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Editors:

C.J. Camphuysen (NZG), Ankerstraat 20, 1794 BJ Oosterend, Texel, The Netherlands, tel/fax + 31 222 318744, e-mail kees.camphuysen@wx.nl

Dr J.B. Reid (Seabird Group), c/o Joint Nature Conservation Committee (JNCC), Dunnet House, 7 Thistle Place, Aberdeen AB10 1UZ, Scotland, U.K., e-mail reid_j@jncc.gov.uk.

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THE STATUS OF THE EUROPEAN SHAG *PHALACROCORAX ARISTOTELIS** POPULATION ON THE ATLANTIC COAST OF THE IBERIAN PENINSULA

KUIFAALSCHOLVERS AAN DE ATLANTISCHE KUST VAN
HET IBERISCH SCHIEREILAND

ALBERTO VELANDO¹, FRANCISO DOCAMPO² & DAVID ALVAREZ³.

¹*Departamento de Ecología e Biología Animal, Universidade de Vigo, 36200 Vigo, Spain, e-mail: avelando@uvigo.es;* ²*Sociedade Galega de Historia Natural, Apdo 330, 15780 Santiago de Compostela, Spain;* ³*Dep. B.O.S., Unidad de Zoología, Universidad de Oviedo, 33071 Oviedo, Spain.*

*A regional analysis of the status of the European Shag *Phalacrocorax* [Stictocarbo] *aristotelis* population on the Atlantic coasts of the Iberian Peninsula is presented. This is the first census to be made of this population. The total population was estimated to be approximately 2239 pairs in 1990-94. The first counts from Euskadi and Cantabria are presented, indicating a population of 57-67 pairs in Euskadi in 1994 and 36-41 pairs in Cantabria in 1992. The first census in Asturias dates from 1986 with 98-124 pairs, and the population has increased at an annual rate of 6%, reaching 199-250 pairs in 1997. There are records of partial counts made in Galicia since 1976. The population appears to have stabilised on the Cíes and Ons Islands (Rías Baixas, Pontevedra), where it was increasing at 8-9% annually. The total count of 1462 breeding pairs on Cíes and Ons accounts for 66% of the Atlantic Iberian population. As far as is known, the population in Portugal has stabilised, but there has been no census of the southern colonies since 1983. On the island of Berlenga there were 60 pairs in 1990-94, the number of pairs having changed very little since the first count in 1939.*

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INTRODUCTION

The European Shag *Phalacrocorax aristotelis* has a distribution that is limited to the western Palearctic, and it breeds from the North Cape to the coasts of Morocco (Cramp & Simmons 1977). There are three subspecies: the Atlantic subspecies, (*P.a. aristotelis*) is the most abundant and its southernmost limit is located on the Atlantic coasts of the Iberian Peninsula. The population of this subspecies has been well documented for the British Isles (Evans 1984; Lloyd *et al.* 1991; Andrews & Carter 1993; Thompson *et al.* 1998, 1999), Norway

Table 1. European Shag population in Euskadi, Spain, 1990-94. Site number (#) refers to number of breeding location in Fig. 1. Shown are number of colonies in each breeding location in 1994 and number of nests in 1990 and 1994.

Tabel 1. Populatie Kuifaalscholvers in Euskadi, Spanje, 1990-94. Kolonie nummers (#) zijn terug te vinden in Fig. 1. Weergegeven zijn het aantal kolonies in 1994 en de aantallen broedparen in 1990 en 1994.

#	location	colonies	1990	1994
1	Planxia	1	1-2	2-4
2	C. Ogoño	1	14-17	20
3	I. Akez	1	6-8	8-10
4	Bakio-Billano	3	18-25	21-27
5	Barrika	1	1-3	6
Total		7	40-55	57-67

Table 2. European Shag population in Cantabria, Spain, 1992. Site number (#) refers to number of breeding location in Fig. 1. Shown are number of colonies in each breeding location and number of nests in 1992.

Tabel 2. Populatie Kuifaalscholvers in Cantabria, Spanje, 1992. Kolonie nummers (#) zijn terug te vinden in Fig. 1. Weergegeven zijn het aantal kolonies en de aantallen broedparen.

#	location	colonies	nests
6	M. Candina	1	6-7
7	M. Buciero	1	5-6
8	C. Quintres	1	7-8
9	I. Mouro	1	1
10	I. Portio	1	5-7
11	I. Conejera	1	9
12	I. Samosa-Desesperada	2	3
Total		8	36-41

(Barrett & Schei 1977; Barrett & Vader 1984; Røv 1990) and France (Guermeur & Monnat 1980; Maout 1990; Cadiou 1996). On the Iberian Peninsula, however, there is an estimate of the overall population only for 1981 (Barcena *et al.* 1984) based on counts taken exclusively on the Galician and Portuguese coasts (Barcena *et al.* 1987; Teixeira 1984). This contrasts with the wealth of information on the Mediterranean subspecies (*P.a. desmarestii*) on the Iberian Peninsula (de Juana 1984; Ferrer *et al.* 1984; Capella *et al.* 1986; Guyot 1993). This paper describes the recent status and distribution of European Shag colonies on the Atlantic coast of the Iberian Peninsula by region.

