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CONTENTS

Effects of North American mink on the breeding success of terns and smaller gulls in west Scotland. By J.C.A. Craik	3
Seasonal and geographical variations in the diet of Common Guillemots <i>Uria aalge</i> off western Scotland. By D.J. Halley, N. Harrison, A. Webb and D.R. Thompson.	12
The status of breeding Arctic Skuas <i>Stercorarius parasiticus</i> and Great Skuas <i>S. skua</i> in Shetland in 1992. By J. Sears, P.M. Ellis, D. Suddaby and H.R. Harrop	21
Increases in the number of Puffins at Eilean Mor and North Rona, Outer Hebrides. By Stuart Murray ...	32
Distant feeding and associations with cetaceans of Gannets <i>Morus bassanus</i> from the Bass Rock in May 1994. By C.J. Camphuysen, Henk J.L. Heessen and Chris J.N. Winter	36
Factors affecting the production of pellets by Shags <i>Phalacrocorax aristotelis</i> . By A.F. Russell, S. Wanless and M.P. Harris	44
Changes in the diet of Great Black-backed Gulls <i>Larus marinus</i> on Skomer Island 1958-1992. By Jim Poole ...	50
Diets of adult and chick Herring Gulls <i>Larus argentatus argenteus</i> on Ailsa Craig, south-west Scotland. By M. Nogales, B. Zonfrillo and P. Monaghan	56
Size variation of Common Guillemots <i>Uria aalge</i> wintering in the northern Skagerrak. By T. Anker-Nilssen and S.-H. Lorentsen	64
Concentrations of Manx Shearwaters off San Antonio, Rio Negro, Argentina. By Patrick Y. Bergkamp	74
Book Reviews	75
The Seabird Group	76
Notice to Contributors ..	78

Effects of North American mink on the breeding success of terns and smaller gulls in west Scotland

J.C.A. Craik

INTRODUCTION

Earlier this century, North American mink *Mustela vison* were farmed for their fur in many parts of the Old World. The descendants of those that escaped are now living and breeding successfully along the coasts and rivers of much of Eurasia. Their present range includes most of the British Isles (Dunstone 1993).

Mink are semi-aquatic carnivorous mammals of the family Mustelidae (weasels, stoats and otters). Their prey range from water-dwelling species, such as fish, frogs and crabs, through aquatic and waterside birds to terrestrial mammals such as rodents and rabbits. Their catholic diet has undoubtedly been one of the reasons for their success in colonising the Old World.

All breeding birds adopt strategies to protect the vulnerable egg and chick stages. Most seabirds nest on the ground or in burrows, and their breeding sites tend to be on cliffs or small islands that are inaccessible to terrestrial predators. Mink are excellent swimmers and regularly reach islands more than a kilometre from the mainland. This study concerns the resulting effects on larids (gulls and terns) which breed at high density on small islands in west Scotland. This is an area with a wealth of small nearshore islands; consequently larids very rarely breed on adjacent mainland.

There is a lack of both evidence and agreement about the effects of feral mink on native prey species. On the one hand, statements such as "Early worries... are largely without foundation" and "the threat to (prey) populations is slight" have been made by those who have spent much time studying feral mink but little time studying seabirds (Dunstone 1993 p.201). On the other hand, there are reports that seabird colonies have disappeared following the arrival of mink in previously mink-free areas (e.g. Olsson 1974; Folkestad 1982; Alexander 1983). Although such statements do not necessarily contradict each other, the standpoints, sentiments and beliefs of the authors sometimes do. In monographs on mink, both Birks (1986) and Dunstone (1993) made special mention of the potential threat of mink at dense colonies of island-nesting birds. However, there are few quantitative data on this topic.

METHODS

The study area lies along the mainland coast of west Scotland, between the towns of Machrihanish and Mallaig (approx. 55° and 57°N). The species investigated were Black-headed Gull *Larus ridibundus*, Common Gull *L. canus*, Common Tern *Sterna hirundo* and Arctic Tern *S. paradisaea*. All but one of the seabird colonies were on small (0.03 - 1 ha) marine islands within 2 km of the mainland of west Scotland; one of the Common Gull colonies was on the mainland coast. In 1992 there were 35 colonies (18, 14, 2 and 1 with one, two, three and all four larid species respectively). In 1993 these figures were 32 (18, 10, 3 and 1). This breakdown excludes small numbers of the target species known to be nesting at some of these colonies but from which breeding success was not recorded. In general, the same larger colonies were studied in both 1992 and 1993, but there were minor variations between years in the numbers and distribution of smaller colonies (those with <30 pairs).

Distribution of mink

Records of the presence of mink up to and including 1965 and 1977 were taken from published material (Alexander 1983). Records for the period 1979 to 1990 inclusive were gathered from

various sources, mainly my own observations but also the records of J. and R. Green of the Vincent Wildlife Trust collected during an otter survey of Scotland in the mid-eighties, records from local naturalists, gamekeepers and other field workers, and responses to requests for information made in the local press. Results were plotted as the presence of mink in standard 10 x 10 km squares of the Ordnance Survey. If a square was known to be occupied in one year, it was assumed occupied in subsequent years.

Measurement of seabird breeding success

Colonies, some of them mixed, were visited during late incubation (ca 20 May for gulls, ca 20 June for terns; terns in this area breed two to three weeks later than in much of the British Isles) and clutches were counted by marking eggs with felt-tipped marker pens. A further visit was made shortly before the peak of fledging to count the large chicks (mid to late June for gulls, mid-July for terns). At Black-headed Gull colonies and at some Common Gull colonies, newly fledged chicks formed rafts on the sea within a few tens of metres of the colony island; where these could be counted from high ground by telescope, this count was taken as the number fledged. Otherwise, large chicks were ringed at colonies after searching by appropriate methods (Common Gull and Common Tern chicks hide in vegetation, while Arctic Tern chicks disperse widely over bare rocks) and the number found was taken as the number fledged. At larger colonies, estimates were made of total numbers likely to be present, based on numbers found and proportion of colony searched. At the largest Common Gull colony (230-300 pairs) and at the largest Common Tern colony (500-600 pairs) the number of large chicks present was determined by mark-and-recapture (Lincoln Index) on two visits one to three days apart. Productivity of each group of colonies A, B and C (see below) was expressed as chicks fledged/pair, calculated as (number of large chicks on second count/number of clutches on first count). In mink-affected colonies, many or most clutches had sometimes been removed before the first visit; in such cases, the number of nests was used as the denominator in this expression.

For comparison of productivity, colonies were classified into three groups. The first group (A) contained those colonies at which mink predation was detected as below. The second group (B) contained those colonies at which there were no signs of predation by mink. The third group (C) contained those colonies at which predation by mink was detected but where one or more mink were then trapped at the colony and killed early in the breeding season (during incubation or the early chick stage). It is known that native predators, such as otter *Lutra lutra*, Peregrine *Falco peregrinus*, Herring Gull *Larus argentatus* and Great Black-backed Gull *L. marinus*, were active at some of these colonies; in no known case did such predation alone result in complete breeding failure. The prey remains left by otter, birds of prey and large gulls are distinctive. Probably because of its relatively recent spread, seabird prey remains left by feral mink appear not to have been described before.

Identification of mink predation

One or more further visits were usually made to each colony, between the times of the above two visits, to look for signs of predation. Mink predation was recorded when at least one of the following four signs was found:

1. Eggs hidden uneaten, one or more of them bearing canine marks or punctures typically 1-2 mm wide and, if paired, ca 10 mm apart on shell; these are respectively the width of the canine tip in most mink at that season (canines become more worn in two-year-old mink) and the distance between either the two upper or the two lower canines. Caches were commonly in dense vegetation or in rock crevices.
2. Large quantities of eggshell in low places, runs, or under overhanging rock or vegetation; on examination, larger pieces of eggshell showed single round holes 1-2 mm in diameter or, more rarely, such holes paired and ca 10 mm apart.

3. Large or small chicks, or adults, dead and often hidden uneaten in vegetation or rock crevices, often thrust hard into the latter so that some force was necessary to extract them.

4. Prey in (3), whether hidden or not, showing neat punctures in neck or head as in (2). Careful plucking of neck and head feathers was necessary to reveal these fully. These punctures were either double (left and right canine) or single (e.g. right). If the latter, more careful examination of the skin often showed a mark or bruise on the skin where the left canine had pressed but not pierced. Sometimes a single, scarcely visible, non-bleeding puncture in the head or neck was the only detectable injury; sometimes this single injury was deep in the ear and visible only as slight bruising around the ear orifice.

Femur, tibia and sternum of large gull chicks that had been eaten were neatly cleared of meat; head and legs were sometimes bitten off.

Mink faeces and mink-sized trails (latter distinguished from otter by much smaller width) in grass on the small islands were sometimes seen accompanying the above. Such predation almost always ceased after one or more mink were trapped in or near the colony. For more details of some examples, particularly of the large numbers of prey that may be killed but not eaten, see Craik (1990, 1991 and 1993). Prey of mink was sometimes so well hidden that considerable searching was required to find it. On at least two occasions, mink made large caches in an inaccessible, invisible space between large intertidal boulders. These caches were found when, at high tides, ten or more bodies of intact tern chicks were seen being flushed out by wave action. Often the only overt sign of mink predation was rows or tiers of empty larid nests at dates when eggs or small young should have been present. Search then usually revealed cached prey or prey remains.

RESULTS

The spread of mink in the study area is indicated approximately by Fig. 1. Mink are secretive and largely nocturnal and can be present in an area unnoticed. Because they are so difficult to detect, Fig. 1 almost certainly understates their absolute distribution in each of the three years; its purpose is to indicate relative change over time. In 1992-3, mink were probably present in almost all coastal 10 km squares on the mainland in this area. It should also be remembered that this system of representation records the known presence of mink but does not indicate abundance or density.

In both 1992 and 1993, colonies (A) at which mink were known to be preying produced no or almost no chicks. Colonies (B) at which predation by mink was not detected produced about 0.2 - 1 chick per pair. Colonies (C) at which mink were killed after preying on seabirds or their young stages had productivity similar to group (B) (Table I).

In 1993, the proportion $(A+C)/(A+B+C)$, i.e. those at which mink were preying and which would presumably have produced effectively no fledged chicks if mink had not been trapped, was: Black-headed Gull, 8/9 colonies and 427/466 pairs (92% of pairs); Common Gull, 14/17 colonies and 901/978 pairs (92%); Common Tern, 12/16 colonies and 890/1519 pairs (59%); and Arctic Tern, 7/9 colonies and 338/361 pairs (94%). The lower percentage of affected Common Terns in both 1992 and 1993 was caused by a large colony, one km from nearest land, which was unaffected by mink, at least until late in the season. Table II shows estimates of productivities of these populations, making the assumptions stated.

Findings at some of the larger colonies will be described. At the largest colony of Common Terns (538 pairs on 21 June 1993, one of the largest colonies of this species in the British Isles and also holding 28 pairs of Arctic Tern) a mink was trapped on 19 July after the disappearance and caching between 11 and 18 July of about a quarter of the 500-600 half-grown tern chicks present; mink predation ceased until 29 July when more, freshly-cached mink-killed tern chicks were found. A second mink was trapped on 30 July. This colony then fledged 350-450 chicks and is in (C).

At the largest colony of Arctic Terns in the study area in 1993, there were 167 clutches on 11 June. (This was the largest colony of this species that has been recorded in the study area since

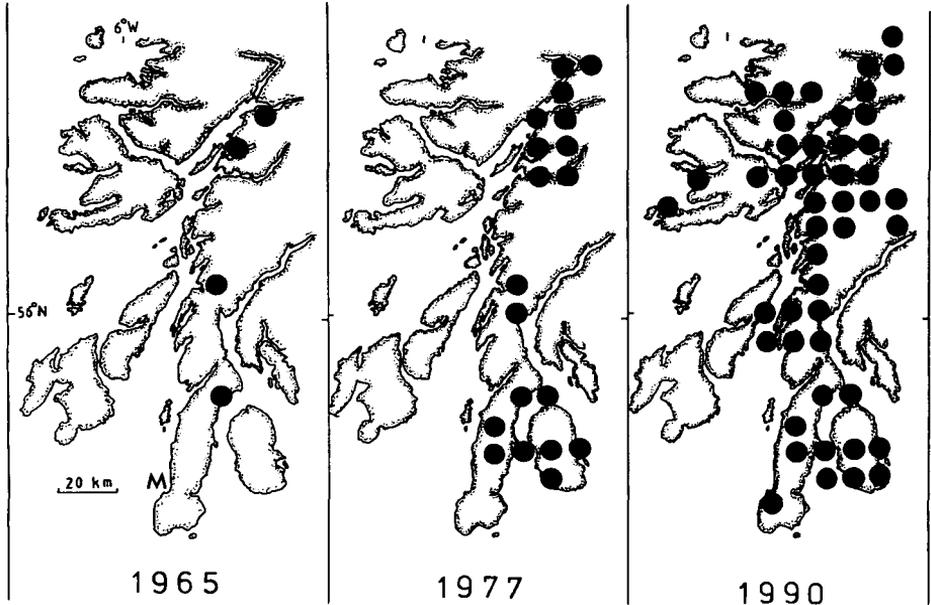


Figure 1. Known distribution of mink in the study area in west Scotland in 1965, 1977 and 1990. The presence of mink in 10 x 10 km squares of the Ordnance Survey is shown by black circles. M is the town of Machrihanish. The town of Mallaig is on the mainland coast about 10 km off the top of the map.

these observations began in 1984.) There were ca 10 pairs of Herring Gull breeding on the same island. All the adult terns deserted before 7 July. Cached tern adults and eggs, and cached chicks of Herring Gull (which also failed to fledge any young) killed by a mink neckbite, were found on that date; this colony is in (A).

At the largest colony of Common Gulls in the study area in 1993 there were 196 clutches and 84 empty nests (280 pairs) at first count on 20 May. No other larids bred on the island. It was clear on that date from egg remains that a mink was preying on eggs; later visits revealed 51 half-grown chicks and 4 adults, killed and cached uneaten in long grass (two chicks had been partly eaten). A mink was caught in the colony on 30 June, the predation ceased, and 70-100 chicks reached fledging size; this colony is in (C). Very similar predation occurred at this colony in 1992 and 1991: mink were not caught in either year; fewer than 16 young are believed to have fledged from 244 clutches and 65 empty nests in 1992 (309 pairs: A) (fledging numbers in 1991 unknown). Such a high proportion of empty nests in mid-May, never recorded at unpredated colonies of Common Gull, was widely found in this work to be a good indicator of predation that, on further investigation, proved to be by mink.

The two largest colonies of Black-headed Gulls in the study area in both years both shared their islands with smaller numbers of Common Gulls. On 22 May 1993 the largest held 161 nests of Black-headed Gulls and, in a separate area about 30 m away, 50 nests of Common Gulls; five adult Common Gulls and six adult Black-headed Gulls killed by mink-sized neckbites were cached intact in crevices between boulders in the colony. Nearby there were remains of mink-eaten eggs of Common Gulls and of Red-breasted Merganser *Mergus serrator*. On 18 June, there very few live chicks (only two Black-headed Gulls and five Common Gulls were seen) but at least 10 dead

Black-headed Gull chicks and two Common Gull chicks, the latter killed and eaten by mink. On 1 July the island was completely deserted and comparison with other colonies, where near-fledged and flying chicks of each species were present at this date, indicated that none had fledged.

At the other large Black-headed Gull colony, on 22 May 1993 there were 148 clutches of Black-headed Gulls and 20 clutches and 11 empty nests (31 pairs) of Common Gulls. On 28 June, when chicks of both species should have been near fledging, the island was deserted by all seabirds (A). In dense vegetation, a live female mink was found under an upturned plastic fishbox surrounded by many empty eggshells. At this island on 27 May 1992, there were 311 clutches of Black-headed Gulls and 74 clutches plus 11 empty nests (85 pairs) of Common Gulls, distributed as in 1993. At the mouth of and near a mink den on the island, 30 m from the Common Gull colony area, there were many mink scats, one eggshell of Common Gull, and 3 adult Black-headed Gulls and 1 adult Common Gull, the adults all cached and killed by mink. On 10 June, most of the Common Gull nests, including all those nearest to the mink den, were empty. Eight small Common Gull chicks were found dead, together with the heads and legs of a further two. There was a dead adult Common Gull (intact) at the den mouth. On 4 July the island was deserted by seabirds. Scattered Black-headed Gull eggshell under mid-island shrubs suggested that the mink had worked through the main Common Gull area before preying in the Black-headed Gull area ca 100 m from the den. As in 1993, breeding of all seabirds at this colony failed; the species concerned are in 1992 (A).

Similar evidence from the other islands showed a very close association between mink predation and total breeding failure at colonies. Colonies at which mink were known to be preying early or mid-season usually failed or had a very low productivity, unless mink were killed. A notable feature of such failures was that most eggs and chicks disappeared but usually only a very small proportion of them were found in caches or as prey remains. It was also remarkable that mink were rarely seen and that evidence of their predation often had to be actively sought. Evidence of attempted breeding elsewhere in the same year by affected birds was sought but never found. Adult birds at affected colonies usually persisted with breeding attempts until it was too late in the season to breed elsewhere.

Comparatively few adult gulls and terns were killed by mink at the colonies. During 1987-1993 there were 44 known cases of mink predation at gull and tern colonies from which quantitative data were obtained. At only one did mink kill more than 10% of the breeding adults (case 2 in Craik 1990, when 60 adult Common Gulls were killed by mink at a colony of 49 pairs). This may not apply to close-sitting species which breed coastally, such as Eider *Somateria mollissima*, or cavity-nesting species such as Black Guillemot *Cephus grylle*. In both these species, considerable numbers of adults attempting to breed (incubating female Eiders, both sexes of Black Guillemot) are killed by mink (Craik 1993 and unpublished results).

Of the four seabird species considered here, only the Common Tern has been accurately counted recently in the study area. Clutch counts in 1987, made as described in Methods, found 1829 clutches in the whole study area (including 728 at the largest colony). In 1993 there were 1553 (538), implying mean annual decreases of 2.69% (4.92%) over this six-year period.

DISCUSSION

This coastal area has been monitored annually for over a decade and its avifauna is well-known. The colonies studied contain most, if not all the birds of these species breeding in the study area. The totals in Table I are 0.6% of the Black-headed Gulls, 7-8% of the Common Gulls, 13% of the Common Terns and 0.3-0.5% of the Arctic Terns breeding on the coasts of Britain (British totals taken from Lloyd *et al.* 1991). The findings are therefore representative and suggest what will happen over a wider area of western Scotland as mink continue to spread and interact with island-breeding colonial seabirds. Because most islets holding seabird colonies are connected to the mainland by chains of other islands, one may speculate that the only regions of west Scotland that will remain mink-free are those that are separated from the mainland by many kilometres of open

TABLE I. BREEDING SUCCESS OF LARIDS IN WEST SCOTLAND IN 1992 AND 1993

		<i>Colonies</i>	<i>Pairs</i>	<i>Fledged (total)</i>	<i>Fledged/ pair</i>
Black-headed Gull					
1992	A	2	343	0	0.00
	B	3	180	50-65	0.28-0.36
1993	A	8	427	0-10	< 0.02
	B	1	39	20-30	0.51-0.77
Common Gull					
1992	A	9	591	16-30	0.03-0.05
	B	5	349	120-145	0.34-0.42
	C	3	300	70-80	0.23-0.27
1993	A	12	486	0-7	< 0.01
	B	3	77	15-35	0.19-0.45
	C	2	415	70-110	0.17-0.27
Common Tern					
1992	A	8	222	0	0.00
	B	8	1182	600-880	0.51-0.74
	C	3	89	97	1.09
1993	A	10	321	0-7	< 0.02
	B	4	629	290-370	0.46-0.59
	C	2	569	350-450	0.62-0.79
Arctic Tern					
1992	A	6	148	2	0.01
	B	7	80	54-64	0.68-0.80
	C	2	23	15	0.65
1993	A	5	298	3-7	0.01-0.02
	B	2	23	7	0.30
	C	2	40	26-28	0.65-0.70

Note: A – Mink known to be preying on eggs or young, sometimes on adults also.

B – No mink predation detected.

C – One or more mink killed early in season at or within 200 m of colony.

(Native predators were known to be active at some colonies in A, B and C.)

Nest counts during incubation and chick counts shortly before fledging gave the estimates of productivity (chicks fledged per nesting pair) in the last column. For example, at the 8 colonies of Common Tern 1992 B, estimates or counts of large young were: 100-140, 47, 400-600, 20-60, 10, 3, 3, 17 = 600-880; some sites were easier to count than others because of size, vegetation, etc.

TABLE II. ESTIMATES OF PRODUCTIVITIES IF MINK HAD NOT BEEN KILLED

		<i>Estimate I</i>	<i>Estimate II</i>
Black-headed Gull	1992	0.10-0.12	Not applicable
	1993	0.04-0.09	Not applicable
Common Gull	1992	0.15-0.19	0.11-0.14
	1993	0.03-0.07	0.02-0.04
Common Tern	1992	0.43-0.63	0.40-0.59
	1993	0.31-0.40	0.19-0.25
Arctic Tern	1992	0.25-0.29	0.22-0.26
	1993	0.03-0.04	0.03-0.04

These are estimates of the productivities (fledged chicks/pair nesting) which the populations would have had if mink had not been killed.

Estimate I was obtained by ignoring colonies C (at which mink were trapped) and calculating the productivity of A and B combined in Table I: e.g. for Arctic Tern in 1992: (56 to 66)/228.

Estimate II was obtained by including C with colonies A and B and assuming that C would have produced no fledged chicks if mink had not been trapped: e.g. for Arctic Tern in 1992: (56 to 66)/251.

water, such as Rum, Canna, Coll, Tiree and Colonsay. Mink are already on Lewis and Harris. The southern isles of the Outer Hebrides are at risk, as possibly is Orkney.

Two striking findings of this investigation were: (a) there was evidence of predation by mink at most colonies of these seabirds in the study area, and most pairs were nesting at colonies where mink were preying, and (b) unless mink were trapped, all colonies so affected produced no or very few fledged young. Finding (a) can be explained by the high density at which mink can live in this coastal habitat. Birks (1986) found densities as high as one or two mink per km along rocky coasts in south-west Scotland. Almost all the coast of west Scotland is rocky, and much or most of this appears able to support mink. Densities as high as this accord approximately with my own limited data from trapping. Such figures must be compared with densities of the two other main predators of terns and the smaller gulls in this habitat, namely, otter and Peregrine. These have coastal territories of ca 2-5 km and ca 10-20 km respectively (Mason & Macdonald 1986; Cramp *et al.*, 1980). Moreover, neither otter nor Peregrine have been reported to indulge in surplus killing (the tendency, found in some carnivorous mammals, of killing much more than can be eaten at the time; Kruuk 1972). Thus the three characteristics of feral mink which together contribute to widespread breeding failures in island colonies of ground-nesting seabirds are their swimming ability, their high linear coastal density, and their propensity for surplus killing.

Comparison of groups A and B in Table I, and the calculations from these data in Table II, together suggest that mink predation severely reduces the productivity of whole populations of these species (although there are no breeding data from the area in the period before the arrival of mink). What are the long-term consequences of this likely to be?

The annual adult mortality rate of Common Terns was found to be 7.5 - 11% by Nisbet (1978) and 8% by DiConstanzo (1980); that of Arctic Terns is 12 - 13 % (Coulson and Horobin 1976). Those of the two gull species are somewhat higher: 16 and 24 % (two estimates) in Black-headed Gulls, and 15 and 26% (two estimates) in Common Gulls (Cramp *et al.* 1983: pp 751 and 792). In populations in equilibrium with all causes of death, including native predators, enough fledged young survive to breeding age to replace these losses. If all breeding were prevented, the adult

populations would decline at about the rates indicated. If, as in the case of mink, an introduced predator species reduces but does not eliminate the productivity of a previously stable population, one would expect the adult numbers to decline at less than the rates indicated, that is at less than about 10% per annum for the terns and less than about 20% per annum for the gulls. Although such declines, if maintained, would have serious consequences for the populations concerned, they would probably go unnoticed for several or many years, given the many inaccuracies inherent in counting seabirds such as larids. The decrease in the total numbers of breeding Common Terns between 1987 and 1993 (see Results) is consistent with such a process, but it is not proven that mink are the cause of this decrease.

Unlike many other causes of regular breeding failures of seabirds, such as bad weather or food shortages, mink predation appears on present evidence to be annual and widespread in west Scotland, and to be increasing steadily in range and severity. It is practically unpreventable over large areas because of the considerable effort, time and expense that are involved in mink trapping, even at a single colony. Its main effect, namely, the widespread breeding failure of colonial ground-nesting birds, is not obvious to casual onlookers. To observers in passing cars or boats, affected colonies appear superficially normal, since approximately the same numbers of adults are present for at least part of the season in successive years. Effects of mink predation are likely to go unnoticed unless productivities are measured at a large sample of colonies from early (clutch) and late (large chick) counts, as in this work. Estimates of productivity based on counts of breeding pairs made when large chicks are counted, for example when ringing, may give results higher than those given here, since adults that have lost their young may have left the colony.

Seabirds would be expected to respond to repeated breeding failures of this nature. Such responses might be behavioural (moving to breed in mink-free areas, for example) or mediated by natural selection (differential survival of those which breed in such a way that mink predation is reduced; for example, by breeding solitarily so that the surplus killing behaviour of mink is not stimulated). Behavioural adaptations would become apparent before evolutionary ones. One might therefore predict that breeding behaviour of these larid species will show marked compensatory changes in response to mink predation.

