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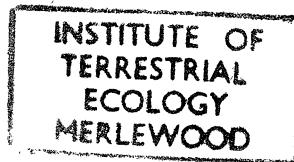
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Population changes in British Common Murres and Atlantic Puffins, 1969-88

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Abstract

The number of Common Murres *Uria aalge* in Britain and Ireland more than doubled, to 1.2 million, between 1969-70 and 1985-88. However, many populations started to decline by the early 1980s. In the North Sea, this decline started earliest in the north and gradually spread south, while the southern populations were still increasing. The decrease at an intensively studied colony appeared to be due to poor recruitment, which probably indicates poor survival of immatures. The number of Atlantic Puffins *Fratercula arctica* in Britain and Ireland increased, but by a smaller proportion, over the same period. The rate of increase in the population of Isle of May decreased after 1981, and by 1988 the population appeared stable. Survival of both adults and immatures was reduced. "Natural" factors were probably responsible for these changes, and there is nothing obvious that can be done in the way of management.

Résumé

Le nombre de Marmettes de Troïl *Uria aalge*, en Angleterre et en Irlande, a plus que doublé, atteignant 1,2 million, entre 1969-1970 et 1985-1988. Cependant, de nombreuses populations ont commencé à diminuer au début des années quatre-vingt. Dans la mer du Nord, cette baisse a commencé dans le nord s'étendant graduellement vers le sud, tandis que les populations du sud continuaient de s'accroître. La diminution, dans une colonie qui fait l'objet d'études intensives, semble attribuable à une diminution du recrutement, qui reflète probablement une baisse du taux de survie des jeunes oiseaux. Le nombre de Macareux moines *Fratercula arctica*, en Angleterre et en Irlande a augmenté, quoique dans une faible proportion, au cours de la même période. Le rythme d'augmentation de la population de l'île de May a ralenti après 1981 et, en 1988, la population semblait stable. Par ailleurs, la survie des adultes et des jeunes a diminué. Des facteurs «naturels» sont probablement à la base de ces changements, de sorte qu'aucune mesure particulière de gestion ne semble appropriée.

1. Introduction

Britain and Ireland have large and internationally important populations of seabirds, and during the last 20 years much effort has been put into monitoring changes in their numbers. Auks have figured prominently in this work because:

- (1) they are numerous and obvious;
- (2) they are peculiarly susceptible to a whole range of pollutants, including oil and chemicals (Bourne 1976);
- (3) they are potential competitors with expanding human fisheries for small fish such as sand lance *Ammodytes* spp. (Evans and Nettleship 1985);
- (4) various species feed in different ecological zones, which allows interesting ecological comparisons to be made; and
- (5) they have great appeal to the general public so that, if they are threatened, funds are often made available for research.

Much attention has focused on the Common Murre *Uria aalge* and the Atlantic Puffin *Fratercula arctica*, although for different reasons: the former is common, obvious, easily counted, and susceptible to oil pollution, whereas the latter has great public appeal and was at one time thought to be endangered.

Most monitoring schemes were originally set up solely to monitor changes in the numbers of seabirds. A recent review of the results of annual counting of murres at sample areas of British colonies concluded that the techniques used provided adequate descriptions of long-term changes in numbers but did not lead to a greater understanding of either the biological process involved or the factors that might be influencing the numbers of birds at the colonies (Rothery et al. 1988). Recent work has, therefore, concentrated on developing schemes to monitor various aspects of the demography and breeding biology of seabirds in an attempt to remedy this shortcoming.

The present paper reports on recent changes in the numbers of murres in Britain and on breeding output and survival at a single Scottish colony, where numbers were increasing rapidly until recently but are now declining. Some comparative data are also presented for the Atlantic Puffin from the same areas, although the results of the detailed studies are reported more fully elsewhere (Harris and Wanless 1991).

2. Methods

2.1. Common Murre

The numbers of individual murres ashore at all British and Irish colonies were counted in 1969–70 (Operation Seafarer) and in 1985–87 (Nature Conservancy Council – Seabird Group Seabird Colony Register). In these counts, it was impossible to separate breeding and nonbreeding birds. At most colonies, only single counts were made, so that the totals are of unknown accuracy. Counts at the same place made on different days can vary by up to 26% (Lloyd 1975), but, on the Isle of May during each June from 1981 to 1989, the mean error of single counts was 12% (95% confidence interval 7–17%, $n = 9$ years).

