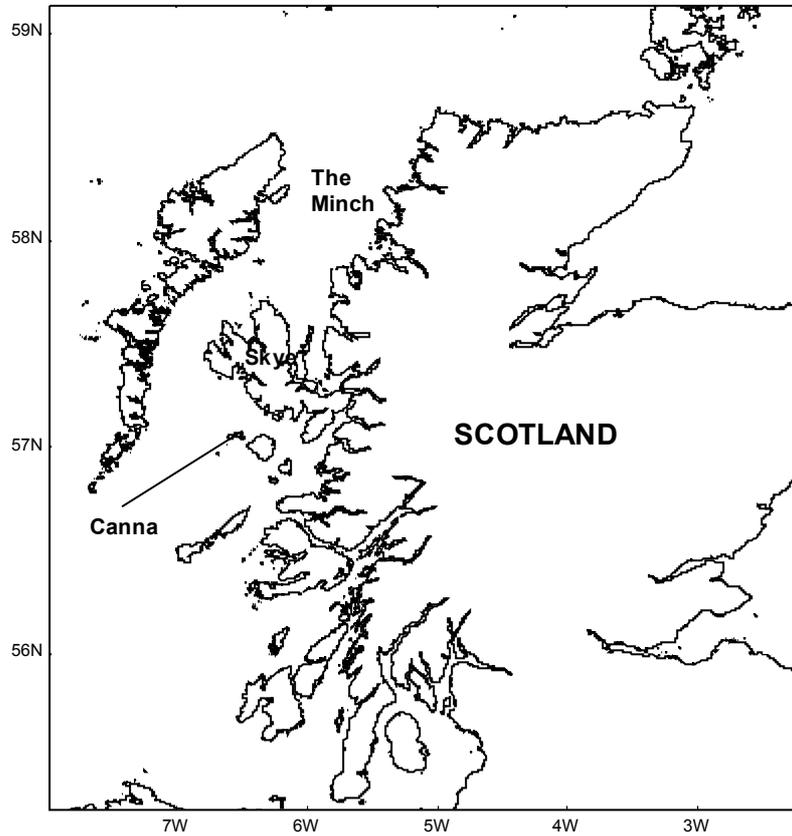


Figure 1. Map of Scotland showing location of Canna.

METHODS

With the exception of Puffins *Fratercula arctica*, all breeding seabirds (including Northern Fulmar *Fulmarus glacialis*, Shag *Phalacrocorax aristotelis*, Kittiwake *Rissa tridactyla*, Common Guillemots *Uria aalge* and Manx Shearwaters *Puffinus puffinus*) are counted each year using standard techniques (see Swann 1997). For some species whole island counts before 1974 are not available. Breeding productivity is also monitored for Manx Shearwater, Fulmar, Shag and Kittiwake; see Swann (1997) for methodology. A major ringing programme is also undertaken annually; as far as possible this involves

the same number of people visiting the same sites each year for the same amount of time to ensure constant effort. To date, around 53 000 seabirds having been ringed on the island since 1969. Recoveries and retraps resulting from this ringing programme have been used to compute survival rates and rates of return to the colony, particularly for auks (Swann & Ramsay 1983; Swann *et al.* 1989; Harris *et al.* 2000) and Shags (Swann *et al.* 1994). These analyses are reviewed and updated in this paper.

RESULTS

Population changes The mean number of Fulmars breeding annually since 1973 is 541 apparently occupied sites (AOS). Numbers appear to have remained fairly stable but have fluctuated considerably in that time (Fig. 2). Since 1995 there has been a particularly pronounced decline in numbers.

The Canna Manx Shearwater colony was first counted in 1973 and 1974 (Swann and Ramsay 1976) and from the 1974 total of 1303 occupied burrows it was estimated that the island population was in the order of 1000-1500 pairs. The occupancy of 60 randomly positioned observation burrows remained fairly constant until 1984 (Swann 1995). It was assumed that for the second complete census of all seabird colonies in Britain and Ireland, the Seabird Colony Register (1985-87) that no major change in numbers had occurred and the population was estimated at >1000 pairs in 1985. It was only in the 1990s that the sudden decline in burrow occupancy rates (Fig. 6) indicated that the breeding population had greatly declined. In late May 1997, using a tape playback method, all known colonies on the island were surveyed (Swann 1997); only 33 calling birds responded from 952 burrows. Using the correction factor of 1.98 given by Brooke (1978) this suggested a total of only 65 occupied burrows. A similar survey repeated in 1999 failed to elicit a response from any burrow.

From the mid-1970s the number of Shags nesting on Canna rose steadily to reach a peak of 1753 nests in 1984, after which numbers decreased to a low of 697 nests in 1993 and then increased to 1140 in 1998, followed by another reduction in 1999 (Fig. 3). Extremely poor weather caused large decreases in 1976 and 1986.

Kittiwake numbers on Canna increased to reach a peak of 991 nests in 1982 (Fig. 4). Numbers then slowly and erratically decreased to 693 nests in 1994, since when there has been a rapid increase to a new peak of 1252 nests in 1999.

Guillemot numbers in Canna study plots at the main colonies on the north of the island increased rapidly up to 823 'nests' in 1983. There then followed a period of relative stability to 1993, after which there is some

evidence of a modest increase, the scale of which has not been fully documented (Fig. 5). The years 1997-99 were characterised by mild winters leading to earlier than average egg laying, which also coincided with slightly later than usual field visits to the study colonies. Consequently, many birds had left the colonies, resulting in underestimated counts. Observations showed that breeding birds had occupied many new sites, suggesting an increase in total numbers in the colony.

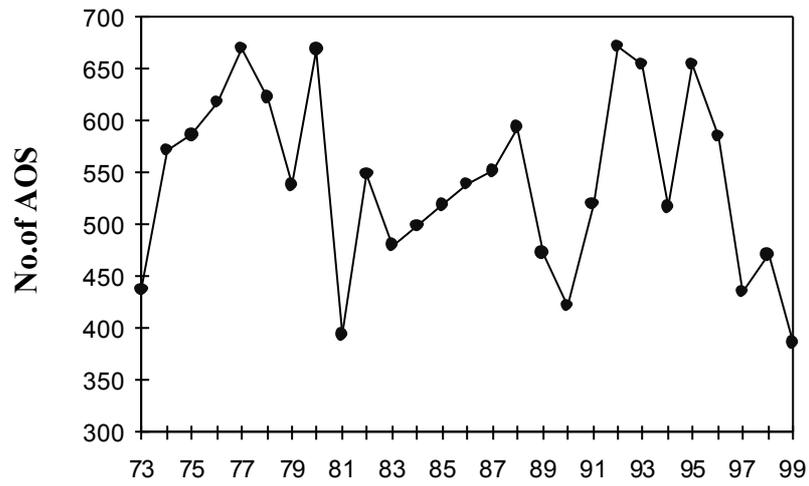


Figure 2. Number of apparently occupied Northern Fulmar sites on Canna 1973-99.

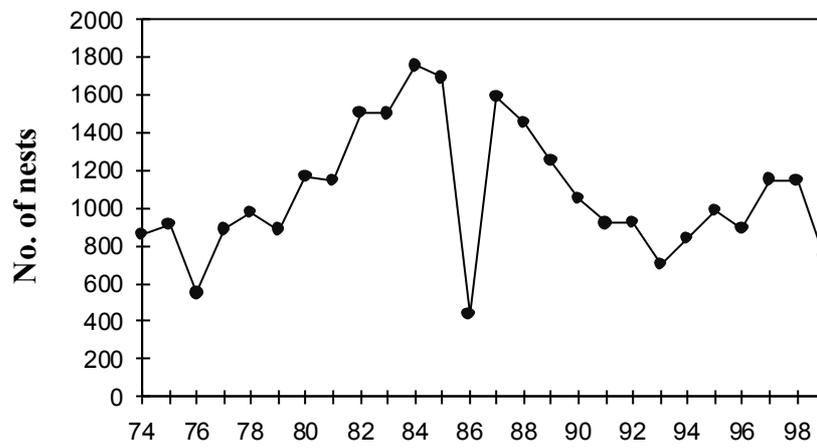


Figure 3. Number of Shag nests on Canna 1974-99

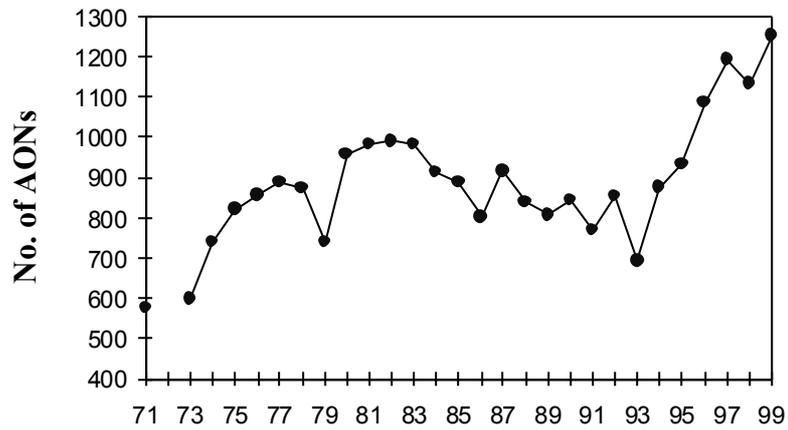


Figure 4. Number of apparently occupied Kittiwake nests (AONs) on Canna 1971-99.

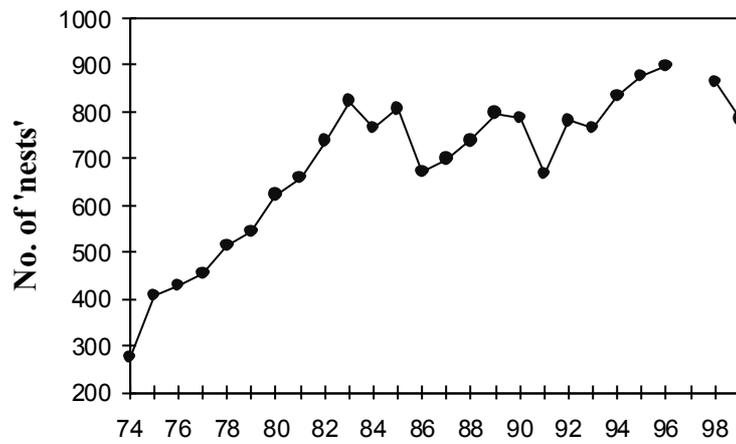


Figure 5. Number of Common Guillemot 'nests' in sample plots on the North cliffs of Canna 1974-99.

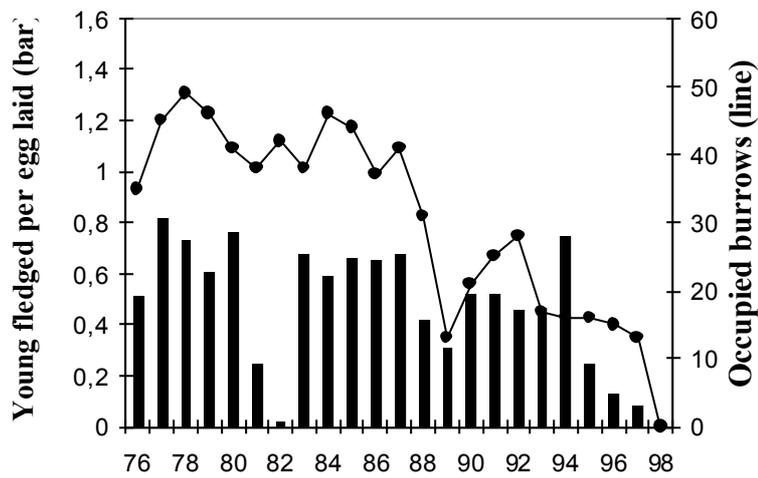


Figure 6. Number of study burrows occupied by Manx Shearwaters on Canna and breeding success as measured by number of eggs in occupied study burrows that produced a large chick.

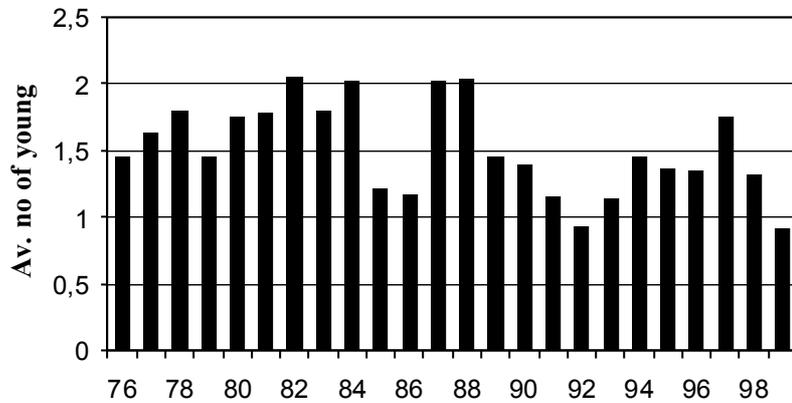


Figure 7. Average number of young Shags fledged per study nest on Canna 1977-99.

Breeding productivity Between 1986 and 1995 the combined number of monitored Fulmar AOS at two study plots varied annually from 42-50 while productivity varied from 0.31 to 0.54 chicks fledged per site per year. There was no significant difference between the two study plots. Since 1995 the number of AOS has declined (to 35 in 1998) and breeding productivity has also declined sharply with only 0.22-0.27 chicks fledged per site. This decline from a 1986-95 mean of 0.37 chicks per AOS to the 1996-98 mean of 0.24 is significant $\chi^2_1 = 5.038, P < 0.05$).

Breeding productivity of Manx Shearwaters up to 1987 was usually around or greater than 0.6 young per pair laying an egg (Fig. 6). Exceptions in 1976, 1981 and 1982 were linked to rat predation, which was counteracted by scattering the rat poison Warfarin throughout the colony in each of the following springs (Swann 1995). After success in 1987, however, the number of occupied study burrows and breeding success began to decline.

Shags are currently monitored at two colonies on the island. Productivity was relatively high between 1977 and 1984 (Fig. 7). It then fluctuated reaching a low in 1992, since when it has improved during a period of rapid colony growth but has not yet returned to the levels of the 1980s.

Kittiwake productivity has been highly variable since monitoring began in 1986 (Table 1), varying from almost total failure in 1988 to 1.21 chicks fledged per AON in 1990. Breeding success was particularly poor between 1986 and 1989, during a period of decline in breeding numbers on the island (Fig. 4).

Table 1. Kittiwake productivity in Sanday study colony 1986-99.

Brood size	86	87	88	89	90	91	92	93	94	95	96	97	98	99
0	99	170	224	109	44	61	86	92	78	89	77	90	113	106
1	70	64	7	52	52	53	79	63	70	69	98	92	101	111
2	18	46	0	22	76	57	30	26	51	61	62	81	44	21
3	0	0	0	0	2	0	1	0	0	3	0	3	2	0
Av*	0.57	0.56	0.03	0.52	1.21	0.98	0.72	0.63	0.86	0.90	0.94	0.99	0.75	0.64

* average number of chicks fledged per AON (apparently occupied nest)

Ringling recovery rates, survival rates and rates of return to the colony

Ringling studies have been used to monitor recovery rates, survival rates and rates of return to the colony of Shags and Guillemots. The recovery rate of Shags ringed on Canna has declined throughout the entire study period (Table 2). This fall in recovery rate was associated with significant changes in recovery circumstances, with far fewer birds being shot and netted than was previously the case (Table 3). This has been associated with significant changes in the location and timing of recoveries, with far fewer ringed Shags now being

reported from the Western Isles and far fewer in winter (Swann *et al.* 1994). These changes are all associated, as large numbers of Shags were formerly shot in the Western Isles in winter for food. There have also been changes in return rates to the colony (Table 4). These were highest during the period 1974-81, then declined and have risen again since 1987. There is no significant correlation between retrap rates (by age 7) and first year recovery rates of different annual cohorts of Shags ringed as chicks on Canna ($r_s = 0.081$, $n = 19$, $P > 0.05$).

Table 2. Recovery rate of Shag chicks ringed on Canna 1961-98.

	no.ringed	no. (%) recovered in first year	no. (%) recovered in 2nd and 3rd year
1961-70	617	45 (7.3%)	12 (1.9%)
1971-81	4005	125 (3.1%)	26 (0.6%)
1982-91	4758	83 (1.7%)	26 (0.6%)
1992-98	3660	43 (1.2%)	4 (0.2%)*

* based on 2310 chicks ringed 1992-96.

Note: Most Shags enter the breeding population in third year of life. Chicks ringed 1971-81 entered the colony during a period of rapid growth, those ringed 1982-91 during a period of decline, and those from 1992 onward during another period of growth. For those ringed 1961-70 there are no details of colony size.

Table 3. Recovery circumstances of Canna Shags in their first year of life.

Reported as:	1961-70	1971-81	1982-91	1992-98
found dead	25	78	67	42
shot	13	30	1	0
netted	7	16	12	1
oiled	0	1	4	0

Table 4. Return rates of Shag chicks to Canna by ages 3-7.

year	no. ringed	no. retrapped	% retrapped in colony
1974-81	3556	132	3.7%
1982-86	2045	33	1.6%
1987-91	2713	58	2.1%

Note: Those ringed in 1974-81 would, by age 7, have been returning during a period of colony growth, those ringed 1982-86 during a period of decline and those ringed 1987 onwards during another period of colony growth.

The recovery rate of Guillemot chicks ringed on Canna in their first year of life has shown major changes over time (Table 5). The recovery rate until 1979 was 1.1%, then significantly increased by more than double between 1980-85 ($\chi^2_1 = 26.14$, $P < 0.001$), since when it has significantly declined, with the 0.8% recovery rate of chicks ringed 1991-98 not significantly different from the 1974-79 cohorts ($\chi^2_1 = 0.017$, $P > 0.05$). The recovery rates of birds in their second and third years were significantly lower in the period 1986-96 compared with 1974-85 ($\chi^2_2 = 26.493$, $P < 0.001$).

These long term changes in the mortality rates of young birds will influence recruitment rates and therefore breeding numbers on Canna. Most Guillemots do not start breeding till at least 5 years old (Harris *et al.* 1994). Return rates were calculated using the percentages of each cohort of ringed chicks retrapped in the colony by age 5. These return rates are highly variable and show significant changes with time (Table 6). The return rate of the 1979-89 cohorts was significantly lower than the 1974-78 cohorts ($\chi^2_1 = 26.952$, $P < 0.001$) and the 1990-94 cohorts ($\chi^2_1 = 15.681$, $P < 0.001$). Return rates also show a negative correlation with recovery rate ($r_s = -0.59$, $n = 20$, $P < 0.01$; Fig. 8). Changes in survival rates of breeding adults will also affect breeding numbers on the island. Mortality rates of breeding adults on Canna based on mark-recapture analysis indicate an average survival rate of known breeders caught between 1983 and 1995 of 92.4% (SE = 0.9; Harris *et al.* 2000). No significant variation in survival rates between years was detected over the study period.

Table 5. Recovery rates of Canna Common Guillemot chicks in their first to third year of life.

	no. ringed	recovered 1st year	Recovered 2nd year	recovered 3rd year
1974-79	2936	32 1.1%	16 0.5%	14 0.5%
1980-85	9518	266 2.8%	52 0.5%	30 0.3%
1986-90	10103	181 1.8%	34 0.3%	15 0.1%
1991-98	16138	128 0.8%	44 0.3%*	16 0.1%**

* based on 15 291 ringed in 1991-97, ** based on 12 659 ringed in 1991-96

Table 6. Return rates of Common Guillemot chicks to Canna by age 5 according to time period ringed.

Time period	no. chicks ringed	no. chicks returned by age 5 to colony	% returned
1974-78	2688	68	2.5
1979-89	17433	213	1.2
1990-94	11631	210	1.8

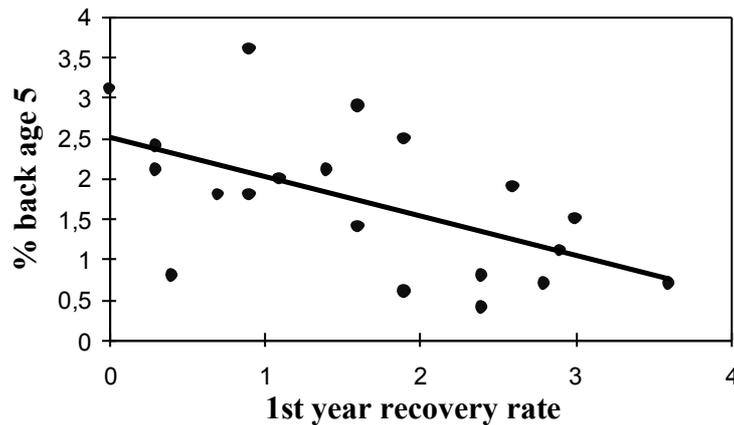


Figure 8. Percentage of young Common Guillemots returning to Canna by age 5 compared to the first-year recovery rate of that cohort.

DISCUSSION

Until 1996, Fulmar numbers and breeding success fluctuated from year to year showing no significant trends. Since 1996, however, there has been a marked decline in both numbers and breeding success. This decline in numbers may be linked to increased predation from large raptors, which bred successfully on the island in 1997 and 1998. As a result of this predation, many Fulmars now nest well back under boulders, which renders them more difficult to count. Increased rates of predation by both avian and mammalian predators are also suspected for the reduction in breeding success.

There is circumstantial evidence, based on partly eaten adults and chicks (Swann 1997), that the decline in breeding success and the total number of Manx Shearwaters breeding on Canna is related to an increase in numbers of mammalian predators, probably cats and rats, possibly due to milder winters. Both species have been seen more frequently on the island in the 1990s than previously. Despite an attempt by the National Trust for Scotland from 1998 to control these predators, the evidence from the 1999 census suggests it is too little, too late and that the Manx Shearwater colony on the island faces extinction.