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SUMMARY

In 1992 and 1993, observations were made of predation by feral North American mink and its effects on the productivity of Black-headed Gulls, Common Gulls, Common Terns and Arctic Terns at more than 30 colonies, some of them mixed and all but one on small islands within two kilometres of the coast of the mainland of west Scotland. Mink predation was detected at most colonies, and most pairs were breeding at colonies where mink were preying. Comparatively few adults were killed by mink, which preyed more heavily on eggs and chicks. Colonies where mink predation was detected produced no or very few fledged young. The implications for populations of these seabirds are discussed.

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Seasonal and geographical variations in the diet of Common Guillemots *Uria aalge* off western Scotland

D.J. Halley, N. Harrison, A. Webb and D.R. Thompson

INTRODUCTION

Although the diet of full-grown Common Guillemots *Uria aalge* in the north-western North Sea and off the northern isles of Scotland has been well documented (Blake 1984; Blake *et al.* 1985; Tasker *et al.* 1987; del Nevo 1990; Harris & Bailey 1992), there are no published accounts of their diet in the area west of Scotland, which differs ecologically and oceanographically from previously studied regions (e.g. Ellet 1979). Knowledge of seabird diet is valuable for modelling energetic requirements of seabirds and estimating their food consumption (e.g. Dunnet *et al.* 1990). We report the results of preliminary investigations into the diet of full-grown Common Guillemots in the region, and attempt to relate the observed pattern of prey consumption to the pattern of prey distribution and to the ecology of Common Guillemots.

METHODS

Full-grown Common Guillemots (i.e. not chicks) settled on the sea were shot under licence from a small inflatable boat using a 12-bore shotgun. Collections were made around the Summer Isles, at the mouth of Loch Broom in the eastern Minch, on 27 April (n=30), 25 June (n=27) and 1-2 November (n=25), 1988. Two collections were also made in the waters around St Kilda on 19 June 1987, one close to shore (n=10) and one c.40km east of the colony (n=10) at the Whale-Rock Bank. Smaller samples were also taken in the North Channel on 7 June 1988 (n=5), a small hydrographic plume Front at the mouth of the Firth of Clyde on 21 June 1988 (n=5), and at a hydrographic front in the the Sound of Jura on 23 August 1988 (n=5) (Fig. 1).

A blunt probe was used to force food in the throat into the crop, and the crop and gizzard dissected out and stored in 80% ethanol. In the laboratory, the digestive tract was opened longitudinally and the contents examined. Fish prey were identified from carcasses, where sufficiently fresh, or from otoliths (and pro-otic bullae for Clupeidae) using a reference collection. Identification was checked and corrected by J.R.G. Hislop of the Scottish Office Agriculture and Fisheries Department. Many fish could not be identified to below generic level. Many samples contained remains of small invertebrates (mainly copepods and euphausiids). In most cases these appeared to have been prey of fish eaten, rather than the prey of the bird itself, although in one case quantities were large enough that it was suspected (though not certain) that the bird could have been feeding on invertebrates directly.

Numbers of fish estimated from each bird were minima based on the number of intact or semi intact bodies and the numbers of otoliths (and pro-otic bullae for clupeids), two similar sized otoliths from the same species (or genus where not specifically identifiable) being taken to indicate one fish. Otoliths were assumed to originate from any partly digested fish bodies present if not in place, so long as body size and otolith size were consistent.

Dietary data were summarised in two ways. The percentage contributions of each fish species were calculated for each collection, based on the total number of fish from all specimens (larval fish excluded). In addition, the frequency with which each prey item (species or genus where species not identifiable, and larval fish separately from adults), occurred in individual stomachs was tabulated. Birds with empty stomachs (3/27 or 11% of the Summer Isles June sample and 1/10 (10%) from the St Kilda Whale-Rock Bank; in all other samples all stomachs contained food) were excluded from this analysis.

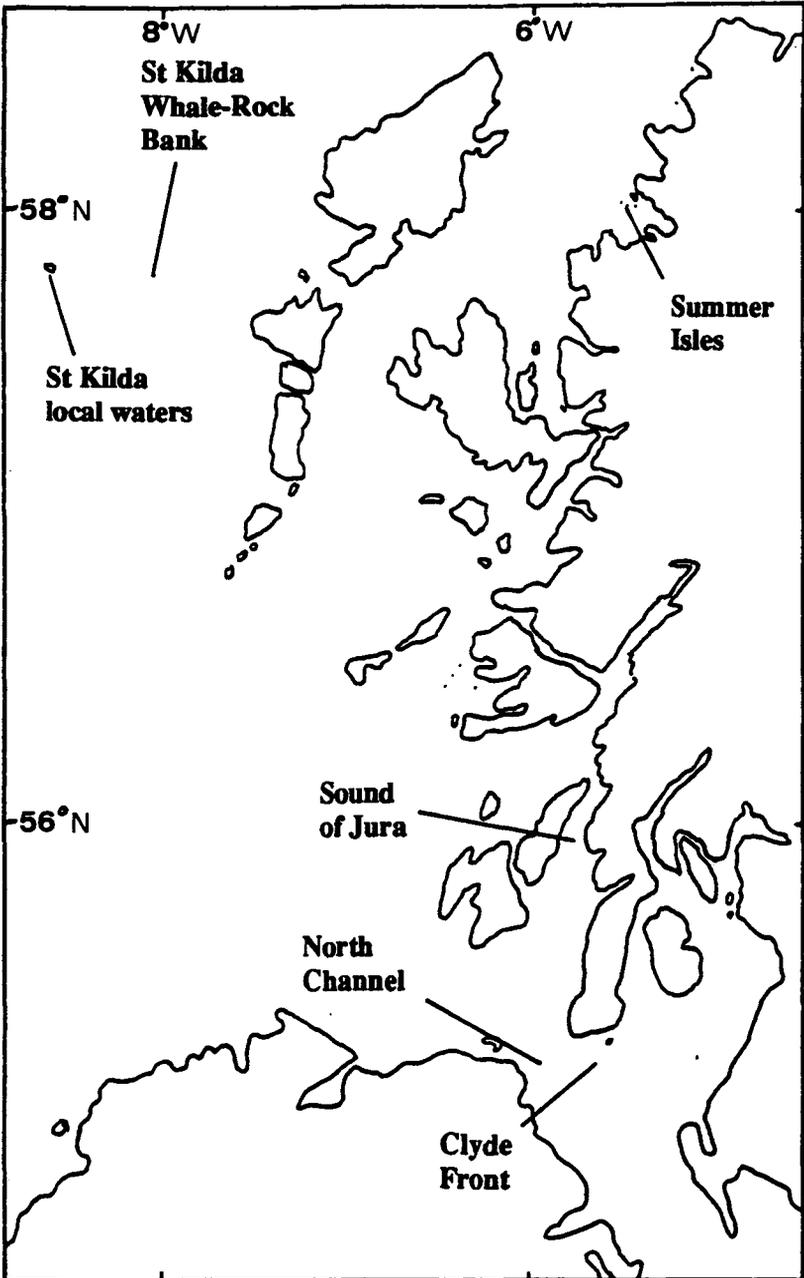


Figure 1. Sampling locations off the Scottish west coast.

The length of time otoliths, bullae and squid beaks remain present in the stomach after ingestion is not known, preventing calculation of the rate of food consumption and potentially affecting the apparent importance of different prey species in the diet. Digestion of flesh in Common Guillemots is rapid (Blake et. al. 1985; Partridge 1986); as a result, relatively few intact prey items were recovered. The maximum fresh weight of food found in an individual was 160g.

Sizes of prey fish were calculated from measurements of intact otoliths using conversion formulae given in Blake (1984).

Statistical tests were performed on the presence or absence of specific prey in individual stomachs, or for fish lengths on the average value from each stomach, to avoid pseudoreplication (Beal & Khamis 1990). In some cases this meant that sample sizes were too small for statistical analysis.

RESULTS

There were no discernable differences in diet between sexes; data have therefore been combined in all analyses. Dietary data for the eight collections are summarised in Tables I and II. In general, juvenile and adult fish were by far the most important prey, with minor amounts of larval fish and squid being taken (although in the small sample from the Clyde Front larval fish were the main prey). Squid eaten were invariably small (beak lower rostral length <2mm). Unidentified jellyfish and shrimp *Crangon vulgaris* were also recorded once each. There were strong seasonal differences in the species of fish eaten in the Summer Isles, and geographical differences between collections made in June.

TABLE I. PERCENTAGE OF TOTAL PREY ITEMS RECORDED FOR EACH SAMPLE.

	<i>Summer Isles, April</i>	<i>Summer Isles, June</i>	<i>Summer Isles, November</i>	<i>St Kilda, local waters, June</i>	<i>St Kilda, Whale-Rock Bank, June</i>	<i>Clyde Front, June</i>	<i>North Channel, June</i>	<i>Sound of Jura, August</i>
n (fish)	383	88	153	78	54	5	52	76
n (birds)	30	24	25	10	9	5	5	5
<i>Ammodytes</i> sp. ¹	98	57	0	0	91	0	96	0
<i>A. marinus</i>	98	50	0	0	44	0	96	0
<i>H. lanceolatus</i>	0	7	0	0	0	0	0	0
<i>G. semisquamatus</i>	*	0	0	0	6	0	0	0
<i>Clupeid</i> sp. ¹	1	0	35	5	4	40	0	99
<i>S. sprattus</i>	1	0	22	0	0	40	0	99
<i>C. harengus</i>	*	0	14	0	0	0	0	0
<i>Gadid</i> sp. ¹	*	43	48	91	4	20	0	1
<i>M. merlangus</i>	0	43	8	0	0	0	0	0
<i>T. minutus</i>	*	0	29	0	0	0	0	0
<i>G. morhua</i>	0	0	12	0	0	0	0	0
<i>T. esmarkii</i>	0	0	0	36	0	0	0	0
<i>C. linearis</i>	0	0	0	0	0	40	3	0
Squid	0	0	16	5	0	0	0	16

Larval fish (which occurred as large numbers of tiny items) excluded. Note that some fish were identified to the generic level only.

¹ Including fish identified both to generic and to species level.

* less than 1%.

TABLE II. PERCENTAGE OF STOMACHS FROM EACH SAMPLE IN WHICH THE SPECIFIED PREY WAS DEFINITELY IDENTIFIED.

	Summer Isles, April	Summer Isles, June	Summer Isles, November	St Kilda, local waters, June	St Kilda, Whale-Rock Bank, June	Clyde Front, June	North Channel, June	Sound of Jura, August
n	30	27	25	10	9	5	5	5
<i>Ammodytes</i> sp.	97	73	0	0	100	0	100	0
<i>A. marinus</i>	97	50	0	0	89	0	100	0
<i>H. lanceolatus</i>	0	23	0	0	0	0	0	0
<i>G. semisquamatus</i>	7	0	0	0	33	0	0	0
Clupeid sp. ¹	6	0	48	20	22	20	0	100
<i>S. sprattus</i>	3	0	26	0	0	20	0	100
<i>C. harengus</i>	3	0	16	0	0	0	0	0
Gadid sp. ¹	3	19	72	100	11	20	0	20
<i>M. merlangus</i>	0	19	9	0	0	0	0	0
<i>T. minutus</i>	3	0	34	0	0	0	0	0
<i>G. morhua</i>	0	0	14	0	0	0	0	0
<i>T. esmarkii</i>	0	0	0	50	0	0	0	0
<i>C. linearis</i>	0	4	0	0	0	20	40	0
Larval fish (<10mm)	0	5	11	10	0	100	5	0
Squid	0	0	36	20	0	0	0	0

Note that some fish were identified to the generic level only, and that many stomachs contained more than one type of prey.

¹ Including fish identified both to generic and to species level.

Seasonal variation

The Summer Isles collection showed seasonal variation in the prey spectrum consumed. In April and June the diet was mainly or substantially composed of sandeels Ammodytidae (overwhelmingly the lesser sandeel *Ammodytes marinus*, but also a few *Hyperoplus lanceolatus* and *Gymnammodytes semisquamatus*). In contrast, sandeels were absent in August and November. Diet was also considerably more diverse in the later part of the year, despite the absence of sandeels, when various clupeids (sprats *Sprattus sprattus* and herring *Clupea harengus*) and gadids *Gadidae* (whiting *Merlangus merlangius*, poor cod *Trisopterus minutus*, and cod *Gadus morhua*) were the major components of the diet.

The only non-fish component of the diet which occurred in more than negligible quantities was squid. Squid were a minor component of the diet inshore off St Kilda in June, but were the third most common prey in the Summer Isles in November, found in over a third of all stomachs and comprising 16% of prey items (but see Discussion).

In the three samples from the Summer Isles, numbers of stomachs containing sandeel sp. declined as the year progressed ($\chi^2 = 55$, 2df, $p < 0.0001$). In contrast, more stomachs contained gadid remains as the year progressed ($\chi^2 = 33$, 2df, $p < 0.0001$), and a higher proportion contained clupeids in November compared to April and June ($\chi^2 = 28$, 2df, $p < 0.0001$).

Geographical variation

The proportions of sandeels and gadids in the diet also varied between the samples collected in June, and were probably related to variations in water mass and substrate (Discussion). The St Kilda (Whale-Rock Bank) and North Channel samples were almost exclusively composed of sandeels. The majority of prey in the Summer Isles sample were lesser sandeels, but whiting were an important secondary element; and the diet of birds collected in the waters close to St Kilda was dominated by gadids (apparently mostly Norway pout *Trisopterus esmarkii*), with sandeels absent. Sandeels were also (except for larvae) absent from the Clyde Front sample, and gadids were a minor item, in a mixed assemblage composed of larval fish, clupeids and crystal gobies *Crystallogobius linearus*.

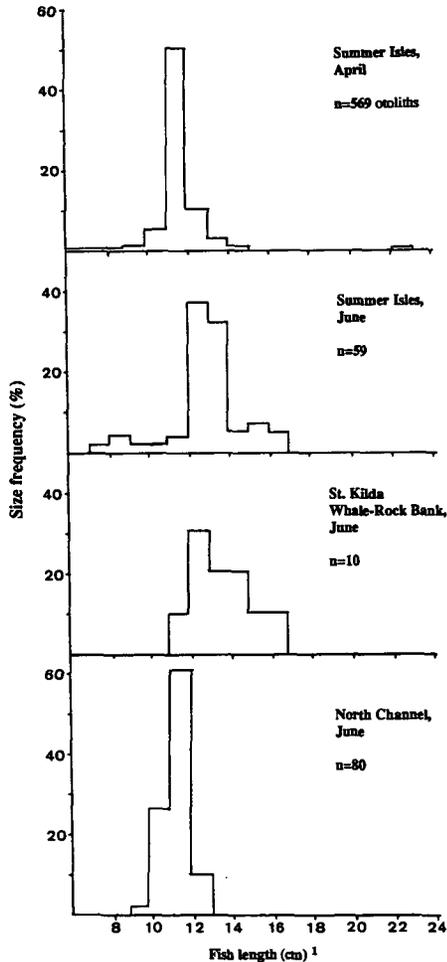


Figure 2. Lesser sandeel *Ammodytes marinus* lengths, calculated from otoliths in Common Guillemot stomachs.

¹ Conversion formula from Blake (1984)

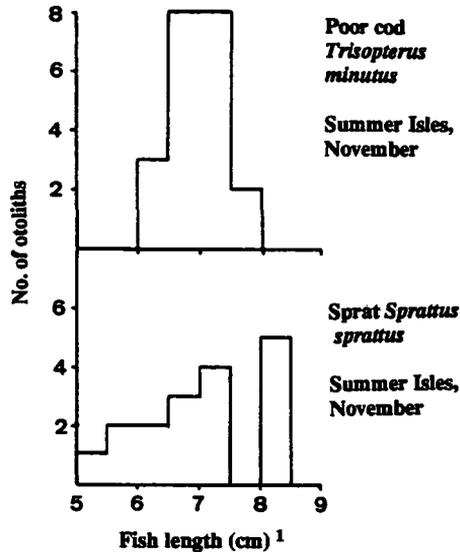


Figure 3. Lengths of non-Ammodyte fish prey calculated from otoliths in Common Guillemot stomachs.
¹ Conversion formula from Blake (1984)

Fish sizes

a) Ammodytidae. The vast majority of specifically identified otoliths belonged to lesser sandeels. The size frequency distribution showed both seasonal and geographical variation (Fig. 2). Lesser sandeels were represented in the prey assemblages from the Summer Isles in April and June. The range of sizes taken was calculated as 64-228mm. In April, lesser sandeel prey averaged 12.2 ± 10.2 mm ($n = 569$) in length; in June 12.8 ± 17.2 mm ($n = 59$). The difference in the average size taken by individual Guillemots in the two samples approached significance (Mann-Whitney $W = 75$, 1 d.f., $p = 0.07$); however, it should be noted that conversion equations are subject to considerable error, and can vary between populations, so that calculated differences between populations should be treated with caution (P. Wright, *pers. comm.*).

The calculated average length of lesser sandeels taken in June at the 3 sites where they occurred as prey also varied: St Kilda (Whale-Rock Bank) 137 ± 16 mm; Summer Isles 129 ± 17 mm; and North Channel 112 ± 6.5 mm. Comparisons of the average lesser sandeel size taken by individual birds in the three groups indicated a significant overall difference in fish length taken between areas (Kruskal-Wallis test statistic = 6.025, 2 d.f., $p < 0.05$). There were no significant pairwise interactions (Multiple-comparisons post-hocs, $p > 0.05$ in each case).

All lesser sandeels in all samples taken were in the 1- and 2- group size ranges, indicating that they had lived through one or two winters respectively (younger fish are termed 0-group); this was confirmed by examination of otolith growth bands. Of the 149 measurable lesser sandeel otoliths in the June samples, none were 0-group. In the Summer Isles, only one otolith was from a 1-group individual; all others were 2-group.

b) Clupeidae. Very few intact herring otoliths were found. The number of intact sprat otoliths from the November sample in the Summer Isles was large enough for an examination of size distribution (Figure 3). Sprats taken averaged 100 ± 19.3 mm, range 65-127mm ($n = 17$); all appeared to be either 1- or 2- group fish.

c) Gadidae. Gadid otoliths were prone to fracture, and again the November sample from the Summer Isles yielded the only adequate assemblage, of poor cod (Fig. 3). The mean size of poor

cod eaten was calculated at 89 ± 8.4 mm; range 74–108mm ($n = 21$). All fish appeared to be 0-group; older fish of this species are presumably too large to be taken by Common Guillemots.

Larval lesser sandeels, gobies (Gobiidae), gadids and clupeids were all eaten. The first two were found in large numbers in some stomachs. A substantial proportion of the diet of birds collected at the Clyde Front in June was composed of larval lesser sandeels and gobies: all contained mainly larvae, and two of the five Common Guillemots collected had been feeding exclusively on them, containing several hundred lesser sandeel and goby larvae each. Crystal gobies appeared to be the main component of larvae taken, followed by lesser sandeels and unidentifiable goby remains.

DISCUSSION

The prey spectrum of the samples collected for this study is similar to those described from other areas around the British Isles (Blake 1984; Blake *et al.* 1985; Bradstreet & Brown 1985 for review). Diet consisted mainly of fish, with small quantities of fish larvae and squid. Other remains found in stomachs, mostly copepods and euphausiid larvae, appeared mainly to be prey of fish ingested secondarily, and in no case could this source be excluded although in one individual (from the April collection at the Summer Isles) the quantity was so large in relation to the quantity of fish prey that it was suspected that it may have been feeding on copepods directly.

The marked seasonal pattern in the types of fish consumed is similar to previous studies (Blake 1984; Blake *et al.* 1985; Bradstreet & Brown 1985; Croll 1990). Sandeels, especially lesser sandeels, predominated in the diet in spring and summer (although in June gadids were important among birds feeding in the waters around St Kilda, and clupeids and gobies on the Clyde Front; see below), but disappeared in autumn, when various gadid and clupeid species became more important in the diet.

This pattern may partly be explained by the biology of the prey species. Sandeels bury themselves in muddy or sandy substrates for much of the time during late summer/early autumn to late winter, and so become less available to Common Guillemots. Sprats are generally found offshore in spring and summer, becoming abundant closer to shore in late summer and autumn (Jones 1976). As a result, they become more available to Common Guillemots in later summer, at the same time that sandeels are becoming unavailable.

However, although usually abundant in spring and summer and often comprising the bulk of total fish biomass in inshore areas (Warburton 1982), sandeels have a relatively low calorific value compared to sprats and herring (Harris & Hislop 1978; Harris 1984), and Common Guillemots and Puffins *Fratercula arctica* appear to select sprats as chick food out of proportion to their low relative abundance during the breeding season (Harris & Hislop 1978; Harris & Wanless 1985; Hatchwell 1991; Hatchwell *et al.* 1992). The dominance of lesser sandeels in breeding season samples presumably indicates the greater availability of the species at that time.

Gadid species are poor in calorific value, and presumably less attractive as prey items except when of high availability, or clupeids and sandeels are scarce. Puffin chicks on St Kilda grew less well and fledged less successfully in years when gadids made up a significant proportion of prey brought back to the colony (Harris 1982); in most years Puffins avoided gadid prey during the breeding season. In the present study, gadids were important in Common Guillemot diets in spring and summer around most oceanic breeding sites, St Kilda (see below). Unfortunately, chick diets, chick growth rates, and productivity of Common Guillemots were not monitored at this colony so that it is not certain whether gadids formed a major source of the chick diet, and if so with what effect. Out of the breeding season, energetic demands for breeding birds are much lower. Birds may be able to subsist comfortably on food of relatively high bulk and low value, and the cost/benefit ratio of taking gadids compared to the other prey fish groups will be lessened as a result.

The absence of 0-group lesser sandeels from the diet in June was perhaps surprising, since in other areas they make up the bulk of prey in summer (Warburton 1982). However, lesser sandeel stocks vary in the timing of breeding and rate of growth (Warburton 1982). The hydrography of

the Scottish west coast is complex (Ellett 1979), but if the local lesser sandeel stock has a relatively late recruitment, the samples in June may have been too early for 0-group lesser sandeel to appear in the diet; and by November they would have moved into the substrate and become unavailable to Common Guillemots. Alternatively, movements of larval and 0-group sandeels are complex (P. Wright *pers. comm.*) so their dispersal pattern may not take them to the area until later. Also, if larger and better-condition 1- and 2- group sandeels are common, birds may be selecting them in preference to 0-group fish. There was no commercial fishery for sandeels in the Summer Isles area of the Minch when samples were taken, presumably resulting in a larger proportion of the older fish remaining available as Common Guillemot prey.

The geographic variation in diet in June must be treated with some caution. The data from both St Kilda samples were obtained in 1987, a year earlier than other samples, so that interannual differences may have affected prey composition. The 1988 samples, other than those from the Summer Isles, were small, taken from five shot birds each. These were collected over a few minutes, and so could have been composed of birds feeding on the same shoal of fish. It is possible, therefore, that the diet of these birds is not representative of the diet of the local population as a whole.

Nevertheless, the importance of gadids and their pattern of occurrence in the diet of Common Guillemots off St Kilda in June is interesting. Of the ten birds sampled from the oceanic waters close to St Kilda, all fed mainly or exclusively on gadids, apparently mostly Norway pout; none had eaten sandeels. In contrast, 6 of 10 birds collected from the mixed (oceanic and coastal origin) Hebridean current waters at Whale-Rock Bank (c. 40 km east of the colony) had fed exclusively on lesser sandeels, three had mainly eaten lesser sandeels, and one contained no prey. In both areas, birds were clearly returning towards St Kilda with food for chicks; this suggests that there may be an energetic trade-off between travelling to shallow waters holding easily accessible, high-quality, prey or remaining close to St Kilda in relatively deep, unproductive oceanic waters holding lower quality prey species.

This small survey demonstrates the broad dietary range of Common Guillemots within a relatively small region, from goby larvae less than 1mm in length (found in stomachs containing only larvae, so that secondary ingestion can be excluded) to 22cm sandeels. Common Guillemots occupy habitats as varied as the inshore semi-estuarine waters of the Clyde and the oceanic waters surrounding St Kilda. These different seas vary in species assemblages and small-scale distribution of prey, and Common Guillemots can vary their diets opportunistically both geographically and seasonally in order to exploit them.

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SUMMARY

Stomach contents were examined from 136 Common Guillemots collected at six sites off western Scotland. Dietary composition was compared for the same location between months and for different locations in one month, June. In April and June sandeels (*Ammodytes* sp.) dominated the diet, except off St Kilda where gadids were dominant among birds feeding in oceanic waters close to the islands. In August and November, sandeels were absent and a wider spectrum of clupeid and gadid fishes were taken. Gobies and larval fish were important at one site in June, and squid composed a substantial fraction of prey in the November sample. The average size of *Ammodytes marinus* sandeels taken in June varied with locality, but almost no 0-group individuals were eaten. Dietary data were considered in relation to available information on fish and Common Guillemot ecology.

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The status of breeding Arctic Skuas *Stercorarius parasiticus* and Great Skuas *S. skua* in Shetland in 1992

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INTRODUCTION

The Great Skua is one of the 79 regularly-breeding British bird species of high conservation importance (a Red Data Bird) on account of its localised breeding distribution and the international importance of the British population (Batten *et al.* 1990). The Arctic Skua is included in the British Red Data list of birds as a candidate species, requiring close monitoring of its status. Within Britain, around 97% of Great Skuas and 92% of Arctic Skuas breed in Shetland and Orkney (Lloyd *et al.* 1991). The Shetland population of Great Skuas is of major international importance, representing nearly half the world breeding population of 13,600 pairs (Lloyd *et al.* 1991).