Commencing in 1969, numbers of murres at several colonies have been monitored annually by counting the individuals present in clearly defined areas on 5–10 d during the chick-rearing period in June (Seabird Group 1981; Stowe 1982). The representativeness of the sample plots used to determine population trends has been questioned (Harris et al. 1983; Heubeck et al. 1986; Mudge 1988), but, during the 1980s, attempts were made to overcome this by siting plots in some objective way (e.g., at random or stratified) or by counting all the birds in the colony (which may again cause problems if it is possible to make only a single count each year). As I am concerned here with long-term changes in numbers and not with year-to-year variation, I have given equal weight to complete and sample counts. The clear patterns that emerge suggest that the approach was justified. The colonies considered are shown in Figure 1 and listed in Table 1. In the Firth of Forth, murres on the Isle of May and all five nearby colonies have been counted regularly, and consequently I have pooled the counts and treated the colonies as a unit (Harris et al. 1987).

The results of complete surveys of all British and Irish murre and puffin colonies come from the reports and data files of Operation Seafarer (Cramp et al. 1974) and the Seabird Colony Register (C.S. Lloyd, pers. commun.). Monitoring of seabirds is carried out by a number of organizations, and there is, as yet, no complete data base of counts. My information included all counts stored in the Seabird Colony Register, with additional published and solicited unpublished data from Benn et al. (1987), Birkhead and Ashcroft (1975), Evans (1989), Harris et al. (1987), Hatchwell (1988), P. Hawkey (unpubl. data), Heubeck (1989a, and pers. commun.), Mudge (1986), K. Rideout (pers. commun.), Royal Society for the Protection of Birds (unpubl. data), Thomas (1988), Wanless et al. (1982), Ward (1987), and reports of the Nature Conservancy Council.

For each colony, counts (\ln) were plotted against year, and any obvious trends in numbers and turning points were assessed visually. All apparent trends involving counts in at least five years were tested using linear regression analysis, and only those significant at the 5% level are included here. Where a significant trend was found, all the years involved were included in the regression; thus, when a trend was reversed, a single year could be included in both a significant decline and a significant increase.

2.2. Atlantic Puffin

Puffins are much harder to census than murres, but the total population was assessed in 1969–70 and 1985–87, whereas that in east Britain (from the Moray Firth to the

Figure 1

Locations of colonies of Common Murres and Atlantic Puffins mentioned in the text. Numbers refer to the colonies listed in Table 1. The arrows indicate the limits of the east British population.