Shag numbers have shown great changes on Canna since monitoring began. Between 1974 and 1984, there was a period of rapid colony growth, ostensibly driven by above average breeding success and also, despite apparently high recovery rates of first-year birds, very high return rates to the colonies. Until 1981, reporting rates of dead first-year birds were greatly inflated by the numbers being shot and reported in the southern islands of the Western Isles. Following protection by the 1981 Wildlife and Countryside Act, the reporting rate declined markedly, although the possibility remains that birds continued to be shot and not reported. From 1984-93, breeding numbers decreased to early 1970s levels. This was characterised by a decline in breeding success and a fall in return rates of young Shags to Canna to breed, indicating that conditions were much less favourable for Shags during that period. Since 1993, breeding success and return rates to the colony have once again improved and this has led to the colony increasing in numbers. Shags on Canna feed on a variety of fish but mainly sandeels and gadoids and there is some evidence that the more sandeels in the diet then the higher the breeding success (Swann *et al.* 1991). It is likely that the amount of fish available to Shags in the Sea of the Hebrides affects breeding success and first year survival rates, which in turn affects recruitment rates and therefore colony growth.

The Kittiwake population on Canna also exhibited a period of growth up to the early 1980s followed by a decline. During the period of decline breeding success was very low. Since 1993, the colony has grown rapidly and there has been a sustained improvement in breeding success. This is perhaps linked with an increase in the availability of sandeels around Canna in recent summers (Swann 1997).

Guillemot numbers steadily increased to peak in 1983 and then stabilised somewhat. The period of population growth was associated with low first-year recovery rates. There is a strong negative correlation between first-year recovery rate and return rates to their Canna breeding colonies of birds up to age 5. During the period of relative stability there was a marked increase in first-year recovery rates and a decline in return rates. As recovery rates have fallen since 1986 return rates have improved and there has been some evidence of colony growth again since 1993 (see Results). It appears that survival rates of birds in their first year of life regulates colony growth, as recovery rates of birds in their second and third years of life are not correlated with changes in colony size and no significant changes have been found in the survival rates of breeding adults.

By continued low level population monitoring it has been possible to track the fortunes of seabirds on Canna and to explain some of these changes by also monitoring breeding performance and diets; the ringing and retrapping programme enables survival rates to be monitored. Several species show a

similar pattern of success with a rise in numbers to the early 1980s, followed by a decline to the early 1990s and followed by another rise. Periods of population decline were generally associated with poorer breeding productivity and lower return rates of chicks to the colony and these are probably linked to the availability of fish. In more recent years increased predation levels are beginning to affect the numbers and breeding success of some species on the island.

ACKNOWLEDGEMENTS

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SAMENVATTING

BROEDVOGELMONITORING VAN ZEEVOGELS OP HET EILAND CANNA, SCHOTLAND, 1969-99

In 1969 werd op het eiland Canna (Small Isles, West Schotland) een jaarlijkse telling van de broedende zeevogels ingesteld. Daarnaast werd het broedsucces van verschillende soorten elk jaar gemeten. Sinds het begin van het onderzoek op Canna werden ruim 53 000 zeevogels geringsd en de talrijke tenngmeldingen en terugvangsten zijn gebruikt om de jaarlijkse overleving en terugkeer van zeevogels op Canna in te schatten. De populatie Noordse Stormvogels Fulmarus glacialis schommelde sinds 1973. Sinds 1996 is sprake van een sterke achteruitgang gepaard gaand met een vermindering van de broedresultaten. In de jaren zeventig werd de populatie van de Noordse Pijlstormvogel Puffinus puffinus op 1000-1500 paar geschat. Eind jaren tachtig begon het aantal bezette nestholten af te nemen, evenals het broedsucces. De soort staat op Canna nu op de rand van uitsterven. Kuifaalscholwers Phalacrocorax aristotelis, Drieteenmeeuwen Rissa tridactyla en Zeekoeten Uria aalge namen alle gestaag toe tot aan het midden van de jaren tachtig, waarna de aantallen weer zijn afgenomen of, zoals in het geval van de Zeekoet, zijn gestabiliseerd. Vanaf begin jaren negentig vertoonden de populaties van de drie soorten weer een toename. Bij zowel de Kuifaalscholwer als de Zeekoet keerden veel jongen naar het eiland terug in perioden dat de populatie groeide, maar het aantal rekruten (tenngkerende jongen als broedvogels in de eigen populatie) liep sterk terug in perioden dat het bestand stabiliseerde of afnam. Gedurende de periode van populatie-afname was het broedsucces bij zowel Kuifaalscholwer als Drieteenmeeuw laag. Aangenomen wordt dat de lokale voedselomstandigheden in die jaren onvoldoende waren. Bij Noordse Pijlstormvogel en in mindere mate Noordse Stormvogel heeft een toegenomen predatie in ieder geval een negatieve invloed op de broedresultaten.

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STATUS, PRODUCTIVITY, MOVEMENTS AND
MORTALITY OF GREAT CORMORANTS
PHALACROCORAX CARBO BREEDING IN
CAITHNESS, SCOTLAND: A STUDY OF A
DECLINING POPULATION

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*This paper describes the results of a study of the Great Cormorant *Phalacrocorax carbo* breeding in Caithness, Scotland, with particular emphasis on its recent status and distribution based on annual surveys carried out between 1992 and 1998, its breeding productivity, diet, mortality and movements. Breeding numbers declined from 842 apparently occupied nests in 1969, to c. 230 in 1985-93, and 90-180 in 1994-98, an overall reduction of 80-90% in 30 years. Over the same period, the number of colonies declined from 12 to five. Breeding productivity varied between 2.18 and 3.20 chicks per successful nest, which is within the normal range of variation found elsewhere in Britain. Nestling diet consisted mainly of sandeels *Ammodytes* spp., according with earlier studies in Caithness. Ringing recoveries show the main winter quarters to be the coasts of the Moray Firth and the rivers that flow into it; fewer numbers move further south along the east coast of Scotland, mainly to the Firths of Tay and Forth but some birds reach southern England. A secondary route extends down the Great Glen (or possibly across the Central Lowlands) to wintering areas along the west coast of Scotland and north-west England, with a few birds crossing to Northern Ireland. Ringing recoveries also show that adult Cormorants from Caithness suffer rather higher mortality rates than birds elsewhere in Britain. The reasons for the declines in breeding numbers are discussed, the most likely cause being reduced adult survival, possibly caused by excessive shooting, although emigration of some birds to other areas to breed is a potential contributory factor.*

Budworth, D., M. Canham, H. Clark, B. Hughes & R.M. Sellers. 2000. Status, productivity, movements and mortality of Great Cormorants *Phalacrocorax Carbo* breeding in Caithness, Scotland: A study of a declining population. *Atlantic Seabirds* 2(3/4): 165-180.

INTRODUCTION

The western European breeding population of the Great Cormorant *Phalacrocorax carbo* has grown dramatically over the past 30 or so years. The

increases have been greatest in Denmark, Germany and the Netherlands, where growth rates of up to 30% *per annum* have been sustained more or less throughout this period (van Eerden & Gregersen 1995). The position in Britain is more complicated, with increases being apparent in some areas, little net change in others and decreases in yet others (Kirby & Sellers 1997). The main areas exhibiting decline are all in Scotland and include the Western Isles, the Northern Isles and Caithness. The population in Caithness declined by 72% between the first national survey of Britain's seabirds in 1969/70 (Operation Seafarer) and the second in 1985-87 (the Seabird Colony Register), the largest decline in any part of Britain between these dates (Lloyd *et al.* 1991). This paper reports the results of an investigation into the causes of these changes, drawing on surveys of breeding Cormorants and study of their productivity in Caithness between 1992 and 1998, and on information on movements and mortality based on ringing recoveries.

METHODS

Complete surveys of all Cormorant breeding colonies in Caithness were undertaken in the seven breeding seasons 1992-98 inclusive; the locations of the colonies are shown in Fig. 1. Counts were made from the shore below the colony at Ord Point (southern section), from the cliff top above the colonies at Ord Point (northern section), Neuk Mhor and Ceann Leathad, and from mainland cliffs at the remainder of the extant colonies, all of which are on stacks 30-50 m offshore. All colonies were counted in late June, when nestlings were mostly well grown, and, if possible, in late May or early June when the nests contained hatching eggs or small young. The Cormorant has a fairly protracted breeding season and although some nests will undoubtedly have failed before the counts were made, others may not have been started. Our counts are likely to be slight underestimates of the actual number of apparently occupied nests (AON), but this will be true of all earlier counts so all counts should be directly comparable. In order to check that no colonies had been overlooked, an aerial survey was undertaken on 25 June 1992. All cliffs from Duncansby Head to the Ord of Caithness, as well as Stroma, Dunnet Head and Holborn Head on the north coast, were checked. The aerial survey also showed that all colonies could be counted accurately from land (i.e. there were no nests on the seaward sides of stacks that could not be seen from land). Historical counts were obtained from the Cormorant Colony Register (Sellers 1997), which draws on the Seabird Colony Register, the results of the Cormorant Breeding Colony Survey (Sellers 1996, 1997) and other published records.

Figure 1. Distribution of Great Cormorant breeding colonies in Caithness: 1 Holborn Head, 2 Dunnet Head, 3 Stroma, 4 Noss Head North, 5 Noss Head East, 6 Stack O'Brough, 7 Stack of Ulbster, 8 Stack of Mid-Clyth, 9 Stacks of Occumster, 10 Ceann Leathad, 11 Traigh Bhuidhe, 12 Berriedale Ness, 13 Traigh Muidhe Cleite, 14 Neuk Mhor, 15 Ord Point. Filled symbols are colonies used in the 1990s; open symbols show sites at which Cormorants have bred in the past.

Information on movements and mortality was derived from ringing recoveries of birds marked as nestlings at the Ceann Leathad and Ord Point colonies at which ringing has been carried out regularly for the past 15 years, and intermittently before that. A list of ringing recoveries from these two colonies was obtained from the British Trust for Ornithology and updated from our records, yielding a total sample of 189 recoveries for analysis. In view of the comparatively limited ringing recovery data we estimated survival rates by fairly crude methods. Breeding performance was determined from observations of nest contents at the end of June or in early July, approximately 1-2 weeks before most nestlings fledge. Information on food was derived from chick regurgitates collected during ringing operations at Ceann Leathad and Ord Point in June 1993, each food bolus being classified with respect to principal fish type.

RESULTS

Distribution of colonies The distribution of all 15 sites known to have been used by breeding Cormorants in Caithness is shown in Fig.1. Two of these, Stroma and Stack of Mid-Clyth, appear not to have been used within the past 40 years or so, but the remaining 13 sites have all been used at one time or another since the late 1960s. A total of 12 colonies was found during the first complete survey in 1969, falling to five by the time of the most recent survey in 1998; only three colonies (Stack of Ulbster, Ceann Leathad and Ord Point) were occupied in each of the 11 complete surveys carried out to date. Of the sites no longer in use, breeding seems to have ceased at four in the 1970s (Dunnet Head, the two Noss Head colonies and Berriedale Ness) and at one in the 1980s (Traigh Muidhe Cleite); the situation at two others (Holborn Head and Traigh Bhuidhe) is unclear but neither seems to have been in regular use within the past 30 years. Nearly all the colonies are (or were) located on the east coast, the main concentration being on the cliffs in the south of the county between Ceann Leathad and the county boundary near Ord Point. Seven of the colonies are (or were) on the tops of stacks, and the remainder on broad rocky ledges or rocky promontories on or associated with cliffs.

Breeding numbers A summary of the 11 complete surveys of Cormorants breeding in Caithness is shown in Table 1. Since the first survey in 1969 the number of breeding birds has fallen from about 842 AON to a current figure of 90-180 AON, a decrease of 80-90%. The trends in the counts at individual colonies have mostly been negative (Fig. 2), although the timing of the downturn varies, and at Ceann Leathad increased somewhat in the 1970s to a peak in 1993.

Figure 2. Trends in breeding numbers at selected Caithness Great Cormorant colonies.

Table 1. Summary of censuses of Great Cormorants breeding in Caithness, 1969-98.

Colony	1969	1977	1985	1986	1992	1993	1994	1995	1996	1997	1998
Holborn Head	5	-	1	-	0	0	-	-	-	-	-
Dunnet Head	2	-	-	-	0	-	-	-	-	-	-
Noss Head North	20	0	-	-	0	-	-	-	-	-	-
Noss Head East	31	0	-	-	0	-	-	-	-	-	-
Stack O' Brough	22	16	0	0	9	8	7	9	2	0	0
Stack of Ulbster	20	14	25	16	11	14	3	4	2	7	5
Stacks of Occumster	46	51	28	32	41	23	0	15	0	20	21
Ceann Leathad	22	34	52	52	56	58	32	40	35	37	52
Traigh Bhuidhe	0	0	-	5	0	0	0	0	0	0	0
Berriedale Ness	22 ^a	0	0	-	0	0	0	0	0	0	0
Traigh Muidhe Cleite	152-172	46	0	-	0	0	0	0	0	-	-
Neuk Mhor	117-137	42	^b	62	18	33	8	15	17	0	4
Ord Point	338-388	81	129	65	95	97	42	94	38	58	93
Total	797-887 ^c	284	235	232	230	233	92	177	94	122	175
No. Colonies	12	7	6	6	6	6	5	6	5	4	5

^a colony listed as Berriedale-Traigh Bhuidhe (see text also)

^b included in total for Ord Point

^c mean 842 AON; however, Lloyd *et al.* (1991) give the total as 825 AON.

'0' indicates that the colony was checked and no birds were present

'-' indicates that the colony was not checked but it was assumed that no birds were present

Table 2. Breeding productivity estimates (brood size 1, 2, 3, or 4) for Caithness Great Cormorants.

Colony	Year	1	2	3	4	<i>n</i>	mean	SE
Ord Point	1993	1	2	10	4	17	3.00	0.19
	1994	2	4	4	0	10	2.20	0.25
	1995	0	1	3	0	4	2.75	0.25
	1998	1	7	10	1	19	2.58	0.16
Neuk Mhor	1993	0	1	7	3	11	3.19	0.18
Ceann Leathad	1993	1	13	17	10	41	2.88	0.28
	1994	1	2	2	0	5	2.20	0.37
	1995	3	13	7	0	23	2.17	0.14
	1996	2	3	9	1	15	2.60	0.21
	1997	3	9	6	1	19	2.26	0.18
	1998	2	17	18	4	41	2.58	0.12
Stacks of Occumster	1993	0	4	5	1	10	2.70	0.21
	1995	1	5	4	1	11	2.45	0.25
Stack of Ulbster	1993	0	1	5	2	8	3.13	0.23
	1994	0	0	3	0	3	3.00	0
Stack O' Brough	1993	0	1	3	1	5	3.00	0.32
	1994	0	4	0	1	5	2.40	0.40
All combined		17	87	113	30	247	2.63	0.05

^aBased mainly on broods 4-5 weeks of age

Breeding performance Estimates of the numbers of nestlings fledged per active nest were made for all occupied colonies in 1993 and at selected colonies thereafter (Table 2). Brood sizes varied between 1 and 4, with broods of 3 and 2 being the most common. No broods of 5 chicks were recorded. The mean number of chicks per successful pair varied between 2.17 and 3.19, typical of the values found elsewhere in Britain (Sellers & Hughes 1996; Sellers 1997; Newson *et al.* 1997).

No systematic estimates of breeding performance have previously been made in Caithness, but from the data quoted by MacKay (1987) a figure of 2.64 chicks per successful brood ($n = 45$) can be calculated for the Ceann Leathad colony in 1987, and from brood sizes recorded during ringing at Ord Point from 1962-72, a figure of 2.17 chicks per successful nest ($n = 14$) can be determined. We have, in addition, consulted a number of ringers and counters who have visited Caithness Cormorant colonies during the past 30 years or so, none of whom recorded unusual numbers of chicks per nest. On the basis of this, albeit anecdotal, evidence we conclude that Caithness Cormorants have shown no substantial change in breeding productivity in the recent past.

Diet During ringing at the Ceann Leathad and Ord Point colonies in June 1993 we collected 24 chick regurgitates. Of these, 22 (92%) contained only sandeels *Ammodytes* spp. and two (8%) flatfish *Pleuronectidae*. Similar results were obtained by MacKay (1987) at Ceann Leathad in 1987 and by Mills (1969) at Ord Point in the 1960s; we conclude that there is no evidence for a recent marked change in the diet of nestling Cormorants in Caithness.

Movements About 40% of recoveries ($n = 189$) were from within 100 km of the colonies, 70% within 200 km of the colonies, and 85% within 300 km. However, a small number of birds travelled much greater distances (Fig. 3), the longest movement recorded being 1133 km (a bird recovered in Finistère, France). Most recoveries were on the east coast of Scotland especially around the Moray Firth (40% of recoveries) and between Rattray Head and the Scottish Borders (33%; Fig. 4). Around 8% moved further south along the east coast into England but there were only a few recoveries south of the River Humber. A further 16% of birds possibly followed a different route south along the Great Glen to winter quarters along the shores of Argyll and around the Firth of Clyde, with lesser numbers further south along the Solway Firth, north-west England and Northern Ireland (although it is possible that some of these may have taken an alternative route via the Firth of Tay or the Firth of Forth, the Central Lowlands and the Clyde Estuary). In addition, a small number of recoveries (3%) were from north of Caithness - three from Orkney, one from North Rona and one from Foula, Shetland.

Figure 3. Frequency distribution of distances moved by Great Cormorants ringed in Caithness.

Most birds were recovered from the coast, but about 23% were recovered inland, mostly on rivers rather than still water (Table 3). Slightly more first-year birds were found inland after 1980 than earlier, consistent with the national trend (Kirby *et al.* 1995; Wernham *et al.* 1999), but the differences were not statistically significant ($\chi^2_1 = 0.75, P > 0.05$).

There were no obvious differences between age groups in terms of distance moved from the natal colony, but birds may have been recovered closer to breeding colonies in the summer than in the winter (Table 4).

Birds begin to move away from the breeding colonies very shortly after the young fledge and by the time the first ringing recoveries appear approximately 50 days after ringing the majority have departed. It is also worth remarking that there are very few recoveries in Caithness itself and none after mid-September (about 75 days after ringing). A few Cormorants do occur in Caithness in the non-breeding season and from the seven available recoveries it seems that these originate mainly from Orkney (2 recoveries), Shetland (4) and north-west Sutherland (1).

Causes of death and mortality rates The recovery data provide only limited information on the cause of death; most birds were reported simply as 'found dead' (Table 5). The other main categories were shot, oiled and caught in fishing nets. The percentage of recoveries reported as shot decreased from 24% before 1980 to 7% thereafter. These results are similar to those found for birds from the Lamb, Firth of Forth (Summers & Laing 1990).

Figure 4. Geographical distribution of ringing recoveries of Great Cormorants ringed in Caithness (not shown, one recovery in Finistère, France). Arrow indicates location of natal colonies.

Table 3. Recovery habitat of Great Cormorants ringed in Caithness.

Age (yr)	No. (%) of recoveries			
	<i>n</i>	coast	inland (river)	inland (still water)
1 (ringed before 1980)	38	31 (82%)	5 (13%)	2 (5%)
1 (ringed after 1980)	87	63 (72%)	18 (21%)	6 (7%)
2	21	17 (81%)	3 (14%)	1 (5%)
>3	43	35 (81%)	3 (7%)	5 (12%)
all	189	146 (77%)	29 (15%)	14 (7%)

Table 4. Median distances (km) moved by Caithness Great Cormorants of different ages.

Season of recovery	Median distance moved		
	1 yr	2 yr	>3 yr
winter (Nov -Feb)	170 (n = 55)	200 (n = 8)	223 (n = 19)
summer (May-Jun)	80 (n = 14)	140 (n = 7)	46 (n = 8)

Table 5. Recovery circumstances of Great Cormorants ringed in Caithness.

Cause of death	Age (yr)			Total	%
	1	2	>3		
<i>Birds ringed before 1980 (n = 65)</i>					
unknown	22	6	14	42	65
shot	11	4	0	15	23
nets	5	0	0	5	8
oil	0	0	3	3	5
<i>Birds ringed after 1980 (n = 124)</i>					
unknown	66	10	20	96	77
shot	9	1	1	11	9
nets	7	0	0	7	6
oil	1	0	0	1	1
tangled	1	0	1	2	2
hit wires	1	0	0	1	1
field record	2	0	4	6	5

Second-year and older birds were found more or less evenly throughout the year, but first-years were more likely to be recovered in the autumn or winter (September to February inclusive; Fig. 5). Most birds were recovered in their first year of life with much smaller numbers in each year thereafter (Fig. 6). The oldest bird recovered was 11 years old. Survival rates based on recoveries of birds ringed before 1988 (i.e. including all those years for which there are unlikely to be any further recoveries) were rather crudely estimated as 0.39 per annum for first-year birds, 0.68 p.a. for second-years and 0.64 p.a. for third-year and older birds.

Figure 5. Timing of recovery of Great Cormorants ringed in Caithness in relation to age.

Figure 6. Age on recovery of Great Cormorants ringed as nestlings in Caithness.

DISCUSSION

Status and distribution Cormorant breeding colonies in Caithness are confined primarily to the east coast. There have been occasional records of breeding on the north coast, but they have not bred here regularly in the recent past. In part, this reflects the shortage of breeding sites, but it is more likely to be due to a

shortage also of suitable feeding areas. Cormorants typically are bottom feeders and seek food in water up to about 10 m deep (Debout *et al.* 1995), and there is very little shallow water along the shores of the Pentland Firth. Even on the east coast there is comparatively little shallow water and this probably accounts for the fact that, except for the cluster of colonies south of Ceann Leathad, colonies are mostly small and distributed well apart. The waters off east Caithness are, however, very productive and support some of the largest concentrations of seabirds in Britain (Lloyd *et al.* 1991). There are no suitable breeding areas south of Caithness on the east coast of Sutherland and this is probably why there is a cluster of colonies in the south of the county and why the most southerly one (Ord Point) is the largest, birds here exploiting the shores of the Moray Firth.

Between 1969 and 1998 the number of birds breeding in Caithness decreased by 79% and the number of colonies by 58%. This is the largest decline suffered by any Cormorant population anywhere in Britain over this period and has occurred against a generally increasing population throughout continental Europe. The only other areas showing decreases are Shetland (54% between 1969 and 1995), the Western Isles (33% between 1969 and 1985) and to a lesser extent Orkney (3% between 1969 and 1985, but 31% between 1985 and 1994). It is perhaps significant that the declines are clustered geographically, and likely that some common factor is responsible. The differences in the timing of the declines should be noted, however.