Both species of skua were counted in Shetland in 1974-75 (Everett 1982) and 1985-86 (Ewins *et al.* 1988). Their breeding populations appeared to be fairly stable or slightly increasing over that period (Ewins *et al.* 1988). Food availability was considered to be the most important factor influencing skua numbers, with human persecution (especially of Great Skuas) and agricultural reclamation of moorland having a local influence (Ewins *et al.* 1988).

Since the mid 1980s several seabird species have suffered reduced breeding success in Shetland due to food shortage (Heubeck 1989, Martin 1989) and some have suffered large declines in numbers (Avery *et al.* 1993). Most notable was the almost complete failure of Arctic Terns, *Sterna paradisaea*, to rear young in most years between 1984 and 1990, as a result of shortage of sandeels, *Ammodytes marinus* (Monaghan *et al.* 1989). Both skua species partially depend on sandeels, obtained either directly or through kleptoparasitism (Furness 1987a). There were concerns that skua populations in Shetland might therefore have decreased since the mid-1980s due to breeding failure. In addition, Arctic Skua numbers and distribution may be limited as a result of predation by Great Skuas (Furness 1977).

In 1992 the Royal Society for the Protection of Birds organised a complete survey of skuas in Orkney and Shetland in order to assess the changes in numbers of both species since they were last counted; 1985-86 in Shetland and 1982 in Orkney. The results of the Orkney survey have been published separately (Meek *et al.* 1994). This paper summarises the results of the Shetland survey and discusses population trends and implications for the future.

METHODS

All areas of potential skua breeding habitat in Shetland were visited between 25 May and 11 July 1992, mostly in early June. Large tracts of moorland were divided into smaller units, where possible using obvious geographical boundaries (streams, ridges or roads). Surveys were not made in adverse weather (winds over Beaufort Force 5, heavy precipitation or poor visibility) or early morning or late afternoon when adults were likely to be away feeding. In areas of low skua density birds were counted by walking transects up to 500m apart, zig-zagging in areas of broken terrain, scanning from suitable vantage points every 200-300m. In areas of high skua density the transects were much closer and colonies were scanned for longer, after birds had settled. After completing the scan, observers walked through the colony recording additional birds and then made a final scan from the other side of the colony, once birds had re-settled.

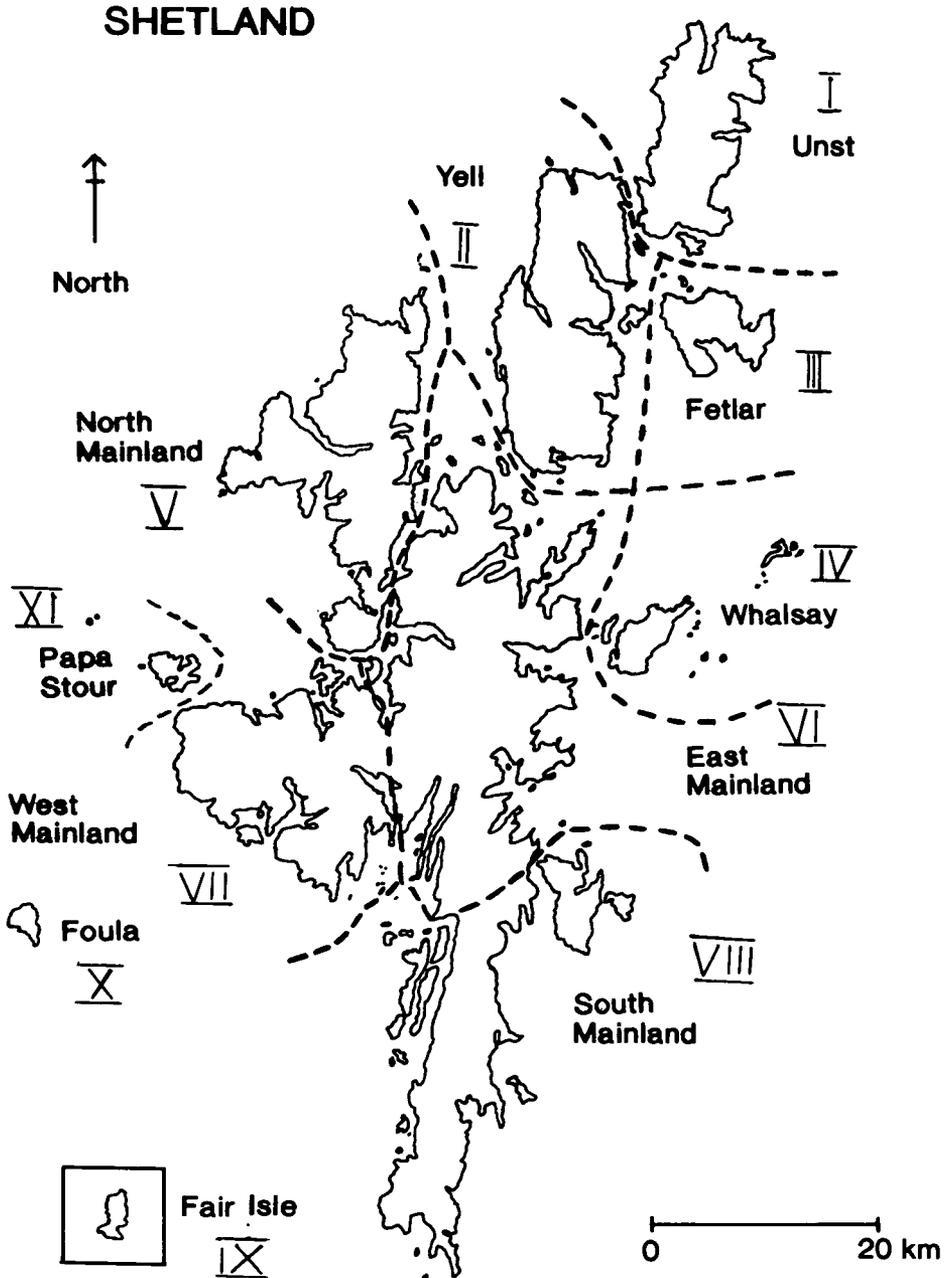


Figure 1. Map of Shetland Islands showing the islands and regional divisions listed in Table I.

The counting unit used was the 'apparently occupied territory' (AOT) as recommended by Furness (1982). This count unit was also used in the 1985-86 survey (Ewins *et al.* 1988). An AOT was scored for any of the following:

- (i) positive signs of breeding (eg. nest, eggs or young)
- (ii) incubating adult
- (iii) distracting or alarming adult(s)
- (iv) pair or single bird in potential breeding habitat and apparently attached to the area.

Skuas flying past, or feeding, or single birds flushed from an area and which flew out of sight were not recorded. Groups of three or more skuas which were seen together regularly but which showed no sign of territorial behaviour were recorded as 'club' (non-breeding) birds.

The positions of all AOTs were plotted on 1:25,000 maps along with the locations of clubs and the number of birds in them. The colour-phases of Arctic Skuas were recorded according to belly colour as either dark (melanic) or pale, using the criteria recommended by P.O'Donald (in Meek *et al.* 1985).

For comparison with the 1985-86 survey, Shetland was divided into the same 11 geographical regions (Figure 1). Since complete coverage of all potentially suitable breeding habitat in Shetland was achieved, it was not necessary to calculate confidence intervals for the estimates of population size as sampling errors are not involved. Statistical analysis was performed using SYSTAT (Wilkinson 1987).

RESULTS

Arctic Skua

1,878 Arctic Skua AOTs were counted in the 11 regions, representing a 1.8% decrease since 1985-86 (Table I). Although there is little difference in the overall population, there have been some changes in distribution since 1985-86 with an increase of 79 AOTs (29.6%) on Unst and decreases of 33 AOTs on each of Fetlar and West Mainland (18.3% and 19.5% respectively). Fair Isle, Foula and Papa Stour continue to be the most densely populated areas, with over 12 AOTs per square kilometre, whilst the lowest densities were in Central, West and North Mainland (Table II).

TABLE I. COMPARISON OF ARCTIC SKUA AOTS IN 1985/86 (FROM EWINS *ET AL.* 1987) AND 1992, AND PERCENTAGE OF 1992 SHETLAND TOTAL OCCURRING IN EACH REGION. ROMAN NUMERALS CORRESPOND TO REGIONS IN FIGURE 1.

Area	1985/6 AOTs	1992 AOTs	Difference	% 1992 Total
I Unst	267	346	+ 29.6	18.4
II Yell	192	175	- 8.9	9.3
III Fetlar	180	147	- 18.3	7.8
IV Whalsay Islands	41	24	- 41.5	1.3
V North Mainland	175	160	- 8.6	8.5
VI Central Mainland & Yell Sound Islands	189	176	- 6.9	9.4
VII West Mainland	169	136	- 19.5	7.2
VIII South Mainland & Islands	326	345	+ 5.8	18.4
IX Fair Isle	115	109	- 5.2	5.8
X Foula	164	159	- 3.0	8.5
XI Papa Stour	94	101	+ 7.4	5.4
TOTAL	1,912	1,878	- 1.8	100

TABLE II. THE DENSITIES OF BREEDING SKUAS PER KM² OF TOTAL LAND AREA IN THE 11 REGIONS OF SHETLAND IN 1992. REGION AREAS (KM²) ARE EXTRACTED FROM EWINS *ET AL.* 1987

Region	Area (km ²)	Arctic Skua AOTs		Great Skua AOTs	
		No	No/km ²	No	No/km ²
I Unst	120	346	2.9	1,567	13.1
II Yell	212	175	0.8	308	1.5
III Fetlar	38	147	3.7	523	13.8
IV Whalsay	27	24	0.9	2	0.07
V N Mainland	228	160	0.7	218	1.0
VI C Mainland and Yell Sound Islands	375	176	0.5	118	0.3
VII W Mainland	213	136	0.6	73	0.3
VIII South Mainland and islands	205	345	1.7	1,079	5.3
IX Fair Isle	9	109	12.1	110	12.2
X Foula	13	159	12.2	2,174	167.2
XI Papa Stour	8	101	12.6	24	3.0
TOTAL	1,448	1,878	1.3	6,196	4.3

Comparisons with the 1974-75 survey are hampered by the different census methods used and the incomplete coverage of the first survey (Ewins *et al.* 1988). The census unit in 1974-75 was 'pairs holding territory' which was not well defined and it is unknown how this counting unit relates quantitatively to the AOTs recorded in 1985-86 and in this survey. However, assuming the two units are directly comparable, Arctic Skua numbers in the three surveys are compared for those areas with complete coverage in 1974-75 (Table III). There appears to have been a sustained increase in numbers on Unst and decrease on Fetlar. Although there was a drop in numbers on Yell between 1985-86 and 1992 it was less than the substantial decrease between 1974-75 and 1985-86. Numbers on Fair Isle have remained remarkably constant but there has been a slight decrease on Foula between each survey. The large increase in numbers in South Mainland, Sandness and on several of the small islands (such as Mousa, Burra and Trondra, Whalsay) between the first two surveys has not continued between 1985-86 and 1992.

Forty-six Arctic Skuas were recorded as non-breeding 'club' birds, most on Fair Isle (13), Foula (10) and in South Mainland (11) (Table IV). This represents a major decline (of 56%) in non-breeders since 1985-86 when 104 were recorded, of which 35 were on Foula and 20 on Fair Isle (Ewins *et al.* 1988). Thirty-three club birds were recorded on Yell in 1985-86 but there were none in 1992.

The colour phase of 3410 territorial birds was recorded of which 767 (22.5%) were pale (Table V). Similar proportions of pale phase were recorded in Shetland in 1985-86 (21.6%).

The colour phases of both members of a pair were recorded for 1548 pairs of which 62% of pairings were melanic x melanic, 32% were melanic x pale and 6% pale x pale (Table VI). Again, similar ratios were found in 1985-86 in Shetland (63%, 32% 5%) and there were no significant differences in the distributions between years (χ^2 , $P > 0.05$).

Great Skua

6,196 Great Skua AOTs were recorded, representing a 9.7% increase since 1985-86 (Table VII). Most of this increase occurred on Unst (+ 310 AOTS), Fetlar (+ 275 AOTS) and in South Mainland & Islands (+ 227 AOTS). On Foula, which continued to have by far the highest densities of Great Skuas (167 AOTs per square kilometre) (Table II) the number of AOTS had decreased by 13% since 1985-86.

TABLE III. COMPARISON OF ARCTIC SKUA BREEDING NUMBERS IN 1974-75 SURVEYS (PAIRS) WITH 1985-86 & 1992 SURVEYS (AOTS), ONLY FOR THOSE AREAS WHERE COVERAGE WAS COMPLETE IN 1974-75 (SEE EWINS *ET AL.* 1987).

Area	1974-75		1985-86	Difference	1992	Difference (%)	
	No prs	Range	AOTs		AOTs	74/75	85/86
<i>Islands</i>							
Unst	193	188-219	265	+ 37.3	342	+ 77.2	+ 29.1
Yell	326	326-327	181	- 44.5	163	- 50.0	- 9.9
Hascosay	18		11	- 38.9	12	- 33.3	+ 9.1
Fetlar	200	200-201	180	- 10.0	147	- 26.5	- 18.3
Whalsay	17		38	+123.5	24	+ 41.2	- 36.8
Nogs	44		22	- 50.0	17	- 61.4	- 22.7
Bressay	104	104-106	70	- 32.7	91	- 12.5	+ 30.0
Burra & Trondra	21	21-23	48	+128.6	46	+119.1	- 4.2
Mousa	5		21	+320.0	26	+420.0	+ 23.8
Foula	175	150-275	164	- 6.3	159	- 9.1	- 3.1
Fair Isle	116	116-136	115	- 0.9	109	- 6.0	- 5.2
Island Total	1,219		1,115	- 8.5	1,136	- 6.8	+ 1.9
<i>Mainland</i>							
North Roe	72		97	+ 34.7	79	+ 9.7	- 18.6
Sutton Voe	26		37	+ 42.3	24	- 7.7	- 35.1
Lunna	8		2	- 75.0	8	0.0	+300
Lerwick	14		9	- 35.7	5	- 64.3	- 44.4
South Mainland	89		155	+ 74.2	147	+ 65.2	- 5.2
Sandness	1		25	+2400	24	+2300	- 4.0
Mainland total	210		325	+ 54.8	287	+ 36.7	- 11.7
Total	1,429		1,440	+ 0.8	1,423	- 0.4	- 1.2

The same problems exist for the comparison of Great Skua numbers in the 1974-75 survey as for Arctic Skuas, but taking these into account, it appears that there was no overall decrease in numbers on Foula between 1974-75 and 1985-86 (Table VIII). There has been a sustained increase in numbers on Unst but most of the increase on Fetlar has been since 1985-86. The increase in South Mainland since 1985-86 was not as high as that between 1974-75 and 1985-86.

Non-breeding Great Skuas were recorded in all 11 regions except the Whalsay Islands (Table IV). Of the 1259 club birds recorded, most were on Unst (446), Foula (259) and South Mainland & Islands (259). Overall, numbers of non-breeders are down 7% since 1985-86 but on Foula they are substantially lower; from 858 club birds in 1985-86 to 270 in 1992 (-68.5%). In several other regions numbers of club birds have increased (Unst, South Mainland, Yell and Fetlar being most notable).

DISCUSSION

Numbers of breeding Arctic Skuas were expected to have decreased since the mid-1980s, as a result of the shortage of sandeels around Shetland. Arctic Skuas in Shetland feed almost entirely by kleptoparasitism, their main hosts being Arctic Terns, Kittiwakes, *Rissa tridactyla*, Guillemots, *Uria aalge*, and Puffins, *Fratercula artica* (Furness 1980, Scanlon & Harvey 1989). Food shortages and population declines suffered by Arctic Terns, Puffins and Kittiwakes during 1984-

TABLE IV. REGIONAL TOTALS OF ARCTIC SKUA AND GREAT SKUA CLUB BIRDS COMPARING NUMBERS IN 1985/86 AND 1992. ROMAN NUMERALS CORRESPOND TO REGIONS IN FIGURE 1.

Region	Arctic Skua		Great Skua	
	1985/86	1992	1985/86	1992
I Unst	0	4	203	446
II Yell	33	0	38	76
III Fetlar	0	0	35	82
IV Whalsay Islands	0	3	4	0
V North Mainland	0	5	7	41
VI Central Mainland & Yell Sound Islands	10	0	4	9
VII West Mainland	0	0	35	9
VIII South Mainland & Islands	6	11	119	259
IX Fair Isle	20	13	54	43
X Foula	35	10	858	270
XI Papa Stour	0	0	0	24
Total	104	46	1,357	1,259

TABLE V. THE FREQUENCY OF PALE PHASE ARCTIC SKUAS IN 1992, COMPARED WITH PREVIOUS SHETLAND AND ORKNEY DATA. NO = TOTAL NUMBER OF INDIVIDUALS WHOSE COLOUR PHASE WAS DETERMINED. PALE = THE NUMBER OF PALE PHASE BIRDS.

Region	No	1992		1986
		Pale	%	%
I Unst	610	117	19.2	21.8
II Yell	315	65	20.6	—
III Fetlar	269	90	33.5	23.4
IV Whalsay Islands	42	14	33.3	—
V North Mainland	281	68	24.2	21.3
VI Central Mainland & Yell Sand Islands	295	74	25.1	27.1
VII West Mainland	240	62	25.8	23.9
VIII South Mainland & Islands	644	129	20.0	19.8
IX Fair Isle	213	36	16.9	15.4
X Foula	313	69	22.1	23.4
XI Papa Stour	188	43	22.9	—
Shetland 1992	3,410	767	22.5	21.6
Shetland 1943-79	1,006	267	26.5	Meek <i>et al.</i> 1985
Foula 1970s	512	138	27.0	Meek <i>et al.</i> 1985
Orkney 1982	1,869	455	24.3	Meek <i>et al.</i> 1985
Shetland 1986	1,615	349	21.6	Ewins <i>et al.</i> 1987
Orkney 1992	1,890	462	24.4	Meek <i>et al.</i> 1994

1990 are therefore likely to have had an adverse effect on Arctic Skuas. Yet the results of this survey compared with the last suggest relatively little change in overall numbers. Also in Orkney similar numbers were recorded in 1992 compared with the last survey in 1982 (+2%) (Meek *et al.* 1994).

However, the comparison between single counts several years apart may only present part of the picture due to dynamic changes in the interim years. On Foula, where numbers were similar in each of the three surveys (175, 164 and 159 pairs/AOTs in 1974-75, 1985-86 and 1992 respectively), annual counts record that numbers peaked at 280 AOTs in 1976 and declined during the mid to late 1980s to a low of 98 AOTs in 1990 (R. Furness, in litt.). Numbers increased markedly in 1991 and 1992 to 141 and 159 AOTs respectively (Walsh *et al.* 1993), coinciding with an increase in sandeel availability (Wright & Bailey, 1993). This suggests that breeding Arctic Skuas were affected by the shortage of sandeels in the late 1980s but could respond rapidly to an increase in food availability. There is evidence from individually marked birds that some breeding adult Arctic Skuas left Foula during 1988-90 but returned in 1991 and 1992 (Furness, 1992a).

TABLE VI. THE COLOUR PHASES OF ARCTIC SKUA PAIRINGS IN SHETLAND IN 1992, COMPARED WITH PREVIOUS SHETLAND AND ORKNEY DATA.

P = pale

M = melanic

N = total no of pairings

Region	N	PAIRINGS (1992)					
		M X M		M X P		P X P	
			%		%		%
I Unst	263	171	65.0	80	30.4	12	4.6
II Yell	146	93	63.7	47	32.2	6	4.1
III Fetlar	126	56	44.4	57	45.2	13	10.3
IV Whalsay Islands	18	11	61.1	4	22.2	3	16.7
V North Mainland	121	72	59.5	44	36.4	5	4.1
VI Central Mainland & Yell Sound Islands	120	71	59.2	39	32.5	10	8.3
VII West Mainland	104	61	58.7	34	32.7	9	8.7
VIII South Mainland & Islands	303	201	66.3	87	28.7	15	5.0
IX Fair Isle	104	75	72.1	23	22.1	6	5.8
X Foula	155	97	62.6	47	30.3	11	7.1
XI Papa Stour	88	52	59.1	31	35.2	5	5.7
Shetland 1992	1,548	960	62.0	493	31.9	95	6.1
Shetland 1943-79 ^a	376	218	58.0	120	31.9	38	10.1
Foula 1970s ^a	256	144	56.3	86	33.6	26	10.2
Orkney 1982 ^a	858	501	58.4	299	34.8	58	6.8
Shetland 1986 ^b	662	418	63.1	210	31.7	34	5.1
Orkney 1992 ^c	845	491	58.1	299	35.4	55	6.5

^a Meek *et al.* 1985

^b Ewins *et al.* 1987

^c Meek *et al.* 1994

TABLE VII. COMPARISON OF GREAT SKUA AOTS IN 1985/86 (FROM EWINS *ET AL.* 1987) AND 1992, AND PERCENTAGE OF 1992 SHETLAND TOTAL OCCURRING IN EACH REGION. ROMAN NUMERALS CORRESPOND TO REGIONS IN FIGURE 1.

<i>Area</i>	<i>1985/6 AOTs</i>	<i>1992 AOTs</i>	<i>Difference</i>	<i>% 1992 Total</i>
I Unst	1,257	1,567	+ 24.7	25.3
II Yell	313	308	- 1.6	5.0
III Fetlar	248	523	+110.9	8.4
IV Whalsay Islands	1	2	+100.0	-
V North Mainland	233	218	- 6.4	3.5
VI Central Mainland & Yell Sound Islands	114	118	+ 3.5	1.9
VII West Mainland	96	73	- 24.0	1.2
VIII South Mainland & Islands	792	1,019	+ 36.2	17.4
IX Fair Isle	84	110	+ 30.1	1.8
X Foula	2,495	2,174	- 12.9	35.1
XI Papa Stour	14	24	+ 71.4	0.4
TOTAL	5,647	6,196	+ 9.7	100

There is also evidence that Arctic Skua productivity in Shetland was adversely affected during 1988-90, when 13-19 monitored colonies fledged an average of only 0.08-0.17 young per AOT (Walsh *et al.* 1990, 1991). By contrast, in 1991, when large numbers of sandeels were available, Arctic Skua productivity in Shetland was much higher, averaging 0.69 young per AOT (Walsh *et al.* 1992) and was even higher in 1992 at 1.13 young per AOT (Walsh *et al.* 1993).

It appears that any reduction in Arctic Skua breeding success during the late 1980s has not yet depressed the adult breeding population to any great extent. However, it may be too early to see a reduction in the breeding population, given that the average age of first breeding for Arctic Skuas is four to five years (Cramp 1983). Thus breeding failures in 1989 and 1990 would not be apparent in the adult population until the period 1993-1995. The fact that numbers of non-breeders in Shetland were considerably reduced compared with 1985-86 supports this prediction. It will therefore be necessary to monitor the population over the next few years.

The Great Skua population was also considered at risk due to the sandeel shortage since, although the adults feed on a variety of items, the young are raised on sandeels (Ewins *et al.* 1988). Overall, Great Skuas appear to have fared better than Arctic Skuas and have continued to increase in Shetland. This is perhaps due to their more catholic diet. Their numbers have increased on Orkney too (+22% since 1982) and at least two more Orkney islands have been colonised since 1982 (Meek *et al.* 1994). Unfortunately Great Skua breeding success in Orkney and Shetland was not well monitored prior to 1991, except on Foula where the average has varied between 0.01 and 0.7 young per AOT during 1987-92 (Furness, R.W. 1987b, 1988, 1989, 1990, 1991, 1992a). There was little or no obvious increase in breeding success in relation to increased sandeel availability in 1991 and 1992 (Walsh *et al.* 1992, 1993).

The overall increase in Great Skua numbers in Shetland masks an important decline in their main breeding area. Foula is by far the largest colony of Great Skuas in the world (Klomp & Furness 1992). It held a peak of 3000 breeding pairs in the late 1970s (Furness 1987a) but has since declined. In 1985-86 a total of 2,495 AOTS were counted and in 1992 there were 2,174, a decline of 13%. Great Skua breeding success was greatly reduced on Foula in 1987-90 and the peak number of non-breeders in 1989 and 1990 had declined by 80% since 1977 (Klomp &

TABLE VIII. COMPARISON OF GREAT SKUA BREEDING NUMBERS IN 1974-75 SURVEYS (PAIRS) WITH 1985-86 & 1992 SURVEYS (AOTS), ONLY FOR THOSE AREAS WHERE COVERAGE WAS COMPLETE IN 1974-75 (SEE EWINS *ET AL.* 1987).

Area	1974-75		1985-86 AOTs	Difference	1992 AOTs	Difference (%)	
	No prs	Range				74/75	85/86
<i>Islands</i>							
Unst	1,075	985-1228	1,254	+ 16.7	1,566	+ 45.7	+ 24.9
Yell	249	249-257	282	+ 13.3	285	+ 14.5	+ 1.1
Hascosay	55	55-60	30	- 45.5	23	- 58.2	- 23.3
Fetlar	237		248	+ 4.6	523	+120.7	+110.9
Noss	255	245-265	378	+ 48.2	424	+ 66.3	+ 12.2
Bressay	160	137-197	115	- 28.1	248	+ 55.0	+115.7
Burra & Trondra	2		9	+350.0	13	+550.0	+ 44.4
Mousa	9		10	+ 11.1	10	+ 11.1	0
Foula	2,400	2150-3000	2,495	+ 4.0	2,174	- 9.4	- 12.9
Fair Isle	17	17-21	84	+394.1	110	+547.1	+ 31.0
Island Total	4,459		4,905	+ 10.0	5,376	+ 20.6	+ 9.6
<i>Mainland</i>							
North Roe	66		140	+112.1	133	+101.5	- 5.0
Sutton Voe	15		15	0	4	- 73.3	- 73.3
Lunna	1		2	+100	2	+100	0.0
Lerwick	16		6	- 62.5	8	- 50.0	+ 33.3
South Mainland	87	87-90	265	+204.6	367	+321.8	+ 38.5
Sandness	7		37	+428.6	29	+314.3	- 21.6
Mainland total	192		465	+142.2	543	+182.8	+ 16.8
Total	4,651		5,370	+ 15.5	5,919	+ 27.3	+ 10.2

Furness 1992). These findings were substantiated by the 1992 survey in which the number of non-breeding Great Skuas on Foula was reduced by 69% compared with 1985-86. This rapid decrease in non-breeders on Foula is believed to have been due to increased recruitment into the breeding population caused by a reduction in adult survival rate since the 1970s (Klomp & Furness 1992). The effects of poor breeding success in 1987-90 will also have affected the number of non-breeders in the last few years. Further decreases in non-breeders may occur on Foula over the next few years leading to a more rapid decline in numbers of breeding birds.