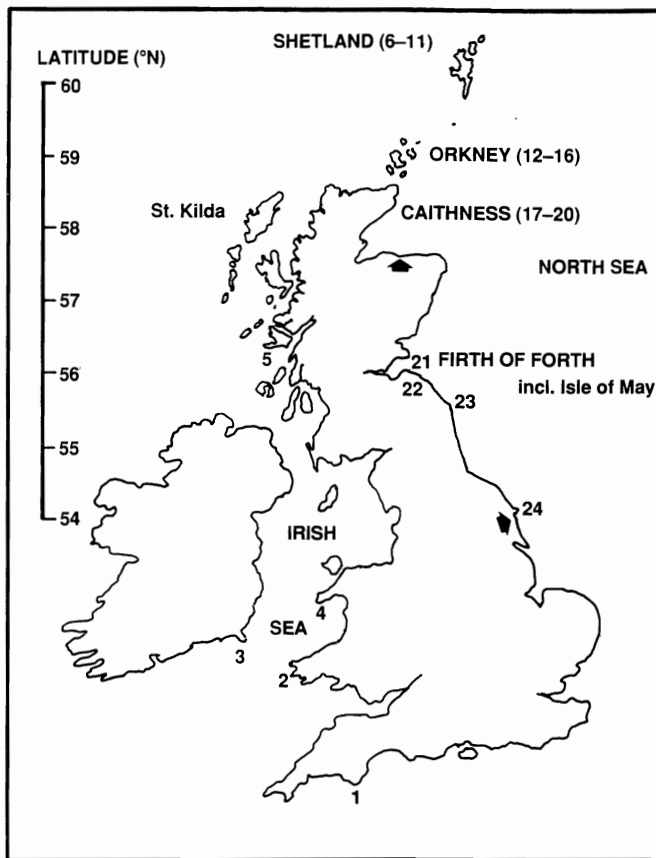


Table 1

Rate of change in the numbers of Common Murres at some British colonies^a

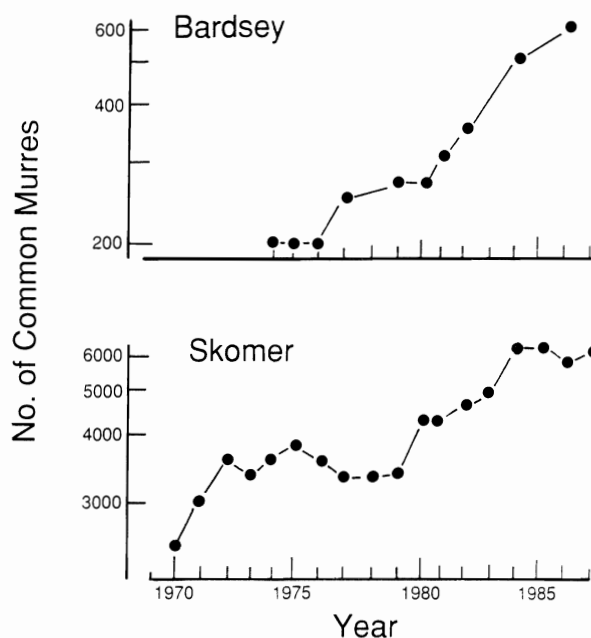
Colony ^b	Period	Type of count	No. of annual counts over which the trend extended	Mean change per annum (%)
1 Berry Head	1976–87	Total	6	+13
2 Skomer	1978–87	Total	9	+7
3 Great Saltee	1978–87	Total	5	+4
4 Bardsey	1976–87	Total	8	+10
5 Canna	1974–83	Sample	9	+11
6 Hermaness	1982–88	Sample	7	–8
7 Noss	1981–88	Sample	8	–7
8 Burrae	1982–88	Total	7	–28
9 Eshaness	1981–88	Total	8	–11
10 Troswickness	1976–82	Sample	7	+3
	1982–88	Sample	7	–12
11 Sumburgh Head	1977–84	Sample	8	+6
	1984–88	Sample	5	–5.5
12 Costa Head	1976–81	Sample	5	+5
13 Marwick Head	1976–80	Sample	5	+6
14 Row Head	1976–80	Sample	6	+6
15 Mull Head	1976–80	Sample	5	+13
	1981–88	Sample	8	–3
16 Gultak	1976–82	Sample	6	+4
	1981–88	Sample	8	–3
17 Skirza	1980–84	Sample	5	–3
	1984–88	Sample	5	+4
18 Inver Hill	1980–86	Sample	6	–6
19 Badbea	1980–87	Sample	8	–2
20 An Dun	1980–88	Sample	9	–3
21 Firth of Forth	1969–83	Total	5	+7
22 St. Abb's Head	1969–88	Total	10	+7.5
23 Farne Islands	1972–88	Total	16	+14
24 Bempton	1975–87	Sample	11	+4

^a Only instances in which there was a significant ($P < 0.05$) linear change over at least five counts are included.

^b Numbers refer to Figure 1. At another Caithness colony, Iresgoe, there was no significant linear change.

Figure 2

Complete colony counts of Common Murres on Bardsey and Skomer, Irish Sea. Note log scale of y axis.



River Humber) was estimated every four to six years. Where possible, counts were made in terms of occupied burrows, but at some colonies estimates were based on counts of the numbers of birds present. The numbers of occupied burrows on Dun, part of Britain's largest colony on St. Kilda (Fig. 1), have been assessed every four to five years, and those at Hermaness and Isle of May, Firth of Forth, have been assessed annually (Harris 1984; Harris and Rothery 1988; Martin 1989).

2.3. Breeding and numbers of Common Murres and Atlantic Puffins on the Isle of May

These data were collected in standardized ways (Harris 1984; Harris and Wanless 1985, 1988). Adult survival rates were based on resightings of colour-banded birds, and immature survival rates come from large-scale resighting and retrapping of birds colour-banded as chicks at the natal and other colonies. Breeding success was taken to be the proportion of young leaving the colony from a known number of eggs laid, assessed without handling the adults. The diet and feeding frequency of young were assessed by observations from blinds and the collection of fish retrieved from adults, chicks on the breeding ledges, or burrows. The energy values of loads were calculated using relationships in Harris and Hislop (1978), up to the maximum values determined from fish taken from auks on the Isle of May.