With the exception of the Herring Gull *Larus argentatus* and the Puffin *Fratercula arctica*, other seabirds breeding in Caithness either have not shown such marked declines or have not declined at all. Thus, between the Operation Seafarer survey in 1969/70 and the Seabird Colony Register survey in 1985-87 the following changes were recorded: Fulmar *Fulmarus glacialis* (+25%), Shag *P. aristotelis* (+71%), Herring Gull (-55%), Great Black-backed Gull *L. marinus* (+11%), Kittiwake *Rissa tridactyla* (-15%), Guillemot *Uria aalge* (+158%), Razorbill *Alca torda* (+1%), Black Guillemot *Cepphus grylle* (+161%) and Puffin (-94%). Whatever is causing Cormorant numbers to decrease is not obviously affecting all these other species, and is probably specific to the Cormorant. As many of these species rely on sandeels during the breeding season, it seems reasonable to conclude that the breeding season food supply is not the factor responsible, unless there is some feature of the way in which Cormorants seek their food (say as in-shore or bottom feeders) that renders them more susceptible to changes in sandeel abundance than these other species. However, the available evidence does not suggest that Caithness Cormorants have experienced any significant difficulty in provisioning chicks with sandeels over the past 30 years, or that food has limited breeding success to any significant extent.

Causes of population decline The decline in the Cormorant population in Caithness has occurred progressively over the past three decades, though apparently somewhat faster between 1969 and 1977 (66% in 8 years) than between 1977 and 1998 (38% in 20 years). The decline has thus not been caused by one catastrophic event, but rather is the result of a chronic problem continuing over several decades. Detailed monitoring over the past seven breeding seasons shows that the population has fluctuated quite markedly between years. In particular, 1994 and 1996 seem to have been difficult seasons for the Cormorant, and probably represent responses to cold springs which are known to depress breeding numbers and in the most extreme cases can result in relatively high numbers of birds failing to produce any young (e.g. Debout *et al.* 1995; Sellers & Hughes 1996). By themselves, however, such events are unlikely to account for the changes recorded. Rather, the long-term decline of Cormorants in Caithness appears fundamentally to be a failure of recruitment to the breeding population to match adult mortality. There are five ways in which this might have happened:

- a) low breeding productivity;
- b) low immature survival;
- c) low adult survival;
- d) increase in the age of first breeding; and
- e) increased emigration.

Breeding success in Caithness has generally been good and the productivity data in Table 2 are within the range of variation seen elsewhere in Britain (1.8 - 3.2) and mostly in the upper half of this range (see Debout *et al.* 1995; Sellers & Hughes 1996; Newson *et al.* 1997). Low breeding productivity may therefore be eliminated as a likely cause of population decline in Caithness.

Our crudely estimated survival rates for first and second-year Caithness birds are quite high but are similar to those found elsewhere in Britain (e.g. Wernham *et al.* 1999). Adult survival, however, is around 20% lower (Sellers 1989), at a rate that is sufficient to account for the population declines observed. Furthermore Wernham *et al.* (1999) suggest that first and second-year Scottish birds may also have lower survival than those in other parts of Britain. The reasons for this are unknown but shooting is an obvious possibility. There is no doubt that Cormorants continue to be subject to a considerable degree of both legal and illegal shooting in Scotland, especially on the salmon rivers of north-east Scotland, one of the wintering areas used by Caithness Cormorants (Kirby *et al.* 1996). In the period 1984-87 an estimated 936-2884 Cormorants, around 20% of the population, were shot in Scotland (Carss 1994) so shooting could well be a cause of excess mortality leading to breeding population decline in Caithness. Shooting probably affects all age groups, and the fact that we have been unable to determine any discernible effect on the mortality rates of

immatures might reflect the fact that these already suffer relatively high mortality from other causes.

Usually, age at first breeding might be deferred in increasing rather than decreasing population (Furness & Monaghan 1987; Newton 1998), so it is unlikely that age of first breeding is increasing in Caithness Cormorants. Although we have no direct information on the age of first breeding in Caithness, third year and older birds are recovered nearer the natal colony in the breeding season than first or second year birds, suggesting that most birds breed around three years of age. However, it should be noted that in a population initially at equilibrium, an increase in the average age of first breeding by one year would cause the population to decline by an amount approximately equivalent to the adult mortality rate. Thus, the declines observed in Caithness could be accounted for by average increases of only a few months in the age of first breeding; such changes would be difficult to detect.

If emigration were the cause of population decline in Caithness over the past 30 years then around 660 pairs must have moved from Caithness to breeding colonies elsewhere in the winter range. In fact there are few such colonies, the chief ones being North Sutor at the mouth of to the Cromarty Firth in Easter Ross and the colonies of the Firth of Forth (Car Craig, Haystack, Inchkeith, Eyebroughty, the Lamb, Craigleith), at the southern end of the main part of the winter range. At all of these colonies there has been a growth in numbers, although at North Sutor there has been a decline in the past few years (Swann 1997). However, the increase at North Sutor (*c.*200 pairs at most) can at best account for only a part of the Caithness declines and the same is true of those in the Firth of Forth colonies (*c.*250 pairs). Furthermore, if substantial numbers of birds had moved to breed at these distant colonies, one would expect there to have been recoveries close by in the breeding season. In fact there have been none in the Firth of Forth nor on the west coast of Scotland, and only three in Easter Ross. What causes birds to shift between colonies is uncertain but generally British Cormorants show high natal site fidelity. Cases are known, however, of birds moving to breed in colonies other than the natal colony, usually to the next nearest colony, but movements up to about 400 km are on record (R.M. Sellers, unpublished results). We note also that movements of this kind could explain both the differences in the timing of the declines at individual colonies in Caithness and the difference in the timing of declines across northern Scotland. However, emigration cannot by itself account for all the declines observed.

In summary, we tentatively suggest the most likely cause of the decline in the Caithness breeding population of the Cormorant is excess adult mortality, perhaps as a consequence of control measures such as shooting in the wintering areas. Emigration to breed in colonies outside Caithness may be a contributory

factor, but cannot solely account for the declines. An explanation based on an increase in the age of first breeding seems unlikely but cannot be eliminated. Breeding productivity is similar to that found elsewhere in Britain and is not a credible causative factor for the declines.

These conclusions account for the observation that it is Cormorants and not other seabirds that are declining and that the declines pertain to Cormorant populations across the north of Scotland and not just Caithness. They also suggest that an obvious action to halt the population declines might be to limit the number of licences granted to control Cormorants in the northern half of Scotland or to restrict licences, say, to the shooting of first-year birds. There is clearly scope for further work on these declining populations. In particular, breeding numbers and other population parameters should be monitored carefully and there needs to be continued and concerted ringing effort in order to monitor mortality and help in the development of a better understanding of the factors that control Cormorant populations. Further research on emigration and the relationship between breeding numbers and food supply would also be merited.

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SAMENVATTING

STATUS, REPRODUCTIE, TREKBEWEGINGEN EN STERFTE VAN AALSCHOLVERS *PHALACROCORAX CARBO* BROEDEND IN CAITHNESS, SCHOTLAND: EEN STUDIE VAN EEN AFNEMENDE POPULATIE

*Dit artikel beschrijft de resultaten van een onderzoek naar de Aalscholvers *Phalacrocorax carbo* die broeden in Caithness, Schotland, met bijzondere aandacht voor de recente afname van het aantal broedparen en de jaarlijkse veranderingen in de verspreiding in de jaren 1992-98, de jongenproductie, de voedselkeuze, jaarlijkse sterfte en trekbewegingen. De broedpopulatie nam af van 842 'kennelijk bezette nesten' in 1969 tot ongeveer 230 in 1985-93 en 90-180 in 1994-98; een totale afname van 80-90% over een periode van 30 jaren. In dezelfde jaren nam het aantal kolonies af van 12 tot vijf. De productiviteit varieerde van 2.18 tot 3.20 kuikens per succesvol nest, hetgeen als 'normaal' beschouwd mag worden in vergelijking met de resultaten van Aalscholvers die elders op de Britse Eilanden nestelen. De jongen kregen hoofdzakelijk zandspiering *Ammodytes* spp. aangevoerd, hetgeen ook al gebleken was uit eerder onderzoek in Caithness. Ringmeldingen laten zien dat de meeste Aalscholvers uit deze provincie overwinteren langs de kust van de Moray Firth (NO Schotland) en langs de rivieren die daarin uitmonden. Kleinere aantallen overwinterden verder*

zuidelijk langs de Schotse kust, zoals in de Firth of Tay en in de Firth of Forth. Enkele exemplaren bleken naar Zuid-Engeland door te trekken. Een tweede trekroute, klaarblijkelijk van geringere betekenis, bracht Aalscholvers via de Great Glen (of misschien dwars over de centrale laaglanden) naar overwinteringsgebieden langs de westkust van Schotland en naar Noordwest-Engeland, met een enkeling die zo Noord-Ierland bereikte. Ringmeldingen wezen uit dat adulte vogels van Caithness te lijden hadden van een aanmerkelijk hogere sterfte dan vogels van andere kolonies op de Britse Eilanden. De mogelijke oorzaken voor de achteruitgang worden bediscussieerd, met intensieve jacht en bestrijding als meest voor de hand liggende oorzaak van de lage overlevingskansen. De afname kan ook door emigratie veroorzaakt zijn.

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BRUCE CAMPBELL'S ISLANDS REVISITED: CHANGES IN THE SEABIRDS OF LOCH SUNART AFTER HALF A CENTURY

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In 1950 and 1998, counts were made of nine bird species breeding on 31 small islands in Lochs Sunart and Teacuis, sealochs that are typical of many in western Scotland. During this 48-year period, some species that were once characteristic breeding birds of islands in sealochs decreased greatly or disappeared; these included Common Eider, Common Gull, Common Tern and Black Guillemot. Numbers of Heron and Oystercatcher changed very little. Herring Gull and Great Black-backed Gull numbers both increased greatly; in recent years these increases took place at a single island at the mouth of Loch Sunart where they bred successfully. The increase in Herring Gull numbers was contrary to a wider regional trend in the period 1989-98. Records from the two lochs of seabird numbers, breeding success and causes of failure during 1990-98 suggest that two quite separate influences were at work. Excess feed from six large salmon farms may have played an important part in the local increase of large gulls, and the arrival and spread of American Mink caused the breeding failures of terns and Common Gulls that accompanied their declines. The decreases reflect changes during 1987-98 over a larger area of west Scotland, where five gull and tern species each declined by c. 40-50% following widespread annual breeding failures that are known to have been caused by mink.

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INTRODUCTION

From Kintyre northwards, the coastline of west Scotland is dissected by numerous sealochs, firths and sounds. Breeding seabirds and seaducks are absent from most of the mainland coast but nest at high densities on many small islands. The principal breeding species of the islands in these enclosed areas of sea are Black-headed Gull *Larus ridibundus*, Common Gull *L. canus*, Herring Gull *L. argentatus*, Lesser Black-backed Gull *L. fuscus**, Great Black-backed Gull *L. marinus*, Common Tern *Sterna hirundo* and Arctic Tern *S. paradisaea*, with smaller numbers of Shag *Phalacrocorax aristotelis*, Oystercatcher *Haematopus ostralegus*, Common Eider *Somateria mollissima*, Red-breasted Merganser *Mergus serrator* and Black Guillemot *Cepphus grylle*. Individual colonies tend to be small, with

* Known as *Lanus graelsii* on the Dutch list

totals of all species almost always under 1000 pairs and usually under 200 pairs. However, the small islands are numerous and together such colonies may hold

Figure 1. Map of Loch Sunart and Loch Teacuis. Fish farms active on 20 July 1998 are denoted by large dots and former sites, now fallow, as large circles. There are 22 islands or groups (a total of 33 islands): 1. Eilean a'Mhuirich (Strontian); 2. Glas Eilean (Laudale); 3. Eilean Mor (Laudale); 4. Eilean an t'Sionnaich; 5. Sgeir Mhali; 6. Garbh Eilean; 7. Eilean a'Chuilinn; 8. Eilean mo Shlinneag; 9. Sgeir an t'Seangain; 10. Dun Ghallain (4 islets); 11. Eilean nam Gillean; 12. Eilean an Fheidh; 13. Risga (1 large, 2 very small islets); 14. Glenborrodale islets (5 islets); 15. Eilean Mor (Glenmore); 16. Caolas Rahuaidh (3 islets) Loch Teacuis (Teacuis Narrows); 17. Eilean nan Gabhar, Loch Teacuis; 18. Eilean nan Eildean, Loch Teacuis; 19. Carna; 20. Eilean na Droma Buidhe; 21. Oronsay; and 22. Sligneach Mor.

significant totals. For example, in 1987, one-eighth of the Common Terns of the British Isles bred along this coast between Mallaig and West Loch Tarbert, a linear distance of only 130 km (Craik, unpublished records).

Because such colonies are numerous, and sometimes inaccessible, survey coverage in north-west Scotland was incomplete in both of the national seabird surveys to date, Operation Seafarer in 1969-70 (Cramp *et al.* 1974) and the Seabird Colony Register census of 1985-87 (Lloyd *et al.* 1991). Many islands that held *Larus* gull colonies in 1998 were not visited in one or both of these surveys. Thus,

it is difficult to obtain reliable regional totals from these surveys against which to monitor subsequent changes.

However, in 1950 and 1952 Bruce Campbell counted seabirds breeding in Loch Sunart and its smaller offshoot Loch Teacuis. Together these two sealochs hold 33 islands or islets in 22 groups (Fig. 1). He wrote two popular accounts of the area and its birdlife (Campbell 1966, 1979). Some years before his death in 1993 (Perrins 1993), Campbell sent Craik his unpublished typewritten records. This typescript shows that in 1950-52 he visited every one of the small islands in these sealochs and recorded the numbers and species of all the breeding birds that he encountered. This therefore allows us to identify with confidence any changes that have occurred in the interim of almost half a century. To make the most of this opportunity, Craik repeated his survey in 1998.

In the mid-twentieth century, American Mink *Mustela vison* ("mink" hereafter) were bred in captivity on fur farms over much of Britain. Some that escaped bred in the wild and gave rise to the feral population that now lives along the coasts and rivers of much of Britain (Dunstone 1993). The approximate timing of the spread of mink in this part of west Scotland was reported by Craik (1995). The main spread in the Sunart-Teacuis area seems to have taken place in about 1985-90.

METHODS

Early visits Campbell visited the islands on 21-22 May 1950 and on 9 and 11 June 1952. He made less extensive visits in 1921, 1926 and on 28 May 1968, 31 May 1971 and 14-15 June 1982. The account below has been compiled from the 1950 records, supplemented where necessary by 1952 records. For example, his 1950 visit was too early for tern clutches, so tern counts are reported for 1952; all the Common Gull colonies were counted in 1950 except Eilean na Droma Buidhe, which was noted as occupied in 1950 but counted in 1952. His records from the other years are not used below unless they give useful insights into long-term changes. In order to obtain breeding numbers Campbell usually counted clutches and empty nests, but sometimes made estimates from adult numbers. For simplicity these have not normally been distinguished below. (In 1950, for example, he made 14 island counts of clutches/nests and five of adults for gulls, and 13 and four respectively for Oystercatchers). Black Guillemots were counted as adults on the sea when the counter was ashore, and separately as clutches/nests. All 33 islands were visited except the two largest, Carna and Oronsay, which are essentially mainland in character.

Recent visits On 7 and 8 June 1998, the 31 islands were searched for nests as thoroughly as possible, using the presence of adult birds as a guide to nesting areas.

Breeding species were identified and their clutches and well-formed empty nests were counted. Sometimes these had already been depredated. The predator species was identified whenever possible by searching the entire island for eggshell or cached eggs. In deep cover (dense vegetation, or cavities in or under rocks) eggshell was often found bearing 1 mm diameter holes, circular or nearly so; these were sometimes in pairs *c.* 10 mm apart, caused by left and right canine teeth applied equally, but more usually there was a single hole, sometimes with a slight mark 10 mm away, caused by unequal application of canine teeth on a curved shell. The presence on islands of hidden eggshell with such single or paired holes was taken as diagnostic of predation by mink, since no similar predator was likely to reach these islands.

Predation by European Otter *Lutra lutra* ("otter") on young seabirds is often revealed by an absence of plucking, by discarded groups of unplucked, unchewed wings, head and legs (one group per chick) and by faeces recognisable by their sweet smell, placed in several prominent positions and consisting of down, feathers and bones. Mink faeces are less easy to find, often deposited in large quantities in a single unobtrusive site, under cover or in a gully, depression or den mouth. Predation by gulls or crows *Corvus* spp. of eggs is usually recognisable by small triangular holes left by the bill tip, often on both sides of the egg. Predation by gulls of chicks, if eaten whole, is sometimes recognised by pellets in the vicinity; or, if not eaten whole, by the twisted, wrenched appearance of the uneaten carcass, some of the feathered skin often being turned inside out over the carcass. Predation by raptors (not detected in this study) is indicated by intense plucking and by "V"-marks in the carina (the "keel" of the sternum). Care should be taken to distinguish such "V"-marks from the superficially similar comb-like appearance of the carina of adult gulls found in mink dens. The numerous fine parallel rips and tears in the carina are caused by repeated dragging and scraping by mink canines. There was no evidence of rats *Rattus* spp. or cats *Felis* spp. on these islands.

A second visit was made to each island on 20 July 1998 to measure breeding success of gulls and terns. Numbers fledged were estimated as the number of large chicks (Walsh *et al.* 1995) or, just after fledging, as the number of flying young settled on the sea and on intertidal rocks (Craik 2000). Whole-colony breeding failure was indicated by absence of adults and young, and confirmed by absence of signs, such as trampled vegetation, faeces or pellets indicative of recent breeding activity. Where such failure was encountered, prey remains were sought as outlined above.

During 1990-98, annual counts were made on the islands Sligneach Mor and Eilean nan Gabhar, respectively the main Herring Gull and Common Tern colonies. In some of these years, a Common Gull colony on the islets at Caolas Rahuaidh (Teacuis narrows) was also surveyed. Occasional pre-1998 observations or records at other islands are also indicated below.

RESULTS

In 1950-52 the two lochs held a rich fauna of breeding seabirds and shorebirds, scattered between the many small islands. By far the most numerous were Common Terns and Common Gulls, with smaller numbers of Herring and Lesser Black-backed Gulls, Oystercatchers and Black Guillemots (Table 1).

Table 1. Numbers of breeding pairs on islands in Lochs Sunart and Teacuis 1950/52 and 1998.

	1950/52	1998
Grey Heron	16	15
Eider	14	0
Oystercatcher	24	22
Common Gull	150	20
Lesser Black-backed Gull	88	1
Herring Gull	64	223
Great Black-backed Gull	3	23
Common Tern	330	2
Black Guillemot*	18	0

*Numbers of Black Guillemots are individual adults

In 1998, except for one colony, the islands held few breeding seabirds. The exception was the island of Sligneach Mor, at the mouth of Loch Sunart, which held a healthy, medium-sized colony of Herring and Great Black-backed Gulls from which many young fledged. Much smaller numbers of a variety of species, mainly Common Gulls and Oystercatchers, were found distributed among other islands. Already on the first visit (7-8 June), most of the Common Gulls and some of the Oystercatchers had empty nests with nearby eggshell indicating predation, often by mink. No other predators were identified in 1998. No Common Gulls fledged anywhere and, apart from at Sligneach Mor, Herring Gulls fledged only two young at one site.

Total breeding numbers of each species in 1950/52 and in 1998 are given in Table 1 and Appendices I-II. Between these two counts, five species had declined greatly in numbers or had been extirpated (Eider, Common Gull, Lesser Black-backed Gull, Common Tern and Black Guillemot). Herring Gulls and Great Black-backed Gulls had increased considerably, but in 1998 both were almost entirely confined to Sligneach Mor. Numbers of Grey Herons *Ardea cinerea* and Oystercatchers showed little change.

Common Gull Survey counts of Common Gulls are presented in Appendix I. In 1950 at least 150 pairs Common Gulls bred on 13 islands. The largest colony, with

52 pairs, was at Glas Eilean and the second largest, with 38 pairs, was at Dun Ghallain. In 1998 there were 20 pairs on seven islands, an 87% decrease, the largest colony being only seven pairs at Sgeir an t'Seangain; there were none at Glas Eilean and one pair at Dun Ghallain.

In 1998 all 20 pairs of Common Gulls failed to fledge young. No small chicks were seen on 7-8 June, when some would have been expected. Thirteen nests and territories were empty (the adults still present) and seven held eggs (three with 3 eggs, one with 2 eggs and three with 1 egg); the small eggs and clutches suggested that some were replacements. Shells at six of the seven islands indicated egg predation and at five of these mink were identified as the predator. In July there was no evidence of young anywhere and most territories were deserted.

From 1990-98, small numbers of Common Gulls (less than ten pairs annually) breeding with terns on Eilean nan Gabhar failed almost annually, as did the terns (Table 4) and probably for the same reason. The colony of Common Gulls at Teacuis narrows declined from 34 pairs in 1987 and 23 pairs in 1989 to 2-3 pairs in 1994-98, and produced few or no fledged young after 1990.

Lesser Black-backed Gull Survey counts of Lesser Black-backed Gulls are presented in Appendix I. In 1950, Campbell recorded at least 88 pairs of Lesser Black-backs breeding at two sites, "50+" pairs at Risga and 38 clutches at Garbh Eilean. In 1982 he reported "tens" and "low tens" of pairs respectively at these two sites. In 1998 the species was absent from both sites. A single pair attempted to breed at Eilean na Droma Buidhe but failed to fledge young; shells of Common Gull and Common Tern there suggested mink predation.

Herring Gull Survey counts of Herring Gulls are presented in Appendix I. In 1950, 64 pairs of Herring Gulls were breeding at three sites in the Lochs. The largest colony, with 41 pairs, was on Sligneach Mor, and there were 15 pairs at Risga and eight at Garbh Eilean. In 1998 there were 223 pairs at five sites, a 3.5 fold increase; almost all of these (216 or 97%) were at Sligneach Mor.