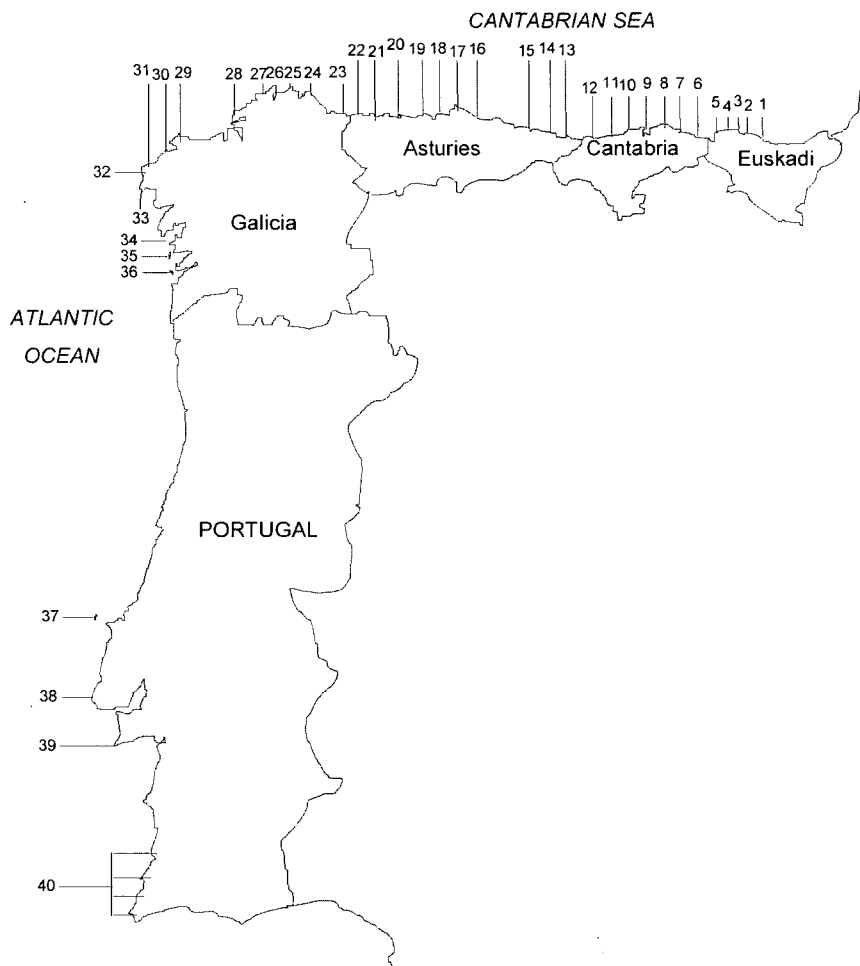


Figure 1. Positions of the main breeding locations of the European Shag in each region of the Atlantic coast of the Iberian Peninsula. Details of the number of colonies and pairs at each location are given in Tables 1-5.

Figuur 1. Ligging van de voornaamste broedkolonies van Kuifaalscholvers langs de Atlantische kust van Spanje en Portugal. Zie verder tabel 1-5.

METHODS

From 1990 to 1997, breeding pairs were counted in all coastal colonies except those on the south-east coast of Portugal, which has not been censused since 1983. For each colony the number of well-built nests was scored as the number

of pairs. For each census we present the minimum number of pairs counted, and for some, an estimate of probable nests or nest sites that were not actually located but where adults were seen to enter. Nearby colonies were grouped into breeding locations for descriptive purposes. In breeding locations that were censused more than three times, the mean annual growth rate was estimated by $N_t = N_0 e^{rt}$, where N_0 is the population size at the outset, t is the time in years, N_t is the population size after time t , and r is the *per capita* growth rate of the population. Annual growth rate was expressed as $r \times 100$.

RESULTS

The location of the European shag colonies on the Atlantic Iberian Peninsula are shown in Fig. 1. A total of 87 colonies was identified at 40 breeding locations. The total population of the Iberian Peninsula was estimated to be 2320-2372 pairs (counts between 1992 and 1994). Details of censuses in each region are presented below.