3. Results

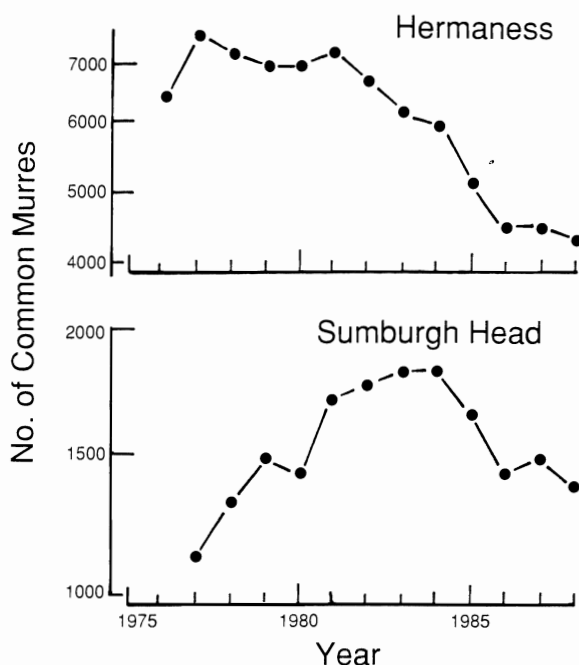
3.1. Population changes

3.1.1. Common Murre

The total British and Irish population increased from about 540 000 individuals in 1969–70 to 1 200 000 in 1985–88. In both surveys, 80% of the birds were at Scottish colonies. In 1982, Stowe and Harris (1984) estimated the population at 1 100 000 individuals by using counts made at 120 (of about 200 known) colonies and the 1969–70 distribution of birds. Increases between 1969–70 and 1985–88 were largest (490%) in southwest Scotland (totaling all colonies) and smallest (50%) in southwest Ireland and southwest England (C.S. Lloyd, pers. commun.).

Figure 3

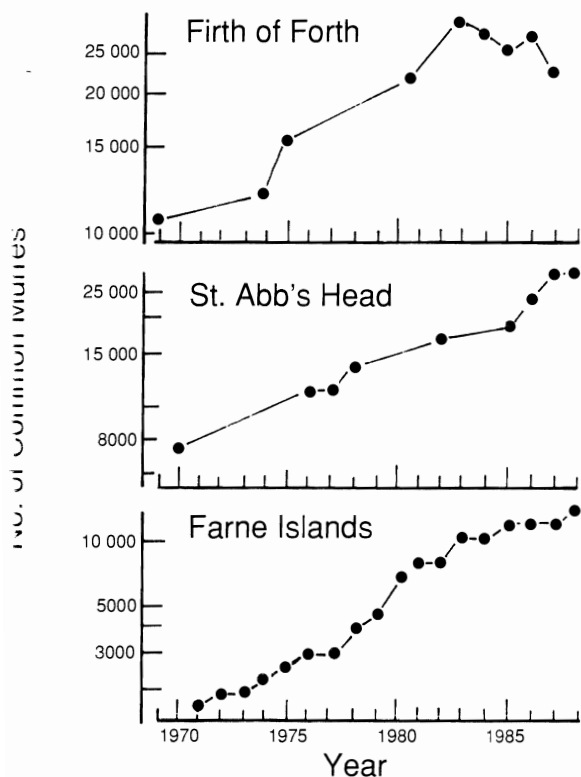
Counts of Common Murres in sample plots at Hermaness and Sumburgh, Shetland Islands. Note log scale of y axis.



Where additional counts were available for intervening years, it was obvious that numbers at some colonies had increased and then declined while still being above the 1969–70 level, and that patterns of change varied greatly between colonies. Murres at Irish Sea colonies were badly affected during a severe national wreck of seabirds in the autumn of 1969, and numbers at many colonies subsequently declined — for example, by 40% on Skomer (Birkhead and Ashcroft 1975). Numbers recovered slightly in the following years and then stabilized, but it was not until the late 1970s that counts indicated a sustained increase, which continued to at least 1987 (Table 1, Fig. 2). Farther north in the Inner Hebrides, numbers on Canna increased at 11% per year between 1974 and 1983 but have since declined slightly (Swann and Ramsay 1984; Swann et al. 1989).

A series of 18 colonies or areas arranged from north to south from the northern tip of Shetland down the east side of Scotland to the Farne Islands has been counted regularly. Numbers increased at all colonies during the 1960s and 1970s, but the most northern colonies started to decline in the late 1970s and early 1980s (Fig. 3); by 1988, all but the most southern colonies counted — those at St. Abb's Head and the Farne Islands — were declining (Fig. 4). Overall, there was a significant negative correlation between the year when numbers were highest and the latitude of the colony (Fig. 5) ($r = -0.60$, $n = 20$, $P < 0.01$). Numbers at some colonies were still declining at the time of the most recent available counts. At others, recent counts were higher than those recorded when counting was initiated. However, in general, the lowest counts in the last 15–20 years occurred much earlier in the southern colonies. Counts at the colony on Helgoland, Germany, which is at the same latitude as the southernmost British North Sea colony that is monitored, showed similar trends, with numbers very low in 1967 and 1973–74 and then increasing steadily up to 1985 before remaining stable in 1986 and 1987 (Vauk-Hentzelt et al. 1986; Kleist and Werner 1987; Meyer 1988). Outside the North Sea, the small population farther south in Brittany has increased from about 250 pairs in 1981 to 350+ pairs in 1988 (P. Yesou, pers. commun.). The

Figure 4
Complete colony counts of Common Murres in the Firth of Forth (total of six colonies), St. Abb's Head, and Farne Islands. Note log scale of y axis.



population in Iberia declined dramatically, from 20 000 birds in the 1950s to 300 in the early 1980s, apparently due to predation and pollution (Barcena et al. 1984), and there are few signs of recovery.