In 1982 Campbell recorded "low tens" of pairs at Garbh Eilean, "tens" at Risga, and "some tens" of pairs at Sligneach Mor. Craik found the latter two sites occupied by similar numbers in 1983-87, although clutches were not counted. In the early 1990s Risga had been abandoned and Garbh Eilean was reduced to very few pairs, and both remained so up to and including 1998. After this decline, breeding numbers increased greatly on Sligneach Mor (Table 2).

In 1998 Sligneach Mor was almost the only colony where young of any seabird species fledged, with 323 of the Lochs' total of 325 young Herring Gulls (99%). Observations during ringing expeditions suggested a very similar pattern in 1994-97.

Table 2. Herring Gulls breeding at Sligneach Mor, Loch Sunart, 1950-98.

Year	No. pairs	No. fledged
1950	41	?
1952	40-60	?
1982	“some tens”	?
1990	50	Some
1991	67	2
1992	75	Some
1993	87	>50
1994	115	>50
1995	128	100
1996	142	150
1997	151	190
1998	216	323

Table 3. Great Black-backed Gulls breeding at Sligneach Mor, Loch Sunart, 1989-98.

Year	No. pairs	No. fledged
1989	present	Some
1990	5	Some
1991	5	0
1992	5-7	Some
1993	4+	Some
1994	7	8
1995	8	10
1996	11	10-15
1997	16	10-15
1998	22	20

Great Black-backed Gull Survey counts of Great Black-backed Gulls are presented in Appendix I. In 1950, Campbell found only three pairs of Great Black-backs, with single pairs at Sligneach Mor, Risga and Eilean a'Chuilinn. In 1998 there were 23 pairs in total, 22 on Sligneach Mor and one on Eilean mo Shlinneag. As with the Herring Gull, the increase of this species at Sligneach Mor occurred mainly from 1994-98 (Table 3). In 1998, Sligneach Mor was the only colony where Great Black-backed young fledged (20 young).

Thus, the rapid increase in numbers of both these large gull species from 1994-98 took place at one site, where they bred successfully almost annually. Their high productivity there contrasted strongly with the mink-related failure of terns and Common Gulls elsewhere in Sunart-Teacuis, and also with several similar

colonies of Herring Gulls elsewhere in west Scotland that failed in 1997 and 1998 because of mink predation on eggs and young (Craik 1998). The landowner at Ardslignish, the headland adjacent to Sligneach Mor, controlled mink on the mainland with specially trained dogs in 1996-97 and reported the area mink-free in 1998 (E. Macdonald, pers. comm.), which may account for the recent breeding success of large gulls there.

The increase in large gulls is also probably related to the development of fish farming in the Lochs. Farming of salmon and trout in cages in sealochs of the Scottish west coast began around 1970. The industry expanded greatly over the next two decades and by 1990 most sealochs were occupied to capacity. Fish farm cage sites in Lochs Sunart and Teacuis in July 1998 are shown in Fig. 1 but no figures are available on the annual production of these.

Common Tern Survey counts of Common Terns are presented in Appendix I. Campbell recorded terns breeding at Eilean nan Gabhar on a visit in 1921. His visit in 1950 was too early (22 May) for terns to have started breeding, although on that date he recorded 42 adults at the two small island sites in Loch Teacuis (Eilean nan Gabhar and the islets at Teacuis Narrows). In June 1952, in his first comprehensive count of terns, he recorded a total in Lochs Sunart and Teacuis of *c.* 330 pairs at ten sites. These were all or mostly Common Terns, but a few Arctic Terns may have been included. In 1952, at least seven sites held colonies of ten or more pairs and the largest colony, with 107 clutches and "150+ pairs", was at Sligneach Mor. In 1982, he counted 61 pairs (55 clutches and six nests) at Eilean nan Gabhar.

In 1998, only two pairs of Common Terns attempted to breed at Lochs Sunart and Teacuis, one at Eilean nan Gabhar and one at Eilean na Droma Buidhe. Both were unsuccessful, and mink was identified as egg predators at both sites.

In 1987-98 Common Terns bred in significant numbers (more than ten pairs) at only two sites: Eilean nan Gabhar and at Sligneach Mor. Single or a few pairs may have bred elsewhere in some years. Breeding at Eilean nan Gabhar was successful only in two of the nine years 1990-98 (Table 4); egg predation by mink accompanied breeding failure in most years. End-of-season predation of large tern chicks here by otter was identified in 1992. Causes of failures of terns at Sligneach Mor (Table 5) could not be identified, although predation of tern chicks by large gulls was recorded in 1987. Terns ceased to breed there after 1993 when Herring Gull numbers increased and occupied most of the two tern areas.

Grey Heron Survey counts of Grey Herons are presented in Appendix II. In 1950, Campbell counted 16 nests (of which 13 held eggs or young) at Eilean nan Eildean. In June 1998, Craik saw none there but recorded 15 nests at Eilean a'Chuilinn. Breeding success was not measured in 1998 since most of the nests were out of reach.

Table 4. Common Terns breeding at Eilean nan Gabhar, Loch Teacuis, 1990-98.

Year	No. pairs	No. fledged young	Notes
1990	27	34	No mammalian predation
1991	83	0	Mink
1992	74	80	One mink was killed 150 m away
1993	31	0	Mink
1994	0	0	
1995	12	0	Mink
1996	35	0	Mink suspected
1997	5	0	Mink
1998	1	0	Mink

Table 5. Common Terns breeding at Sligneach Mor, Loch Sunart, 1952-98.

Year	No. pairs	No. fledged young	Notes
1952	150	?	
1987	129	?	plus 1 pair Arctic Terns
1988	28	0	
1989	41	0	
1990	27	0	
1991	0	0	
1992	56	47	
1993	158	0-2	
1994-98	0	0	excluded by increased number of Herring Gulls

Common Eider Survey counts of Eiders are presented in Appendix II. Although not ideal, census methods used for Eider in 1998 followed those used in 1950/1952 in order that comparisons could be made. In contrast to some Scottish sealochs, such as Loch Fyne and Loch Etive, Lochs Sunart and Teacuis have never held large numbers of breeding Eiders. In 1950, Campbell recorded 14 clutches or broods at seven sites. On 15 June 1982 he counted a total of seven females and one nest in addition to (uncounted) "ducks and ducklings" in Glenborrodale Bay.

In 1998 no nests, clutches, broods or adults were seen. The dates of 7-8 June are slightly late for finding clutches of this species, but ducks with broods should have been obvious on the water. However, counts were restricted to islands and would have missed birds that nested on the shore of the mainland.

Oystercatcher Survey counts of Oystercatchers are presented in Appendix II. In sealochs such as Lochs Sunart and Teacuis, Oystercatchers breed both along the

mainland shore and on islands, whereas all, or nearly all, the gulls and terns breed on islands. This study was confined to islands so included all the gulls and terns but only a small proportion of the Oystercatcher population of the Lochs.

Oystercatchers were the most widespread of all the species surveyed. In 1950 there were 24 pairs on 19 islands and in 1998 there were 22 pairs on 14 islands. Of this 1998 total, two pairs had young on 20 July, the outcome of four pairs was unknown, and 16 pairs were considered (from the behaviour of the adults) to have failed. Of these 16, mink were identified from eggshells as the cause of failure of six pairs, while the cause of failure of the other ten was unknown (mink not excluded). Thus, no more than two of 18 pairs (11%) were successful.

Black Guillemot Survey counts of Black Guillemots are presented in Appendix II. Black Guillemot nests are difficult to count, and Campbell mainly reported counts of both adults and clutches. As a boy in 1926, he found a chick in a nest crevice at Eilean a'Chuillin in Loch Sunart. He found Black Guillemots breeding in the same crevice in 1950 and again in 1982. In 1950 he recorded eight adults and six clutches at Risga, the species' stronghold in the Lochs, and adults were present at Garbh Eilean. In 1952, 16 adults and four clutches were found at Risga, but other sites were not visited. In 1982, Campbell recorded 13 adults and, with less searching than in 1952, two clutches, distributed between these three sites.

In June 1998, no Black Guillemots were seen at any of Campbell's sites or at any other islands in the Lochs, although small numbers may have bred undetected on the mainland shore.

Ideally, this species should be censused earlier in the year (Wash *et al.* 1995) but the absence of adults in early June 1998, when onshore searches were made of all these small islets, certainly indicated either that none bred or that the breeders had failed. No eggshells were found, suggesting that none had attempted to breed.

DISCUSSION

Reliable quantitative records of breeding seabirds from as early as 1950 are rare, particularly in west Scotland, an area where seabirds are still under-recorded at the beginning of the twenty-first century. Loch Sunart and Loch Teacuis are typical of the many sealochs of west Scotland, so the long-term changes described above are likely to be representative of a larger part of the coast.

Breeding numbers of Herring Gulls and Great Black-backed Gulls in both lochs increased mainly between 1994 and 1998, while Common Eiders, Common Gulls, Common Terns and Black Guillemots either greatly decreased or became extinct between 1950 and 1998. Campbell's counts of 18 Black Guillemots in 1950 and 13 in 1982 (Appendix II) suggest that this species decline occurred mainly after 1982. Several factors may have caused these changes.

In a larger area of west Scotland, between Mallaig ($57^{\circ} 00' N 5^{\circ} 50' W$) and Machrihanish ($55^{\circ} 25' N 5^{\circ} 42' W$), including Lochs Sunart and Teacuis, Herring Gull numbers decreased by *c.* 37% between 1989 and 1998 (from *c.* 10143 pairs at 73 colonies to 6,388 pairs at 44 colonies). This decline was caused by widespread annual whole-colony breeding failures caused by mink predation of eggs and chicks (Craik 1998). Thus the large increase of Herring Gulls breeding in Lochs Sunart and Teacuis took place against this wider regional decrease.

The perennial supply of food pellets at fish farms provides a source of food for large gulls that is probably substantial (Furness 1996). This, together with the successful breeding almost every year at Sligneach Mor, is a likely reason for the local increase in their breeding numbers. However there are no regular counts from Sligneach Mor before 1990, so any changes then remain undetected.

It is tempting to argue that the species' declines in Lochs Sunart and Teacuis may have been caused by large gulls preying on the eggs and young of the other species and/or taking over their breeding sites. However, there is little evidence for this. In 1998, almost all the Great Black-backs and Herring Gulls (96% and 97% respectively) bred on Sligneach Mor, 6 km from the tern colony at Eilean nan Gabhar and 16 km from the largest of the extant Common Gull colonies. Predation by large gulls was not detected at tern and Common Gull colonies (except of young terns at Sligneach Mor in 1987). Also with the exception of Sligneach Mor, where Herring Gulls increased to occupy areas formerly occupied by terns, all the former breeding sites of terns and Common Gulls remained uncolonised by other species. Thus, there was probably little competition between species for breeding sites.

There is clear evidence that mink predation of eggs was often the cause of repeated whole-colony breeding failures of terns between 1990 and 1998 (Table 4), and of the failure in 1998 of most, possibly all, the Common Gulls and at least some of the Oystercatchers. Between 1965 and 1994, mink increased in this area from being scarce and thinly distributed to become common and widespread along shores and rivers (Craik 1995). Much of this increase in Loch Sunart occurred after 1985. From 1987-98, mink were responsible for decreases of *c.* 40-60% in tern and gull numbers in a west Scotland study area that included Lochs Sunart and Teacuis (Craik 1997, 1998). Mink predation of eggs and young is therefore the most plausible explanation of the declines of terns and Common Gulls in Lochs Sunart and Teacuis since 1990. Caution should be exercised, however, in applying this recent evidence to the whole period since 1950.

Breeding success of Eiders, Lesser Black-backed Gulls and Black Guillemots was not measured, so the reasons for their declines cannot be supported by direct evidence. However, mink predation of incubating adults has been recognised as a cause of the disappearance of Black Guillemots from several other areas in west Scotland in the early 1990s (Craik 1993). Also, between 1990 and

1998, at Eilean nan Coinean-Eilean Fraoich in the Sound of Jura, an important mixed seabird colony with *c.* 200 pairs of Lesser Black-backed Gulls plus similar numbers of Shags and Herring Gulls and smaller numbers of Black Guillemots, was extirpated (except for a small number of Herring Gulls). This coincided with well-documented annual whole-colony breeding failures caused by mink (Craig 1998 and unpublished results). The declines in Loch Sunart at the same time as mink-related declines of these species and terns and Common Gulls elsewhere are therefore likely to have been due to mink predation.

Why were Herons and Oystercatchers, numbers of which changed little between 1950 and 1998, apparently unaffected? Herons breed in trees and, although mink are able to climb trees (Larivière 1996), this behaviour is not common. In 1998, the breeding success of Oystercatchers in the Lochs was reduced by mink but some pairs did succeed in raising young. In contrast to the colonial habit of gulls and terns, Oystercatchers always breed singly and, for that reason, their eggs and chicks may be less vulnerable to mink. Having found one clutch or brood, a mink would be less likely to find the offspring of neighbouring pairs. Consequently, surplus killing by mink, stimulated by a high density of helpless prey (Kruuk 1972), would not be elicited. Moreover, Oystercatchers are abundant in this and in other habitats and many breed inland, far from water and probably also from mink. Only those Oystercatchers breeding on islands were monitored in this work. Oystercatcher populations as a whole may be sufficiently robust to withstand the extra predation pressure that prevails in mink habitats.

Campbell's records alert us to what almost certainly must have happened in sealochs throughout much of west Scotland where early seabird counts were never made. While not all the losses in Lochs Sunart and Teacuis since 1950 can be proved to have been caused by mink, there is little evidence that other factors have greatly affected this group of species. Within the years 1988-98, other areas in west Scotland (Lochs nan Ceall, Don, Creran, Crinan, Sween, Caolisport and the Sound of Luing) have also lost all or most breeding seabirds, all after mink-related whole-colony breeding failures, in most cases recorded in successive years. Terns and Common Gulls still breed in some other areas where there is local annual control of mink such as Lochs Ailort, Leven, Etive, Feochan, Melfort, Craignish, West Loch Tarbert and the Sound of Mull (Craig 1998).

SAMENVATTING

DE EILANDEN VAN BRUCE CAMPBELL OPNIEUW BEZOCHT: VERANDERINGEN IN DE ZEEVOGELPOPULATIE VAN LOCH SUNART NA EEN HALVE EEUW

In 1950 en 1998 werden tellingen uitgevoerd van de aantallen broedparen van negen soorten zeevogels op 31 kleine eilandjes in de Lochs Sunart en Teacuis, zeearen die karakteristiek zijn voor talloze andere in West-Schotland. In de loop van deze 48 jaren zijn verscheidene soorten die ooit karakteristiek waren voor dit kustgebied, sterk afgenomen of zelfs vrijwel geheel verdwenen, waaronder de Eider Somateria

mollissima, de Stormmeeuw *Larus canus*, het Visdiefje *Sterna hirundo* en de Zwarte Zeekoet *Cephus grylle*. Het aantal Blauwe Reigers *Ardea cinerea* en Scholeksters *Haematopus ostralegus* is daarentegen nauwelijks veranderd. Zilver- *Larus argentatus* en Grote Mantelmeeuw *L. marinus* zijn toegenomen, maar de laatste jaren is die toename beperkt gebleven tot één eilandje in de monding van Loch Sunart. De toename van Zilvermeeuw stond in schril contrast met de overheersende trends in de rest van deze regio in de jaren 1989-98. De aantalsontwikkelingen, het broedsucces en de oorzaken van mislukte broedsels in de jaren 1990-98 doen vermoeden dat twee factoren een rol spelen. Bij de grote meeuwen lijkt gemorst voedsel in een zestal grote zalmwekerijen te hebben bijgedragen aan een relatief ruim voedselaanbod. Bij metname Stormmeeuwen en stems heeft de komst en vervolgens de sterke uitbreiding van de Amerikaanse Nerts *Mustela vison* tot veel nestplunderingen geleid, hetgeen in veel gebieden populatieafnames tot gevolg heeft gehad. De resultaten zijn representatief voor de ontwikkelingen in een veel groter deel van de Schotse westkust, waar vijf soorten meeuwen en stems met 40-50% zijn afgenomen na jaren met een slechte reproductie veroorzaakt door de Amerikaanse Nerts.

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Next page: Appendix I. Number of pairs of Common Gull, Lesser Black-backed Gull, Herring Gull, Great Black-backed Gull and Common Tern counted in islands of Lochs Sunart and Teacuis, 1950/52-98. Figures in brackets indicate number of young fledged. Island numbers refer to those in Fig. 1.

Appendix II. Counts of Black Guillemot (individual adults), Eider (nests, clutches or broods), Heron (active nests) and Oystercatcher (pairs) in islands of Lochs Sunart and Teacuis, 1950/52-98.

Appendix I Island	Common Gull		L Bl-b Gull		Herring Gull		Gr Bl-b Gull		Common Tern	
	1950/52	1998	1950	1998	1950	1998	1950	1998	1952	1998
1. Eilean a'Mhuirich									30-40	0(0)
2. Glas Eilean	52	0 (0)							present	0(0)
4. Eilean an t'Sionnach	15	1 (0)							35	0(0)
5. Sgeir Mhali										
6. Garbh Eilean			38	0 (0)	8	4 (2)				
7. Eilean a'Chuilinn	10	0 (0)			0	1 (0)	1	0 (0)		
8. Eilean mo Shlinneag							0	1 (0)		
9. Sgeir an t'Seangain	1	7 (0)								
10. Dun Ghallain	38	1 (0)							25-30	0(0)
11. Eilean nam Gillean	1	0 (0)								
12. Eilean an Fheidh										
13. Risga	5	0 (0)	50+	0 (0)	15	0 (0)	1	0 (0)	4	0(0)
14. Glenborrodale islets	Present	5 (0)			0	1 (0)			25	0(0)
15. Eilean Mor										
16. Caolas Rahuaich	2	3 (0)			0	1 (0)			10	0(0)
17. Eilean nan Gabhar	Several	1 (0)							1	1 (0)
18. Eilean nan Eildean	Several	0 (0)								
20. Eilean na Droma Buidhe	20	2 (0)	0	1 (0)					35	1 (0)
22. Sligneach Mor	6	0 (0)			41	216 (323)	1	22 (20)	150	0(0)
Total	150+	20 (0)	88+	1 (0)	64	223 (325)	3	23 (20)	315-330	2 (0)

Appendix II Island	Black Guillemot			Eider		Heron		Oystercatcher	
	1950/52	1982	1998	1950	1998	1950	1998	1950/52	1998
1. Eilean a'Mhuirich								1	1 (0)
2. Glas Eilean				3	0			1	2 (?)
4. Eilean an t'Sionnach				1	0			1	1 (?)
5. Sgeir Mhali								1	0 (0)
6. Garbh Eilean	present	6	0	3	0			2	2 (0)
7. Eilean a'Chuilinn	2*	1*	0			0	15	1	0 (0)
8. Eilean mo Shlinneag								1	1 (0)
9. Sgeir an t'Seangain				1	0			1	1 (0)
10. Dun Ghallain								3	3 (1+)
11. Eilean nam Gillean								1	1 (0)
12. Eilean an Fheidh								1	? (?)
13. Risga	16	6	0	4	0			2	1 (0)
14. Glenborrodale islets								1	4 (2)
15. Eilean Mor								1	? (?)
16. Caolas Rahuaich								1	2 (0)
17. Eilean nan Gabhar				1	0			1	1 (0)
18. Eilean nan Eildean				1	0	16	0	2	? (?)
20. Eilean na Droma Buidhe								1	1 (0)
22. Sligneach Mor								1	1 (?)
Total	18+	13	0	14	0	16	15	24	22 (3+)

* Eggs in 1950 and 1982 were in same rock cavern as chick in 1926.

THE BREEDING *LARUS* GULLS ON SKOMER ISLAND NATIONAL NATURE RESERVE, PEMBROKESHIRE

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*The populations of breeding Lesser Black-backed Gull *Larus fuscus*, Herring Gull *Larus argentatus* and Great Black-backed Gull *Larus marinus* on Skomer Island have all changed dramatically since the island became a National Nature Reserve in 1959. The role of human activities in these changes is marked and includes bird protection and other conservation measures, reduction in numbers by culling, and changes in food availability. Gulls and other seabirds have been well-studied on Skomer and population trends are considered in relation to adult survival rates, annual productivity and other factors.*

Perrins C.M. & S.B. Smith 2000. The breeding *Larus* gulls on Skomer Island National Nature Reserve, Pembrokeshire. *Atlantic Seabirds* 2(3/4): 195-210.

INTRODUCTION

Skomer Island, Pembrokeshire, has been a National Nature Reserve (NNR) since 1959 and forms part of the Skokholm & Skomer Special Protection Area, designated under EC Directive 79/409. Owned by the Countryside Council for Wales (CCW), it has been managed since it was declared an NNR by the Wildlife Trust, West Wales (WTWW) and its predecessor bodies. Not only is Skomer one of the most important seabird colonies in southern Britain, but the waters around the island have been designated a Marine Nature Reserve. Seabird monitoring fits within a broader framework of monitoring marine and terrestrial organisms on and around the island. Skomer is one of the four "key sites" that form part of the Seabird Monitoring Programme, co-ordinated by the Joint Nature Conservation Committee (JNCC).

The seabird populations have been monitored since the early 1960s, enhanced by the introduction of measurements of annual adult survival of Lesser Black-backed Gull *Larus fuscus** and Herring Gull *L. argentatus* by the Edward Grey Institute of Field Ornithology, University of Oxford starting in 1978, and of annual productivity surveillance in the 1980s and 1990s (e.g. Poole

* Known as *Larus graelsii* on the Dutch list

& Smith 1998). Along with the Great Black-backed Gull *L. marinus*, these species have been the focus of a number of research projects (Smith 1998ab).

This paper briefly assesses the results of monitoring of Lesser Black-backed Gull, Herring Gull and Great Black-backed Gull on Skomer since 1960 (see Sutcliffe (1992) for a detailed review of population change). Up to 25 pairs of Black-headed Gull *L. ridibundus* nested on Skomer between 1966 and 1970, but they are not discussed further.