By contrast, at the main colony in Orkney (Hoy), there was little change in the numbers of non-breeding Great Skuas and a 21% increase in the number of AOTs between 1982 and 1992, possibly suggesting a lower rate of adult mortality than on Foula (Meek *et al.* 1994).

Numbers of Great Skuas in Shetland may also be affected by future changes in fishing practices, particularly by any reduction in the discarding of undersized fish and offal at sea, for example through changes in mesh size regulations or reductions in fishing effort. Adult Great Skuas depend heavily on discards of whitefish from fishing boats around Shetland (Hudson & Furness 1988). Plans to limit this practice within EU waters are currently under discussion. It has been predicted that Great Skuas would suffer major breeding failures if there was a reduction in suitable length

discards coincidental with a shortage of sandeels, and that numbers of breeding Great Skuas would decrease considerably as a result of a 30% reduction in fishing effort or an increase in mesh size to 120 mm, or both (Furness 1992).

Any change in Great Skua numbers or food supply may have a knock-on effect on the numbers and distribution of Arctic Skuas since the chicks of birds such as Arctic Skuas are included in the Great Skua diet. Newly fledged Arctic Skua chicks are particularly heavily predated by Great Skuas on Noss (McKay & Crossthwaite 1985, Harvey & Suddaby 1986). In 1988, all recorded predation of Arctic Skua chicks on Noss (13 cases) and Hermaness (8 cases) was caused by Great Skuas (Scanlan & Harvey 1989). The continuing decline in Arctic Skua numbers on Fetlar may be associated with the increase in Great Skuas, which more than doubled between 1985-86 and 1992.

To conclude, although the numbers of breeding skuas of both species have not declined overall compared with the 1985/86 survey, it may be too early to record any effects of reduced breeding success during the late 1980s. However, there has been a major decrease in the number of Great Skuas breeding at the most important colony in the world, on Foula. Also of concern is the decline in the number of non-breeders of both species since it is likely that this will limit future recruitment into the breeding population. It is therefore necessary to monitor the populations of both species closely over the next few years to detect these changes and any that may occur as a result of changes in fishing practices such as a re-opening of the Shetland sandeel fishery or a reduction in discards. In order to achieve this, a complete survey of skua populations in Orkney and Shetland should be repeated every five years.

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SUMMARY

A survey of skuas in Shetland in 1992 indicated that, since the last survey in 1985-86, numbers of breeding Arctic Skuas had remained stable at around 1,900 apparently occupied territories (AOTs) and numbers of Great Skuas had increased by 10% to around 6,200 AOTs. However, numbers of Great Skuas at their main colony on Foula had continued to decline. Declines in numbers of non-breeders were evident for both species and the possibility of future reductions in adult populations are discussed.

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Increases in the number of Puffins at Eilean Mor and North Rona, Outer Hebrides

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INTRODUCTION

The numbers of Puffins *Fratercula arctica* in Scotland declined during the early and mid parts of this century, but most information suggests that these decreases had mostly ceased, and in some places had been reversed by the late 1970s (Harris 1984). Numbers appear to have remained more or less static during the 1980s (Lloyd *et al.* 1991) but in recent years there has been renewed speculation about the health of Puffin colonies on some of Scotland's remoter island groups. (Taylor 1990). This note reports on increases during the last 17 years of numbers at two medium sized colonies in the Outer Hebrides, Western Isles. Eilean Mor, the largest island in the Flannans group (32 km west of Lewis) and North Rona (74 km north of the Butt of Lewis).

METHODS AND RESULTS

Eilean Mor

This island was visited between 21 and 28 June 1975. The Puffin colonies were located and mapped and the two largest measured by pacing out a marked rope. The main colony, south and east of the lighthouse covered approximately 11500 m² and the western colony centred around the ruined Macphails bothies, about 1200 m². The colony was revisited on 23/24 May 1992.

The irregular shape of the colonies and the varying angle of the slopes makes a precise measurement of both areas difficult to achieve. The area totals are, if anything, an underestimate of the ground occupied by Puffins. To sample burrow density three transects were taken through the main colony and two through the western colony. All the transects were started above the upper limit of burrows and run down slope through the colonies, ending at steep cliffs beyond the limit of Puffin occupancy. The numbers of occupied burrows (ie. those showing signs of digging, droppings, broken egg shells etc) were counted in each transect. The slight differences in areas covered by the transects in 1975 and 1992 were due to the loss of marker pegs on the grass slopes above the colony.

In 1992, the occupied burrows in the transects were counted and some colony mapping was also done. Puffins were present at all the sites they had been seen at in 1975. In the main colonies there were no obvious changes to colony extent. An additional transect placed outside, and on the extreme western edge of the main colony, had no burrows in either 1975 or 1992. The remaining three transects had increased numbers of occupied burrows in 1992, compared with 1975. The two transects in the western colony had also increased (Table I). A minimum population estimate for both years was calculated by multiplying the average occupied burrow density, after totalling the

TABLE I. COUNTS OF OCCUPIED BURROWS IN TRANSECTS ON EILEAN MOR IN 1975 AND 1992.

Transect number	Area (m ²)	1975		1992		
		Occupied burrows	Density per/m ²	Area (m ²)	Occupied burrows	Density per/m ²
1	369	68	0.184	297	97	0.326
2	117	40	0.341	117	54	0.461
3	234	71	0.303	216	93	0.430
4	273	57	0.208	243	103	0.423
5	63	26	0.412	72	49	0.680

five transects, by the total area of both east and west colonies. In 1975 this was 0.248 occupied burrows/m² x 12700 m², giving 3150 occupied burrows, and in 1992, 0.325 occupied burrows/m² x 12700 m², giving 5320 occupied burrows.

Problems in estimating the total number of breeding Puffins, arise from the variations in burrow density within the colonies and difficulties in delimiting the overall size. I have no check on the accuracy of these estimates, but I am confident that the areas surveyed contained between 3000-5000 pairs in 1975, and between 5000-6000 pairs in 1992. In addition to the areas surveyed, Puffins occupied other parts of the island, notably among boulder scree above the north cliffs. No attempt was made to count these subcolonies, but they were present in both years, and numbers were estimated at 500 to 1000 pairs.

North Rona

I visited North Rona in June or early July in 1976, 1980, 1986 and 1993. During the first two visits, transects were established on the largest colony on the east cliffs, but these were not recounted until the most recent visit between 14-24 June 1993.

The first map of the puffin colonies on the island was made by Bagenal and Baird (1958). It is difficult to judge from their map what the relative size of each sub-colony might be, but clearly many of the west and south coast colonies are very small. Evans (1975) produced a similar map for 1972 and there are few apparent differences between them. Away from the main concentrations, the location and number of smaller subcolonies are consistent between years. Since then the colonies have been mapped in detail in 1986 (Benn *et al.* 1989) and in 1993 by Murray and Love (Scottish Natural Heritage unpublished).

In both these years the coast was checked for the presence or absence of birds ashore to give some assessment of colony size. The only area not counted was the main colony on the east cliffs. There was no change in the number or positions of sub-colonies found in 1986 compared with 1993. At 12 out of a total of 18 sub-colonies, numbers seen ashore in 1993 were higher than in 1986. However birds coming ashore at colonies are notoriously fickle, so changes in numbers cannot be inferred from single annual counts.

Evans (1975) estimated the breeding population at 6200 pairs in 1972. This figure was based on counts of birds ashore and burrow density in three coastal and three inland colonies. The average occupied burrow density for these areas were, 0.097 occupied burrows/m² and 0.130 occupied burrows/m² respectively. The only other transect counts of burrow density were four made in 1976 and one in 1980 (Table II). No population estimates were calculated from these counts.

The transects ran through the main concentrations of Puffins on the east cliffs below and to the south of the island summit. However to reach them it is necessary to negotiate steep slopes, unstable vegetation and high numbers of Fulmars *Fulmarus glacialis*. Access is particularly hazardous after heavy rain, and for this reason transect 4 on the steepest and most exposed cliff, was not repeated in 1993 (Table II).

TABLE II. COUNTS OF OCCUPIED BURROWS IN TRANSECTS ON NORTH RONA IN 1976, 1980 AND 1993.

Transect number	Area (m ²)	1976/1980		1993		
		Occupied burrows	Density (burrows/m ²)	Area (m ²)	Occupied burrows	Density (burrows/m ²)
1	117	37	0.316	126	46	0.365
2	72	60	0.833	72	85	1.180
3	72	27	0.375	72	71	0.986
4	144	55	0.381	No count		
5	255	29	0.113	255	33	0.129

Note: 1976 Transects 1 to 4; 1980 Transect 5.

Transects 1-3 in 1976 had a combined total of 124 occupied burrows and 75 classed as unoccupied. In 1993, the total of occupied burrows had risen to 202, which suggests all usable burrows were occupied. Support for this came from the marginal quality of some of the occupied burrows, which were so short or eroded that incubating or brooding birds could easily be seen. This may encourage a slow expansion of the colony into other areas.

However, transect 5 which appears to have the greatest potential for expansion, showed only a slight increase between 1980 and 1993, with the number of occupied burrows increasing from 29 to 33 (Table II). Puffins may be deterred for some reason from using this slope, which is a steep grassy gully hemmed in by cliffs on both sides. The overall steepness of the cliffs makes it impossible to map the colony with any degree of confidence. Thus no extrapolated estimates of total colony size based on transect data were attempted. The range of population estimates for the entire island, 4000 to 7000 pairs, is based solely on counts of birds on land in 1986 and 1993.

DISCUSSION

There has been no decline in Puffin numbers on either Eilean Mor between 1975 and 1992 or on North Rona between 1976 and 1993. On the contrary there have been substantial increases within the largest colonies on both islands, but with no obvious changes in colony extent. All the transects have shown increases, but at a variable rate, and overall, numbers of occupied burrows have risen by 38% on Eilean Mor and 39% on North Rona. Both islands have had continuous Puffin occupation for at least the past century. The Flannans were visited by Harvie Brown (1882) and he described the Puffin on Eilean Mor as abundant. On North Rona, Swinburne (1885) described them as 'swarming wherever they could burrow'. Most subsequent visitors to both islands have used the same broad but imprecise language in describing the colonies. This has led, in the case of North Rona, to an assumption that in recent historical time the Puffin colonies were considerably larger, than at present. The inference that they have declined owes much to Darling's (1940) vague estimate of 100,000 birds; (a calculation made on the erroneous assumption that the Puffin formed the main prey item for the resident population of Great Black-backed Gulls *Larus marinus*).

Subsequent investigation has shown this not to be the case. Even with a population in excess of 2000 pairs of gulls, predation on Puffins was remarkably low (Evans 1975). Evans did conclude however, that the Puffin colonies had declined between 1938 and 1958.

On the Flannans group, Puffins have been noted on all the main islands. Surveys of the seabirds, including Puffins have been made previously in 1959 (Anderson *et al.* 1961), 1969 (Cramp *et al.* 1974) and in 1988 (Lloyd *et al.* 1991). The only attempt at detailed mapping of the largest Puffin colony in the group, on Eilean Mor, was made in 1975 (S. Murray unpublished).

On Eilean Mor there is no major evidence of a decline in numbers. From the description in Anderson *et al.* (1961) it does seem that the limits of the main Puffin colony have retreated eastwards, and there may also be burrow loss due to erosion around cliff edges, particularly above the south landing. Neither effect will necessarily result in a loss of breeding pairs.

In conclusion, the high density of occupied burrows in parts of North Rona's main colony, suggests it may have reached its limit for viable burrows. If so a slow expansion into adjacent areas is likely. By contrast, on Eilean Mor, even at the highest density found in 1992, there could still be room for growth within present colony limits. The sizes of the breeding populations on both islands are difficult to calculate, but both hold similar numbers in the range 4000 to 7000 pairs.

ACKNOWLEDGEMENTS

I am grateful to Kenny Taylor for arranging my trip to the Flannans in 1992, in association with the Scottish Wildlife Trust 'Operation Puffin' fieldwork, Mary Harman for inviting me to North Rona in 1993, and Mike Harris who improved an earlier draft of this paper.

SUMMARY

Five transects were set up in the largest Puffin colony on Eilean Mor in the Flannans group in 1975, and recounted in 1992. All five showed increases in the numbers of occupied burrows present, and overall these had increased by 38% between 1975 and 1992. On North Rona, four transects were placed on the east cliffs in 1976 and a fifth added in 1980. Four out of five were recounted in 1993, and all showed increases in the numbers of occupied burrows present, with an overall increase of 39% between 1976 and 1993. There were no marked changes in Puffin colony extent on either island between years.

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Distant feeding and associations with cetaceans of Gannets *Morus bassanus* from the Bass Rock, May 1994

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INTRODUCTION

The feeding range of breeding Gannets *Morus bassanus*, deduced from the time spent away from the nest and a known flight speed, has been estimated at 320-480 km (Nelson 1978). In contrast, on the basis of ship-based surveys in the North Sea, Tasker *et al.* (1985) concluded that fishing trips rarely exceed 150 km from the colony and that most are well below one-third of that distance. Further surveys, collected for the European Seabirds At Sea Database, confirmed that high densities of Gannets in May are confined to areas within 150 km around most large colonies (ESAS unpubl. data). A ship-based survey in the North Sea in May 1994 showed that mass feedings of Gannets, white-beaked dolphins *Lagenorhynchus albirostris* and white-sided dolphins *L. acutus* occurred at the Dogger Bank in the central North Sea. The feeding movements of Gannets found in May 1994 were reconstructed and analysed, in order to determine the origin of the Gannets. Feeding behaviour, group size, presence and feeding success at fishing vessels, prey and associations with cetaceans are described.

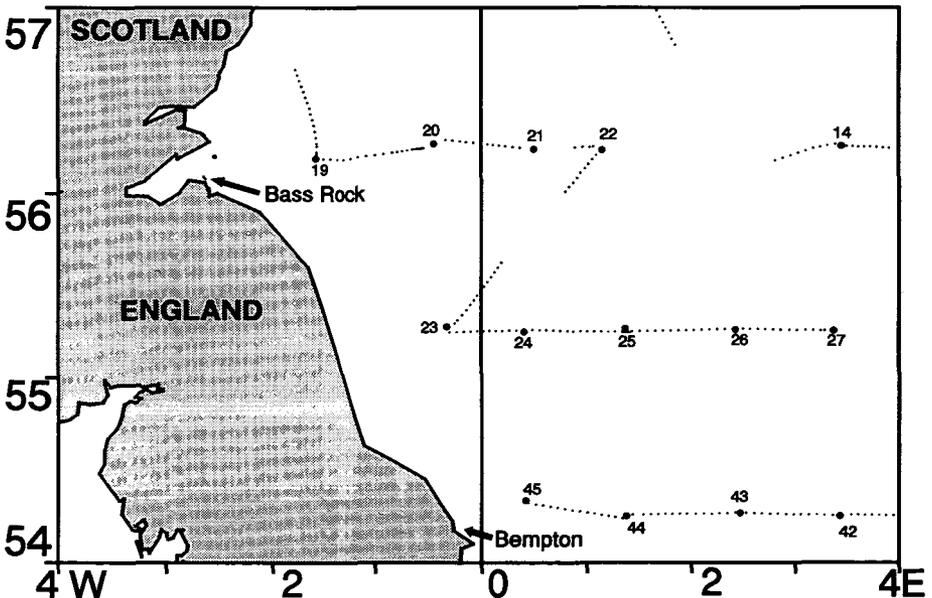


Figure 1. Study area off NE England, strip-transect counts (small dots), numbered hauls, and location of gannetries.

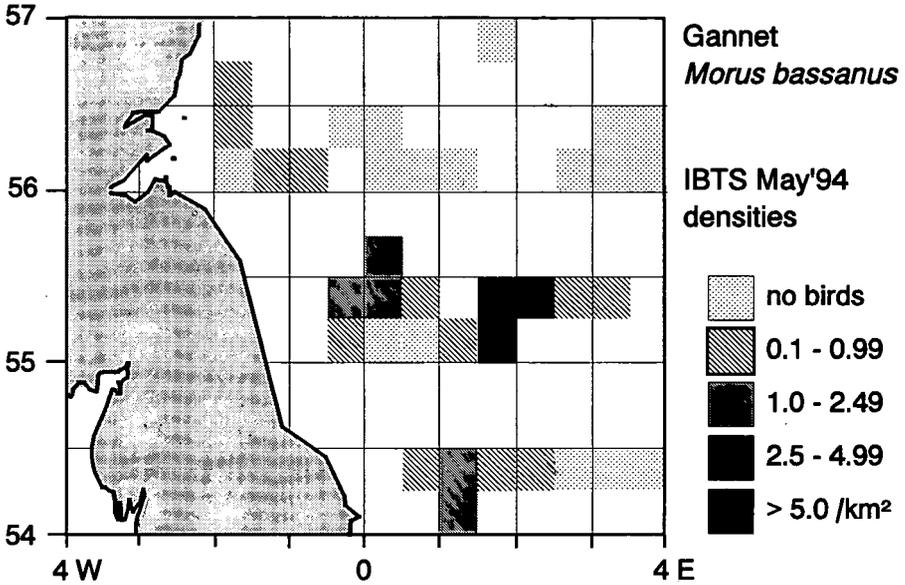


Figure 2. Densities (n/km²) of Gannets per quarter ICES square, May 1994, RV Tridens.

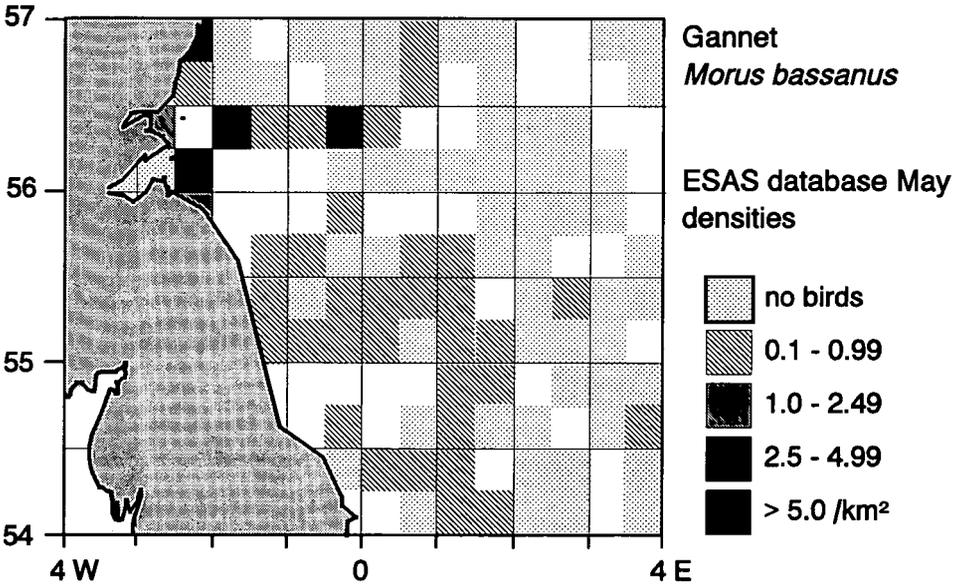


Figure 3. Densities (n/km²) of Gannets per quarter ICES square in May (ESAS Database unpubl.).

METHODS

The distribution of seabirds at sea was assessed onboard the fishery research vessel *Tridens* during the ICES co-ordinated International Bottom Trawl Survey (IBTS) from 2 to 27 May 1994, which enabled broad coverage of the North Sea between 52°N and 57°30'N. Counts presented are in the form of densities (birds per km²) obtained from a 300 m wide band-transect method (Tasker *et al.* 1984). All times are given as Greenwich Mean Time. Gannets outside the band-transect were recorded in a 180° scan ahead of the ship (not used to calculate densities), but individuals at more than 2 km away from the ship were ignored. Gannets were aged by plumage and counted in 10-minute periods, while notes were made on the direction of flight if the birds were clearly not attracted or influenced by the ship. Feeding associations of dolphins and Gannets were recorded and described. Fish leaping out of the water during interactions of dolphins and Gannets were identified whenever possible.

The ship trawled for half an hour in each ICES square visited, steaming for approximately 2 hours between fishing stations (Fig. 1). Seabirds were counted only during steaming, while the number of attracted birds was counted separately during periods of fishing (maximum number of each species present at each haul). Both during steaming and fishing, the numbers of commercial trawlers fishing were assessed at 30 min intervals within 3 nautical miles around the ship using radar and a visual check outside to identify vessels. Flocks of birds associated with nearby trawlers were counted.

IBTS surveys use the otter trawl (Knijn *et al.* 1993), which is an inefficient sampling method for pelagic, shoaling fish such as herring *Clupea harengus* and sprat *Sprattus sprattus*. The only available information on fish abundance, however, were otter trawl catches at 14 stations within the study area. Quantities of fish caught on 10 May were expressed as 'number of fish per hour fishing' for each station.

Results are presented here for an area to the east of NE England (54-57°N, 3°W-4°E). The distribution of seabirds at sea was compared with similar data collected previously for the European Seabird At Sea Database (ESAS unpubl. data). Directions of flight (only if a series of

TABLE I. SHIP'S ACTIVITIES, NUMBER OF GANNETS ATTRACTED DURING FISHING AND OBSERVATIONS OF FEEDING, MOVING OR RESTING GANNETS AND DOLPHINS, 10 MAY 1994, RV TRIDENS (SEE FIG. 3).

Time (GMT)	Ship's activity	haul	Gannet <i>M. bassanus</i>	dolphins <i>L. albir./ acutus</i>
03.55-05.55	steaming SW		(59) passage SE	none
05.55-07.15	fishing	23	21 attracted	
07.15-08.45	steaming E		(47) passage SE-NW	none
08.45-10.15	fishing	24	10 attracted	
10.15-12.55	steaming E		(164) passage SE-NW	none
12.55-13.35	fishing	25	(300) fishing 5 attracted	(100) feeding
13.35-15.35	steaming E		(825) resting	(70) passage W
15.35-16.45	fishing	26	12 attracted	none
16.45-18.25	steaming E		(39)	none
18.25-19.15	fishing	27	1 attracted	none

flocks were heading steadily in the same direction) were used to suggest the origin of flocks of Gannets at sea on 10 May, while the distance of high density areas to the nearest coast and to the nearest colonies (the Bass Rock at 56°05'N, 02°40'W and Bempton Cliffs at 54° 10'N, 00°08'W) were calculated.

RESULTS

Gannet

Gannets were scarce or absent offshore in much of the study area (Fig.2). Near the Bass Rock, low densities were recorded on 9 May, but Gannets were absent more than 100km from the nearest coast, contrary to results obtained in previous surveys in this region (ESAS unpubl. data; Fig.3). In the early morning of 10 May, very large numbers of Gannets were observed flying from northwest to southeast while the ship was steaming southwest off Newcastle (03.55-05.55h; Table I, Fig.4). In this area (ca. 55°27'N, 00°01'E), flocks of adult Gannets moving from northwest to southeast could only originate from the Bass Rock, 180 km away. The birds ignored the vessel completely. From 07.15h (at 55°15'N, 00°13'W) onwards, the ship moved in an easterly direction and the stream of Gannets moving in a southeasterly direction was again picked up roughly an hour later at 00°09'E. Between 08.15 and 12.25h, 210 Gannets were observed in small groups, the majority were moving towards the southeast, but some were returning to the northwest. Many more birds, outside the transect, were showing similar behaviour.

When fishing commenced at 55°14.4'N, 01°26.4'E, the ship had just reached an area where hundreds of white-beaked dolphins and white-sided dolphins were breaching and feeding, with an overall movement of cetaceans in a westerly direction (Fig.5). Small flocks of Gannets (totalling at least 300 birds) were feeding in close association with these dolphins, or following herds of dolphins which were moving rapidly. Neither dolphins nor Gannets showed any interest in the ship and only five Gannets were attracted when the net was lifted. Further east, large flocks of inactive Gannets were observed (13.35h, after the period of fishing) and between this spot and a point at 02°15.40'E (reached at 15.05h) the mean density was 27.6 Gannets per km² (392 adults in transect, 14.2km² surveyed). Dolphins became progressively scarcer, but were still moving westwards, and most Gannets were resting on the sea. These concentrations occurred ca. 170-205 km away from the nearest coast, 280-320 km away from the Bass Rock.