The annual rates of increase and decrease at the various British colonies that showed significant sustained year changes are given in Table 1. The mean rate of increase at 17 colonies was 7.3% per year (SE = 0.9), including Burra, a small colony where some adults are shot by vandals (M. Heubeck, pers. commun.), the mean rate of decline was 5.8% (n = 11, SE = 1.03). All declines occurred at colonies in or near the North Sea during the 1980s, and there was a significant relationship between the rate of decrease and latitude, the numbers at northern colonies decreasing most rapidly (Fig. 6) ($r = 0.78$, $P < 0.01$). There was no significant relationship between the rates of increase and latitude.

2. Atlantic Puffin

The total British and Irish population in 1984–88 is about 600 000 occupied burrows, with approximately 2% in Scotland. This figure suggests an overall increase of about 20% since 1969–70. In part, this could be an artifact resulting from improved coverage of some of the large isolated colonies, but the increase is supported by the regular monitoring counts on Dun, St. Kilda, which show an increase of 18% between 1977 and 1987 (Harris and Gentry 1988). Numbers at the large colony at Hermaness have remained fairly stable through 1973–88 (A.R. Martin, pers. commun.).

There have been proportionally large increases at the small southern colonies in England and Wales. In northeast Britain, the total number of pairs of puffins between Troup Head (Grampian) and Bempton (Humberside) (Fig. 1) was estimated at 10 000 in 1969, 17 000 in 1974, 24 000 in 1979, and 49 000 in 1984, which indicates a steady rate of increase of 10% per year.

Figure 5
Year of recent maximum count of Common Murres at 19 British colonies in relation to latitude. All the colonies were in northeast Britain. Arrows indicate where the maximum count was at the start or end of the period of counts.

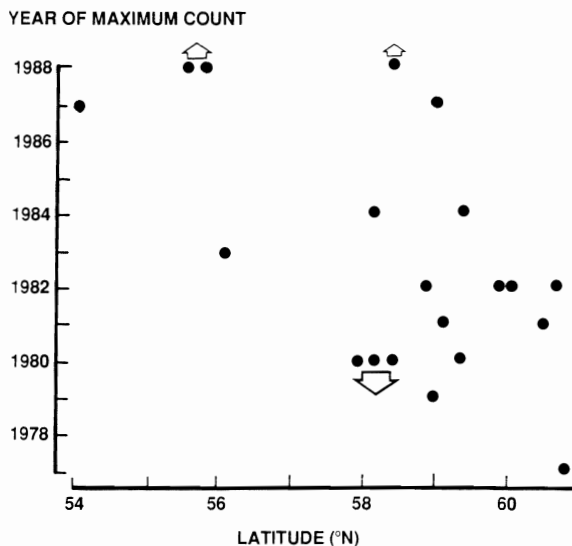
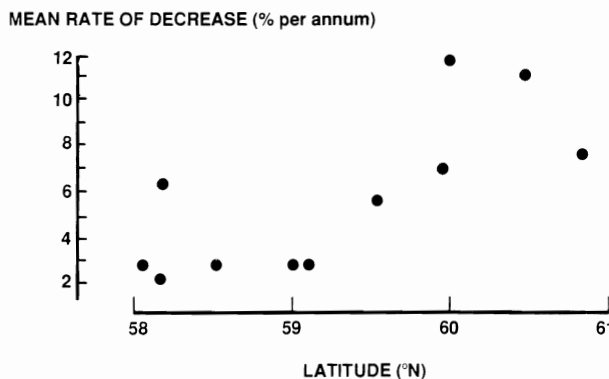


Figure 6
Rates of decrease of the numbers of Common Murres at 11 colonies in northeast Britain in relation to latitude



3.2. Demography and breeding on the Isle of May

3.2.1. Common Murre

Counts increased during the 1970s and early 1980s (Harris and Galbraith 1983), stabilized about 1983, and declined significantly from 1986 onwards (Fig. 7). The numbers of pairs known to breed in study plots stabilized slightly later and did not decline. The reduction in total numbers was attributed to a combination of fewer nonbreeding birds and changes in attendance behaviour of breeding adults.