SPECIES ACCOUNTS

Lesser Black-backed Gull

Population size The population of Lesser Black-backed Gulls nesting on Skomer (plus the population of some 4000 pairs on the adjacent island of Skokholm) is important because it comprises a significant proportion of the total world population of the subspecies *L. f. graellsii*. At the time of the last national census (Lloyd *et al.* 1991), the Skomer colony was one of the three largest in Britain and Ireland, the other two being on Walney and the inland colony at Abbeystead.

Counting breeding numbers of this gull can be particularly difficult on Skomer due to high density, plateau nesting and the habit of nesting in areas on which the vegetation becomes tall by the time the birds are nesting. Until the late 1970s, "eye-counts" of the population were probably underestimates (Sutcliffe 1997). From 1980 onwards, the census method was improved to include repeated counts of incubating pairs/territories (from standardised view points since 1987). Some areas are then physically counted by a team walking through the area and placing a cane by each nest so as to obtain an actual number of nests. This number, divided by the number counted by eye (which was always smaller) gave a "correction factor" which is applied to all the eye-counts so as to yield a best estimate of the total. Comparison of whole-island estimates with nest counts in study plots shows that the method does produce results that match the changes in the study plots (Poole & Smith 1998), thus suggesting that the method does give meaningful estimates.

Although this method probably provides a truer estimate of the actual numbers than just using the simple eye-counts, it is not without problems. The method cannot correct for non-breeding adult birds present in the colonies, which is suspected to occur on Skomer (Sutcliffe 1992) and has been noted at other colonies (Calladine & Harris 1997). Another concern is the number of empty nests found during the counts; this has varied from 14% to 40% from 1991-98 and seems to have become more common (Poole & Smith 1998). We do not know whether 1) a proportion (and if so, what proportion) of the adults build more than one nest, as has been reported elsewhere (O'Connell *et al.*

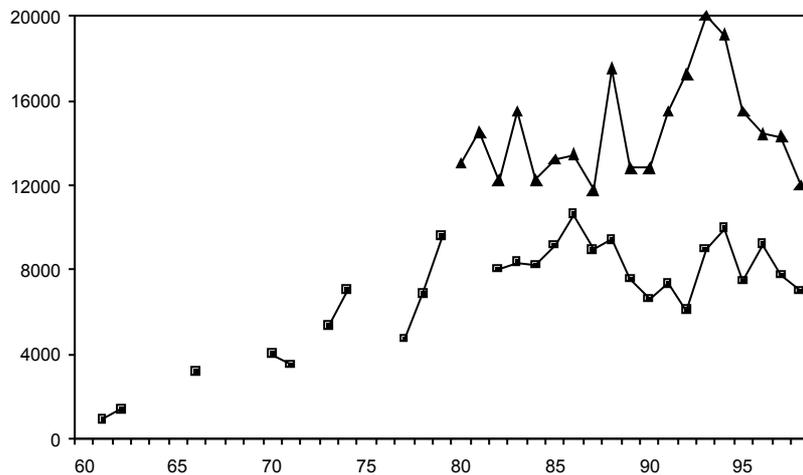


Figure 1. Lesser Black-backed Gull numbers on Skomer Island 1962-98. Squares show the "eye-counts" and triangles the numbers adjusted as a result of the "cane counts" (see text).

1997); 2) whether these nests are ones from which the eggs have been lost; or 3) whether these are nests in which late-comers will try to breed.

Survival has been measured by colour-ringing breeding adults and recording their subsequent breeding histories. Survival rates have been measured by applying the programme SURGE (Lebreton *et al.* 1992).

Estimated breeding numbers (Fig. 1) increased steadily through the 1960s and early 1970s, and more rapidly in the second half of the 1970s. From about 1980 the number of breeding pairs increased more slowly. Trends may be partially obscured by culls of some 4000 adults during the years 1981-87, due to concerns about gull predation on auks and waders (Donovan 1973; Sutcliffe 1991). Numbers peaked at 20,200 pairs in 1993, since when they have steadily decreased to 12,000 pairs in 1998. Even so, this may still be 14% of the British and Irish population (using the figures in Lloyd *et al.* 1991).

Breeding success and adult survival We know something of the demographic characteristics of the population since the late 1970s. For most years since 1982 overall productivity has been estimated (see Fig. 2) using a capture-re-sighting method (e.g. Southwood 1978). This involves ringing about 500 chicks prior to the first chicks' fledging and then, when the chicks have fledged, counting

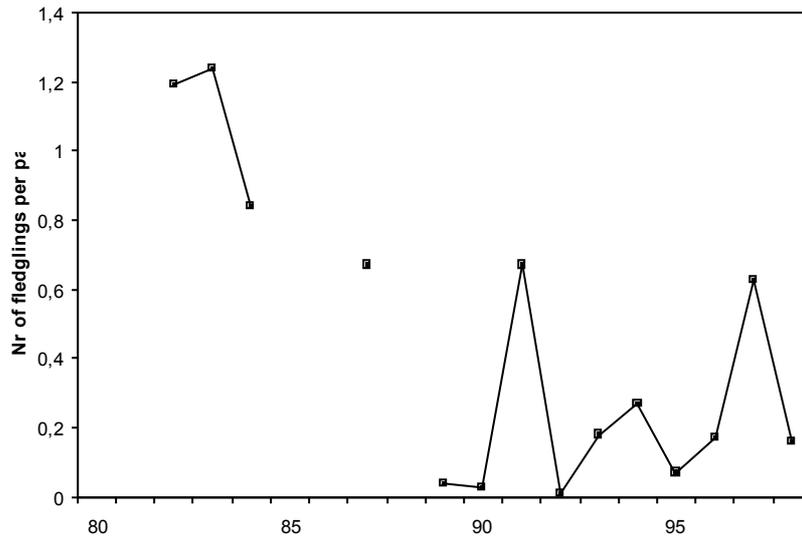


Figure 2. Lesser Black-backed Gull productivity on Skomer Island 1982-98 (estimated number of fledglings per breeding pair).

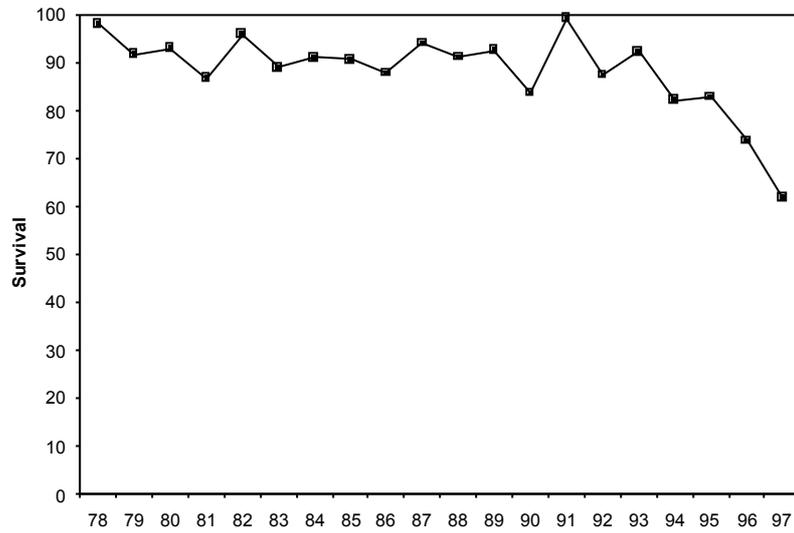


Figure 3. Lesser Black-backed Gull annual adult survival on Skomer Island 1978-97.

ringed and unringed fledglings and applying a capture-recapture calculation. This technique meets all the criteria for capture-recapture estimations except perhaps one; this is that we cannot rule out some immigration by fledglings from nearby Skokholm. We think that this will be small, but more importantly, it would have the effect of increasing the number of unmarked fledglings resighted, thereby increasing the estimates of number fledged; in any case, the estimates are very low.

Since 1987 productivity has been very low (Fig. 2), with almost complete breeding failure (0.01-0.07 young fledged pair⁻¹) in 1989, 1990, 1992 and 1995, and less than 0.20 fledged pair⁻¹ in 1993, 1996 and 1998. Other methods of estimating productivity, e.g. nest histories in fenced and unenclosed plots also record a decrease from the early 1980s (Todd 1986; Perrins 1991, 1992), but in some years the clearest evidence for very low productivity was the difficulty of locating the required number of chicks to ring; in 1989 and 1990 it was not possible to find enough chicks to ring the normal annual sample (Perrins 1992).

Survival rates of breeding adults have been measured since 1978 (Fig. 3). Although there has been a gradual decline in the breeding population in recent years, presumably due to the very poor (until recently) breeding success, there has been no very convincing evidence that adult survival has also declined. However, the data from 1987-97 now show a significant downwards trend ($r^2 = 54\%$, $P = 0.006$, Perrins (2000)), starting with 1994. We cannot, of course, distinguish between death and emigration. It is very unusual for adult birds to move far from an established breeding site, but in the face of continued breeding failure, it remains possible that some of the missing birds may have moved elsewhere.

Causes of population changes The increase in numbers in the early 1960s was probably due to increased protection by virtue of the acquisition and management of Skomer by conservation bodies and a reduction (later cessation) of egg collecting for local consumption, and perhaps aided by increased safety from predation due to increased bracken cover in parts of the island (Todd 1986). The rapid increase in the late 1970s has been attributed to an abundant food supply, notably whitefish discards from French trawlers fishing for Norway Lobster *Nephrops norvegicus* (Stone *et al.* 1992; Sutcliffe 1992).

The declines in numbers in the last 15 years or so are probably also associated with changes in the food supply, especially with a decrease in availability of fishery discards, although the details remain unclear; information on fisheries and discards is limited and occasionally confusing (e.g. Dunn 1993). Although French fishing effort and the quantity of whitefish discards in the southern Irish Sea increased during the late 1980s (despite an increase in

mesh size), the fishing may not have been within easy foraging distance for Skomer gulls (Stone *et al.* 1992). Dunn (1993) suggested the change to a smaller number of larger fishing vessels, combined with the reduction of the practice of continuous gutting, may have changed food availability for gulls since discard locations may have been more concentrated and available over shorter periods of time. Other factors may include an increase in inter-specific competition for discards.

Todd (1987) confirmed earlier studies (Harris 1965; Alexander & Perrins 1980; Alexander 1981) that earthworms *Lumbricus terrestris* were important food items early in the season with a shift to fish during the chick rearing period. In recent years, with discards apparently less available, birds have continued to forage on mainland agricultural land during the chick rearing period; for example, in July 1991 over 80% of chick regurgitates were of earthworms (Perrins 1991) compared with about 80% that were fish in 1985 (Todd 1986). The years of worst breeding failure are also those of very dry summers when presumably worms are more difficult to find (Thompson 1995). Attempts to study the direction of gull feeding trips are hampered by the fact that many leave before dawn, but studies in 1990-91, 1994-5, 1998 and 1999 found that most of the gulls leaving the island were heading inland (Orsman & Sutcliffe 1990; Perrins 1991, 1992; Davies 1994; Thompson 1995; Perrins unpublished data). However, in late July 1991 and 1995, there was evidence that gulls fed their chicks on fish; this may mean that late/replacement layers and those chicks that had survived until then benefited in those years although earlier breeders are usually more successful.

What is clear is that in most years since 1988, the majority of the chicks have died within a week of hatching. Most were clearly underweight and the food, as judged by the regurgitates, was mostly earthworms. This accords with the observation that the birds are going inland to collect food. Hence it seems that while the parents themselves may be able to survive on a diet of earthworms, they may be unable to collect sufficient earthworms for a rapidly growing brood. For example, in 1992, of 159 chicks that hatched 73 (46%) were found dead or had disappeared by day 5, a further 46 (total 75%) by day 10, and only six survived to day 20, of which probably only two fledged (Bradbury & Griffiths 1999; Bradbury pers. comm.).

In addition to chick losses, the low breeding success since 1987 has been due to the abandonment of nests before laying, high intra-specific predation of eggs which was linked to reduced parental attendance (presumably due to hunger), or the death from starvation, usually within a few days, of those chicks that did hatch (Dunn 1993; Perrins 1991, 1992; Sutcliffe 1997; Thompson 1995). Although most of the increased losses are likely to be the result of decreased attendance, changes to a more open vegetation in some areas

of the island may also have led to increased predation of eggs and chicks (Sutcliffe 1997).

The increased predation (mostly by other Lesser Black-backs) resulting perhaps from reduced attentiveness may explain the increase in the number of empty nests noted at the annual census.

Records also show that clutch sizes have decreased from 2.70 in 1960-62 to 2.19 in 1991 and 1.86 in 1995 (Harris 1964; Perrins 1992; Thompson 1995), although some of the smaller clutches may have partly been predated. Eggs measured in 1995 were similar in size to those measured in 1978, but both were lower than in 1982, about the time when the population was beginning to grow rapidly (de Wijs 1982; Thompson 1995).

Even in those years when most chicks were dying and seemed only to be being fed worms, a small proportion of the chicks grew well and regurgitated fish, indicating that sources of fish were available but that few parent gulls were able to find them. This observation need to be borne in mind when comparing data on chick diets because if most chicks are fed only worms and die young and the only young to survive are being fed fish, then samples taken from larger young are likely to be fish. Nevertheless, there are some indications that birds feeding during the early chick-rearing period may have reverted largely to marine sources. Fish were found in 54% of chick regurgitates in 1994 (Davies 1994) and 58% in 1995 (Thompson 1995). The species, which were identified in the latter year, suggested that the most likely source was again fishery discards (Thompson 1995). Regurgitates in 1997 and 1998 were almost entirely fish; only one chick of almost 500 ringed regurgitated pellets containing worms in 1998 (Barton, pers. comm.). Nevertheless, overall breeding success remains low; indeed it fell again in 1998 to an estimated 0.16 fledglings per pair (Fig. 2), roughly one-sixth of what would be required to maintain a stable population.

Herring Gull

Population size In contrast to the Lesser Black-backed Gull where the Skomer population is an important component of the British population, the Herring Gull breeds in a large number of colonies around the British and Irish coasts and the Skomer population even at its highest levels has never comprised more than 1-2% of the total population of Britain and Ireland (Lloyd *et al.* 1991).

Census methodology is much more straightforward for this species than for the Lesser Black-backed Gull and has not changed since the 1960s. Counts are made of incubating birds or occupied territories from various vantage points and by walking the coastline.

Numbers increased during the 1960s to 2200 Apparently Occupied Territories (AOTs) in 1969 (Fig. 4), and then remained fairly stable through the 1970s (although the counts for 1979 showed a marked increase to 2940 pairs).

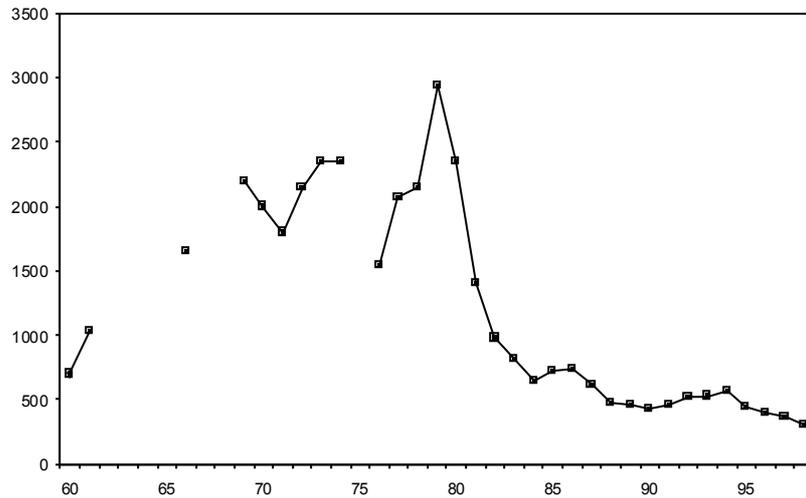


Figure 4. Herring Gull numbers on Skomer Island 1962-98.

From 1980 the population then decreased dramatically, being only 645 pairs in 1984. For a while thereafter, numbers remained fairly stable, although they declined slightly until the early 1990s, since when the population has declined further, reaching the lowest recorded level of 299 pairs in 1998.

The proportion of inland nesting birds, typically found close to rock outcrops, stone walls, etc. increased significantly during the period 1960-92 (Sutcliffe 1992), but has consistently remained at about 25% inland:75% coastal nesters every year since then.

The continued decline is in line with the national picture; the total British and Irish population of Herring Gulls seems to have declined by almost half between the two previous national seabird censuses (1969-70 and 1985-87; Lloyd *et al.* 1991). However, some other colonies of Herring Gulls in the region have been increasing. This includes neighbouring Skokholm, which after following a similar pattern to Skomer until 1996, recorded an increase of 70 pairs 1996-98; in the same period the Skomer population decreased by 102 pairs. The population on Middleholm, a small islet off Skomer, remained the same in 1997-98.

Breeding success and survival Annual measures of breeding success are not available for Skomer. However, low breeding success was reported in 1984 and 1985 when the birds raised only 0.48 and 0.59 chicks pair⁻¹ (Todd 1986),

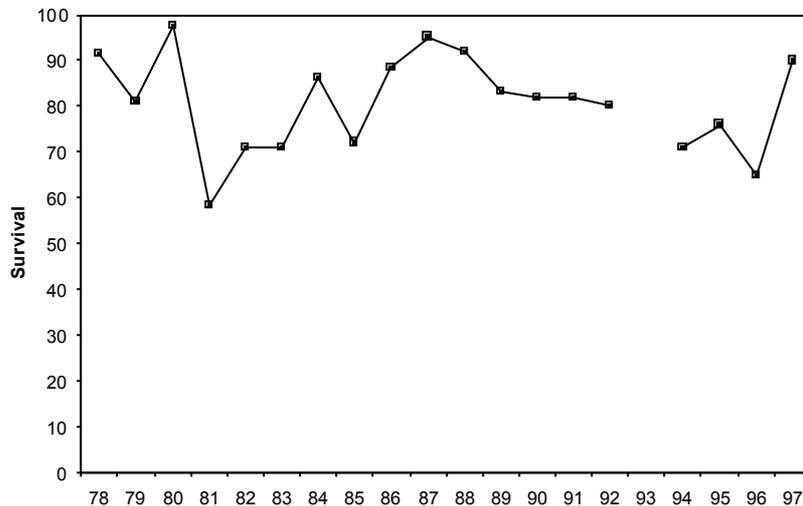


Figure 5. Herring Gull annual adult survival on Skomer Island 1978-97. The survival for 1993 was high, but can not be estimated accurately.

although these are similar to the 0.6 young pair⁻¹ recorded in 1962 when the population was increasing (Harris 1962). Recent breeding success does not appear to have been particularly low (1.09 per AOT in 1994, 1.21 in 1996, 1.24 in 1997 and 0.75 in 1998), but was lower than those recorded on Caldey Island (1.94 in 1996, 1.53 in 1998; Sutcliffe, pers. comm).

The annual adult survival rates were measured as for Lesser Black-backed Gulls. In a "healthy" population these might be expected to be around 90% or higher (see Discussion). For the Herring Gulls on Skomer, survival rates (Fig. 5) for two of the first three years of the study were not dissimilar to this, but declined sharply 1981-83, almost reached a level that might be expected for a normal Herring Gull population in four of the five years 1984-88, but were low again during the years 1989-92, and very low in three of the last four years (1993-96). Survival rates from 1987-97 show a highly significant downward trend (adj $r^2 = 87.6\%$, $P < 0.001$), although survival from 1997-98 was higher than it had been for some years. However, the sample size of the study group is now smaller than desirable.

Causes of population changes The early increase in numbers probably occurred for the same reasons as in the Lesser Black-backed Gull, namely protection of

the island colonies after Skomer became a National Nature Reserve in 1959. As the population increased, some attempts were made control it because of perceived problems of predation on and kleptoparasitism of breeding auks and waders (Donovan 1973). Egg-pricking during the years 1969-72 may have contributed to the decline in numbers to 1550 pairs by 1976 (Sutcliffe 1992) and about 100 adults were accidentally killed in the culls of Lesser Black-backs in 1981-87.

The Herring Gull forages out at sea less than the Lesser Black-backed Gull and many Herring Gulls, but almost no Lesser Black-backs, visited the Milford Haven fish-docks when these still flourished (Davis 1973). The decline of the fish-docks (Harris 1970; Davis 1973) must have had a serious effect on the availability of food for those individuals who visited the docks regularly. Thus, when the fish-docks closed many of them switched to feeding at rubbish-tips. The rubbish tips at this time were a source of botulism *Clostridium botulinum*, probably caused by the introduction of black plastic refuse bags, which heated the waste. Consequently, many adult gulls were found dying on Skomer in the breeding season and botulism was confirmed as the cause of death in a number of individuals. The major decline in numbers of Herring Gulls coincides with the timing of these poisoning outbreaks. Since then, better management of tips, including gull exclusion, caused birds to revert to feeding on fields and inter-tidal areas (Sutcliffe 1992; Thompson 1995). As a result, the decline halted, but not only have numbers not increased, they are now decreasing still further. The reasons for this are not known.

Great Black-backed Gull

Population size As with the Herring Gull, the Skomer population of Great Black-backed Gulls does not represent a significant proportion of the British and Irish population, but it is perhaps 10-20% of the total Welsh population.

In common with the Herring and Lesser Black-backed Gulls, the Great Black-backed Gull also increased after the island became an NNR in 1959, reaching a peak of 283 pairs (AOTs) in 1962. Thereafter, numbers declined to less than 100 pairs by 1976 (Fig. 6) and to 25 pairs in 1984. They then increased until 1994 (68 pairs), but there has been little change since then (53 pairs in 1998 and 65 pairs in 1999). Much of the decline in 1997 and 1998 was due to the reduction in numbers of inland nesters on rocky ridges, after a period when they appeared to be reforming their inland colony structures (Sutcliffe 1992, 1997).

Breeding success and survival Breeding success has been measured only since 1996, but is perhaps what we might expect for a stable population (1.14 chicks fledged AOT⁻¹ in 1996, 1.17 in 1997, 1.10 in 1998 and 0.96 in 1999).