Within the study area, Gannets occurred in small numbers when the ship was fishing and were absent at fishing stations nearest to the Bass Rock. A maximum of 21 Gannets were attracted to the trawl, just to the south of the area where an extensive southeasterly passage occurred (55°15'N, 00°12'W). Of all scavengers at the trawl (n = 1988 birds; 14 hauls), 3.7% were Gannets. During experimental discarding on 10 May, 5.3% of all scavengers were Gannets (n = 928), which were feeding highly successfully, taking five times more roundfish than other scavengers, as expected from their numerical abundance ($\chi^2 = 26.5$, df = 1, p < 0.0001). There were few trawlers within the study area, and only 0.1 commercial (stern) trawlers were found fishing per 100 km² between 1°W and 1°E. A small number of beamtrawlers, fishing for flatfish, were encountered in the southeast sector of the study area. No trawlers were observed elsewhere. Only three Gannets were seen on 10 May at four active trawlers. On that day, 96.3% of 904 Gannets aged during strip-transect counts were adults, whereas at the trawl (including both counts at the research vessel and at nearby commercial trawlers), 25.0% of 60 were immatures ($\chi^2 = 48.3$, df = 1, p < 0.0001).

Cetaceans

Feeding dolphins were herding fish shoals in small groups (5-15 dolphins) which were surface rushing towards a focal point. As a result of this co-operative action, fish shoals were concentrated near the surface, and many fish were seen leaping out of the water and were moving in a 'frenzied' manner close to the surface between two groups of dolphins porpoising in from opposite directions (cf. Evans 1982). Gannets immediately circled over these spots and dived near, but not between,

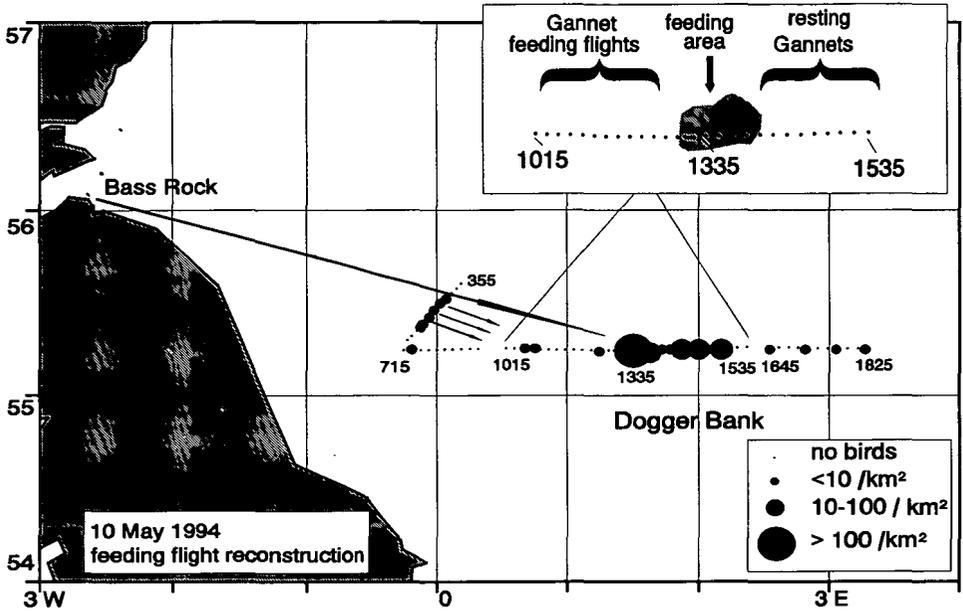


Figure 4. Gannet concentrations at sea and flight directions (small arrows), 10 May 1994, RV Tridens.

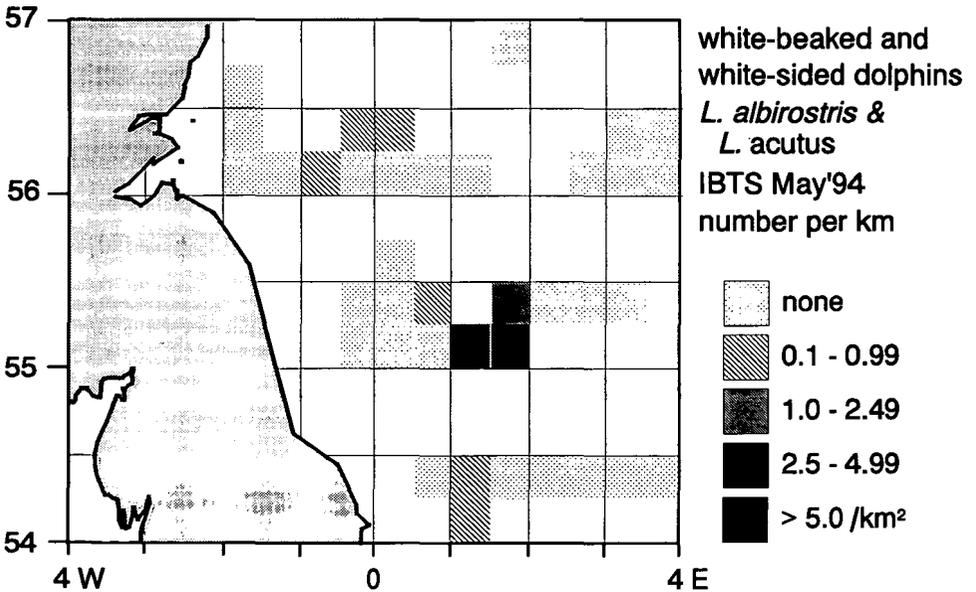


Figure 5. Number of white-beaked and white-sided dolphins per km per quarter ICES square, May 1994, RV Tridens.

the feeding dolphins. White-beaked dolphins were most actively (or obviously) feeding, and were not seen to co-operate with white-sided dolphins in the area.

Fish

Trawlcatches on 10 May were dominated by herring, sprat and Norway pout *Trisopterus esmarki*, with smaller quantities of small whiting *Merlangius merlangus*, cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, sandeel *Ammodytidae*, and grey gurnard *Eutrigla gurnardus* (Table II). Substantial catches were hauls 23 and 24 (mainly herring and sprat), but the number of seabirds reported near these fishing stations was small. Large herds of dolphins were actively feeding around trawling station 25. When feeding herds surfaced, many small (estimated maximum length 20 cm) fish were seen leaping out of the water and all fish which could be recognized were, according to the estimated length, young herring. However, in haul 25 a rather small amount of fish was caught, including immature herring and sprat (Table II), which suggests that the presence of these fish was mainly confined to the upper water layers.

DISCUSSION

TABLE II. OTTER TRAWL ROUND FISH CATCHES, EXPRESSED AS NUMBER OF FISH PER HOUR TRAWLING, 10 MAY 1994 (RIVO UNPUBL. DATA)

Haul	herring < 24	herring ≥ 24	sprat	others
23	6384	11552	22496	13104
24	1312	256	2816	22084
25	204	–	636	680
26	–	–	–	204
27	–	4	56	462

Few commercial trawlers were fishing in the area studied and attracted few Gannets. However, those Gannets which were feeding in association with the research vessel were highly successful scavengers, in being able to swallow larger fish, by robbing all other scavenging species and by obtaining significantly larger amounts of fish than expected from the relative abundance of Gannets. Despite this apparent success, fishing vessels were almost totally ignored by Gannets, and it was clear that most birds were travelling purposefully to a distinct area far out in the North Sea. Normally, Gannets searching for food check out any boat within sight, simply by altering course and passing near the ship. Such behaviour was not observed on 10 May, when a constant stream of Gannets, mainly moving from northwest to southeast, all completely ignored the steaming or fishing research vessel. Of the small number of Gannets attracted to the ship during fishing, a significant proportion were immature.

Gannets were seen diving in numbers only in an area where white-beaked dolphins were actively feeding. Feeding herds of dolphins were moving from east to west and the flocks of Gannets arriving from the west started feeding immediately. Resting Gannets encountered further to the east (where dolphins were only seen travelling or, after 14.25h, were absent) appeared satiated and were apparently loaded with fish. The ship, splitting swimming groups of Gannets in two, seldom forced the birds to fly and those that took off made very laboured progress. Associations between Gannets and cetaceans are well known (Evans 1982). The presence of feeding dolphins, which drive fish shoals to the surface, may be crucial for Gannets to reach herring and sprat which are normally close to the bottom during the day. White-beaked dolphins

are commonly found north of the Dogger Bank in May, but are usually highly concentrated (pers. obs. and ESAS unpubl. data). It is difficult to understand how Gannets know their way over very long distances away from the colony towards such isolated feeding areas, but the presence of feeding dolphins suggests that the area may represent a 'predictable' source of food. The total number of Gannets feeding north of the Dogger Bank is unknown, because the area used by feeding dolphins and Gannets has not been estimated and because the turnover rate is unknown. However, since over 1000 Gannets were actually observed during the survey, and the total feeding area was larger than that visited, at least 2% of the Bass Rock Gannets (recent estimate *ca.* 22,000 pairs; Lloyd *et al.* 1991) might have been feeding in this area. The area northwest of the Dogger Bank was the only area in the North Sea where high densities occurred in May 1994 (Camphuysen *et al.* 1994). The early-season food for Gannets breeding on the Bass Rock consists mainly of sandeels and possibly sprat (Nelson 1978). The Wee Bankie and the Firth of Forth approaches are well known feeding areas (Tasker *et al.* 1987, M.L. Tasker pers. comm.). Pelagic shoaling fish such as herring, sprat or mackerel *Scomber scombrus* are important food fish for Gannets in other colonies and perhaps also for Gannets on the Bass Rock (Wanless 1984, Martin 1989). Wide feeding ranges for Gannets were assumed from the time that adults spent away from the nest (Nelson 1978, Wingham 1985). Recent studies of seabirds at sea have demonstrated that feeding flights of over 300 km away from the Bass Rock in May are highly unusual, with concentrations of Gannets usually restricted to an area well within 150 km of the colony (Tasker *et al.* 1985). Variations in feeding patterns of marine birds have been suggested to reflect fluctuations in fish availability (Furness & Monaghan 1987, Montevecchi *et al.* 1988), thus the exceptionally large foraging range recorded in May 1994 may have been a response to poor feeding conditions nearer to the colony.

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SUMMARY

Large numbers of Gannets were observed moving towards a small feeding area north of the Dogger Bank on 10 May 1994. Feeding occurred in close association with feeding white-beaked and white-sided dolphins. From the direction of the movements and the number of birds involved it was concluded that the Gannets originated from the Bass Rock, some 300 km away from the feeding area. Previous surveys around the Bass Rock and in the North Sea suggested that distant feeding is highly unusual during the breeding season. The Gannets occurred in small numbers at trawlers but were highly successful as scavengers compared with other species. Trawlers occurred in very low densities in this offshore area but did not attract many birds. Most Gannets ignored the fishing vessels completely.

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Factors affecting the production of pellets by Shags *Phalacrocorax aristotelis*

A. F. Russell, S. Wanless and M. P. Harris

INTRODUCTION

Many species of cormorant Phalacrocoracidae regurgitate mucus-covered pellets which typically contain undigested prey remains eg fish bones and otoliths, fragments of crustacea, cephalopod beaks, as well as small stones and/or grains of sand. Several studies have exploited the fact that the species, number and size of fish prey can be determined from otolith characteristics (Härkönen 1986) and pellets have been utilised to provide information on the diet of several cormorant populations (e.g. Ainley *et al.* 1981; Barrett *et al.* 1990; Harris and Wanless 1991; Linn & Campbell 1992). Two studies have demonstrated that the method consistently underestimates the number and sizes of prey items taken (Duffy & Laurenson 1983; Johnstone *et al.* 1990). However there are at least two other potential sources of error in the technique. First, pellet production could differ between different age, sex or breeding categories and second, the frequency with which birds produce pellets might vary. Given these potential sources of error it is surprising that there is remarkably little published information about pellet production in free-living cormorants. The main aim of this study was therefore to collect data on the status of birds producing pellets and the frequency of pellet production at a colony of Shags *Phalacrocorax aristotelis* in south-east Scotland.

METHODS

The study was carried out on the Isle of May in the Firth of Forth, in June and July 1992. The influence of age, sex and breeding status on a) whether or not Shags produced pellets, b) the diurnal pattern of production and c) how often birds produced pellets was investigated by direct observations made from a hide c. 15 m from the study colony. Data were collected from adults: five breeding and five non-breeding pairs; immatures: three two-year-old and three one year-old-birds (aged by plumage); juveniles: three birds aged between seven and eight weeks which had recently left the nest but were still dependent on their parents for food; chicks: ten nestlings from four broods aged between two and six weeks. All the adults had previously been ringed with unique colour combinations and were therefore individually identifiable. The sex of these birds had been established by extensive observations of courtship and mating behaviour (J.A. Graves pers. comm.). The sex of the immatures, juveniles and nestlings was unknown.

The incidence and diurnal pattern of pellet production was estimated from 40 hours of observation spread over six days, such that the daylight period 02:30 to 22:30 h (all times in GMT) was completely covered twice. As pellet production appeared to be almost entirely confined to the early morning (see Results), further observations to determine the number of days elapsing between the production of successive pellets by individual Shags were made between 02:30 and 08:30 h on seven consecutive days. These estimates of the frequency of pellet production assumed that birds did not cough up pellets away from the vicinity of the breeding site, or in the case of nonbreeders, the roosting area (see Discussion).

The findings from the observations were tested experimentally (under licence) by feeding birds a single coloured plastic bead concealed in a small fish. The beads were 5 mm in diameter, a size similar to stones commonly present in regurgitated pellets. They were resistant to acid of pH 1 and were therefore, unlikely to dissolve in a Shag's stomach. To minimize disturbance of the birds

used in the observations, the bead experiment was carried out in another part of the colony. Beads were fed to 30 adult Shags (five pairs with young, five pairs incubating eggs and five pairs which were not breeding) and ten chicks all about 6 weeks old. The area around the nests of these birds and nearby sea rocks were searched at 09:00 h on seven consecutive mornings after the beads had been fed. All pellets present were collected and subsequently examined for beads.

To determine the amount of stomach contents expelled in a pellet, five adult breeding Shags were stomach flushed (details in Wanless *et al.* 1993) after they had been seen producing a pellet. Their pellets were collected and digested in Biotex to release the contents (details in Johnstone *et al.* 1990). All means are given \pm standard error.

RESULTS

Adult Shags regurgitated pellets irrespective of their sex or breeding status. Pellet production was also recorded in immatures, and juveniles aged seven to eight weeks, but not in any of the ten nestlings. Results from the bead experiment accorded well with these findings although immatures and juveniles were not tested. Thus pellets containing beads were obtained from adult Shags regardless of their breeding status or sex (see later) but none of the beads fed to chicks still in the nest were recovered.

Pellet production occurred in the early morning (Fig. 1). Of the 18 pellets produced during this part of the study, most (78%) were egested between 04:30-06:30 h (median 05:15 h) and none were seen being regurgitated after 08:20 h. These results were supported by trials in which pellets were cleared from the colony. Thus after removal of pellets at 09:00 h, no new pellets were found at dusk of the same day ($n = 3$ clearances/searches). Similarly after three clearances just prior to

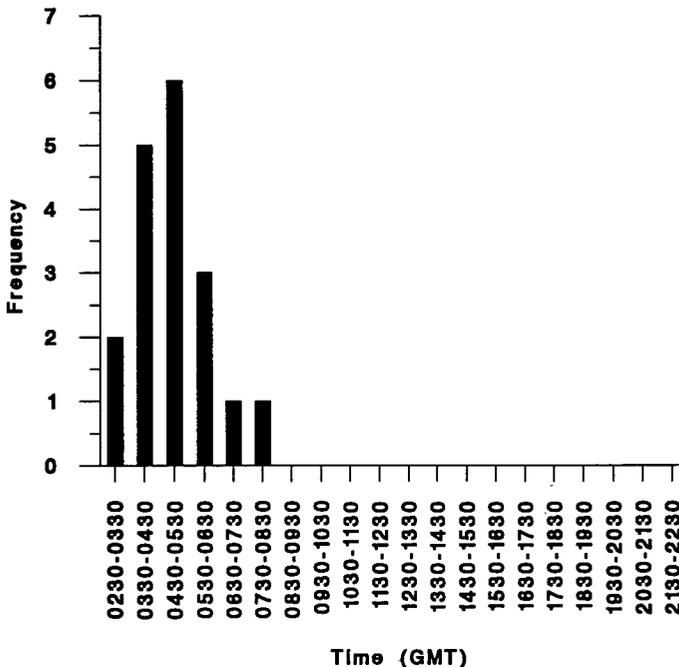


Figure 1. Diurnal pattern of pellet production by 18 Shags on the Isle of May in June-July 1992.

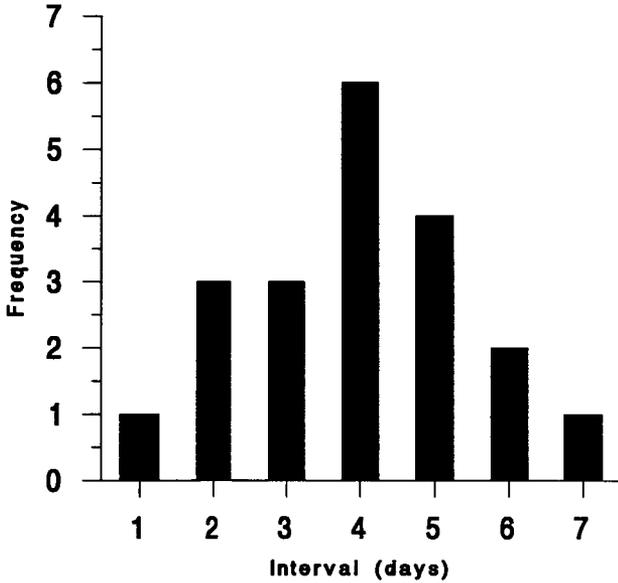


Figure 2. Frequency of production of pellets (days between pellet production) by 20 adult Shags on the Isle of May June-July 1992.

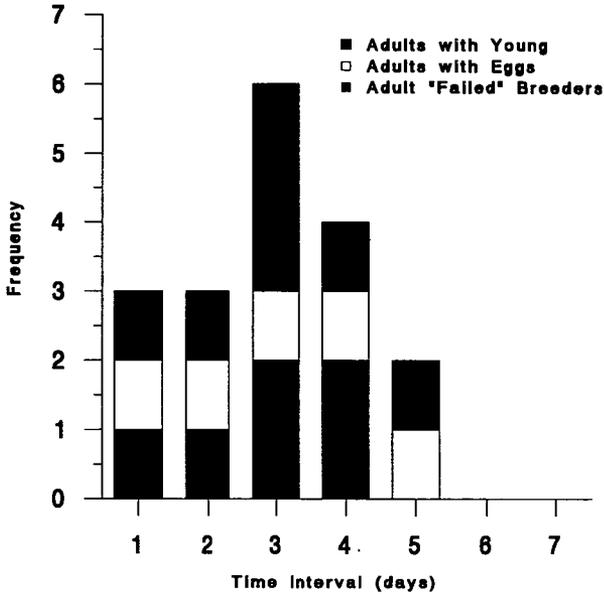


Figure 3. Frequency histogram of the time elapsing between the ingestion of a bead by 18 adult Shags and their recovery in a pellet.

dusk, no pellets were found the following dawn. There was no suggestion that the diurnal pattern of production was influenced by sex or breeding status (Kruskal Wallis $H = 1.08$, $df = 3$, ns).

Observations of the 20 individually recognisable adult Shags indicated that birds did not produce a pellet each day with the interval between successive pellets ranging from one to seven days (mean 3.7 days \pm 0.25, $n = 20$, Fig. 2). There was no significant sex or breeding status effect on the production interval (Kruskal Wallis $H = 1.52$, $df = 3$, ns).

Beads were recovered from pellets of 18 (60%) adult Shags. Recovery rate was not influenced by sex (males 10/15, females 8/15, $\chi^2_1 = 0.6$, ns) or breeding status (brooding 7/10, incubating 5/10, non-breeding 6/10, $\chi^2_2 = 0.8$, ns). In the cases where beads were recovered, the interval between ingestion and expulsion varied from one to five days (mean 2.9 days \pm 0.3, Fig. 3). There was no obvious difference in this interval between the above categories of birds although sample sizes were small (Fig. 3).

Results from the five Shags which were stomach flushed after producing a pellet, indicated that between 90% and 100% (mean 95.4 \pm 1.9%) of prey remains were removed in the pellet (Table I).

TABLE I. PREY REMAINS (NUMBER OF ITEMS) IN PELLETS AND STOMACH-FLUSHINGS OF FIVE ADULT SHAGS WHICH HAD JUST PRODUCED THE PELLETS.

Bird	Number of items collected from:		% removed in pellet
	Pellet	Stomach- flushing	
1	28	3	90
2	24	1	98
3	12	1	92
4	64	2	97
5	10	0	100

Note: prey items in Birds 1-4 were all fish otoliths, Bird 5's pellet contained fragments of chitin.

DISCUSSION

Results from both the observations and the bead experiment indicated that age was the only parameter which influenced whether birds produced pellets with pellets being egested by all age groups except nestlings. Pellets were however, regurgitated by juveniles which like nestlings, depend on their parents for food. Thus pellet production was not confined to individuals which had been catching prey for themselves, but also occurred among birds which were receiving partially digested prey. The lack of pellets produced by nestlings may be explained by their having a more acidic gastric environment (Van Dobbin 1952).

Previous studies have concluded that cormorants and shags typically produce one or two pellets per day which are regurgitated overnight (e.g. Guanay *P. bougainvillii*, Jordan 1959; Cape Cormorant *P. capensis*, Duffy & Laursen 1983; Shag, Johnstone *et al.* 1990). During our study the frequency of production was considerably lower, averaging about one pellet every four days (Fig. 2). Although casual observations would have indicated that pellets were produced "overnight", detailed watches and the clearance of areas established that pellets were, in fact, coughed up predominantly in the early morning. Less systematic observations indicated that a few pellets were regurgitated outwith this period (one breeding and two non breeding adults were seen coughing up pellets in the afternoon) but it was clear that most were produced before birds departed on the first feeding trip of the day.

Our studies (both observational and experimental) were focused on the breeding area and nearby sea rocks and we could not, therefore, be certain that Shags had not coughed up pellets elsewhere. In the bead experiment, we failed to recover beads from 40% of the birds. Stomach flushing after pellet production indicated that the bulk of stomach contents were removed and we considered that it was unlikely that beads were preferentially retained in the stomach. We have never seen a Shag cough up a pellet when it was on the sea and we know of no records of such behaviour from other studies. Pellet production therefore seems to occur only on land. Assuming this to be the case, birds with chicks appear to have little opportunity to cough up pellets away from the breeding area as this group seldom spends any time on land away from the breeding area (Wanless & Harris 1992, additional unpublished data). Incubating birds, failed breeders and immatures do occasionally come ashore away from the breeding area (Wanless & Harris 1992, additional unpublished data) and could therefore potentially have produced pellets during these times. However, the recovery rates of beads from incubating and non-breeding birds were not significantly lower than those with young and the most plausible reason for the disappearance of beads would therefore seem to be that pellets were overlooked because they had lodged in a crack or fallen in the sea, or had been eaten by Herring Gulls *Larus argentatus* before the search was carried out.

In a previous paper Harris and Wanless (1991) commented that it was harder to find Shag pellets on the Isle of May when birds were breeding compared with earlier or later in the season. Since the number of Shags associated with the colony did not change dramatically over the period, they speculated that the effect was due to the onset of breeding with breeding birds, having a lower frequency of pellet production. Four Shags from the Isle of May taken into captivity prior to breeding, normally produced a single pellet each day (Johnstone *et al.* 1990). Our results for June and July indicated that on average, birds egested one pellet every four days which suggests that pellet production may indeed be depressed during the summer. However, neither our direct observations of different categories of birds nor the bead experiments provided any evidence of a sex or breeding status effect on pellet production during June or July. Thus the reduction in pellets may be a seasonal rather than a breeding effect but clearly more work is needed on this aspect of pellet production.

The finding that the average frequency of pellet production was much less than one per day, has important consequences for the use of pellets to estimate energy requirements of phalacrocoracids, since such models have generally assumed that pellet contents give an estimate of daily food intake (e.g. Linn & Campbell 1992). Several studies have cautioned that pellet contents may greatly underestimate the number and/or size of prey items taken (Duffy & Laurenson 1983; Jobling & Breiby 1986; Johnstone *et al.* 1990). In addition our findings indicate that for Shags on the Isle of May in June and July 1992, the assumption that a pellet's contents reflect the remains of food taken during a 24 hr period was invalid.

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SUMMARY

The status of Shags egesting pellets and the frequency with which pellets were produced were investigated on the Isle of May during June and July 1992. Adults, immatures and juveniles all regurgitated pellets but nestlings were never seen to produce them. Most pellets were egested in the morning between 04:30-06:30 h. The interval between the production of pellets varied from one to seven days and averaged 3.7 days. This frequency was markedly lower than the daily production frequently assumed for models of prey consumption by cormorant populations.

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Changes in the diet of Great Black-backed Gulls *Larus marinus* on Skomer Island 1958-1992

Jim Poole

INTRODUCTION

Great Black-backed Gulls *Larus marinus* are formidable predators, scavengers and food pirates, they are also very catholic in their choice of prey taking a wide range of items and carrion. They are essentially opportunistic, and their diet changes markedly with locality and season depending largely on food availability, however, marked individual preferences also occur (Cramp 1983).

Skomer Island National Nature Reserve, 2km off the south-west coast of Wales, is important for its seabirds, particularly its Manx Shearwater *Puffinus puffinus* colony numbering some 160,000 pairs (Sutcliffe 1990). Great Black-backed Gulls eat many shearwaters, for example in 1959 an estimated 5000 were killed by about 300 pairs of Great Black-backed Gulls (Mylne 1960). The numbers of gulls were controlled during the 1960s and 1970s in an effort to reduce this predation. It is therefore of interest to monitor changes in the gulls' diet in order to assess the damage done to the shearwater population for conservation management purposes.