Euskadi and Cantabria - Most of the recent data on Iberian Peninsula breeding colonies is from the Cantabrian coast. The first census undertaken in Euskadi dates from 1990 (40-55 pairs), and in 1994 between 57 and 67 pairs were recor-

Table 3. European Shag population in Asturias, Spain, 1976-94. Site number (#) refers to number of breeding location in Fig. 1. Shown are number of colonies in each breeding location in 1994; - = unoccupied colonies during the year census was made. Shown are number of colonies in each breeding location in 1994 (- = unoccupied colonies during the year census was made) and number of nests in 1986-97.

Tabel 3. Populatie Kuifaalscholvers in Asturias, Spanje, 1976-94. Kolonie nummers (#) zijn terug te vinden in Fig. 1. Weergegeven zijn het aantal kolonies in 1994 en de aantallen broedparen in 1986-97 (- = kolonie niet bezet).

#	location	colonies	1986	1989	1991	1992	1994	1997
13	Franca-S. Emeterio	2	3-6		2-5	3-5		1-2
14	Ribesella-Vidiagu	5	7-21	10-24	16-20	24-29		12-26
15	Tazones-Rodiles	2	1-6	-				
16	Campa Torres	1	-	1-2				1
17	Cabu Peñes	1	1	1-2	1-2	2-4	4	10-13
18	La Deva	1	-	2-3	6	2	8	13
19	Porceberas-Gavieru	8	40-41	59-65	72-78	72-74	68-70	67-87
20	Raposera-Osa	4	9	15-25	17	15-17	11-13	6-10
21	Gaivoteiro-Castelo	4	23	32-35	18-21	7-10	18-19	41-45
22	Pantorgas-Talaya	4	14	18	21-28	32		48-53
Total		32	98-124	138-174	153-177	157-173		199-250

Table 4. European Shag population in Galicia, Spain, 1976-94. Site number (#) refers to number of breeding location in Fig. 1. Shown are number of colonies in each breeding location in 1994 (- = unoccupied colonies during the year census was made) and number of nests in 1976-94.

Tabel 4. Populatie Kuifaaalscholvers in Galicia, Spanje, 1976-94. Kolonie nummers (#) zijn terug te vinden in Fig. 1. Weergegeven zijn het aantal kolonies in 1994 en de aantallen broedparen in 1976-94 (- = kolonie niet bezet).

#	location	colonies	1976	1981	1986	1994
23	Punta Niño do Corvo	1	-			1
24	Ansarón- San Ciprian	4	20-31			39
25	Coitelo-Tres Martas	2	-			16
26	C. Ortegal	3	6			38
27	P. Candiera	1	-			7
28	C. Prior- I. Gabeiras	4	11			49
29	I. Sisargas - Malpica	2	54	27		61
30	Corme-Laxe	2	-	29		8-15
31	C. Vilan	1	15	28		46
32	P. Buitra-Muxia	2	20-25	18		17
33	Finisterre	7	101	88		123
34	I. Sagres- I. Noro	2	-	-		12
35	I. Ons	1	122	193	305	557
36	I. Cíes	1	190	292	398	905
Total		33	539-555			1932

ded in seven colonies (Sociedad Ornitológica Lanius, Table 1). The difference between the first and second census estimates may be attributable to an improvement in the census methods applied. The most important colony in Euskadi is at Cabo Ogoño with 20 pairs in 1994. The only census in Cantabria (Table 2) was carried out in 1992, and indicated that 36-41 pairs were breeding in eight colonies (G. Orizaola, unpublished data).

Asturias - The first count in Asturias was made in 1986, and indicated a total of 98-124 pairs (Coordinadora Ornitológica d'Asturias). The population has been increasing and in 1997, 199-250 pairs were counted, representing an average annual rate of increase of 6% (Table 3). The population is distributed among small colonies each containing fewer than 25 pairs. The most important breeding area is located between the Porceberas Islands and the cliffs of Gaviero (no. 19, Fig. 1), where a total of 67 well-built nests was recorded in 1997. This locality hosts eight colonies, the largest of which (La Caladoria) holds eight pairs. Most colonies exhibited irregular growth; numbers of nests in the breeding areas of Gaivotero-Castelo (no. 21, Fig. 1) and Ribesella-Vidiagu (no. 14, Fig. 1) fluctuated over the years the censuses were carried out; the colonies

Table 5. European Shag population in Portugal, 1981-94. Site number (#) refers to number of breeding location in Fig. 1. Colonies = number of colonies in each breeding location in 1994; - = unoccupied colonies during the year census was made.

Tabel 5. Populatie Kuifaalscholvers in Portugal, 1981-94. Kolonie nummers (#) zijn terug te vinden in Fig. 1. Weergegeven zijn het aantal kolonies in 1994 en de aantallen broedparen in 1939, 1981-83 en 1990-94 (- = kolonie niet bezet).