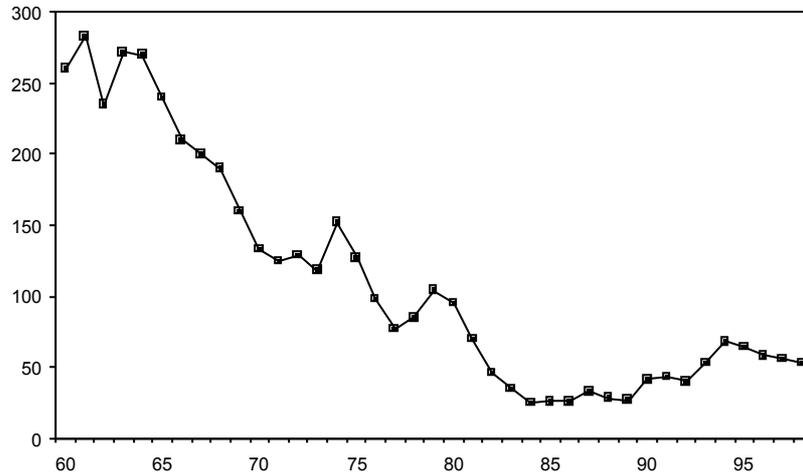


Figure 6. Great Black-backed Gull numbers on Skomer Island 1962-98.

The population has not been intensively studied, largely because the pairs are widely separated and the adults difficult to catch; hence there are no measures of survival rates.

Causes of population changes The initial increase in numbers was almost certainly again due to the protection afforded by Skomer becoming an NNR. The subsequent decline was due to culling throughout the 1960s and 1970s instigated because of concern over predation on other birds, especially Manx Shearwaters *Puffinus puffinus* (Mylne 1960; Sutcliffe 1992), but also Puffins *Fratercula arctica* (Harris 1964; Donovan 1973). This culling resulted in the fragmentation or loss of most of the inland plateau subcolonies. The size of the population was then further reduced by the outbreaks of botulism, and this led to the cessation of control measures in the late 1970s.

Diet studies in the 1970s indicated a change from mainly shearwaters, fish remains and rabbits *Oryctolagus cuniculus* in the early 1960s (Harris 1965) to feeding on human refuse (Corkhill 1973). The reasons for this are unclear; a diet study in 1992 found a reversion to mainly "natural foods" with shearwaters and rabbits the main items (Poole 1995). On Skokholm (as at other local colonies) numbers have risen since the end of the botulism outbreaks; the number of pairs have increased from 14 in 1988 to 50 in 1998 (Thompson, pers.

comm.). Mean breeding success on the two islands during the years 1996-98 has been similar (1.22 chicks fledged AOT⁻¹ on Skokholm, 1.13 on Skomer).

DISCUSSION

Population increases in all three species of large gulls seemed to be closely associated with the creation of Skomer as an NNR in the late 1950s. Protection, reduced disturbance and, especially, the prevention of regular incursions by local people collecting eggs during the spring must have been important in allowing bird numbers to build up.

Healthy, stable populations of large gulls such as these might be expected to lay clutches of approaching three eggs per pair (Cramps & Simmons 1983) and to raise about one chick per pair (Harris 1970 and references therein; Davis 1973); annual adult survival rates should be around 90% or better (Chabrzyk & Coulson 1976). During the course of this study, production of both Lesser Black-backed and Herring Gulls has fallen well below these levels and not surprisingly, the populations have declined.

However, one other characteristic of these species may mask changes in populations for some time and this is the age of first breeding. In the two smaller species, Herring and Lesser Black-back, the birds do not normally start breeding until they are about 3 or 4 years old; in the Great Black-backed Gull maturity is probably about one year later than this, at age 4 or 5 (though these may vary with population size or food supply). At any time, therefore, there are three to five cohorts of birds which are non-breeders.

This may have some quite striking effects on population size. For example, complete breeding failure for four years will not result in any immediate diminution of the breeding population; only after the fourth year (and even then only if there is no immigration) will the population start to decline. This effect can be seen to some extent in the Lesser Black-backed Gull; the birds' breeding success declined markedly from 1988 onwards, but no decline in breeding numbers was apparent for several years after this. It is largely for this reason that culling eggs is so unsuccessful as a method of population control in the short term. If one adds in the number of pairs that lay repeat clutches and allows for increased survival of the clutches that were missed during the cull, then egg-culls may be very ineffective even in the long term, unless a high proportion of the eggs are removed over a long period of years.

For long-lived species such as these, it follows that population size is much more sensitive to changes in adult survival rates. Even small changes in this rate can dramatically lower the mean expectation of further life for individuals, and hence lifetime breeding output. In all three species, declines can be associated with lowering of the adult survival rates. In the Lesser Black-

backed Gull the main reason for the change in adult survival rates is not clear, but presumably it is related to the loss of food, which is so apparent in the breeding season. In the case of the Herring Gull, the earlier decline was clearly associated with botulism contracted at rubbish tips, although the reasons for the current decline are unclear. The main reason for the decline in Great Black-backed Gulls was culling of adults, perhaps exacerbated by botulism.

There is also much we do not know. Currently, all three species are either in decline (Lesser Black-back and Herring) or stable at a much lower density than formerly (Great Black-back); in the case of the two smaller species at least, survival rates of the adults are insufficient to maintain a healthy population whatever the reproductive output. Yet while the cause of the low survival of the Lesser Black-backed Gull, as suggested above, may be associated with its currently poor food supply, it is not clear why the other two species are not faring better. The number of breeding pairs of Herring Gulls is now much lower than it was formerly and yet the adults are still, apparently, unable to find sufficient food for themselves (if it is food supply that is limiting their numbers). Yet in the breeding season they seem to be being reasonably successful at raising their broods, in contrast to the Lesser Black-backs.

In some ways the slow decline of the Great Black-backs is the most puzzling of all. Although we do not know whether their adult survival rates are low, we do know that the food that many of the pairs rely on is actually on Skomer itself, namely rabbits, Manx Shearwaters and Puffins. These are as abundant, or possibly even more abundant, than they have been at any time in the last 50 years. Hopefully these foods are free from contamination, which might not be the case with, say, worms in fields or waste taken by the other two species. Yet for some reason the Great Black-backs are unable to regain their earlier numbers in the face of apparent plenty. It is tempting to draw the parallel with Peregrines *Falco peregrinus* where coastal breeding pairs, taking a diet of seabirds, raise fewer chicks than those breeding inland (Ratcliffe 1993).

Gulls are not always everybody's favourite birds, as evidenced by the fact that all three species have been culled at one time or another on Skomer with the aim of protecting habitats for other species. Yet currently all three species are in decline and we do not know why; their ecology still merits further study.

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SAMENVATTING

BROEDENDE *LARUS*-MEEUWEN OP SKOMER NATIONAAL NATUURRESERVAAT, PEMBROKESHIRE

De populaties van Kleine Mantelmeeuw Larus graelsii, Zilvermeeuw Larus argentatus en Grote Mantelmeeuw Larus marinus op Skomer zijn sterk veranderd sinds dit eiland in 1959 een nationaal natuurreservaat is geworden. Sinds de instelling als natuurreservaat zijn de drie soorten toegenomen als gevolg van beschermings- en beheersmaatregelen, waardoor het rapen van eieren is verminderd en later zelfs is gestopt. De toename van de Kleine Mantelmeeuw in de jaren zeventig is waarschijnlijk veroorzaakt door een groter voedselaanbod op zee in de vorm van visafval (discards) van Franse kreeftenvissers. Een verminderde beschikbaarheid van deze discards is mogelijk de oorzaak van de afname in de laatste 15 jaar. De Zilvermeeuw is minder afhankelijk van de voedselsituatie op zee, maar meer van de nabijgelegen vissershaven. Na sluiting van de vissershaven verschoof de Zilvermeeuw naar een vuilstort, waardoor botulisme uitbrak. Deze uitbraak viel samen met een periode van sterke afname van de populatie. Ook de Grote Mantelmeeuw profiteerde aanvankelijk van de beschermingsmaatregelen. In de jaren zestig en zeventig werd deze soort echter bestreden om predatie van Noordse Pijlstormvogels Puffinus puffinus en Papegaaiduikers Fratercula arctica te verminderen. Nadat de populatie door botulisme verder gereduceerd was, werd de bestrijding gestaakt. De afname van de onderzochte soorten wordt uiteindelijk veroorzaakt door slechte broedresultaten én door een verminderde jaarlijkse overleving van volwassen vogels. Vanwege het directe effect op de populatiegrootte lijkt de laatste factor het meest van belang.

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Great Black-backed Gull (photo S.C.V. Geelhoed).

POPULATION TRENDS OF LITTLE AND SANDWICH TERNS *STERNA ALBIFRONS* AND *S. SANDVICENSIS* IN BRITAIN AND IRELAND FROM 1969 TO 1998

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*Population trends of Little Terns *Sterna albifrons* and Sandwich Terns *S. sandvicensis* were determined between 1969 and 1998 using counts from sample colonies throughout the UK and Ireland. The Sandwich Tern population increased from c. 12 000 pairs in 1969 to c. 17 000 pairs in 1971, but then fell to c. 13 000 pairs in 1974. It then recovered at a rate of 6% per annum to c. 17 000 pairs in 1979 and fluctuated around 16 000 pairs until 1992. There was a second large population decline of 20% between 1992 and 1995, resulting in a total of c. 13 000 pairs in 1995. This decline appears to have halted up to 1998, when population size remained relatively stable at 13 500-14 000 pairs. The Little Tern population increased from 2000 pairs in 1969 to 2600 pairs in 1971 and then decreased to c. 1800 pairs in 1973. It increased again to a peak of 2800 in 1975 but then entered a long-term decline at an average rate of 1.23% per annum, punctuated by increases in 1988 and 1996. The population of c. 1700 in 1998 was the lowest recorded during the 30 year study and represents a 39% decline compared with 1975. The decline in Sandwich Tern populations appears to be confined primarily to the North Sea, with decreases being associated with events at individual colonies rather than at all colonies within the area. The declines in Little Tern populations appear to have occurred throughout the species range and are probably symptomatic of a chronic, widespread problem. Possible reasons for the declines in these populations are discussed and recommendations are made for further research, monitoring and conservation measures.*

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INTRODUCTION

The Little Tern *Sterna albifrons* and Sandwich Tern *S. sandvicensis* populations in Britain and Ireland are internationally important, hosting c. 15% and c. 40% of the European population respectively (Lloyd *et al.* 1991). Little and Sandwich Terns are included on the 'Amber' list of Birds of Conservation Concern (Gibbons *et al.* 1996) and listed in Annex 1 of the EC Birds Directive (Batten *et al.* 1990). All tern populations are sensitive to an array of threats, including disturbance (Lloyd *et al.* 1975), predation (Craik 1997; Becker 1998), flooding (Haddon & Knight 1983; Becker 1998), food availability (Monaghan *et al.* 1989;

Suddaby & Ratcliffe 1997; Stienen & Brenninkmeijer 1998), pollutants (Becker 1991) and trapping during winter (Dunn & Mead 1982, Stienen *et al.* 1998). This potential for tern populations to undergo rapid declines is exemplified by the crash of Roseate Terns *S. dougallii* in Britain and Ireland during the 1970s (Cabot 1995), of all tern species in the Wadden Sea during the 1960s (Becker 1991) and of Arctic Terns *S. paradisaea* on the Orkney and Shetland Islands between 1980 and 1994 (Bullock & Gomersall 1981; Avery *et al.* 1989; Brindley *et al.* 1999). It is essential that tern populations be monitored so that adverse population trends can be identified and ultimately diagnosed and reversed. Effective monitoring of terns in Britain and Ireland should therefore be regarded as a high priority and an international responsibility.

The low site-fidelity of terns makes census work difficult as they readily abandon sites, form new colonies and move among established ones (Lloyd *et al.* 1991). Therefore changes in numbers at sample colonies may not be representative of trends of others in the region, and the variability of trends among colonies produces wide confidence limits around population estimates. In order to overcome this problem, periodic complete national censuses or an annual sampling strategy that includes a high proportion of the colonies within the nation (and preferably in other countries within the metapopulation) need to be conducted. Data from both these sources are available for Sandwich and Little Terns in Britain and Ireland.

There is a long history of censusing tern colonies in Britain and Ireland that dates back to the beginning of the century (Parslow 1967; Cramp *et al.* 1974). These were generally non-systematic counts of a small sample of individual colonies by amateur ornithologists. The first national Little Tern census was in 1967 (Norman & Saunders 1969) and was followed by the 1969-70 'Operation Seafarer' census (Cramp *et al.* 1974), which censused all tern colonies in Britain and Ireland. Another complete survey was conducted in 1985-87 (Lloyd *et al.* 1991) and incorporated data from the 1984 'All Ireland Tern Survey' (Whilde 1985) for those sites not surveyed in western Ireland. These surveys showed an increase in the population size of both Little and Sandwich terns. The Irish tern survey was repeated in 1995 (Hannon *et al.* 1997), detecting declines in Little and Sandwich Terns since the mid 1980s. A third national tern census of Britain and Ireland is planned for 2000.

In addition to the infrequent national censuses, a sample of tern colonies have been counted annually by reserve wardens and volunteers throughout Britain and Ireland since 1969. These data are a valuable supplement to the national censuses as annual population changes can be described, allowing adverse trends to be detected and diagnosed more quickly and patterns of change between censuses to be studied. The counts have been collated by The Royal Society for the Protection of Birds (RSPB) and the Seabird Group, and total

numbers of breeding terns at monitored colonies between 1969 and 1984 have been reported as population sizes and raw trends (Lloyd *et al.* 1975; Thomas 1982; Thomas *et al.* 1989). This simple analysis produces minimum population estimates and biased trends, because changes in population size reflect temporal patterns in the colonies included in the sample as well as real changes in population size (Sears & Avery 1993).

In 1986, the annual tern monitoring scheme was integrated with the national Seabird Monitoring Programme and trends have since been presented as chain indices (Marchant *et al.* 1990) that compare percentage changes only at those colonies counted in consecutive years. These indices suggest that Little and Sandwich Terns have declined in the UK since 1986 (Thompson *et al.* 1999). Sears & Avery (1993) also used chain indices to describe annual population changes for Little Terns in Britain and Ireland between 1969 and 1989. This showed an increase up to 1972, followed by a sharp fall in 1973. The population then recovered to a peak in 1976 followed by a gradual decline up until 1989.

From the above, it is clear that a holistic interpretation of the annual tern population trends from 1969 to the present day is not feasible because the data are not held centrally and have been analysed using different, non-comparable methods. The evidence that Little and Sandwich Tern populations have decreased since 1986 needs to be investigated more thoroughly in the light of earlier population trends. This paper describes the population trends for Sandwich and Little Terns in Britain and Ireland using data from sample colonies over a 30-year period. Possible reasons for changes in population size are discussed and recommendations are made for further demographic studies, including more analyses of tern population trends.

METHODS

Counts of tern colonies were made by volunteers and reserve wardens throughout Britain and Ireland between 1969 and 1998 and were submitted to a central co-ordinator for collation. Count units were the number of breeding pairs, derived primarily from counts of nests or Apparently Incubating Adults (Walsh *et al.* 1995). Peak fledgling counts (the maximum number of fledged young counted at a colony, Walsh *et al.* 1995) were also available from many Little Tern colonies and were used to provide a crude measure of productivity. Movements of fledglings among colonies, count errors and sampling bias in the counts create inaccuracies in this measure of productivity, and so it should be regarded at best as a crude index.

Sandwich Terns tend to breed in a few large colonies, most of which are in nature reserves and are counted annually. The 38 regularly censused Sandwich Tern colonies represented approximately 80% of the national population in 1985-

87, so trends described from these colonies should be accurate. These colonies were distributed throughout the Sandwich Tern's British and Irish breeding range, although the small colonies in Orkney, Stroma and some parts of western Ireland were counted neither regularly nor systematically enough to include in the sample. Some of the smaller colonies included in the sample were not counted annually, so gaps occur in these colony histories (6.4% of all cases).

Little Terns tend to nest in small, single-species colonies on beaches and spits, many of which are on nature reserves. Survey coverage was not as comprehensive as it is for Sandwich Terns because smaller, declining colonies and abandoned colonies were rarely monitored (Sears & Avery 1993); this tends to result in conservative estimates of downward trends. The total number of Little Terns at the 110 sampled colonies represented around 65% of the national total during 1985-87 complete survey. Sampled colonies were distributed throughout the species breeding range in the North and Irish Seas. The consistency of counting at the monitored colonies is far lower than for Sandwich Terns and so there are more gaps in colony histories (32.2% of all cases). Estimates of Little Tern population trends will therefore be less robust than for Sandwich Terns, but are likely give a reasonably accurate index of long-term population changes.

Due to the gaps in the colony census histories, simple summation of annual totals would result in biased population trends that are influenced by the temporal pattern of missing counts. Chain indices (Marchant *et al.* 1990) have been used to assess changes in population size at colonies counted in consecutive years (Sears & Avery 1993; Walsh *et al.* 1994). However, this method makes poor use of the available data as any counts at a colony that are not repeated in the following year are discarded. The program TRIM (Pannekoek & van Strien 1996), a log-linear model specifically designed to model trends in data with missing counts, was used to produce indices of population change with 95% confidence limits.

The TRIM indices give changes in population size relative to that in the first year measured (1969), which is scaled to an arbitrary value of 1. In order to derive annual population sizes rather than merely indices of change, all index values for both species were multiplied by the total British and Irish population sizes during the 1969-70 'Operation Seafarer' survey. The population estimates for the entire period are therefore dependent on the 1969-70 survey being comprehensive and accurate.

Regional trends were also computed in order to compare them with national trends. Studies of Roseate Tern natal fidelity and inter-colony movements suggest that sub-populations of the NW European metapopulation occur in the Irish Sea, the English Channel and the North Sea (Ratcliffè 1997). Population trends for Sandwich and Little Terns were therefore examined within

these regions on the assumption that their metapopulation structures were similar. The small number of colonies monitored in western Scotland and Ireland were pooled with the counts from the Irish Sea. The trends were analysed using TRIM, and the results presented as indices rather than population sizes.

Productivity of Little Terns was determined by summing the total number of pairs and total number of fledged young at colonies for each year of available data. Productivity may be calculated by dividing the total number of chicks fledged by the total number of pairs and trends investigated by regressing these values against year. However, analysis of trends using these summary statistics would result in uneven weighting of cases due to variation in sample sizes among years (Crawley 1993). Instead, a code of 1 was assigned to denote successes and 0 to denote failures. The value for successes was weighted by the total number of fledged chicks and the value for failures was weighted by the total number of pairs minus the total number of fledged chicks. Thus if 100 pairs produced 25 chicks, there would be 25 successes and 75 failures. This scheme produces identical annual estimates of productivity to the simple division of fledged young by number of pairs providing the overall annual productivity does not exceed one chick per pair, as was always the case for Little Terns. A logistic regression was used to determine the significance of productivity trends by testing the effect of year on success as a continuous covariate. The square of year was fitted in addition to year in order to test for Gaussian (bell-shaped) trends in productivity through time. The logistic models were fitted using the maximum likelihood ratio.

RESULTS

The British and Irish Sandwich Tern population during the last 30 years has been highly variable, with annual fluctuations and notable peaks and troughs (Fig. 1). The population increased from *c.* 12 000 pairs in 1969 to *c.* 17 000 pairs in 1971, an increase of 42%. This was followed by a sharp decline of 23% to *c.* 13 000 pairs in 1974. It then recovered at a rate of 6% *per annum* to *c.* 17 000 pairs in 1979 and fluctuated around 16 000 pairs until 1992, with a notable peak of 18 000 pairs in 1988. There was a second population crash of 20% between 1992 and 1995, with a total of *c.* 13 000 pairs in 1995. The population has been relatively stable from 1995-98 at 13 500-14 000 pairs. The population size in 1986 was estimated at *c.* 15 500 pairs using the modelled trend since 1969, whereas the complete census in 1985-87 (with most counts in 1986) was 18, 400 pairs (Lloyd *et al.* 1991). This suggests either that the colony trends were negatively biased or that the 1969 survey was an underestimate.

Analyses of regional trends show that the 1992-95 population crash was sustained primarily on the British North Sea coast (Fig. 2) where the population

during 1996-98 was lower than previously recorded. The North Sea hosted 73% of the British and Irish Sandwich Tern population in 1969, so it is not surprising that trends here have a large influence on the national population size. Examination of trends at individual colonies show the Sands of Forvie (Grampian, *c.* 1000 pairs in 1992) and Firth of Forth (473 pairs in 1991) declined and were ultimately abandoned between 1992 and 1995 without commensurate increases occurring at other colonies along the British North Sea coast. There was also a net loss of 1500 pairs from Northumberland between 1992 and 1995 due to declines at the Farnes that were not fully compensated for by observed increases at nearby Coquet Island. The colonies at Foulness and Havergate Island in Suffolk, which collectively contained 580 pairs in 1995, also declined and were abandoned in 1998.

In the English Channel (2% of the British and Irish population in 1969) the Sandwich Tern population was stable until 1980, but doubled in the following year (Fig. 2) due to increases at Dungeness and the Solent. The population has since fluctuated around this new level, with no notable changes during the period of the national population decline (Fig. 2).

In the Irish Sea (25% of the 1969 population) numbers increased by 50% in 1970 due to colony growth at Ravenglass (Cumbria), Green Island (Co. Down) and Tern Island (Co. Wexford) and then fluctuated around this level until 1986. The population then increased by a further 50% due to increases at Green Island, Strangford Lough (Co. Down) and Lady's Island Lake (Co. Wexford). There followed a decline of 25% between 1989 and 1992, which occurred at colonies in Strangford Lough and Cumbria (Fig. 2).

The Little Tern population increased from 2000 pairs in 1969 to 2600 pairs in 1971 and then decreased to *c.* 1800 pairs in 1973 (Fig. 3). It increased to a peak of 2800 in 1975 but then entered a long-term decline at an average rate of 1.23% *per annum*, punctuated by increases in 1988 and 1996 (Fig. 3). The population of *c.* 1700 in 1998 was the lowest recorded during the 30-year study and represents a 39% decline compared to 1975. The 1986 population estimate using the modelled trend since 1986 was *c.* 2300 pairs which again is lower than the complete census total of 2800 in Lloyd *et al.* (1991).