Adult survival and most measures of breeding output remained very high from 1981 to 1988 (Table 2). Two murres of known age had been found breeding on the Isle of May up to 1988; one was three years old (and was brooding a small chick when caught), and the other was six (and had been present for the two previous seasons but had certainly not bred). Of 133 chicks colour-banded in 1983, 11 (8%) were identified during intensive daily searches of the breeding areas and loafing rocks, and only four (3%) were known to have definitely survived until five years of age. Of 250 chicks marked in 1984, 11 (4.5%) were present at four years of age. Despite thorough searches of other colonies in east Britain, only two chicks reared at the Isle of May have been found elsewhere, both on the Farne Islands; one of these was subsequently seen back on the Isle of May.

3.2.2. Atlantic Puffin

The annual counts of burrows in about a quarter of the colony showed that the population increased at 19% per year between 1973 and 1981, after which the increase slowed; for the first time, numbers declined slightly between 1987 and 1988 (Fig. 8). There was little variation in breeding success or the mass of food fed to chicks during the 16 years (Table 3), but fledging weight declined ($r = 0.812$, $n = 15$, $P < 0.001$). The population increased each year until 1987, so it is unclear whether the decrease in fledging weight was due to increasing intraspecific competition for food (Gaston 1985) or to changes in the overall food supply.

Adult survival decreased quite abruptly after the winter of 1980–81, at exactly the same time that the rate of population increase slowed down. The most recent survival estimates could be too low, as not every adult is recorded every year, so that some missing birds could still be alive. However, recalculating the survival rates using Leslie models (Leslie and Chitty 1951) to allow for this confirmed the reduction in survival: the mean of nine estimates from 1973 to 1981 was 96.0% (SE = 1.8), and the mean of five estimates from 1981 to 1987 was 91.4% (SE = 1.8). The survival of adult puffins is also monitored on Skomer, where survival declined from a mean of 95.8% per year in 1973–78 to a mean of 88.4% per year in 1978–86 (C.M. Perrins, unpubl. data).

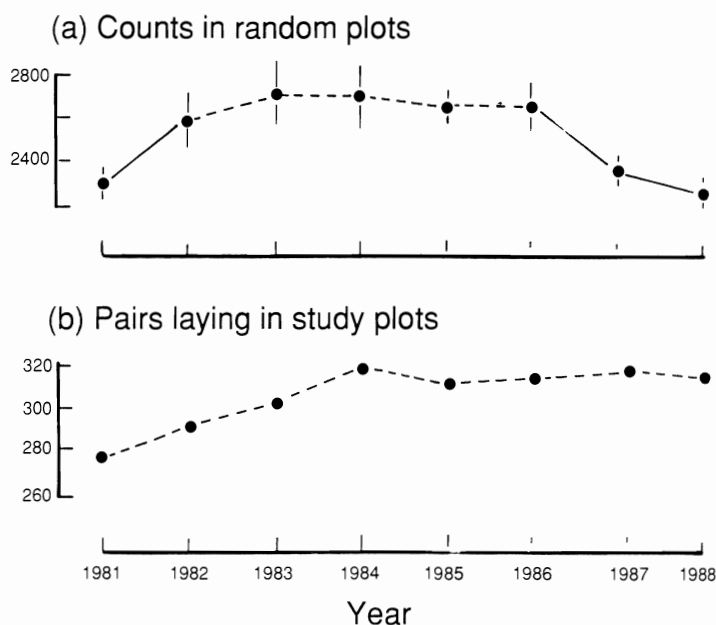
Estimates of immature survival (calculated from fledging until the median age of first breeding at five years for birds returning to the island) are available for chicks fledging each year from 1973 to 1978. The mean survival of the 1973–77 cohorts was 28%; that of the 1978 cohort was 18% (Harris and Wanless 1991). Large-scale colour-banding and subsequent checking of many British colonies indicated that at least 46% of young puffins recruited to colonies away from where they hatched, which suggests that about one-half of the young survived to breeding age from the cohorts produced during the 1970s. Immature puffins can be separated from adults by bill characters, and the proportions of such birds present on the Isle of May declined from 37% in 1980 to 0–10% in 1985–88, which also suggests that survival of immatures had decreased in recent years (or that more birds were emigrating and fewer were immigrating).