The diet of these gulls on Skomer has been documented three times before. Mylne (1960) recorded the predation of shearwaters by the Great Black-backed Gulls and their effects on other seabirds. Harris (1965) considered the whole diet by examining stomach contents and found that shearwaters and rabbits *Oryctolagus cuniculus* were the main prey species in 1962. Corkhill (1973) collected remains at nest sites on Skomer throughout the season and found that refuse and commercial fish species were important. In 1991, during visits to nest sites to ring chicks, I noted that the frequency of the various prey remains was rather different from that noted by Corkhill and therefore collected data more systematically in 1992.

METHODS

It is not practical to count the number of shearwaters killed due to the size of the island, the fragile nature of the soil over shearwater colonies and the loss of many corpses on steep slopes or cliffs or in the sea. However an indication of the relative levels of predation comes from the number of corpses found at gull nest sites during the breeding season.

In 1992, 33 nests were visited up to four times each at fortnightly intervals to identify and record prey remains. Shearwaters were recorded as (a) complete corpses, (b) pairs of wings, (c) pellets composed of feathers, (d) heads, and (e) assorted bones. An attempt was then made to quantify the actual number of shearwater corpses represented at each site. Rabbits and other items were identified, counted and categorized into descriptive headings. Each site was cleared of remains at each visit.

A comparison of the results of the 1992 work with earlier studies was possible at the level of frequency of occurrence, ie the number of nests at which a particular category was recorded. A similar study was carried out on Skokholm, 4km to the south of Skomer (Betts 1992). The results of the 1991 study were not considered directly comparable because they were obtained from a single visit towards the end of the breeding season.

RESULTS

Shearwaters and rabbits predominated through the season (Table I), augmented by gull and auk eggs and chicks as they became available. Refuse was also found increasingly in late June and

July. There was, however, a wide variability of food remains from individual nest sites which the table cannot show, with some birds showing more specialised feeding habits than others.

Shearwaters were recorded at 80% of the site visits (Table II) and the absolute frequency of remains was 8.4 shearwater corpses per nest per season. Five sites recorded comparatively large numbers of shearwaters (5-8) at a single visit, but none did so more than once.

Gull remains were recorded at 16% of visits, however there was a noticeable increase through the 1992 season as Herring Gull *Larus argentatus* and Lesser Black-backed Gull *L. fuscus* eggs and chicks became available.

Few other birds featured among the prey remains. Auks, mainly puffins *Fratercula arctica*, occurred at only 5% of site visits, with two sites having relatively large amounts of Puffin remains on one occasion only, with little or none on the other visits. Young of Carrion Crows *Corvus corone*, Jackdaws *Corvus monedula* and Magpies *Pica pica* were the only non-seabird species, again recorded at 5% of visits.

Rabbit was recorded at all nest sites on two dates, and at most nest sites on the other dates. It proved impossible to calculate the number of rabbits taken; some sites had many pellets of fur and large amounts of loose fur and bones that could not easily be quantified.

The frequency of all fish remains was 16%. Commercial and small fish were recorded separately in 1973, but were combined for this study as it was not always possible to state the origin of the items involved. In 1992 Great Black-backed Gulls were seen to feed on discarded bait from lobster pots on two occasions in June, and this was possibly the source of medium-sized fish backbones found at as a small number of sites throughout the season.

The occurrence of intertidal items was 5%, with only five records of edible crab and one of bones from the front flipper of a young grey seal *Halichoerus grypus* pup.

Refuse was recorded on 14% of the visits. Corkhill (1973) included an "agricultural" category but was vague in its definition. No remains that could be attributed to this source were recorded in 1992.

TABLE I. NUMBER OF GREAT GREAT BLACK-BACKED GULL NESTS AT WHICH EACH PREY ITEM WAS FOUND ON SKOMER IN 1992

	Date of Check			
	25-26 May	7-8 June	24-25 June	9-10 July
Total number of nests checked	33	33	28	28
Birds				
Manx Shearwater	22	26	25	24
Gull	0	3	5	10
Auk**	0	5	2	3
Other bird	1	2	2	1
Rabbit	33	31	28	26
Fish*	1	6	5	5
Refuse	3	4	6	10
Intertidal	3	2	1	0
Agricultural	0	0	0	0

Notes:

* = Commercial and small fish combined

** = Puffins with two records of Guillemot

TABLE II. COMPARISON OF THE FREQUENCY PERCENTAGE OF PREY REMAINS FOUND AT GREAT BLACK-BACKED GULL NESTS ON SKOMER AND SKOKHOLM, 1973-1992

	<i>Skomer 1973</i> <i>Up to 7 visits</i> <i>per site</i>	<i>Skomer 1991</i> <i>Single visit</i>	<i>Skomer 1992</i> <i>4 visits most</i> <i>sites</i>	<i>Skokholm 1992</i> <i>Up to 7 visits</i> <i>per site</i>
Sample size	56	30	33	24
Birds				
Manx Shearwater	67.9	96.7	80.2	89.2
Gull	16.0	3.3	16.0 *	17.2 *
Auk	12.5	10.0	4.7 ***	12.9
Other bird	19.6	3.3	4.7	8.6
Rabbit	58.9	70.0	96.7	88.2
Commercial fish	30.4	3.3	15.5**	9.7
Small fish	28.6	10.0	15.5**	14.0
Refuse	53.6	16.7	13.5	2.2
Intertidal	8.9	10.0	5.0	5.4
Agricultural	?	?	0	1.1
No of shearwater carcasses (sites)	137(38)	192(29)	205(24)	286(24)
Mean no of carcasses per site	3.6	6.6	8.4	11.9

Notes:

* = including eggs and chicks

** = commercial and small fish combined

*** = puffin, and two records of guillemot

Skomer 1973 data from Corkhill (1973).

Skokholm 1992 data from Betts (1992).

DISCUSSION

Great Black-backed Gull food on Skomer

Where Great Black-backed Gulls nest close to other seabirds, predation can provide most of the food for the breeding birds and their young for several months of the year (Harris 1965). In 1992 Great Black-backed Gulls shared Skomer with about 16,000 pairs of Lesser Black-backed Gulls, 160,000 pairs of Manx Shearwaters, 6,000 pairs of Puffins, 3000 Razorbills *Alca torda* and 8,000 Guillemots *Uria aalge* (Poole & Sutcliffe 1992). Rabbits were also abundant.

In the 1960s there was considerable concern about the effect of Great Black-backed Gulls on other seabird species breeding on Skomer. Buxton & Lockley (1950) estimated that these gulls killed 2,500 Manx Shearwaters out of an estimated population of 25,000 pairs, 5,000 Puffins from a population of about 50,000 pairs, and 10,000 young rabbits from 5,000 does. The Puffin figures are now thought to be over-estimates (Mylne 1960). Mylne also estimated a total annual mortality at between 5,000 and 10,000 adult shearwaters. Great Black-backed Gulls were subsequently controlled, and the population declined from over 300 pairs to about 40 over 20 years (Skomer Island records). Shearwater numbers have increased during this time as have the total number of shearwaters found at the gull nest sites. Puffin numbers have been stable throughout whilst the cliff-nesting auks initially declined and increased later (Skomer Island records).

In 1992 Great Black-backed Gulls on Skomer fed their chicks almost entirely on shearwaters and rabbits, with no other category of prey remains being found on more than 16% of visits to nest sites. The results for 1992 were similar to those indicated from a single visit to nests in 1991, to the data from Skokholm in 1992, and to Harris's study in 1962 but very different to Corkhill's birds in 1973 (Table II).

The frequency of occurrence of Manx Shearwaters at Great Black-backed Gull nest sites increased from 68% in 1973 to 80% in 1992. The estimated shearwater population was 95,000 pairs in 1971 (Corkhill 1973), and 160,000 in 1990 (Sutcliffe 1990), while Great Black-backed Gull numbers had decreased from about 300 pairs (including those on Midland Isle) to about 40 pairs. Thus the shearwaters were a more available source of food and their importance in the diet of an opportunistic feeder such as these gulls would be expected to increase. There was also an increase from 67% on the first visit to 85% at the last in 1992. Immature shearwaters which are prospecting for burrows and spending a great deal of time on the surface are particularly vulnerable to predation by Great Black-backed Gulls (Brooke 1990). Those nests which had most shearwater remains in 1992 did so at the time when the number of prospecting birds was increasing. The majority of sites, however, did not show any increase in the number of shearwater remains at this particular time. In 1991 all but one gull nest had shearwater remains; this was probably due partly to the single nest visit being made at a time when there were many prospecting shearwaters visiting the island, and partly to the fact that the visit recorded an accumulation of items over the season rather than over a two week period as in 1992.

The 1992 study recorded an average of 8.4 shearwater corpses per gull nest site and this compares with Mylne's study which recorded 9.3 in 1959, and Harris who recorded 8.25. The 1973 figure of 3.6 corpses is therefore unusually low.

Although Manx Shearwaters were again being taken at their 1958-1962 levels, the shearwater colony had increased in size and there was no cause for concern during the gull breeding season. In fact, the peak level of shearwater mortality occurs in September and October when fledglings leave their burrows and are easy prey even for inexperienced gulls (Brooke 1991). Young shearwaters suffering from *Puffinosis* are particularly vulnerable, but would almost certainly die even if not predated. Harris (1965) suggested that perhaps one third of the shearwaters killed were youngsters which had never left the island.

The high frequency of rabbit remains at nest sites in 1992 may have been due to a severe summer outbreak of myxomatosis: rabbits were therefore easily available as prey or carrion. Myxomatosis occurs almost annually on Skomer, but at varying levels of intensity. Many nest sites appeared to be virtually carpeted with rabbit fur, suggesting that the amount of rabbit actually taken was greater than in 1991. Comparisons with Skokholm (where a single myxomatosis outbreak was recorded in 1988 only) in 1992 showed that rabbit featured there almost as regularly as on Skomer. Rabbits have always been a substantial part of the gulls' diet on Skomer: the frequency of occurrence was 59% in 1973, Harris recorded rabbit remains at 14 of the 21 nests he studied in 1962 (65 rabbits out of 420 prey items), while Mylne recorded rabbits at up to 19 out of 23 sites in 1959.

Of the auks, Puffins are the most frequent prey items for Great Black-backed Gulls, but they are often caught at sea, or taken to sea to be eaten (Harris 1965). Mylne (1960) believed that Lockley's estimate of 5000 Puffins taken on Skomer in 1946 and Davis's estimate of 500-1000 Puffins in 1958 were likely to be over-estimates. Mylne counted only four Puffin corpses in an area of 120 acres in the west of Skomer, and Harris recorded Puffin remains at only six nest sites in 1962, compared with eight Puffins at four nests in 1992. Puffins were clearly a more important food item thirty years ago than they are today.

Harris recorded only 16 *Larus* chick remains amongst 420 items from Great Black-backed Gull nests in 1962. The frequency was similar in 1973 and in 1992 even though the population of Lesser Black-backed Gulls had increased from 1400 pairs to 16,000 in 1992. However in 1992

most Lesser Black-backed Gull chicks starved to death at a few days old, so that there may well have been fewer chicks available to the Great Black-backed Gulls than 30 years ago.

The decrease in the number of "other bird" items from 20% in 1973 to 5% in 1992 may simply have happened as a result of the abundance of other prey items. Although most of Corkhill's records were of "crow remains", the gulls used to kill lots of Jackdaws as well (M.P. Harris pers. comm.). In 1992 Jackdaws and Magpies were the main items. Magpies were not breeding on the island in 1973, and the Carrion Crow breeding population has declined from 18 pairs in 1973 to six pairs in 1992.

Comparison with other localities

No high degree of food specialization was recorded on Skomer, although this has been documented at some other colonies (Cramp 1983). On Great Saltee Island, Co. Wexford, Hudson (1982) found that the diet of chicks for about 300 pairs of Great Black-backed Gulls nesting colonially comprised mainly fish and crabs (67%) whereas solitary nesters took more (68%) auks and gulls, nearly all chicks. Rabbits and shearwaters featured amongst "other food", the population of Manx Shearwater on the island in 1978 was recorded as 100-150 pairs (Lloyd 1982), while rabbits were "as numerous as ever" between myxomatosis epidemic years (Flux & Fullagar 1992).

The influence of food on Great Black-backed Gull status in Wales

Great Black-backed Gulls are able to obtain a substantial proportion of their diet within a short distance of their breeding sites, but they will also take advantage of 'easy pickings' at greater flight distances. Great Black-backed Gulls have increased in numbers and extended their breeding range in the present century (Cramp *et al.* 1974). The increase correlates with the increasing availability of artificial foods such as rubbish, discarded fish and offal. Grieg *et al.* (1986) noted that the numbers of Great Black-backed Gulls feeding at rubbish tips were inversely related to the amount of fish landed at local ports, suggesting that when fish offal was not available, the gulls switched to rubbish as an alternative.

The marked decline of Great Black-backed Gulls in south Wales since 1960 (Lloyd *et al.* 1991) has been largely due to control measures, but their habit of feeding on rubbish contributed to the decline in the early 1980s when botulism killed large numbers of adult birds (Sutcliffe 1986). In the late 1970s and early 1980s dying birds showing symptoms of botulism were found on Skokholm and Skomer. Since then the management of refuse tips has changed substantially. The small open landfill sites in West Wales have been replaced by a single large site which is permanently covered by netting to prevent birds feeding on the rubbish. Nevertheless the birds still scavenge a small amount of refuse.

The reduction in the fish component of the diet has also been forced on the gulls. Mylne (1960) comments that fish may have come "... from Milford Haven fish market where thousands of gulls live comfortably off the cleanings from the fish." Harris (1965) found more fish remains than rabbit remains in his survey of nest sites in 1962. Davis (1974) also noted that Milford Haven was a major source of food in the early 1970s. The fishing industry has severely declined since then, and now provides little food for the gulls.

The diet of Great Black-backed Gulls in 1959 and 1962 was very similar to that found in 1992. The differences recorded in 1973 may have been as a result of opportunity in that a plentiful food supply was available from refuse tips and fish docks, but these sources were equally available (in fact more available as there were many small local rubbish tips) in earlier years. Perhaps the high level of persecution of Great Black-backed Gulls on Skomer in the 1960s (e.g. by trapping, shooting, nest control etc.) made them reluctant to scavenge or hunt around the reserve and the 1973 study reflected this 'enforced' change. They very effectively adapted to other food sources and have subsequently returned to a 'normal' diet following the cessation of control.

SUMMARY

The food remains at nests of Great Black-backed Gulls on Skomer were collected in 1992 and the results compared with those of studies made 20-30 years ago. The main prey items were rabbits and Manx Shearwaters, with other gull chicks during part of the season. Fishery waste and rubbish from tips no longer formed a significant part of the diet due to the decline of the local fishing industry and the closure or covering of rubbish tips in the area.

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Diets of adult and chick Herring Gulls *Larus argentatus argenteus* on Ailsa Craig, south-west Scotland.

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INTRODUCTION

The Herring Gull *Larus argentatus*, is widely distributed over the Holarctic region (Cramp & Simmons 1983), and, although in terms of breeding biology and behaviour, is a relatively well-studied species, its diet has received comparatively little detailed attention over much of its range. Some dietary studies have been made in Europe, e.g. Spärck 1951, Ehlert 1961, Harris 1965, Andersson 1970, Spaans 1971, Spitzer 1976, Mudge & Ferns 1982, but there has been little information on the diet of both chicks and adults during the breeding season (see Spaans 1971, Monaghan 1977). There is also some contradiction, one researcher having concluded that the diet of chicks is similar to adults (Threlfall 1968), while others have reported the contrary (Ehlert 1961, Spaans 1971).

The aim of this study is to describe the food spectrum of adult and chick Herring Gulls in the Firth of Clyde area of south-west Scotland, by analyses of pellets, regurgitations and prey remains during a single season.

METHODS

Field work was carried out on the island of Ailsa Craig, Strathclyde Region, from 17 May to 6 August 1991. The first chick hatched on 24 May with most hatched by 5 June.

Around 2,000 pairs of Herring Gulls breed on the island, mainly on the upper vegetated slopes and screes, but also around the boulder beach below the cliffs surrounding the island. Three study plots were demarcated. The first was below the bird cliffs on rock screes (40 nests), the second was above the cliffs in an area of large boulders (10 nests) and the third was on a more open grassy slope below the summit (20 nests). These areas were chosen to avoid any possible confusion with the nests of Lesser Black-backed Gulls *Larus fuscus*, which were mainly in discreet sub-colonies.

The dietary data of these 70 nests is based on analysis of 408 adult pellets collected around the nests each fifteen day period, 125 regurgitations from 42 chicks, obtained by weekly monitoring of chick growth, and 83 prey remains. "Prey remains" are here defined as items of food collected at the nest but of uncertain origin being neither pellets from adults nor regurgitations of chicks. For example, remains of mammals or large fish skeletons which may have been delivered or regurgitated at the nest by adults and then pecked clean by chicks or ignored by them. The prey remains found around the nests were removed weekly for studying the variation in the prey selected, and are listed separately in Table II.

Pellets were collected at 15 day intervals, sealed individually in plastic envelopes, and analysed using a x 8 binocular microscope shortly after collection. Chicks can also produce small pellets at very early ages (Goethe 1937), therefore the few (< 10), very small pellets found during the entire period of the study were excluded from the analyses. After the chicks are older than 4 weeks, they attain a similar body size to adults, but their pellets are usually still much smaller. To avoid any possible confusion as to the origins of the few small pellets they were not itemised. The food composition of the chick regurgitations obtained during the present study (soft food) suggested that the chicks were fed little indigestible material.

Two sites near nests at the base of the bird cliffs were those of egg-specialist Herring Gulls.

Undeveloped egg contents would not be evident in pellets but fragments of eggshell were recorded in pellets from 15 days after the chicks had hatched.

Data on the food of chicks and adults are only comparable to a certain degree due to the fact that soft-bodied animals, such as earthworms Oligochaeta, marine invertebrates such as some jawless Polychaetes, and discarded fish offal, do not appear in pellets. However, similar studies of Western Gulls *Larus occidentalis* by Annett & Pierotti (1989) and of Herring Gulls by Spaans (1971) concluded that pellets accurately reflect the adult dietary compositions.

The development and growth rate of the chicks from hatching was studied by measuring the wing length and weight each week. Eight chicks were weighed and measured weekly at least 6 times. We use the term "white fish" in this study, to define mainly Gadoids but also all other discarded commercial species. Where not specified, "meat" is usually that of birds, rabbits *Oryctolagus cuniculus* and farmed animals.

RESULTS

Adult Herring Gulls are omnivorous but there is a marked difference between parental diet and that of chicks (see Tables I, II and III). While the food spectrum of the chicks was largely based on white fish and meat, the adult pellets frequently included vegetable material and refuse (inorganic material such as foil, concrete, glass and plastic), two components which are not common in the chick diets.

TABLE I. ANALYSIS OF THE DIET OF HERRING GULL CHICKS ON AILSA CRAIG SHOWING PERCENTAGE OCCURRENCE OF THE DIFFERENT FOOD COMPONENTS IDENTIFIED IN THE CHICK REGURGITATIONS EACH WEEK. THE FIRST WEEK BEGAN ON 2 JUNE 1991. (- = zero.)

Food	Age of chicks (weeks)						Total
	First	Second	Third	Fourth	Fifth	Sixth	
Fish	68.2	52.2	47.1	40.0	26.1	8.0	39.2
Meat	9.1	21.7	41.2	40.0	60.8	76.0	42.4
Gannet pulli	-	-	-	20.0	4.3	16.0	6.4
Guillemot pulli	-	-	-	-	4.3	-	0.8
Rabbit (only)	-	-	-	-	-	4.0	0.8
<i>Invertebrates</i>							
Crustacea	13.6	4.3	11.8	-	-	-	4.8
Coleoptera	4.5	4.3	-	-	4.3	-	2.4
Lepidoptera	4.5	8.7	-	-	-	-	2.4
Hymenoptera	-	4.3	-	-	-	-	0.8
Cephalopoda	9.1	8.7	-	-	-	-	3.2
Gastropoda	-	-	-	-	4.3	-	0.8
Oligochaeta	13.6	-	-	-	-	-	2.4
<i>Plant Material</i>							
Vegetable matter	-	8.7	-	-	-	-	1.6
Bread	13.6	4.3	-	-	4.3	16.0	7.2
<i>Non-foods</i>							
Rubbish/refuse	-	-	-	-	4.3	-	0.8
Total No of regurgitations examined	22	23	17	15	23	25	125

TABLE II. ANALYSIS OF PREY REMAINS AT NESTS WITH HERRING GULL CHICKS ON AILSA CRAIG SHOWING PERCENTAGE OF OCCURRENCE OF THE DIFFERENT FOOD COMPONENTS DETECTED AS PREY REMAINS AT THE NESTS. THE FIRST WEEK BEGAN ON 2 JUNE 1991.

Food	Age of chicks (weeks)						Total
	First	Second	Third	Fourth	Fifth	Sixth	
Fish	80.0	63.6	53.8	45.5	40.0	16.6	48.2
Meat	6.7	36.4	46.2	45.5	60.0	44.4	39.8
Gannet (pulli)	—	—	—	9.0	—	22.2	6.0
Guillemot (pulli)	—	—	—	—	—	5.6	1.2
Razorbill (pulli)	—	—	—	—	—	5.6	1.2
Rabbit (only)	—	—	—	—	—	5.6	1.2
Crustacea	13.3	—	—	—	—	—	2.4
Total No of samples	15	11	13	11	15	18	83

The main items taken by adults showed a significantly greater proportion of pellets containing bird meat, coleoptera and vertebrate food in the last 3 periods (3 June-16 July) than in the first ($\chi^2_3 = 16.18$, $p < 0.01$ for birds, $\chi^2_3 = 64.68$, $p < 0.001$ for Coleoptera, $\chi^2_3 = 24.21$, $p < 0.001$, for all vertebrate matter). In contrast, the frequency of vegetable fibres and refuse varied little throughout the breeding period (Table III).

A few distinctive, unworn fish otoliths were identified with certainty during the analysis of the pellets, and these were gobies *Gobius* sp. (2 otoliths), cod *Gadus morhua* (4), dragonet *Callionymus lyra* (7), whiting *Merlangius merlangus* (6), flounder *Platichthys flesus* (1) and mackerel *Scomber scombrus* (2).

Part of the "bird" remains (4.9% in frequency of occurrence) were eggshells. Observations showed the remains of 64 eggs near one nest at the base area to be those of Guillemot *Uria aalge* (39%), Gannet *Morus bassanus* (34%), Razorbill *Alca torda* (14%), Fulmar *Fulmarus glacialis* (6%), Kittiwake *Rissa tridactyla* (5%) and Gulls *Larus* spp. (2%).

Most of the fish regurgitated by the chicks was muscle which is difficult to identify to species level. Four species were recorded, confirmed by attached distinctive skin and scales: dragonet, mackerel, whiting and herring *Clupea harengus*.

The results from regurgitation analyses show a marked dietary change in food composition with chicks of 1-2 weeks old fed fish and worms, chicks of 3-4 weeks old where the diet showed an equal percentage of meat and fish, and chicks of 5-6 weeks old where meat was more important than fish (Fig. 1). These frequencies of occurrence shown a clear, very highly significant difference ($\chi^2_2 = 26.91$, $p < 0.001$). The prey remains seen around the nests reflect the regurgitation results. Invertebrates, marine and terrestrial, were not very important quantitatively in the general context of the chick's overall diet, appearing mainly during the first two weeks. However their function in the chick development may be crucial. They may provide small but essential quantities of minerals and vitamins necessary for growth.

As the chick develops the percentage of fish in the diet decreases and the percentage of meat increases (Fig. 1). The growth curve (Fig. 2) shows that the chicks increased in weight on the diet they received during this season and fledged successfully. The data show significant differences in the weight of chicks during the first and second weeks, compared with the second and third weeks (Wilcoxon's Test $T_8 = 0.52$, $p < 0.02$) and between third and fourth weeks compared with fourth and fifth weeks ($T_8 = 3$, $p < 0.05$). These changes reflect the changes in diet.

TABLE III. ANALYSES OF PELLETS FROM ADULT HERRING GULLS BREEDING ON AILSA CRAIG SHOWING PERCENTAGE OCCURRENCE OF FOOD AND NON-FOODS CONSUMED. THE FIRST PERIOD BEGAN ON 20 MAY 1991. THE POST-HATCH PERIOD IS IN THE SECOND 15-DAY STAGE.