Analysis of regional trends show that declines have occurred throughout Britain and Ireland over the last two decades. The numbers in the English Channel (23% of the 1969 population) have decreased most and are approximately half of what they were in 1969 (Fig. 4). Numbers in the North Sea and western coasts (46% and 31% respectively of the 1969 population) have shown a less severe decline after the 1970s and are now at levels similar to those in 1969 (Fig. 4).

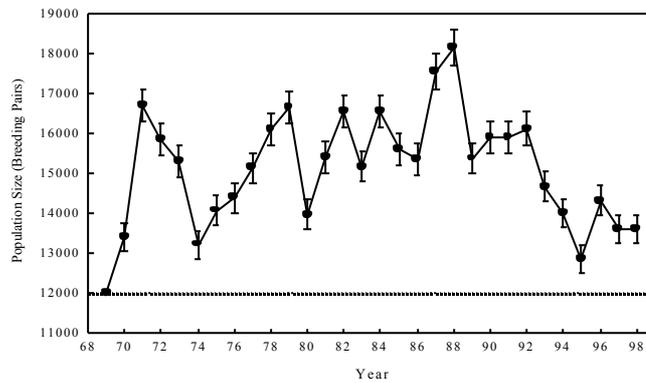


Figure 1. Population size and trends of Sandwich Terns in Britain and Ireland between 1969 and 1998. Error bars represent 95% confidence limits of the population estimates.

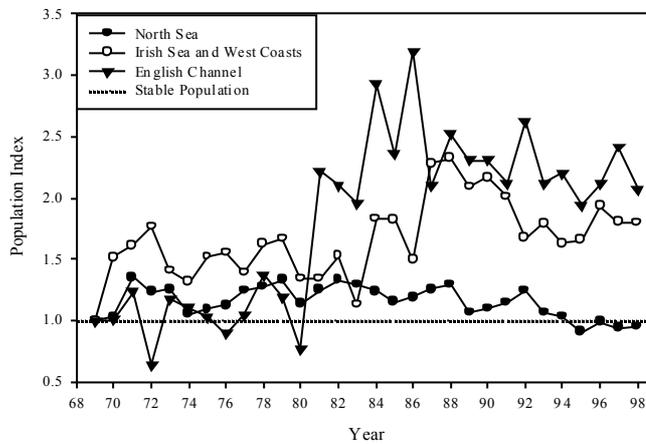


Figure 2. Population trends of British and Irish Sandwich Terns in the North Sea, Irish Sea and English Channel. Values are index values scaled as proportional change in population size compared with the population in 1969, which is given an arbitrary value of 1. The dotted reference line represents a stable population trajectory.

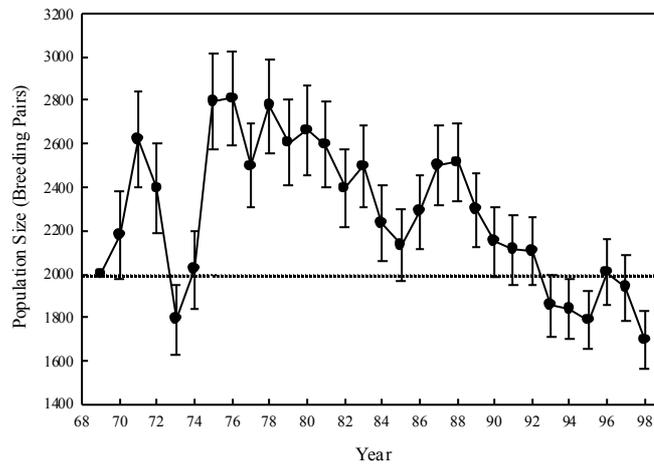


Figure 3. Population size and trends of Little Terns in Britain and Ireland between 1969 and 1998. Error bars represent 95% confidence limits of the population estimates.

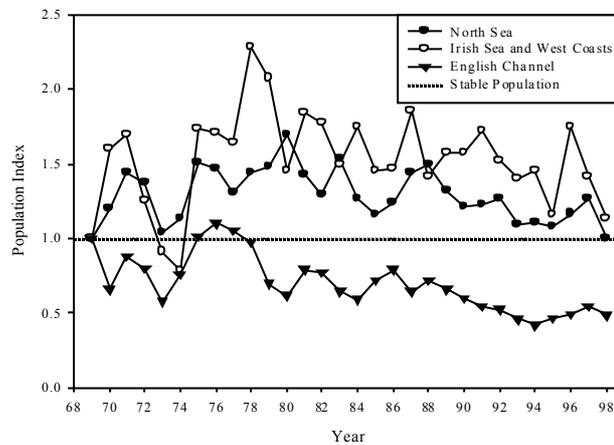


Figure 4. Population trends of British and Irish Little Terns in the North Sea, Irish Sea and English Channel. Values are index values scaled as proportional change in population size compared with the population in 1969, which is given an arbitrary value of 1. The dotted reference line represents a stable population trajectory.

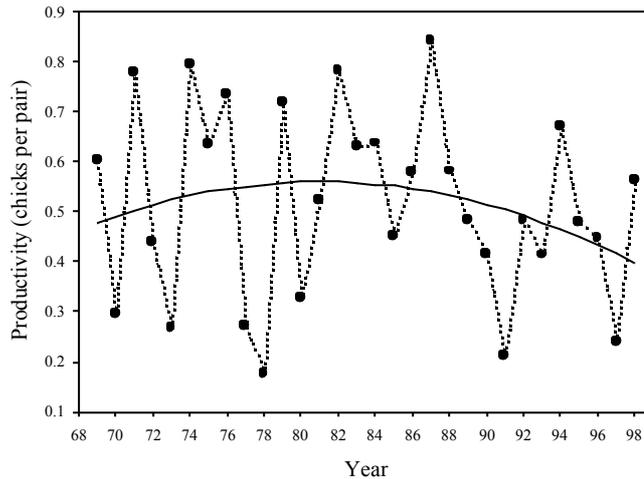


Figure 5. Trends in productivity of Little Terns between 1969 and 1998. Productivity estimates represent the number of chicks per breeding pair pooled over all colonies for which data were available in each year. The solid line represents the best fit logistic regression line.

A logistic regression showed that productivity increased significantly up to the early 1980s and then declined subsequently ($G_2 = 280.35$, $P < 0.0001$; Fig. 5), this Gaussian curve being a significantly better fit than the logistic one (improvement of fit from adding year² to model including year: $G_1 = 103.43$, $P < 0.0001$). However, the overall fit of the trend is poor ($r^2 = 0.01$) due to the large annual fluctuations in productivity.

DISCUSSION

Monitoring of sample colonies of Little and Sandwich Terns has revealed population declines in both these species that are of conservation concern. These downward trends may have been exaggerated because the modelled trend underestimated the size of the population compared with the national census estimates in 1986 (Lloyd *et al.* 1991). This may be because the sample colonies declined at a faster rate than the population as a whole or because the 1969 counts were underestimates. However, since the proportion of the populations of

both species that is monitored annually is large, it is unlikely that the trends are wholly unrepresentative and so the declines were probably real. The complete census of British and Irish tern populations planned for 2000 is timely so that long-term population trends can be determined with complete confidence and any bias in the sample monitoring programme can be investigated more thoroughly.

Detecting a decline only instructs conservationists that a problem exists, not what that problem is nor how to mitigate it. Identifying the factors responsible for tern population trends is difficult as terns are migratory and spend much of their lives at sea, so direct assessment of threats in declining colonies can be problematical. Effective interpretation of tern population trends depends on long-term monitoring of productivity (Becker 1998), survival (Croxall & Rothery 1991; Wendeln & Becker 1998), an understanding of inter-colony movements (Spendlow *et al.* 1995) and knowledge of migratory routes and wintering areas.

Unfortunately, data on tern demography and movements are few compared with those on population trends. Productivity data tend to be collected using peak counts of fledglings, but these are prone to errors due to inter-colony movements of juveniles; collection of these data also tends to be *ad hoc* rather than systematic. Analysis of dead recoveries is unlikely to yield precise estimates of survival rates because most birds are ringed as chicks, which confounds estimation of age-specific survival and reporting rates (Green *et al.* 1990). There are also few studies in Britain and Ireland that have estimated survival from resightings of colour-ringed terns. Therefore, a robust analysis of demographic parameters that have changed and precipitated the population declines described in this paper is not possible. However, several factors are likely to have affected Sandwich and Little Tern population trends at the breeding colonies.

The decline in the Sandwich Tern population in the 1990s appears to be due to localised events at individual colonies rather than widespread declines across its range. The abandonment of colonies at the Sands of Forvie (Grampian), Foulness and Havergate (Suffolk) and Foulney (Cumbria) during the early 1990s appears to have been in response to several years of Fox *Vulpes vulpes* predation that caused breeding failures in previous years (Thompson *et al.* 1996, 1997, 1998). All these sites are on mainland beaches or islets in lagoons, and so are vulnerable to mammalian predation. The reasons for the complete abandonment of the Forth colonies are more obscure since they are on offshore islets and inaccessible to mammalian predators. The main colony at Inchmickery was abandoned after several years of breeding failure and may have been due to encroachment of the increasing gull population onto the breeding area (D. Fairlamb, pers. comm.). Sandwich Terns attempted to breed on Long Craig islet between 1991 and 1996, but the Firth of Forth was completely abandoned by

1997. The reasons behind declines on the Farne Islands, which are also offshore and free from mammalian predators, are also obscure. Increases on nearby Coquet Island partially explain this decline, but there was still a net loss of 1500 pairs from Northumberland.

While abandonment of colonies by Sandwich Terns has been documented in the past, these have usually been followed by commensurate increases at other nearby sites (Lloyd *et al.* 1991). In the recent series of colony abandonment this appears not to have occurred. The birds must either have died, deferred breeding or emigrated to colonies outside Britain. Since the declines have been confined to the North Sea, emigration to the large colonies in the Netherlands and Germany might explain decreases in Britain. The populations there have indeed increased (Fleet *et al.* 1994; van Dijk & Meininger 1995; Südbeck & Hälterlein 1997) following catastrophic declines due to organochloride poisoning (Rooth 1981). However, the population growth has been at a steady rate and there is no evidence of sudden increases during the early 1990s that could explain the disappearance of over 2000 pairs from Britain, so emigration to eastern North Sea coasts appears not to explain the decline. Sandwich Tern populations experienced declines of similar magnitude in the early 1970s but rapidly recovered, so it is possible that the current population crash is another short-term perturbation in the longer term population trend. Further monitoring is clearly necessary to ensure that future recovery or further decline is recorded.

Concerns about decline in the Little Tern population predate 1969 (Parslow 1967) and prompted the first complete survey in 1967 (Norman & Saunders 1969). Little Terns prefer to nest on mainland beaches; increased use of the coast for human recreation probably led to increased breeding failure through disturbance and trampling (Norman & Saunders 1969). In the 1970s and 1980s many Little Tern colonies were designated as nature reserves and measures were taken to reduce disturbance, including wardening and sign-posting (Haddon & Knight 1983). Following a decline in the early 1970s, the Little Tern population increased, possibly due to improved breeding success of birds accorded protection from disturbance in nature reserves (Sears & Avery 1993).

Despite this protection there has been a long-term decline in the population since 1975, culminating in the lowest population recorded in Britain and Ireland during the 30 years of study in 1998 (see Results). Elsewhere in Europe, the fortunes of Little Terns have been mixed. The Netherlands population has declined from 400-500 pairs in the early 1980s to 350 pairs in 1992 (van Dijk & Meininger 1995). Numbers in the German Wadden Sea increased through the late 1970s and early 1980s before declining sharply during the mid 1980s (Fleet *et al.* 1994). There is some evidence of a recovery in the 1990s (Flore 1998) but the population is still below previous levels.

Population decline in Britain and Ireland has been associated with a downward trend in productivity since the early 1980s (see Results) and the resultant lower recruitment into the breeding population probably explains the decline. While the rate of decline may have been steeper had colonies not been protected from disturbance, it is clear that Little Tern reserves are not meeting their objectives of maintaining or increasing the population size. Factors other than disturbance are clearly responsible for the decline in productivity of Little Terns within these reserves.

Predation is listed as a major problem at many colonies, with foxes, Carrion Crows *Corvus corone* and Kestrels *Falco tinnunculus* being listed as the main predators (Norman & Saunders 1969; Lloyd *et al.* 1975; Haddon & Knight 1983; Thompson *et al.* 1998). Increased predation at colonies could be due to increases in fox and corvid populations (Tapper 1992; Gregory & Marchant 1996), or to the terns breeding in fewer, larger and fixed colonies that predators can exploit more easily (Sears & Avery 1993). Complete surveys are required to examine trends in the number and size of colonies; the only such survey to include the years of the decline in Little Terns was in Ireland (Whilde 1985; Hannon *et al.* 1997), which showed that the number of colonies halved from 40 in 1984 to 20 in 1995.

Efforts have been made to guard against mammalian predation at many colonies by erecting electric fencing (Haddon & Knight 1983; Brindley 1995, 1996, 1998; Behmann 1998; Pickerell 1998). Electric fencing reduces the likelihood of fox incursion, but occasionally foxes can avoid them and cause significant damage (Patterson 1977; Haddon & Knight 1983; Brindley 1995, 1996, 1998; Pickerell 1998). Nocturnal patrols of the colony perimeter by wardens appear to be the most effective way of deterring fox predation (Brindley 1998; Pickerell 1998). Other methods of reducing mammalian predation at colonies include use of chemical deterrents (Haddon & Knight 1983) and ultrasonic scaring devices (Brindley 1998), which appear to be ineffective. Attempts to counter avian predation have included provision of chick shelters (Brindley 1998) and supplementary feeding of Kestrels (Durdin 1992). Methods of controlling predation are generally applied in an *ad hoc* manner rather than experimentally and the limited monitoring of their effects on predation rates does not allow assessment of their efficacy in improving productivity (Sears and Avery 1993).

Flooding during spring tides is also a problem at many colonies (Lloyd *et al.* 1975; Haddon & Knight 1983; Pickerell 1998) and this may have increased due to long-term rises in sea levels (Norris & Bussion 1994). Sea level rise is likely to be a particular problem in the Little Tern stronghold of East Anglia, where rates of rise are likely to be highest and strong sea defences prevent reformation of natural coastal profiles further inshore (Norris & Bussion 1994).

This could reduce breeding habitat for Little Terns and render remaining sites more vulnerable to flooding. Attempts to counter flooding at Little Tern colonies have included major restructuring of a few colonies and removal of eggs from marked scrapes just prior to an incoming spring tide and replacing them afterwards (Haddon & Knight 1983).

Further studies of tern demography are required to monitor survival rates, interpret effects of varying productivity on population changes and to assess inter-colony movements. Survival rate estimates could be obtained for Sandwich Terns by integrating ring-recovery analyses with count and productivity data (Green *et al.* 1990), but this is unlikely to yield precise estimates for Little Tern survival due to the low number of recoveries (Toms *et al.* 1999). Accurate estimates of survival and inter-colony movement rates for both Little and Sandwich terns are likely to depend on colour-ringing or field-readable metal rings (Casey *et al.* 1995) or PIT tags (Wendeln & Becker 1998) that allow live adults to be re-sighted in consecutive years (Massey *et al.* 1992; Renken & Smith 1995; Spendelow *et al.* 1995; Ratcliffe 1997; Wendeln & Becker 1998). This demands capture of adults in order to produce a representative age structure for the population within a short time; problems with disturbance should be minimal if established protocols are followed (Brubeck *et al.* 1981; Nisbet 1981; Massey *et al.* 1988; Hill & Talent 1990). Such studies require a great deal of effort to be successful and should be initiated only in a few accessible colonies.

Further research into management of tern colonies is also required. The efficacy of the various methods employed in tern reserves to reduce predation needs to be tested experimentally by comparison of clutch and chick survival rates under different treatments. Recommendations for effective anti-predator management may then be formulated.

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SAMENVATTING

POPULATIEONTWIKKELINGEN VAN DWERGSTERN *STERNA ALBIFRONS* EN GROTE STERN *S. SANDVICENSIS* IN GROOT-BRITANNIË EN IERLAND VAN 1969 TOT 1998

*Van 1969 tot en met 1998 werden de aantallen broedende Dwergstems *Sterna albifrons* en Grote Sterns *Sterna sandvicensis* in Groot-Brittannië en Ierland steekproefsgewijs geteld. De Grote Stern nam toe van c. 12 000 paren in 1969 tot c. 17 000 paren in 1971, maar nam vervolgens af tot c. 13 000 paren in 1974. Sindsdien groeide de populatie met 6% per jaar tot c. 17 000 paren in 1979,*

waama tot aan 1992 de populatie schommelde rond 16 000 pairs. Een tweede opmerkelijke afname in de populatie (20%) werd waargenomen tussen 1992 en 1995, zodat in 1995 nog maar c. 13 000 paren tot broeden kwamen. Deze afname lijkt nu tot stilstand te zijn gekomen, aangezien de populatie zich gestabiliseerd heeft op een niveau van ongeveer 13 500-14 000 paren.

De Dwergstem nam toe van 2000 paren in 1969 tot 2600 paren in 1971, om vervolgens af te nemen tot ongeveer 1800 paren in 1973. Een korte periode van herstel tot liefst 2800 broedparen in 1975 werd gevolgd door een langdurige periode van gestage neergang met gemiddeld 1.2% per jaar, afgewisseld met korte perioden van herstel in 1988 and 1996. De in 1998 gemeten populatiegrootte, c. 1700 broedparen, was het laagste gedurende de 30 jaren van onderzoek en betekent een afname van 39% sinds 1975. De neergaande trend bij de Grote Stern blijkt zich vrijwel geheel te hebben beperkt tot de Noordzee en bovendien werd de afname veroorzaakt door teleurstellende resultaten in een klein aantal kolonies. In tegenstelling daarmee lijkt de afname bij de Dwergstem een structureel en wijdverbreid probleem te zijn. Mogelijke oorzaken van de teruggang worden besproken en aanbevelingen worden gedaan voor toegepast beheer, toekomstig onderzoek en een voortgezet monitoringprogramma.

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POPULATION TRENDS OF KITTIWAKE *RISSA TRIDACTYLA*, BLACK GUILLEMOT *CEPPHUS GRYLLE* AND COMMON GUILLEMOT *URIA AALGE* IN SHETLAND, 1978-98

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Kittiwake Rissa tridactyla numbers in Shetland, monitored by periodic nest counts at all colonies, declined from 54 600 pairs in 1981 to 23 000 pairs in 1998, probably due to low food availability and increased predation by Great Skuas Catharacta skua. Pre-breeding counts of Black Guillemots Cepphus grylle along selected stretches of coastline showed variable trends. In Yell Sound, an increase of 155% between 1983 and 1998 probably represented recovery after mortality from oil pollution in 1979. Elsewhere, some decreases were associated with localised oil pollution. Common Guillemot Uria aalge numbers at four colonies increased in the late 1970s and early 1980s, but then declined up to 1990; thereafter, numbers increased at all colonies. At the largest colony, Guillemot numbers had returned to their previous peak by the mid 1990s, but at the three smaller colonies they remained at c. 50% of early 1980s levels. Large-scale change in food availability in the North Sea is thought to have caused increased winter mortality during the early 1980s, whereas reduced abundance of sandeels may have contributed to reduced colony attendance of non-breeding and off-duty birds and therefore apparently low population levels from 1989-91.

Heubeck M. 2000. Population trends of Kittiwake *Rissa tridactyla*, Black Guillemot *Cepphus grylle* and Common Guillemot *Uria aalge* in Shetland, 1978-98. *Atlantic Seabirds* 2(3/4) Special Issue: 227-244.

INTRODUCTION

Twenty-one species of seabird breed regularly in Shetland, many in populations of national or international importance (Lloyd *et al.* 1991). Some of the larger multi-species colonies are world-reknowned and have long been afforded protected status such as that of National Nature Reserve. Shetland's seabird populations attract thousands of tourists to the islands each year and so are an integral component of the local economy.

The discovery in 1971-72 of oil 150 km north-east of the islands and the siting of an oil terminal at Sullom Voe in the north Mainland of Shetland resulted in concern of possible pollution, and led the local authority and the oil industry establishing the Sullom Voe Environmental Advisory Group (SVEAG).

Opposite page: figure 1. Map of Shetland showing the location of Yell Sound, Kittiwake breeding stations (squares 1-12, named in Fig. 3), Black Guillemot monitoring sites (circles, A-O, named in Fig. 6) and the four monitored Guillemot colonies (named).

Figure 2. Map of Yell Sound showing the six monitoring areas for Black Guillemot, and the location of the Sullom Voe Terminal (S.V.T.). Cliff coastline over 50 m high is indicated by solid black.

During 1974-76, SVEAG and the then Nature Conservancy Council initiated baseline surveys of seabird distribution and numbers. In early 1978, the Shetland Oil Terminal Environmental Advisory Group (SOTEAG), the successor to SVEAG, established a programme of seabird monitoring based upon these earlier studies (Richardson *et al.* 1981; Dunnet & Heubeck 1995). This programme continues, and this paper describes population trends over a period of approximately 20 years for Kittiwake *Rissa tridactyla*, Black Guillemot *Cepphus grylle*, and Common Guillemot *Uria aalge*, three species that have shown considerable changes in breeding numbers.

METHODS

Kittiwake Initially, Kittiwake monitoring consisted of repeated counts of occupied nests in study plots at Sumburgh Head, Troswick Ness, Eshaness and Burravoe (Fig. 1). The proportion of nests included in these plots varied from 18% (Sumburgh Head) to 100% (Burravoe); neither colonies nor plots were selected randomly, but were chosen to provide a degree of geographic spread of the islands (Dunnet & Heubeck 1995). Complete surveys in 1981 and 1985-87 indicated that both increases and decreases in numbers had occurred, and at greatly varying rates, at different colonies (Richardson 1985; Heubeck *et al.* 1986).