4. Discussion

The most likely reason for the decrease in total numbers of Common Murres while the numbers breeding remained constant is a reduction in the numbers of immature murres returning to the colony. Hudson (1985) listed 10 estimates of the survival of chicks until breeding age; the mean of these was 30% (SE = 2), and even the lowest estimate (17%) was far in excess of the numbers found back on the Isle of May. Most of these published estimates were based on banding returns and so are probably not directly comparable with sight records. However, on Skomer, similar methodology indicated that 17–23% of young survived to return to the colony between 1973 and 1977 when numbers were stable (Hudson 1979); in 1987, 13 (9%) of 148 chicks ringed in 1985 were seen, compared with only 10 (1.2%) of 796 young recorded on the Isle of May at a similar age (Hatchwell 1988; pers. obs.). On the Isle of May in 1989, 33 (17%) of 199 young colour-banded in the main study colony in 1986 were seen at the colony, which suggested that survival of that cohort was high and supported the conclusion that most of the young

Figure 7

Mean counts (± 2 SE) of (a) individual Common Murres in monitoring plots, and (b) pairs laying in study plots on the Isle of May, 1981–88. Solid lines joining points indicate significant differences (t-tests; $P < 0.05$).



ringed in 1983–85 had died, rather than been overlooked on the Isle of May or elsewhere.

Immature murres are known to visit other colonies, but there are no quantitative estimates available on the rates of emigration or immigration. It is possible that some young reared on the Isle of May have recruited into the nearby colonies at St. Abb's Head or the Farne Islands, as these are still expanding, but careful searches have failed to locate any. Details of this aspect of murre biology are needed urgently.

Banding recoveries provide some indication on the age and cause of death of murres from the Isle of May. Of 45 recoveries of murres ringed as chicks in 1981–87, 29 (64%) were reported in the first year after leaving the colony, 13 (29%) in the second year, and only three (7%) when older. Although more older birds will doubtless be reported in the future, there is obviously a large mortality in the first year and, to a lesser extent, second year. There have been wrecks involving large numbers of immature murres found dead or dying, apparently of starvation, in the North Sea in several winters during the 1980s (e.g., Underwood and Stowe 1984). Of 73 recoveries of murres of all ages banded on the Isle of May, 51 (70%) occurred between November and February, which coincided with the timing of these wrecks. Most recoveries were of birds found dead on the shore (47%), whereas fewer were oiled (25%), tangled in fishing nets (25%), or shot (3%).

Although breeding output was high right up to 1988, there was evidence that in the later years the duration of feeding trips for adults with young had increased (MPH and S. Wanless, unpubl. data), suggesting that birds were having to travel farther to feed or taking longer to catch prey in the feeding area. There is, therefore, some evidence of a recent reduction in food availability during the chick-rearing period, which would result in lower counts, as fewer off-duty adults would be present (Gaston and Noble 1986). So far this has not been reflected in a reduction in the daily energy intake of the young. However, adults appear to be approaching the time when they cannot extend their

Table 2
Details of breeding, food of young, and adult survival for Common Murres on the Isle of May, 1981–88

Year	Median laying date (May)	Lost eggs replaced (%)	Young fledged/pair	Leaving weight (g) ^a	Feeds/day	Value of fish (kJ)	Daily intake		Adult survival ^b
							g	kJ	
1981	8	60	0.81	?	5.2	113	61	590	?
1982	8	39	0.79	249	3.4	104	45	354	93.0
1983	7	52	0.77	250	4.1	94	44	386	93.2
1984	5	43	0.70	262	3.6	82	36	295	93.5
1985	7	41	0.86	262	3.8	64	30	244	93.7
1986	10	52	0.81	264	3.9	69	33	269	97.3
1987	8	45	0.80	252	3.7	86	37	319	92.6
1988	6	86	0.86	252	3.5	113	39	396	92.4

^a Leaving weight is the mean weight of chicks with wing lengths of more than 60 mm.

^b Survival refers to survival over winter between year *n* and year *n* + 1.

Figure 8
Counts of occupied Atlantic Puffin burrows in sample areas on the Isle of May, 1973–88

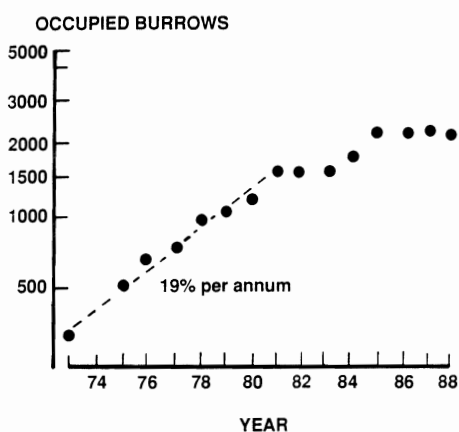


Table 3
Details of adult survival, breeding success, food intake, and fledging weights of chicks and immatures present for Atlantic Puffins on the Isle of May, 1973–88

Year	Adult survival ^a (%)	Chicks fledged per pair	Intake of chicks per day		Fledging weight (g)	% immatures ^b
			g	kJ		
1973	94.6	0.74	?	?	?	?
1974	98.4	?	?	?	289	?
1975	94.7	?	57	435	293	?
1976	97.9	?	37	249	304	12
1977	95.0	0.73	65	513	281	15
1978	93.6	0.87	42	310	289	28
1979	95.5	0.90	46	348	278	22
1980	95.0	0.76	27	194	285	37
1981	86.1	0.89	43	330	272	15
1982	87.5	0.92	40	284	279	15
1983	86.0	0.79	47	316	273	22
1984	93.9	0.88	49	353	270	14
1985	89.2	0.79	47	330	270	5
1986	84.3 ^b	0.80	36	259	281	10
1987	76.1 ^b	0.93	43	315	270	0
1988	?	0.88	47	310	264	0

Note: See Harris (1984) and Harris and Wanless (1991) for methods and sample sizes.