Food	First	15 day period number			Total
		Second	Third	Fourth	
Total Mammals	7.2	11.2	5.5	7.1	7.6
Rat	—	3.3	0.9	—	0.5
Rabbit (only)	1.8	3.3	—	—	0.5
Total Birds	7.2	15.7	22.9	24.4	18.6
Poultry	—	3.3	2.8	4.7	2.5
Egg fragments	—	9.0	6.4	3.9	4.9
Nestlings	—	5.6	6.4	11.0	5.6
Total Fish	30.1	15.7	25.7	18.1	22.3
Gadoids	3.6	3.4	9.2	3.9	5.2
Total Crustacea	8.4	12.4	7.3	3.9	7.6
<i>Nephrops norvegicus</i>	6.0	2.2	3.7	2.4	3.4
<i>Cancer pagurus</i>	—	2.2	—	0.8	0.7
<i>Ligia oceanica</i>	1.2	2.2	2.8	0.8	1.7
Total Mollusca	6.0	1.1	1.8	2.4	2.7
<i>Littorina saxatilis</i>	3.6	1.1	—	—	1.0
Polychaeta	1.2	—	—	—	0.2
Total Insecta	24.1	60.7	74.3	74.0	61.0
Coleoptera	24.1	60.7	74.3	74.0	61.0
Other insects	1.2	2.2	0.9	—	3.9
<i>Total Animal</i>	79.5	87.6	95.4	97.6	91.2
Plant fibres	62.7	73.0	69.7	73.2	70.1
Wheat & Chaff	1.2	2.2	0.9	2.4	1.7
Seeds	2.4	2.2	3.6	—	1.5
Algae	2.4	1.1	—	1.6	1.2
<i>Total Plants</i>	73.5	77.5	77.1	77.2	76.5
<i>Non-foods</i>					
Paper	25.3	18.0	18.1	16.5	19.1
Glass	14.5	10.1	11.0	14.2	12.5
Aluminium foil	15.7	14.6	6.4	14.2	12.5
Plastic	13.3	3.4	2.8	6.3	6.1
Polythene	15.7	15.7	23.9	27.6	21.6
Other items	8.4	—	4.5	6.3	4.9
<i>Total Rubbish</i>	47.0	40.4	46.8	46.5	43.1
Grit	50.6	51.7	23.9	39.4	40.2
Total No of Pellets	83	89	109	127	408

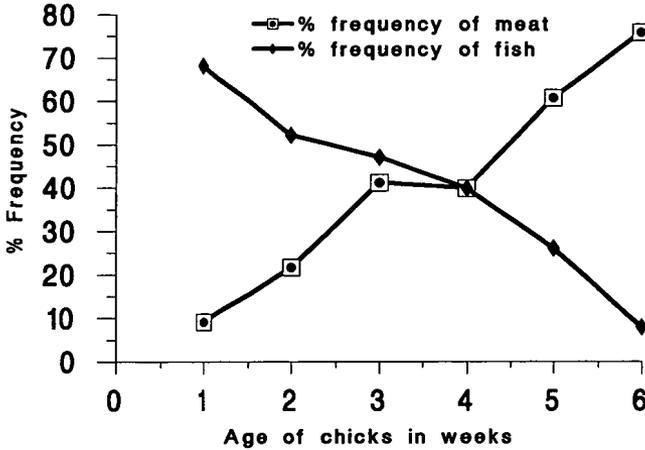


Figure 1. Temporal variation of frequency of fish and meat in the regurgitations of Herring Gull chicks on Ailsa Craig.

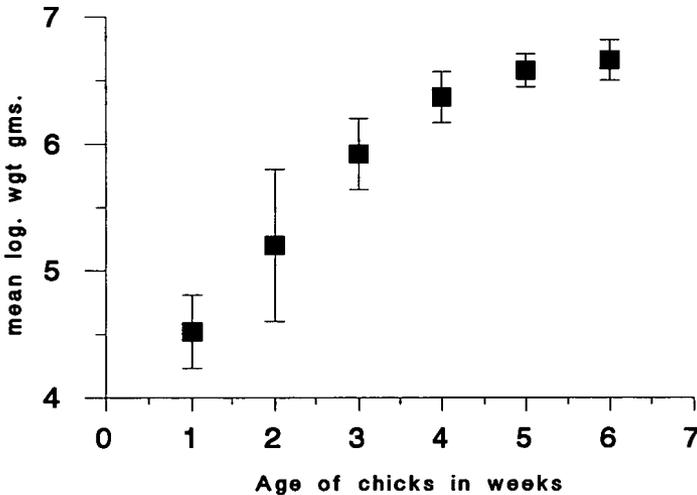


Figure 2. Growth rate of Herring Gull chicks ($n = 8$) in their first six weeks on Ailsa Craig. Means (\pm s.d.) have been transformed to natural logarithms.

DISCUSSION

The results from the present study show differences in the diet of the adult Herring Gulls and that of their chicks. It appears that parents select foods with the highest possible nutritional value and lowest possible indigestible material to provision their young. These data agree with the ideas of Spaans (1971) and Noordhuis & Spaans (1992) in the Netherlands. Monaghan (1977) saw garbage as second in importance (34% of the regurgitations) in an urban colony, demonstrating the wide adaptability of Herring Gulls to exploit available food supplies in different situations. Observed differences in diet between adult and chicks may be due to non-random feeding by adults. By

feeding themselves first, after leaving the nest site during chick rearing, and then gathering foods more suitable to the requirements of the chick the items retained may thus be separated. Observations from the upper study area showed that after adults fed the chicks they consistently washed, preened and then foraged on the littoral zone at the base of the island, the latter pattern governed only by tidal conditions. After a period of around one hour they would regularly fly out to sea. If suitable but large prey were soon caught e.g. a commercial sized fish from a trawler, this could not be immediately fed to the young chick but regurgitated at the nest, and may be the origins of the "prey remains".

The presence of important quantities of fish in the diet of Herring Gull chicks has been commented upon by Spaans (1971), Noordhuis & Spaans (1992) and Monaghan (1977). In this study, the progressive change from white fish to meat may be due to various reasons. Firstly, fish and earthworms are food presumably easier for a young chick to digest than a more cohesive substance such as mammal meat. Spaans (1971) postulated that during the digestion of fish bones, substances might be released that are of importance for building the skeleton, the development of which does not terminate until the sixth week. The development of the digestive system in the chick may take time to become sufficiently adapted to handling solid foods. The tendency of switching from fish to meat may correspond with different energetic requirements in the growth rate of the chick. As the chick grows its maintenance requirements will also increase and this may be satisfied with different foods. Herring Gulls do not actively catch live commercial sized fish (Witt *et al.* 1981) thus most fish probably originated from scavenging behind trawlers. The energy expended in this form of foraging is probably very high and the intra and inter-specific competition is undoubtedly intense. All fish species taken are frequently caught by trawlers fishing in the Firth of Clyde during summer, and from their size, all appear to indicate that they are scavenged by the gulls from boats. Observations of birds at the trawlers operating within close range of the island show large numbers of Herring Gulls, Lesser Black-backed Gulls, Great Black-backed Gulls *L. marinus*, Kittiwakes and Gannets constantly in attendance. These species assemblages also make up most of the summer scavenging seabirds around trawlers in northern waters (Hudson & Furness 1988a).

Hudson & Furness (1988b) found that Herring and Lesser Black-backed Gulls were dominated by their more aggressive competitors, Fulmars, Great Black-backed Gulls and Gannets. After the chicks are approximately three weeks old, energy expenditure may perhaps be reduced by the adults going to the mainland (15 km away) where food can be found more easily. This kind of food is usually meat (processed human food), mainly pork and poultry remains. However part of these types of foods could originate from the frequent passenger ferries which cross the Firth of Clyde, and from Scotland to Ireland. The distance from Ailsa Craig to the mainland is not great. The foraging range of the Herring Gull has been estimated at 40 km (Witt *et al.* 1981) and 30-60 km (Götmark 1984). In Western Gulls, which are similar in size to Herring Gulls, a switch from "garbage" in the pre-hatching period to marine fish after chick hatching was highly significant (Annett & Pierotti 1989). Noordhuis & Spaans (1992) found that Herring Gulls on the Dutch coast switched from bivalves to marine fish for their young, immediately after the hatching of the first chicks, and that birds whose eggs were prevented from hatching showed no dietary change.

The food spectrum of the adults showed them to be omnivorous. The occurrence of young birds as food in the last three periods coincides with the availability of eggs and chicks of most other seabirds on the island. Opportunistic feeding on resources abundant temporarily has also been mentioned by Andersson (1970) and Götmark (1984). The avian material in the diet was mainly eggshell and chicks, but some bird meat probably originated from the many seabird carcasses on the island. Food specialisation by certain Western Gulls in California showed them selecting Pigeons *Columbia livia* and mice *Mus* sp. (Annett & Pierotti, 1989). Selective predatory behaviour of Herring Gulls has also been described by Rogers (1968), Cleaves (1969) and Kosonen (1983). Only a very few Herring Gulls specialised in egg stealing on Ailsa Craig.

An item of food more difficult to explain is the presence of many coleoptera beetles in the adult pellets during the last three periods. These may be specifically sought after by the gulls or may simply reflect their local abundance. The presence of quantities of insects in the pellets may indicate dietary switching after the chicks hatch. Insects are probably consumed immediately after the period when chicks have been fed. Chicks are clearly not fed quantities of insects nor inorganic items, which the adult will continue to consume regularly during the chick rearing period.

The high frequency of vegetable matter (mainly grasses) is also quite difficult to explain because these types of food could be ingested incidentally together with the invertebrates or other soft-bodied items (for instance caterpillars), or may have been consumed deliberately. It is interesting to note that other researchers have found important quantities of vegetable material in the pellets of this species (Rintoul & Baxter 1925, Someren 1930, Gillham 1952, Davis 1956, King 1969, Morton & Hogg 1989, Noordhuis & Spaans 1992). It may be that material such as grass helps pellet formation for ridding the crop of the indigestible carapaces and legs of many insects, which may irritate the proventriculus. Virtually all grass pellets had insect remains intermingled to some extent.

The origins of the food of the adults shows a high percentage dependent on man's activities. Much of the food may originate from the rubbish tips near the towns of Ayr, Girvan and Stranraer on the mainland. There are also abattoirs in the Girvan area, from which much of the meat eaten by adults and fed to chicks may be derived. The use of this feeding strategy has been observed in other parts of the species' range as in the north west of Europe (Monaghan 1977, Mudge & Ferns 1982, Lüttringhaus & Vauk-Hentzelt 1983) or the Mediterranean area (Isenmann 1976, Witt *et al.* 1981). While soft material digested by adults would not show in pellets, hard material such as insects and inorganic refuse would show in chick regurgitations. The fact that the latter were not important in the chick diet appears to indicate a deliberate decision by the adults on what foods are given to their chicks. During the breeding period, others researchers have commented that in some areas of Europe, Herring Gulls consumed food mainly of "natural" origin (marine invertebrates, fish, insects, etc.) (Conder 1952, Mejerin 1954, Ehlert 1961, Spitzenberger 1961, Löhmer & Vauk 1970, Wietfeld 1977). This has also been observed in the Atlantic Ocean (Mougin & Stahl 1981, Hamer *et al.* 1989) and some areas of North America (Mendall 1939). The ingestion of items of non-food such as glass and concrete (some pieces as large as the proventriculus) are presumably an extension of the normal intake of small stones and grit for the gizzard.

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SUMMARY

The diet of chick and breeding adult Herring Gulls on Ailsa Craig was studied by analysing 125 chick regurgitations, 83 prey remains collected around nests and 408 adult pellets. While the basis of the chick diet was fish and meat of birds and mammals, the adult pellets frequently included vegetable material, insects and refuse. Adults ate a wide variety of scavenged items, whereas the food of small chicks was mainly soft and of a high energy value and obtainable from the immediate surrounding environment. Gradual changes in the food of chicks, from fish to meat, coincided with changes in growth rate.

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Size variation of Common Guillemots *Uria aalge* wintering in the northern Skagerrak

T. Anker-Nilssen and S.-H. Lorentsen

INTRODUCTION

Some of Europe's most important wintering grounds for Common Guillemots *Uria aalge* are found in the eastern parts of the North Sea (e.g. Carter *et al.* 1993). The birds arrive in late summer, and in August 1987 and 1988 numbered about 200 000 individuals (Skov *et al.* 1992). In 1989–1992, an estimated 100–200 000 individuals were found in the Kattegat in January–February each year (J. Durinck & H. Skov pers. comm.). High concentrations of Common Guillemots also winter in the southwestern Skagerrak (e.g. over the Egersund Bank) and off the Danish Skagerrak coast, as well as along the coast of Østfold and Bohuslän southeast of Oslofjord. Most birds arrive in the Skagerrak during July–August and leave in March–April (Carter *et al.* 1993). In other words, many individuals spend the better part of the year in these waters.

That high numbers of Common Guillemots winter in the northern Skagerrak was also demonstrated during the small but disastrous *Stylis* oil spill in December 1980, which killed an estimated minimum of 60 000 individuals (Anker-Nilssen & Røstad 1982). Eighteen percent were adult birds, and their morphometry indicated that maybe two thirds were from colonies in Scotland and (probably to a lesser extent) southern Norway and the Faroes. Most of the other birds probably originated from northern Norway (Anker-Nilssen *et al.* 1988).

It is, however, difficult to assess if the *Stylis* episode killed a representative sample of Common Guillemots wintering in these waters. This paper discusses the morphometry of Common Guillemots killed in fishing nets set along the northeastern coast of Skagerrak during the winters 1987/88, 1988/89 and 1989/90. The results are compared with those from the *Stylis* episode (Anker-Nilssen *et al.* 1988), to further elucidate the origin and structure of this important winter population.

METHODS

During the winters 1987/88, 1988/89 and 1989/90, a total of 1157 Common Guillemots that drowned in fishing nets along the coast of Østfold county (c. 59°10'N 10°50'E), S.E. Norway was collected (Table I). Østfold lies on the eastern side of the outer Oslofjord. The sampling periods were January–February 1988 (n=126), November–March 1988/89 (n=231) and October–March 1989/90 (n=800). The corpses were stored in a freezer for up to one year before they were examined at the Norwegian Institute for Nature Research (NINA) in Trondheim according to the procedures described by Jones *et al.* (1982). Additionally, a sample of 46 immature birds from the *Stylis* oiling incident was stored in a freezer, and examined by persons 1 and 2 in this study in November 1988, 8 years after they were collected.

Birds were thawed at room temperature and, with few exceptions, inspected after their plumage had dried. Among the variables recorded were head plumage (4 categories: winter, summer, and the two transitional stages), whether or not the specimen was bridled, winglength (maximum flattened chord) and head length (head+bill) to the nearest 1 mm, culmen length (tip to proximal end of sheath), bill depth at gonys and the minimum inter-orbital breadth across the supra-orbital ridge (cf. Gaston 1984) to the nearest 0.1 mm, and body mass (if dry plumage) to the nearest 5 g. Birds were sexed from gonadal inspection and aged as "immature" or "adult" according to the presence or absence of cloacal bursa, respectively.

Various persons were involved in the examinations of corpses (Table I). Regrettably, no birds were measured by several persons, and there has been no later possibilities to test for the consistency of measurements between measurers. However, in order to take full advantage of the data set and minimize bias caused by differences in measuring techniques for external metric variables, each measurement made by persons 2–4 for such variables were adjusted to resemble those of person 1 (who was the most experienced measurer). This was done by assuming that the mean size of birds in samples examined by different persons should not differ as long as birds belonged to the same sex and age group and originated from the same time period. The calibration factors were calculated as the mean of the deviations calculated for males and females and was based upon comparisons of mean values for immature birds from February 1988 (person 2 vs person 1) and November–December 1989 (persons 3 and 4 vs person 1). Such adjustments were made irrespective of the statistical significance of the differences. The 5 birds not measured by persons 1–4 were omitted from the biometric analyses.

TABLE I. NUMBERS OF COMMON GUILLEMOT CORPSES EXAMINED IN RELATION TO SAMPLING PERIOD AND DIFFERENT EXAMINERS.

Winter	Month	Examined by person				other	Total
		1	2	3	4		
1987/88	Jan	–	1	–	–	–	1
	Feb	54	70	–	–	1	125
1988/89	Nov	1	–	–	–	–	1
	Dec	40	–	1	–	–	41
	Jan	57	–	–	–	–	57
	Feb	114	–	2	–	–	116
	Mar	16	–	–	–	–	16
1989/90	Oct	17	–	11	–	4	32
	Nov	113	–	17	19	–	149
	Dec	–	–	235	73	–	308
	Jan	–	–	–	57	–	57
	Feb	–	–	1	203	–	204
	Mar	–	–	–	50	–	50
Total		412	71	267	402	5	1157

RESULTS

Age, sex and bridling

Only 10% of the birds that were aged were classified as adults (Table II). The proportion of adults in February, when there was a reasonable sample from all three years, varied significantly ($\chi^2=31.55$, $df=2$, $p<0.001$) from zero in 1988 to 22% in 1990. The sex distribution was strikingly different in adults and immatures (Table II), with almost twice as many females than males among adults ($\chi^2=6.75$, $df=1$, $p=0.009$) and significantly more males than females among immatures ($\chi^2=6.61$, $df=1$, $p=0.010$). There was no significant variation in the monthly sex ratio in immatures in either season (1988/89: $\chi^2=1.80$, $df=3$, $p=0.615$; 1989/90: $\chi^2=5.46$, $df=5$, $p=0.362$).

Altogether, 13.3% of the birds (147 of 1109 examined) were bridled. There were no significant differences linked to sex or age with respect to this feature (sex: $\chi^2=2.15$, $df=1$, $p=0.143$, age: $\chi^2=1.47$, $df=1$, $p=0.225$, combined: $\chi^2=5.24$, $df=3$, $p=0.155$), but the proportion was twice the 6.8% reported by Anker-Nilssen *et al.* (1988) for 950 birds collected in 1980/81 ($\chi^2=22.1$, $df=1$,

TABLE II. THE MONTHLY DISTRIBUTION OF AGE AND SEX RATIOS (NUMBER OF BIRDS WITH PROPORTIONS GIVEN IN BRACKETS) OF COMMON GUILLEMOTS CAUGHT IN COASTAL FISHING NETS OFF ØSTFOLD COUNTY, S.E. NORWAY DURING THREE CONSECUTIVE WINTERS.

Winter	Month	Adults (without bursa)			Immatures (with bursa)			Total
		males	females	total	males	females	total	
1987/88	Jan	0	0	0	0	1	1	1
	Feb	0	0	0	59	64	123	123
1988/89	Nov	1	0	1	0	0	0	1
	Dec	0	2	2	18	20	38	40
	Jan	0	1	1	26	30	56	57
	Feb	7	6	13	58	45	103	116
	Mar	0	2	2	7	7	14	16
1989/90	Oct	0	0	0	23	8	31	31
	Nov	1	4	5	75	65	140	145
	Dec	13	27	40	134	115	249	289
	Jan	1	1	2	29	19	48	50
	Feb	16	23	39	81	61	142	181
Mar	1	2	3	27	20	47	50	
Total		40 (37%)	68 (63%)	108 (10%)	537 (54%)	455 (46%)	992 (90%)	1100

$p < 0.001$). However, Anker-Nilssen *et al.* (1988) pointed out that it is difficult to detect bridling in oiled, winter-plumaged birds, and found that 13% of 62 birds were bridled when birds in winter plumage were omitted from the analysis. This result does not deviate from the corresponding 18% bridled of 189 birds in summer or transitional head plumage in our study ($\chi^2 = 0.540$, $df = 1$, $p = 0.462$).

Intra-seasonal size variation

The sample of adult birds was too small to make monthly comparisons meaningful. Among immatures there was a significant monthly variation in head, culmen and gonyes lengths for males within the last season (Table III), which was primarily due to an overall increase in these variables (Fig. 1). In immature females, there was no corresponding variation, although culmen length did tend to increase over the season. With the exception of inter-orbital breadth in females, there was no significant monthly variation in morphometry in immatures during the 1988/89 winter, but the collection of birds started two months later in that season. There was a clear variation in body mass of both sexes of immatures throughout the 1989/90 winter, with the lowest masses recorded in October–November 1989 (Table III, Fig. 1).

Inter-seasonal size variation

Adult birds were slightly smaller in the 1989/90 season than in the preceding winter, but the differences were only significant for gonyes depth in males and all three head variables in females (Table IV). There was a similar trend for some variables in immature birds, where sample sizes allowed an analysis of data from the same month (February) in all three seasons (Table V). In this comparison, birds from February 1988 appeared to be of intermediate size to those collected one and two years later, but this pattern was not uniform.

TABLE III. RESULTS OF ANOVA TESTS FOR MONTHLY VARIATION IN MORPHOMETRY AND BODY MASS OF IMMATURE COMMON GUILLEMOTS CAUGHT IN COASTAL FISHING NETS OFF ØSTFOLD COUNTY, S.E. NORWAY DURING THE WINTERS 1988/89 (DECEMBER-MARCH) AND 1989/90 (OCTOBER-MARCH). THE DATA WERE GROUPED ACCORDING TO SAMPLING MONTH AND ARE PRESENTED IN FIGURE 1.

Variable	Winter	Males				Females			
		F	df	p	F	df	p		
Winglength	1988/89	0.09	3, 105	0.963	ns	2.10	3, 99	0.104	ns
	1989/90	1.46	5, 357	0.200	ns	0.15	5, 278	0.979	ns
Head length	1988/89	0.67	3, 102	0.576	ns	1.75	3, 97	0.160	ns
	1989/90	2.59	5, 335	0.025	*	0.87	5, 266	0.500	ns
Culmen length	1988/89	2.01	3, 101	0.117	ns	0.65	3, 96	0.591	ns
	1989/90	6.63	5, 336	<0.001	***	2.23	5, 264	0.051	ns
Gonys depth	1988/89	0.26	3, 105	0.855	ns	2.63	3, 98	0.054	ns
	1989/90	5.90	5, 351	<0.001	***	0.55	5, 275	0.740	ns
Inter-orbital breadth	1988/89	1.97	3, 105	0.121	ns	3.63	3, 99	0.015	*
	1989/90	1.30	5, 356	0.264	ns	0.25	5, 281	0.940	ns
Body mass	1988/89	0.31	3, 105	0.818	ns	2.54	3, 99	0.060	ns
	1989/90	7.52	5, 355	<0.001	***	3.00	5, 280	0.012	*

TABLE IV. MORPHOMETRY (IN MM) OF ADULT COMMON GUILLEMOTS CAUGHT IN COASTAL FISHING NETS OFF ØSTFOLD COUNTY, S.E. NORWAY IN THE WINTERS 1988/89 AND 1989/90. RESULTS OF STUDENT'S *t*-TESTS ARE INDICATED.

Sex	Variable	Winter 1988/89			Winter 1989/90			<i>t</i> -test		
		<i>n</i>	Mean	<i>SD</i>	<i>n</i>	Mean	<i>SD</i>	<i>t</i>	<i>p</i>	
Males	Winglength	8	206.1	6.1	32	205.0	6.9	0.44	0.663	ns
	Head length	8	114.1	3.4	30	111.9	4.5	1.28	0.210	ns
	Culmen length	8	49.1	3.0	30	47.6	2.8	1.32	0.197	ns
	Gonys depth	8	13.09	0.99	30	12.17	0.77	2.82	0.008	**
Females	Winglength	11	206.7	3.3	57	205.3	4.3	1.04	0.305	ns
	Head length	11	111.9	3.0	55	109.8	2.4	2.58	0.012	*
	Culmen length	11	47.7	2.2	55	46.3	2.0	2.11	0.039	*
	Gonys depth	11	12.66	0.73	57	11.91	0.66	3.42	0.001	***

Comparisons with body measurements of birds from the Styliis incident

Compared to the birds examined after the *Styliis* incident, the birds caught in fish nets appeared to be generally smaller than those killed by oil 8–9 years earlier (Tables VI and VII). The comparison of data for the immature *Styliis* victims measured by Anker-Nilssen *et al.* (1988) and for the equivalent sample measured by examiners in the present study almost 8 years later (Table VIII) suggests that this could be the result of potential differences in measuring techniques (e.g. for head length). However, of the three body parts involved in the comparison, the two that were significantly smaller in the stored sample (wing and head) involves more muscle tissue and were thus probably more susceptible to shrinkage during storage than the third (the bill), which mostly consists of horn and bone structures. Moreover, the much greater deviation in winglength for males than for females is difficult to explain by anything but chance. If data for the two sexes are

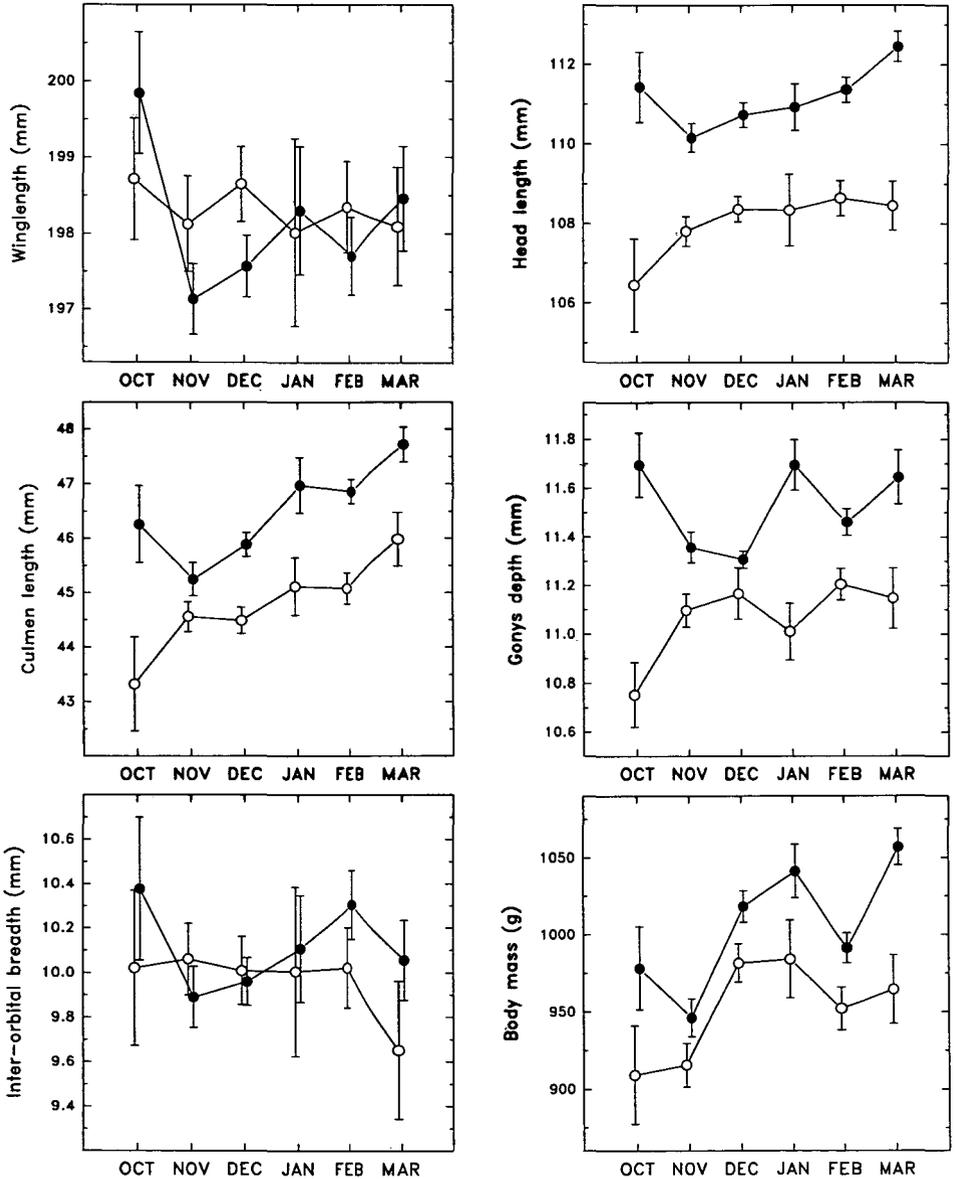


Figure 1. The intra-seasonal variation (monthly means \pm 1 SE) in body mass and morphometric variables of immature male (filled circles) and female (open circles) Common Guillemots caught in coastal fishing nets off Østfold county in October 1989–March 1990. See Table III for statistics. Sample sizes varied with month, sex and variable, ranging in males from 19–20, 69–73, 121–133, 26–29, 80–81 and 26–27, in October–March, respectively. The corresponding samples of females were 7, 62–65, 108–115, 18–19, 56–61 and 19–20.