The monitoring strategy soon developed to survey all Shetland colonies at intervals not exceeding three years, and to check other suitable cliff habitat for new colonies. Many colonies were not visible from land and so these surveys were carried out from an inflatable boat. Since this method depended on favourable wind and sea conditions, surveys were made on an opportunistic rather than planned basis and instead of regular three-yearly counts, coasts were surveyed at intervals of one to five years. In order to estimate change in the overall population, the numbers of nests at breeding stations in years when no counts were made were predicted from mean annual rates of change between sets of actual counts. The totals of actual and predicted nest counts were summed to estimate the Shetland breeding population for each year (Heubeck *et al.* 1999).

Since 1986 breeding success (chicks fledged per nest in which eggs were seen or assumed to have been laid) has been monitored at several colonies, using standardised methodology (Harris 1987; Walsh *et al.* 1995).

Black Guillemot Baseline surveys of Black Guillemots and methodology development were carried out by Oxford University during 1982-84 (Ewins 1985, Ewins & Tasker 1985), and population monitoring began in 1985. Birds were counted in the pre-breeding season (late March to early May), when adults spend the first hours of daylight close inshore, or ashore, displaying near prospective nest sites. Counts were made between 0400 and 0800 h GMT only in favourable weather and sea conditions. Birds ashore were flushed onto the sea and birds in adult plumage within 200 m of the coast were regarded as being associated with potential breeding sites; their location was marked on 1:25 000 maps. Adults further offshore or feeding, and immature birds, were recorded separately and are not considered here.

As well as variable daily attendance of adults, the number of birds counted can be affected by sea and weather conditions, and by their willingness to leave cliff perches (where they are more likely to be overlooked than on the sea). Pre-breeding colony attendance of *Cepphus* spp. can also be affected by

tidal state, with some birds opting to feed rather than display on mornings of particularly low tides (Vermeer *et al.* 1993). However, the constraint of suitably calm weather meant surveys could not be limited only to periods of high tide.

The aim was to survey twice per season and in alternate years the entire coast of Yell Sound, mostly by inflatable boat, and 15 other sites around Shetland from land (Fig. 1); however, poor weather prevented strict adherence to this schedule.

A complete survey of Yell Sound usually takes eight mornings so for recording purposes the coastline was divided into six areas, each differing considerably in the extent of suitable nesting habitat (Fig. 2). Where two surveys were made the higher count of each area was used to calculate an overall total for Yell Sound.

Common Guillemot Between 1976 and 1998, Guillemots were counted during June in study plots at one large (Sumburgh Head) and three smaller colonies (Troswick Ness, Eshaness and Burravoe; Fig. 1). All birds visible from the clifftop were counted at Eshaness and Burravoe, and almost all at Troswick Ness; plots were selected non-randomly at Sumburgh Head to include a range of cliff types and different parts of the colony. Counts followed established protocols regarding time of day and weather conditions (Walsh *et al.* 1995). Until 1985 counts were made on up to 10 different dates throughout June, but in subsequent years this was reduced to five dates during the first three weeks of June. An annual mean was calculated for each colony from the total daily counts, and an annual population index was calculated based on the 1978 mean (assigned a value of 100). Between 1989 and 1998, breeding success was monitored at a single plot at Sumburgh Head, and provides counts of site-holding and egg-laying pairs (Walsh *et al.* 1995).

RESULTS

Kittiwake Counts of nests in study plots during 1976-88 have been published elsewhere (Heubeck *et al.* 1986; Dunnet & Heubeck 1995). Since the monitoring strategy changed to periodic counts of all nests in all Shetland breeding stations, variation in trends in numbers at individual stations has become increasingly apparent (Fig. 3). Some, such as Eshaness and Saxavord, have shown marked increases followed by even greater decreases, while decreases followed by increases occurred at some smaller stations such as Griskerry and Clett Head. This reinforces the need to monitor the population through counts at all stations.

The total population of 54 600 pairs in 1981 declined by 51% to 27 000 pairs in 1997 (Heubeck *et al.* 1999), with a further decline to an estimated 23 000 pairs in 1998 (Fig. 4).

Opposite page: figure 3. Counts of nests at selected Kittiwake breeding stations, 1981-98. 1. Ramna Stacks; 2. Eshaness; 3. Papa Stour; 4. Vaila; 5. Griskerry; 6. Horse Island; 7. Saxavord; 8. Burravoe; 9. Clett Head; 10. Noss; 11. Troswick Ness; 12. Boddam. See Fig. 1 for locations.

Figure 4. The estimated Shetland Kittiwake breeding population, 1981-98.

Breeding success varied considerably, both between years (Fig. 5) and between colonies in the same year (Heubeck *et al.* 1999). Average breeding success was very low (< 0.2 young fledged per pair) during 1988-90 and again in 1997 and 1998, and exceeded 0.8 only in 1992. Most Kittiwakes first breed when 4-5 years old (Wooller & Coulson 1977), and while it would appear that the low breeding success during 1988-90 was followed by rapid population decline in 1992-94, that decline continued during 1996-98 despite greatly improved breeding success in 1992-94.

Figure 5. Mean annual Kittiwake breeding success (young fledged per nest at which eggs were seen or assumed to have been laid) at 5-10 monitored breeding stations.

Black Guillemot Full coverage of Yell Sound was achieved in eight years, but two complete counts were made in only four of these (Table 1). The 1985-98 surveys were conducted in the same manner and within the same time limits, but the mix of land/sea-based surveys differed in 1983, when some surveys continued beyond 0800 h. Of the 29 occasions when second surveys were made, the first and second counts were each higher in 14 instances and were identical in one, indicating an equal chance of obtaining a higher count on first and second surveys. While comparison of the results of a single survey (1983) with the higher counts obtained per area on two complete surveys (1998) is not strictly valid, the percentage change *per annum* between 1983 and 1998 (+6.4% p.a.) was only marginally higher than between 1985 and 1998 (+6.3% p.a.), both years when two complete surveys were achieved in favourable conditions.

Between 1983 and 1998 the number of Black Guillemots increased by 155%. This increase probably represents recovery from the December 1978 *Esso Bernicia* spill of 1174 tonnes of bunker fuel oil at the Sullom Voe Terminal, following which 729 Black Guillemots were found oiled, mostly on beaches in Yell Sound (Heubeck & Richardson 1980).

The mean annual rate of increase in Yell Sound declined from 12.1%

during 1983-88, to 5.3% during 1988-93, and to 2.1% during 1993-98. Indeed, since 1993 numbers have increased only along the high cliffs of West Yell (Area 1), the longest continuous stretch of suitable breeding habitat in Yell Sound. With 738 adults along 8.5 km of coast this is one of the largest breeding concentrations of Black Guillemots in the UK (Lloyd *et al.* 1991). In southern Yell Sound (Areas 5 and 6) where cliffs are low and colonies small and scattered, the number of adults associated with particular sites and islands has fluctuated markedly between years. For example, at Copister Broch 15 adults

Table 1. Pre-breeding counts of Black Guillemots in Yell Sound, 1983-98. Counts are of 'associated adults' recorded on the first and second survey (where made) of each of six areas. Most counts were made in good weather and sea conditions throughout; other counts (in italics) may be underestimates caused by suboptimal survey conditions. Totals given are (A) the sum of the first and second surveys, and (B) the sum of the higher count per area.

Area	1983 1st/2nd	1985 1st/2nd	1987 1st/2nd	1988 1st/2nd	1990 1st/2nd
1	<i>131/ -</i>	202/145	<i>264/ -</i>	372/335	<i>322/ -</i>
2	<i>226/ -</i>	226/231	<i>247/275</i>	254/262	291/288*
3	<i>59/ -</i>	89/82	<i>117/ -</i>	135/128	<i>99/ -</i>
4	<i>35/ -</i>	28/30	<i>53/ -</i>	61/58	<i>54/ -</i>
5	<i>34/ -</i>	41/41	<i>72/ -</i>	65/85	<i>69/ -</i>
6	<i>70/ -</i>	50/40	<i>74/ -</i>	69/65	<i>89/ -</i>
Total A	<i>555/ -</i>	636/569	<i>827/ -</i>	956/933	<i>924*/ -</i>
Total B	555	643	855	984	924*
% change per annum		+ 7.6 1983-85	+15.3 1985-87	+15.1 1987-88	

Area	1991 1st/2nd	1993 1st/2nd	1996 1st/2nd	1998 1st/2nd	1983-98 % change
1	422/ -	<i>585/ -</i>	<i>652/499</i>	697/738	+463
2	295/-	298/340	<i>323/301</i>	310/343	+52
3	155/ -	147/ -	<i>144/141</i>	142/145	+146
4	72/ -	<i>50/67</i>	71/65	57/70	+100
5	65/ -	75/ -	37/48	47/56	+65
6	76/ -	61/ -	52/83	<i>64/57*</i>	-9
Total A	1085/ -	1216/ -	1279/1137	1317/1409	
Total B	1085	1275	1321	1416	+155
% change per annum	+ 3.3 1988-91	+ 8.4 1991-93	+ 1.2 1993-96	+ 3.5 1996-98	+ 6.4 1983-98

* incomplete coverage of the area

Figure 6. Counts of Black Guillemots at 15 monitoring sites, 1982-98. Solid symbols are actual counts, open symbols are estimates calculated by mean annual percentage change between actual counts. Letters denote site locations (see Fig. 1).

were counted in 1983, 29 in 1985, 39 in 1987, 21 in 1990, 33 in 1993, and 16 in 1998. Although variable attendance patterns may have contributed to these differences, some birds at this and other sites on low islands have been depredated by Otters *Lutra lutra* in recent years (Fowler 1995; *pers. obs.*).

Numbers at other Shetland monitoring sites showed no uniform trend since the early 1980s (Fig. 6). Generally, however, numbers increased slightly or remained rather stable during the 1980s. Some subsequent changes followed known localised mortality of Black Guillemots from oil pollution incidents, most notably the decreases in 1993 in south-west Mainland (Sites E and F), on Fair Isle (O), and possibly at Site N in south-east Mainland following the *Braer* oil spill in January 1993 (Heubeck 1997). Each of these decreases was followed by an increase. Smaller incidents involving oiled Black Guillemots also occurred in early 1985 and 1991 in south-east Mainland (sites L-N; Heubeck 1995a). At one site (M) where a 44% decrease between 1987 and 1992 was followed by little or no increase in numbers, predation at nest sites by Otters is thought to have increased in recent years. However, the causes of other apparent changes, such as the fluctuations at Site K and the 1997-98 decrease at Site O, are not known.

Common Guillemot At the four monitored colonies, numbers increased or were stable between 1976 and 1984 (Fig. 7). A decline to a uniformly low level in 1990 began earlier and was greater at the three smaller colonies than at Sumburgh Head. Numbers at Sumburgh Head then increased, and by 1995 exceeded the previous peak in 1984. Although numbers at the other three colonies increased between 1990 and 1992/93, they then remained relatively stable at *c.* 60-70% of 1978 levels.

The census unit for Guillemots is the number of birds present at the colony (Walsh *et al.* 1995). Standardisation of the time of counts can control for diurnal and seasonal variation in colony attendance of off-duty and non-breeding birds, but attendance is also affected by wind speed and precipitation (Birkhead 1978), and by food abundance (Uttley *et al.* 1994). Over the years, breeding numbers have certainly changed in Shetland; one plot at Sumburgh Head held seven pairs in 1978 but 200 in 1995, and some plots at Eshaness and Burravoe were abandoned by 1987/88. There is a significant correlation (Spearman rank correlation, $r_s = 0.466$, $n = 22$, $P = 0.029$) between the mean population index for the four colonies and changes in estimates of sandeel *Ammodytes marinus* abundance around Shetland (Fig. 8), suggesting that at least some of the inferred changes in Guillemot populations may relate to changes in colony attendance.

At Sumburgh Head there was little change between 1989 and 1991 in the number of site-holding and egg-laying pairs in the only plot in which breeding success was monitored (Fig. 9), but the population index recorded at other plots fell significantly between 1988 and 1989 ($t = 5.89$, $df = 8$, $P < 0.001$)

and between 1989 and 1990 ($t = 6.70$, $df = 8$, $P < 0.001$), then rose significantly between 1990 and 1991 ($t = 4.56$, $df = 8$, $P < 0.001$), and also between 1991 and 1992 ($t = 5.21$, $df = 8$, $P < 0.001$). Similarly, the population index fell significantly between 1997 and 1998 ($t = 2.35$, $df = 8$, $P < 0.05$), although numbers in the breeding success plot continued to rise.

Figure 7. Indices (1978 = 100) of mean annual counts of Guillemots in study plots at four breeding colonies plotted on a log scale. Actual counts (1978): Sumburgh Head 1326; Troswick Ness 282; Eshaness 699; Burravoe 334. See Fig. 1. for colony locations.

Figure 8. Mean annual index (1978 = 100) of Guillemots (●) in study plots at four breeding colonies, and estimates of total stock biomass (TSB) of sandeels (I) at 1 July in the Shetland assessment area (1998 = 567 634 tonnes), plotted on a log scale. Sandeel data courtesy of the Scottish Executive Rural Affairs Department.

Figure 9. Mean annual index (1978 = 100) of Guillemot numbers in eight study plots at Sumburgh Head (solid symbols indicate a statistically significant change from the previous year; see text) and the actual number of site-holding and egg-laying pairs in a single breeding success study plot.

DISCUSSION

A population monitoring programme should be able to answer two questions: 1) are any changes recorded real or an artefact of the methodology?; and 2) are the changes confined to the sites sampled or have they occurred in the wider population? Ancillary studies such as ringing programmes, beached bird surveys and monitoring of breeding success might suggest causes for the observed changes. From a conservation viewpoint, population declines are of particular interest. Since SOTEAG's monitoring programme is funded by the partners in the Sullom Voe Oil Terminal, any impact of oil pollution is of concern. The breeding ecology of Kittiwakes, Black Guillemots and Guillemots are very different, and this has resulted in different approaches to monitoring changes in their breeding population. Their wintering ecology also differs, and Kittiwakes and Guillemots face threats such as oil pollution, food shortage, or entanglement in fishing gear in areas far from Shetland.

Kittiwake Kittiwakes breed colonially in traditional sites and build conspicuous nests, so monitoring changes in breeding numbers is straightforward. Trends at particular breeding stations differed in direction and rate, but periodically surveying all stations from the sea and checking suitable habitat for new colonies ensured complete coverage. Although weather and sea conditions prevented some stations being surveyed for four or five years, counts at those surveyed most frequently suggest that while rate of change can be high, abrupt reversals of its direction or fluctuation in numbers occur rarely. All the evidence shows that the Shetland Kittiwake population is in decline.

The most likely causes of this population decline have been low breeding success, especially during the late 1980s, and increased predation of adults by Great Skuas *Catharacta skua*. Low breeding success was associated with reduced local sandeel abundance during the late 1980s (Hamer *et al.* 1993; Wright & Bailey 1993), while predation of Kittiwake eggs, chicks and adults by Great Skuas that increased as sandeel abundance declined is also believed to have caused considerable desertion by breeding adults of the most affected colonies (Hamer *et al.* 1991; Furness 1997; Heubeck *et al.* 1997). By the mid-1990s predation of adult Kittiwakes was considered to be at an unsustainable level (Furness 1997).

The only other possible factor contributing to the decline is emigration of breeding adults to colonies in Orkney, where numbers increased during the late 1980s when the decline in Shetland was greatest (Heubeck *et al.* 1999). Oil pollution around Shetland appears not to have contributed to the decline since between 1979 and 1992 only 4.2% of over 4000 dead Kittiwakes found on beached bird surveys in Shetland were oiled. This proportion is lower than has been found in the southern North Sea (Camphuysen 1989). Beached bird survey data indicate only one instance of large-scale, non oil-related mortality - a 'wreck' in January 1993 that followed prolonged south-westerly gales, and that also coincided with the *Braer* oil spill. However, this probably involved birds breeding mainly north of Shetland (Weir *et al.* 1996).

Black Guillemot As Black Guillemots are largely resident in Shetland and, apart from those breeding on isolated exposed islands, probably do not move far from their natal colonies during their lifetime (Ewins 1988), interpretation of the causes of population change is easier than for many other seabirds. However, Black Guillemots are difficult to monitor since they nest mainly in crevices on rocky coasts. Counting pre-breeding adults may be the best method of monitoring, but it does have some drawbacks. Firstly, some coastlines are inherently more difficult to survey accurately because of topography, cliff height and sea conditions (e.g. persistent tide rips). Secondly, the number of birds in adult plumage attending potential breeding sites compared with actual breeding

numbers varies considerably between colonies (Ewins 1985). Thirdly, on some mornings attendance at sites is either low or non-existent (*pers. obs.*), birds presumably having decided to feed rather than display. Finally, counting Black Guillemots during the pre-breeding season is not easy, especially in early May when birds can be difficult to flush from cliffs. An observer's familiarity with the coastline, with favoured perches and the likely number of birds present probably increases both the number of Black Guillemots recorded and the consistency of successive counts.

Despite these caveats, it is reasonable to conclude, firstly, that a substantial increase in breeding numbers occurred in Yell Sound from at least 1983 onwards, which probably represented population recovery from losses caused by the *Esso Bernicia* oil spill of early 1979. Secondly, declines at other sites followed localised mortality of Black Guillemots from oil pollution, but numbers have tended to soon recover rather quickly.

Common Guillemot Although Guillemots are relatively easy to count, variation in attendance patterns of off-duty and non-breeding birds makes interpretation of counts difficult. With new areas of cliff being colonised at Sumburgh Head during the early 1980s, and breeding ledges being deserted at Eshaness and Burrae in the late 1980s, there is little doubt that the overall Shetland Guillemot population did increase up to the early 1980s and then decreased, but uncertainties remain over the scale of these changes. The marked reduction in numbers in 1990 in particular, and possibly also in 1989 and 1991, is likely to have been at least partly due to low colony attendance during a period of low sandeel abundance (Heubeck *et al.* 1991; Uttley *et al.* 1994). There was no significant overall trend in Guillemot numbers in Shetland during 1986-98, in contrast to Orkney and east Scotland where numbers increased (Thompson *et al.* 1999). However, there was a marked contrast between trends at Sumburgh Head, where numbers declined less and then increased beyond their previous peak levels by the mid-1990s, and the three other colonies, where numbers decreased sooner and more rapidly but then remained relatively stable at about half their previous peaks.

Analysis of recoveries of ringed birds revealed that many immature Guillemots from Shetland colonies were killed by oil pollution in the Skagerrak and south-eastern North Sea in the winter of 1980/81, and it was suggested that this mortality might result in a reduction of at least 6-9% in breeding numbers by 1985 (Baillie & Mead 1982); between 1980 and 1985 the population index at the four monitored Shetland colonies fell by 17%. Further analysis of ringing returns of Guillemots ringed in Shetland colonies indicated an increase in recovery rates of birds of all ages during the early 1980s, with a subsequent reduction in the late 1980s (Heubeck *et al.* 1991). Drowning in fishing nets in Scandinavia, oil

pollution in the southern North Sea, or simply being found dead but not oiled on beaches (mainly on the east coast of Britain) were the three main reported causes of death, and each followed the same pattern of increase and decrease. A similar increase in first-winter recovery rates of Guillemots ringed as chicks on the Isle of May also occurred during the 1980s (Harris & Bailey 1992). In contrast to Shetland, there was no reduction in the late 1980s and adult survival rates remained high. The Isle of May population declined slightly between 1983 and 1990 having previously increased rapidly.

Sprats *Sprattus sprattus* are an important component of the diet of Guillemots wintering in the North Sea (Blake *et al.* 1985), and a decline in the North Sea sprat population in the early 1980s and a southerly shift in its centre of distribution is thought to have led to changes in the winter distribution of Guillemots in the North Sea (Camphuysen 1990; Corten 1990; Harris & Bailey 1992). This shift may have brought Guillemots into areas of higher risk of mortality from oil pollution or entanglement in fish nets (Peterz & Olden 1987; Camphuysen 1989). Change in sprat abundance may have been at least partially responsible for the large wreck of auks on the east coast of Britain in February 1993 (Blake 1984), one of a series that occurred during the 1980s, and which continued sporadically until 1996 (Heubeck *et al.* 1992; Heubeck 1999).

Oil pollution in Shetland waters is unlikely to have contributed significantly to changes in the Guillemot population. The numbers of oiled Guillemots found on beached birds surveys decreased during the 1980s and have generally been considerably lower than on coasts further south in the North Sea (Camphuysen 1989; Heubeck 1995b).

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SAMENVATTING

POPULATIEONTWIKKELINGEN BIJ DRIETEENMEEUW, ZWARTE ZEEKOET EN ZEEKOET OP SHETLAND, 1978-98

*Uit periodieke tellingen van nesten op alle kolonies is gebleken dat de aantallen Drieteenmeeuwen *Rissa tridactyla* op de Shetland Eilanden zijn afgenomen van 54 600 paren in 1981 tot 23 000 paren in 1998, vermoedelijk door een afgenomen voedselaanbod in combinatie met een toegenomen predatie door Grote Jagers *Catharacta skua*. Tellingen van Zwarte Zeekoeten *Cephus grylle* juist voorafgaande aan het broedseizoen langs geselecteerde stukken kustlijn leverden wisselende*

resultaten op. In Yell Sound werd tussen 1983 en 1998 een toename van 155% geconstateerd; herstel van de populatie na een olie-incident in 1979. Elders werden afnamen geconstateerd, steeds samenhangend met olie-incidenten. De aantallen Zeekoeten *Uria aalge* in vier geselecteerde kolonies (study plots) namen toe gedurende de tweede helft van de jaren zeventig en het begin van de jaren tachtig, maar namen vervolgens af tot in de jaren negentig. Sindsdien namen de aantallen in alle gevolgd kolonies toe. In de grootste kolonie waren de aantallen Zeekoeten medio jaren negentig terug op het eerder bereikte piekniveau, maar op de drie resterende kolonies bleven de aantallen steken op ongeveer de helft van het niveau van begin jaren tachtig. Toegenomen wintersterfte, samenhangend met grootschalige veranderingen in voedselbeschikbaarheid begin jaren tachtig, wordt gezien als de oorzaak van deze populatieontwikkelingen. Daarnaast kan de teruggelopen beschikbaarheid van zandspiering *Ammodytes marinus* in de zomer hebben geleid tot een verminderde aanwezigheid van niet-broedende exemplaren in de kolonies in 1989-91.

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