^a Survival from year *n* to year *n* + 1.

^b In mist-net catches during the chick-rearing period.

feeding trips farther and still guard the chick, and, if conditions become worse, chick production could be affected.

The Isle of May is the only British colony for which detailed information on numbers and ecology is available for the Atlantic Puffin. During the 1970s, numbers increased at an average rate of 19% per year compared with the 16% per year expected from the demographic data, indicating that the colony must have been receiving recruits from other colonies (Harris 1984). During the 1980s, a less complete data set indicated that although the proportion of birds breeding and breeding success remained high, adult and immature survival had both decreased, and that this should result in the stabilization of the population, a prediction borne out by counts of the colony (Harris and Wanless 1991).

4.1. Implications for management

A period of rapid increase for British murre and puffin populations appears to have ended recently. Numbers in 1988 were more or less stable or declining. Young auks disperse widely (Mead 1974), and birds from different natal areas occur in the same areas. Immature murres banded on the Isle of May have been recovered all around Britain. It is, therefore, difficult to envisage a regular latitudinal ranking of wintering areas, although critical data are lacking. The sequential latitudinal trend in the timing of this change among colonies in the North Sea points to a cause operating during the breeding season.

However, whereas murres on the Isle of May had been making longer feeding trips during the chick-rearing period in the later few years, this was not reflected in a reduced breeding output. Similarly, at none of the many colonies visited each year during monitoring counts or chick banding did observers report any serious breeding failures. The same appeared to be true for puffins up to 1986; however, during the last three breeding seasons, pairs at two of the largest colonies in Shetland, Hermaness and Foula, reared very few chicks, apparently because the adults were unable to obtain small sand lance (Furness 1989; Martin 1989). This food shortage also resulted in breeding failures of Arctic Tern *Sterna paradisaea* and Black-legged Kittiwake *Rissa tridactyla* (Monaghan et al. 1989; Heubeck 1989b). The reduction in numbers of sand lance around Shetland appears to be a natural event (perhaps exacerbated by a human fishery) and part of a widespread change in the marine environment of the northern North Sea (Kunzlik 1989; Harris and Wanless 1990).

Thus, although there is some evidence that conditions during the breeding season have deteriorated recently, and a possibility that this occurred first in northern colonies, it is difficult to reconcile these findings with the observed population changes. All the evidence suggests that a reduction in immature survival and also, in the case of the puffin, in adult survival outside the breeding season has been responsible for the leveling off or decline in numbers, but with this explanation it is hard to see why systematic, geographic differences should have arisen.

The similar declines in the annual survival rates of puffins nesting on Skomer, which winter to the south and east of Britain, and birds on the Isle of May, which winter mainly in the North Sea, suggest that recent changes must be acting over a wide area. Further, the coincidence in changes of population trends of Isle of May puffins, which winter well offshore, and murre, which winter closer to land (Tasker et al. 1987), suggests that a range of habitats may be affected. Despite recent advances in our knowledge of auks at sea, we still know almost nothing of their ecology in winter. Auks in Britain get oiled, get caught in fishing nets, accumulate heavy metals, PCBs, and other chemicals, and are (rarely) shot, but present knowledge suggests that these threats are now fairly minor (Evans and Nettleship 1985), although there is increasing concern about the numbers of auks drowned in fishing nets (Mead 1989). Changes in the marine environment are the most likely reasons for recent changes. We can fairly easily protect the birds while they are at their breeding sites, but it is difficult to protect them at sea, except by reducing the pollution of the sea and managing fish stocks sensibly.

Attaining these aims will be no small achievement. Rigorous population studies will probably do little to help the birds directly but must continue, as they will enable us to identify the magnitude of problems once they become apparent. The detailed work on the puffins on Røst, Norway, and their repeated failures to rear young (Lid 1981) is a good example of a problem being highlighted before the population declined noticeably. However, care must be exercised not to claim a species as endangered or threatened after a minor decline in numbers or breeding success. Auks are much more resilient species than they sometimes appear.

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