TABLE V. MORPHOMETRY (IN MM) AND BODY MASS (IN G) OF IMMATURE COMMON GUILLEMOTS CAUGHT IN FEBRUARY IN COASTAL FISHING NETS OFF ØSTFOLD COUNTY, S.E. NORWAY IN THREE CONSECUTIVE WINTERS, 1987-1990. ANOVA TEST RESULTS ARE INDICATED.

Variable	Sampling period	Males			Females		
		n	Mean	SD	n	Mean	SD
Winglength	Feb 1988	55	197.6	4.0	59	200.4	4.4
	Feb 1989	58	199.5	4.5	45	200.5	4.6
	Feb 1990	81	197.7	4.6	61	198.3	4.7
		(F=3.59, p=0.029) *			(F=4.09, p=0.018) *		
Culmen length	Feb 1988	53	47.3	2.3	60	45.8	2.4
	Feb 1989	57	47.7	2.2	44	45.5	2.3
	Feb 1990	80	46.9	2.0	56	45.1	2.2
		(F=2.88, p=0.057) ns			(F=1.50, p=0.225) ns		
Head length	Feb 1988	53	111.2	3.2	60	109.1	3.3
	Feb 1989	57	112.9	2.8	44	108.6	3.2
	Feb 1990	80	111.4	2.8	56	108.6	3.3
		(F=5.97, p=0.003) **			(F=0.47, p=0.630) ns		
Gonys depth	Feb 1988	56	11.72	0.63	61	11.42	0.64
	Feb 1989	58	11.84	0.49	44	11.42	0.55
	Feb 1990	81	11.46	0.49	61	11.21	0.50
		(F=9.43, p<0.001) ***			(F=2.62, p=0.074) ns		
Inter-orbital breadth	Feb 1988	57	10.24	1.22	63	9.80	0.93
	Feb 1989	58	10.27	0.90	45	10.03	1.09
	Feb 1990	81	10.30	1.40	61	10.02	1.40
		(F=0.05, p=0.944) ns			(F=0.73, p=0.489) ns		
Body mass	Feb 1988	55	1006	79	60	947	99
	Feb 1989	58	1051	87	45	1022	74
	Feb 1990	81	991	88	61	952	108
		(F=8.58, p=0.001) ***			(F=9.34, p=0.003) **		

combined, the deviation between the two samples of immatures from the *Stylis* incident (Table VIII) is still not significant for culmen length and gonys depth (0.69 mm, $t=1.49$, $df=663$, $p=0.138$ and 0.12 mm, $t=1.23$, $df=695$, $p=0.220$, respectively), but appears to be in the same order of magnitude as those documented between birds from *Stylis* and the birds netted in the late 1980s (Tables VI and VII).

DISCUSSION

The skewed sex and age ratios of wintering Common Guillemots found in this study are difficult to explain. The dominance of females among adults could indicate a segregation of sexes with the adult males, who accompany the flightless young for several months after they leave the colony (e.g. Harris & Birkhead 1985), tending not to winter in the Skagerrak. It is also possible that the males arrive there later in the season, but the skewness of the sex ratio in the first half of the season (October–December) was not significantly different from that in the second half of the season

TABLE VI. MORPHOMETRY (IN MM) OF ADULT COMMON GUILLEMOTS WINTERING IN THE NORTHERN SKAGERRAK. BIRDS FROM WINTER 1980/81 WERE BEACHED AFTER AN OFFSHORE OILSPILL IN LATE DECEMBER (DATA FROM ANKER-NILSSEN *ET AL.* 1988), WHILE BIRDS FROM WINTERS 1988/89 AND 1989/90 WERE KILLED IN COASTAL FISHING NETS OFF ØSTFOLD COUNTY, S.E. NORWAY. RESULTS OF STUDENT'S *t*-TESTS ARE INDICATED.

Sex	Variable	Offshore oilspill winter 1980/81			Coastal fishing nets winters 1988/89 and 1989/90			t-test		
		n	Mean	SD	n	Mean	SD	t	p	
Males	Winglength	68	206.4	4.0	40	205.2	6.6	1.18	0.240	ns
	Head length	34	114.9	2.6	38	112.4	4.4	2.89	0.005	**
	Culmen length	61	49.6	2.1	38	47.9	2.8	3.40	0.001	***
	Gonys depth	65	12.82	0.66	38	12.36	0.89	3.15	0.002	**
Females	Winglength	73	208.4	5.3	68	205.5	4.2	3.55	0.001	***
	Head length	32	112.1	3.2	66	110.1	2.6	3.39	0.001	***
	Culmen length	68	47.6	2.4	66	46.5	2.1	2.89	0.005	**
	Gonys depth	71	12.66	0.64	68	12.03	0.72	5.58	<0.001	***

($\chi^2=0.834$, $df=1$, $p=0.361$). On the other hand, the tendency for a decline in the winglength of immatures between October and November 1989 (Fig. 1) hints at an increasing proportion of first-winter birds in the sample and would support the idea of a later arrival of males and young. The preference for different prey found between the sex-age groups (Lorentsen & Anker-Nilssen in manuscript) could have been an effect of corresponding differences in the birds' distribution and foraging behaviour and thereby in their chances of being caught in fish nets, but we have too little data on the distribution of prey stocks and fish nets to elucidate this point. That immature males and females may have slightly different winter distributions in this area, is also supported by data from the oiling incident of December 1980, but then there was an excess of females in the sample from this part of the coast and the opposite tendency in the sample from Bohuslän, western Sweden (Anker-Nilssen *et al.* 1988).

As the size of Common Guillemots generally increases with latitude (see e.g. Table 12 of Anker-Nilssen *et al.* 1988), the tendency for adults to be smaller in 1989/90 than in 1988/89 suggests a more southerly origin of the birds in the latter winter. However, the test results were ambiguous, and the (to some extent) unavoidable bias involved with respect to different examiners and measuring techniques must be kept in mind (e.g. Barrett *et al.* 1989). The similar, but even less clear-cut variation in size of immatures could easily have been biased by regional differences in reproductive success, since it is reasonable to assume that most immatures are first-winter birds (cf. Mead 1974). With respect to the range of size variation found within the species and the unknown variation in the age structure of the immature population from year to year, the inter-seasonal variation may be regarded as relatively insignificant in 1988-90. However, the comparison with data from the *Styris* incident suggests that there was an overall decrease in body measurements of both adult and immature Common Guillemots wintering in the northern Skagerrak during the 1980s. Such a decrease could have been brought about by more British birds entering the area in the last winters and, by so doing, outnumbering the larger northern birds to a greater extent than in the previous season.

Another (or complementary) explanation is that a change in size distribution could be a direct effect of the dramatic decrease in numbers of Common Guillemots in northern Norway and on Bear Island after the capelin *Mallotus villosus* collapse during the second half of the 1980's (Vader

TABLE VII. MORPHOMETRY (IN MM) FOR IMMATURE COMMON GUILLEMOTS WINTERING IN THE NORTHERN SKAGERRAK. BIRDS FROM 1980/81 WERE BEACHED AFTER AN OFFSHORE OILSPILL IN LATE DECEMBER (DATA FROM ANKER-NILSSEN *ET AL.* 1988), WHILE BIRDS FROM 1987-1990 WERE KILLED IN COASTAL FISHING NETS OFF ØSTFOLD COUNTY, S.E. NORWAY. RESULTS OF STUDENT'S *t*-TESTS ARE INDICATED.

Sex	Variable	Offshore oilspill winter 1980/81			Coastal fishing nets winters 1987/88, 1988/89 and 1989/90			t-test	
		n	Mean	SD	n	Mean	SD	t	p
Males	Winglength	323	200.1	4.8	527	198.1	4.5	6.06	<0.001 ***
	Head length	170	112.8	3.7	500	111.3	3.2	5.25	<0.001 ***
	Culmen length	296	48.0	2.6	500	46.5	2.5	8.14	<0.001 ***
	Gonys depth	305	11.86	0.61	522	11.54	0.56	8.03	<0.001 ***
Females	Winglength	334	200.4	4.5	447	198.9	4.7	4.53	<0.001 ***
	Head length	141	110.2	3.1	434	108.6	3.3	5.29	<0.001 ***
	Culmen length	306	46.1	2.4	431	45.0	2.4	6.06	<0.001 ***
	Gonys depth	319	11.54	0.58	445	11.25	0.77	5.91	<0.001 ***

TABLE VIII. MORPHOMETRY (IN MM) FOR IMMATURE COMMON GUILLEMOTS BEACHED AFTER AN OFFSHORE OILSPILL IN THE SKAGERRAK IN LATE DECEMBER 1980. SAMPLE 1 WAS MEASURED WITHIN A FEW WEEKS AFTER THE CORPSES WERE COLLECTED (DATA FROM ANKER-NILSSEN *ET AL.* 1988), WHILE BIRDS IN SAMPLE 2 WERE STORED IN A FREEZER FOR ALMOST 8 YEARS BEFORE THEY WERE EXAMINED BY OTHER PERSONS (PERSONS 1 AND 2 OF THIS STUDY, CF. TABLE I). RESULTS OF STUDENT'S *t*-TESTS ARE INDICATED.

Sex	Variable	Sample 1 examined 1981			Sample 2 examined 1988			t-test	
		n	Mean	SD	n	Mean	SD	t	p
Males	Winglength	323	200.1	4.8	19	195.3	4.5	4.09	<0.001 ***
	Head length	170	112.8	3.7	12	110.4	3.3	2.48	0.014 *
	Culmen length	296	48.0	2.6	15	47.6	1.5	0.71	0.476 ns
	Gonys depth	305	11.86	0.61	19	11.81	0.46	0.47	0.642 ns
Females	Winglength	334	200.4	4.5	24	199.5	5.3	0.95	0.344 ns
	Head length	141	110.2	3.1	15	107.6	2.8	3.18	0.002 **
	Culmen length	306	46.1	2.4	17	45.1	1.7	1.69	0.092 ns
	Gonys depth	319	11.54	0.58	21	11.37	0.60	1.37	0.173 ns

et al. 1990a, 1990b, Anker-Nilssen & Barrett 1991), since it is probable that significant numbers of birds from that region visit Skagerrak in winter (Anker-Nilssen *et al.* 1988). A note of caution is, however, appropriate since this effect would in part be counteracted by the somewhat less dramatic decrease recorded in some British Guillemot populations during the same time period (Heubeck *et al.* 1991). Furthermore, it is not known to what extent the birds' risk of being netted or oiled is independent of their body size, nor if birds of very different origins were distributed differently within the area. This last question could easily have been the most important, since the oiling occurred offshore whilst the fishing nets were set relatively close to land.

Ringed recoveries document that many young Guillemots from colonies in Shetland visit the Skagerrak area, particularly during the last decade (cf. Mead 1974, Heubeck *et al.* 1991). Not surprisingly, the 10 ringed Guillemots present in our sample all originated from the British Isles (9 from Scottish colonies and 1 from Ireland). These birds had all been ringed as nestlings and 8 of them were recovered in their first winter. Unfortunately, a detailed study of the Norwegian ringing results has not yet been made. However, of 133 Guillemots ringed as chicks in south Norway and recovered in winter (October-March) when less than 4 years of age, only 15 (11%) were found in the Skagerrak and Kattegat area (east of 6°30'E), and the corresponding result for chicks ringed in north Norway was only 1 (1%) of 129 birds (data provided by V. Bakken). When including recoveries of birds when more than 4 years old, these numbers were 15 of 143 and 2 of 135, respectively. Such results should be interpreted with great caution, especially since of the 339 Norwegian Guillemots ringed as chicks and later recovered, 277 (82%) were found prior to 1980 and only 3 (1%) were found during the winters of this study. Nevertheless, these data strongly indicate that the Skagerrak is a less preferred wintering ground for Guillemots from northern colonies.

Overall, our results confirm that the major breeding areas of Common Guillemots wintering in the Skagerrak are found in Great Britain. The intra-seasonal variation documented for immature birds most likely reflects the continuing growth of young birds during their first winter. A suggested decrease in the size of birds during the 1980s may have both methodological and biological explanations and does not invalidate the conclusions of Anker-Nilssen *et al.* (1988) that significant numbers of birds may originate from colonies in northern Norway (including Bear Island).

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SUMMARY

The morphometry of 1157 Common Guillemots killed in fishing nets at the northeastern coast of Skagerrak during the last three winters of the 1980s is discussed. Only 10% of the birds were adults (lacking a cloacal bursa). The intra-seasonal variation in size measurements documented for immature birds most likely reflected the continuing growth of young birds during their first winter. The results confirm that the major breeding areas of Common Guillemots wintering in the Skagerrak are found in Great Britain. A suggested decrease in the size of birds during the 1980s could have both methodological and biological explanations, and does not invalidate the earlier findings that this important winter population also recruits birds from breeding colonies in northern Norway (including Bear Island).

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Concentrations of Manx Shearwater off San Antonio, Río Negro, Argentina

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From September 1992 to May 1993 I collected data on seabirds, waders and waterfowl along the coast of San Antonio Oeste, Río Negro, Argentina. From the second week of October until the first week of December, Manx Shearwaters *Puffinus puffinus* were regularly seen far off at sea (usually at more than 300 m offshore). Total numbers seen did not usually exceed c. 500 birds.

On 1 November, however, a group of c. 650 birds was present 100 m off the coast, near the entrance of Bahía San Antonio 40°48'S 64°55'W, between two sandflats, Banco Reparo in the west and Banco Lobos in the east. The following day the number of birds had increased to an estimated 1,400. The flock was slowly moving towards Banco Lobos (where I was observing at that time) and more shearwaters, arriving from the east were joining this group. After one hour I estimated that 13-15,000 birds were present. While the birds were gathering, the main group was flying in circles counter clock-wise (diameter 1.0 km) at less than 10 m above the sea. Only occasionally did birds sit down on the water to rest. When the group reached its peak number more birds sat down for a while, apparently to rest or to search for food, as close as 50 m off Banco Lobos. The majority, however, continued to fly in circles. After c. 15 minutes the group started to move in a southeastern direction towards the open sea, meanwhile continuing the circling movement. Even then birds were arriving from the east, but in smaller numbers, and this went on until at least 2 hours after the highest estimate when I left the area. Therefore, in total, there must have been more than 15,000 Manx Shearwaters in the Golfo de San Matias at that time.

The population size of the Manx Shearwater, which breeds in the NE Atlantic, is 250,000-300,000 pairs (del Hoyo *et al.* 1993), of which the majority winters off eastern South America from 10°S to 50°S (Harrison 1983). Flocks of this size appear not to have been reported close to South American shores, neither has the observed behaviour been described. Although, the circling behaviour is very similar to that shown by birds in rafts offshore from colonies at dusk (Brooke 1990).

The presence of large quantities of food might have caused such a concentration and the performance of the peculiar circling behaviour. However, because the majority of the shearwaters did not make any attempt at foraging, this explanation seems doubtful, also because none of the 2,100 Kelp Gulls *Larus dominicanus* and more than 300 terns *Sterna* spp (mostly South American Tern *S. hirundinacea*) left their roosts in the vicinity of the area to join the shearwaters.

Another possibility could have been that strong eastern winds blew the shearwaters towards the coast, although the wind at the time (Beaufort Force 4-6) came from the southwest. Furthermore, in the week prior to this date the wind had been south-southwest force 6-8. Possibly this long-distance migrant gathers in certain areas off eastern South America after its southward migration. Shearwaters are not known to migrate in flocks of more than a few hundred birds. From current knowledge there does not seem to exist a satisfactory explanation for the observed circling movement.

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BOOK REVIEWS

CAMPHUYSEN, C.J., K. ENSOR, R.W. FURNESS, S. GARTHE, O. HUPPOP, G. LEAPER, H. OFFRINGA & M.L. TASKER. 1993. Seabirds feeding on discards in winter in the North Sea. EC DG XIV research contract 92/3505. NIOZ Rapport 1993 – 8, Netherlands Institute for Sea Research, Texel. 140pp. ISSN 0923-3210.

This is the report of an international project, funded by the European Commission, to investigate the extent to which wintering seabirds feed on discards from commercial fishing trawlers in the North Sea. The list of questions to be answered was ambitious given the timing and duration of fieldwork (January-February 1993): what species scavenge at trawlers in different parts of the North Sea, in what numbers, and what do they eat?; which fisheries attract most birds?; how do different seabird species interact at boats?; how many seabirds could be supported by fishery waste; what effect would reducing waste quantities have?

Fieldwork was carried out by teams of observers on six fisheries research vessels operating in different sectors of the North Sea, and the bulk of the report summarises the mass of observations made during different fishing operations and during experimental discarding of fish. Of the problems faced, the weather was probably the least. The lay-out of the vessels and consequent fishing practices varied and despite an initial cruise to standardise methods, inconsistencies arose. Furthermore, one vessel covering the NW sub-region of the North Sea was diverted for much of the time because of the *Braer* oil spill. Despite these hindrances, the aims of the project were largely achieved.

If I had one main criticism of the report it would be that the layout makes it difficult to access the wealth of information contained within it. In double-column format, some paragraphs extend the length of the page while subject headings (which should have been in bold type) could usefully have been listed at the beginning of each section, as they do not appear on the contents page. Similarly, a summary list of the 51 Figures and 66 Tables would have helped the reader find raw data more easily. On the plus side the two summaries at the beginning (one for 'scientists' and one for 'non-specialists') were excellent, and printed on a different coloured paper for easy access. There were inconsistencies in the use of statistical tests to support sometimes surprising statements, e.g. that in Kittiwakes "immatures appeared clearly more successful than adults" at scavenging experimentally discarded fish, while I came across a few annoying errors (e.g. p.101 Figure 4.4.1-3 should read 4.1.1-3).

The authors commendably draw attention to the fundamental problem in extrapolating from their work, i.e. that fishing activities and seabirds scavenging patterns may (and probably do) differ between research and commercial trawlers, and studies to ascertain the extent of this difference is one of the recommendations made. In summary, this is a valuable contribution to our understanding of the relationship between seabirds and the fishing industry, and a welcome sign of political acceptance of the need for research into the way that fishery practices, and changes in them, affect other parts of the marine food chain.

The report, published by the Netherlands Institute for Sea Research (P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands), unfortunately is now out of print.

Martin Heubeck

THE SEABIRD GROUP 1995

The Seabird Group was founded in 1966 to circulate news of work in progress on seabirds and to promote research. It is run by an elected Executive Committee and maintains close links with the three major British national ornithological bodies – the British Ornithologist's Union, the British Trust for Ornithology, and the Royal Society for the Protection of Birds. Membership (£10 per annum, £9 if paid by banker's order, £5 for students) is open to all with an interest in seabirds; for details please contact the Membership Secretary (address below) – payment by banker's order helps the Group.

Current Executive Committee The present Committee comprises: Chairman K. Taylor, Secretary M. Heubeck, Treasurer R.W. Furness, Membership Secretary S. Russell, Editor of *Seabird* S. Wanless, Newsletter Editor M. Tasker, also K.C. Hamer, M.P. Harris, J.D. Okill and E.K. Dunn.

Newsletters and Meetings Three Newsletters are circulated to members each year. They contain all sorts of items including reports on seabird conservation issues and research projects, news from seabird groups in other countries, book reviews, details of meetings, etc. The Newsletter Editor (address below) welcomes contributions from members. The usual venue for the Group's annual meeting is the BTO Ringing and Migration Conference at Swanwick, except when the Group holds its own conference, in which case the meeting is combined with that. Our conferences draw seabird workers from many countries to join in a forum of topical interest. In keeping with our desire to promote work in the field, practical manuals and guidelines evolve from the workshop sessions which cater for specialist topics within the conference theme.

Seabird Group Grants Each year the Group has some money available to help fund research conducted by members. All grant applications should be submitted to the Secretary by the end of February, and will be considered by the Executive Committee by the end of March. Successful applicants are required to submit a typed report, not exceeding 500 words, by the end of October of the same year for inclusion in the Newsletter. A full typed report (in triplicate) must be submitted by the end of the year.

Seabird Colony Register The Seabird Group has always sought to organise and implement national schemes involving the active participation of its membership, now standing at 350 members. The Group membership played a major role in the national Operation Seafarer survey whose results were published in 'The Seabirds of Britain and Ireland' (1974). The Group completed the Seabird Colony Register fieldwork in 1988, in cooperation with the Nature Conservancy Council, and the results were published in the book: 'The Status of Seabirds in Britain and Ireland' in 1991. This register was begun in 1985 to gather together all existing data on breeding seabird numbers in the British Isles, to bring our knowledge of their status up to date by detailed field surveys and to establish a computerised database which can be easily updated in the future. Although this round of survey work has been completed, it is important to continue monitoring of seabird breeding numbers: anyone eager to conduct counts on a regular basis should contact Paul Walsh, JNCC, 17 Rubislaw Terrace, Aberdeen AB1 1XE.

Seabird Journal In November 1984 the Group launched its new-look journal *Seabird*, numbered 7 in deference to its pedigree of Seabird Group Reports 1-6. Our priority is to maintain a high volume and quality of content and the current editor, Sarah Wanless, welcomes offers of papers (see Notice to Contributors, and address below). Members of the Seabird Group receive *Seabird* free of charge; additional copies to members, and any copies to non-members are £10 + 50p postage within the British Isles, £10 + £1 postage overseas. Postage overseas is by surface mail, unless the recipient can make prior provision for air mail. The subscription to Libraries is £15 per copy. To help reduce costs, overseas subscribers are kindly asked to make payment by international money order rather than by cheque. Back issues of *Seabird* 11, 12, 13, 14, 15 and 16

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All submissions, of which *three* copies are required, must be typewritten, on one side of the paper, with double spacing and adequate margins. The approximate position of figures and tables should be indicated in the margin. Authors are advised to consult a recent copy of *Seabird* and follow the conventions for section headings, tables, captions, references, quotation marks, abbreviations etc. The Editor may return without consideration any submission that departs from the *Seabird* form of presentation. Spelling should conform with the preferred i.e. first-cited spelling of the *Shorter Oxford Dictionary*. Details of experimental technique, extensive tabulations of results of computation procedures, etc. are best presented as appendices. A full-length paper must include a summary not exceeding 5% of the total length.

On first mention a bird species should be designated by an English vernacular name drawn from *The Status of Birds in Britain and Ireland*, or from an authoritative faunistic work treating the appropriate region, followed by systematic binomial; author and date need be cited only in taxonomic papers. Thereafter only one name should be used, preferably the English one. Capitals should be used for the initial letters of all single words or hyphenated vernacular names (e.g. Great Black-backed Gull, White-eyed Gull) but not in a group name (e.g. gulls, terns). Trinomials should be used only if the subspecific nomenclature is relevant to the topic under discussion. Underlining is used for all words of foreign languages, including Latin, other than those which have been adopted into English. Underlining should also be used for phonetic renderings of bird vocalizations. Underlining is not needed for emphasis.

Measurements should be given in SI (International system of units), but if the original measurements were made in non-SI units, the actual values and units should be given, with SI equivalents inserted in parentheses at appropriate points. Measurements may be given in cm.

Figures and diagrams should be drawn in black ink on white board, paper or tracing material, with scales (for maps), and lettering given in Letraset. In designing drawings, authors are asked to note the page-size and shape of *Seabird*; originals should be 1½-2 times final size. Tables should be typewritten and spaced appropriately. References should be quoted in the text in the format indicated by the following examples: Harris 1980, Cramp & Simmons 1980, Monaghan *et al.* 1980. References at the end of the paper (following acknowledgements) should be given in the following format:

COULSON, J.C. and WOOLER, R.D. 1976. Differential survival rates among breeding Kittiwake Gulls *Rissa tridactyla* (L.). *J. Anim. Ecol.* 45: 205-213.

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