#	location	colonies	1939	1981-83	1990-94
37	Berlengas	1	70	70	50-60
38	Cabo da Roca	1		5	5
39	Cabo Espichel	1		5	5
40	SW Coast	4		50	
Total		7		130	

of Pantorgas-Talaya (no. 22, Fig. 1) showed an annual increase of 11% between 1986 and 1997; and the colonies located in Porceberas-Gavieru (no. 19, Fig. 1) increased by 12% annually between 1986 and 1991, stabilising at around 70 pairs between 1991 and 1997.

Galicia - Galicia is currently the most important region with 34 colonies and 86% of the total population of the Atlantic Iberian Peninsula. The first census made in this region was in 1976, when the population was estimated at 539-555 pairs (Rodríguez-Silvar & Bermejo 1977). A partial census taken on the west coast in 1981 did not indicate any major changes, except on the Cíes and Ons Islands. In 1994, our census recorded a total of 1932-1939 breeding pairs. The breeding distribution of the European Shag in Galicia is extensive, but is not uniformly distributed; 77% of the population here is located in only two colonies (the Cíes Islands and the island of Ons, Table 4). On the Galician coast there are a substantial number of average-sized colonies, such as on the Isle of Anserón (no. 24, Fig. 1) which has 30 pairs, Los Aguillons on Cabo Ortegal (no. 26, Fig. 1) with around 40 pairs, Gabeiras Islands (no. 28, Fig. 1) with 22 pairs, Sisargas Islands (no. 29, Fig. 1) with 60 pairs, Cabo Vilán (no. 31, Fig. 1) with 50 pairs, and the colonies of Fisterra (no. 33 Fig. 1) holding approximately 100 pairs. The population on the Cíes Islands and the island of Ons (two colonies located less than 15 km apart) numbered 703 pairs in 1986 (Callejo *et al.* 1986), and has doubled during the last eight years to 1462 pairs. This indicates average annual rates of increase of 9% on the Cíes Islands and 8% on the island of Ons.

Portugal - There are around 130 breeding pairs distributed among scattered colonies in this region. The largest colony is on the Berlengas Islands with 50-60 pairs (Table 5, Teixeira & Granadeiro, unpublished data). This colony

Table 6. Growth of the European Shag population in the Atlantic Iberian Peninsula, 1981-1994. The 1981-83 data are from Barcena *et al.* (1984) and the 1990-1994 data from this study. Site numbers (#) refer to numbers of breeding locations in Fig. 1.

Tabel 6. Groei van de populatie Kuifzwaluwen langs de Atlantische kust van Spanje en Portugal. De gegevens over 1981-83 zijn ontleend aan Barcena *et al.* 1984, de recente gegevens komen uit de huidige studie. Kolonie nummers (#) zijn terug te vinden in Fig. 1.

#	breeding area	1981-83	1990-94
1-23	Cantabrian coast	90	251
24-28	Rías Altas	220	149
29-33	Costa da Morte	200	255
34-36	Rías Baixas	500	1474
37-40	Portugal	130	110 ¹
Total		1140	2239

¹the SW Portugal population was assumed not to have changed from 1983 (see Table 5).

appears to be well-established, with no major changes since 1939 when Lockley (1952) estimated the population to be approximately 70 pairs. The colonies on the south-west coast have not been counted since 1983.

DISCUSSION

We estimated that the population of European Shags on the Atlantic Coast of the Iberian Peninsula was 2239 pairs in 1990-94 (Table 6). This represents a 100% increase since the 1981-83 census (Bárcena *et al.* 1984), an increase that may be attributable to several different causes. Firstly, it must be noted that the 1981-83 data from the entire Cantabrian coast and the Rías Altas are not exact counts but are estimates. The increase in the number of pairs in this census could reflect the more accurate information now available from breeding localities, especially if account is taken of the fact that the first census made in Asturias in 1986 already revealed more pairs than those estimated in 1983 for the entire Cantabrian coast. It also reflects a real increase in some of the breeding colonies as was found to occur in several colonies in Asturias and Galicia. Thus, the Galician and Portuguese populations appear to have stabilised since the counts of 1981-83 (Teixeira 1984; Bárcena *et al.* 1987), exceptions being the population of the Cíes and Ons Islands. Here, there has been large population growth and the islands presently account for 66% of the Atlantic subspecies in the Iberian Peninsula, rendering them the most important breeding grounds of the European Shag at its southernmost limit.

The Cíes and Ons Islands populations exhibited a yearly growth rate of between 8 and 9%, with a maximum on the Cíes Islands of 15% annually between 1986 and 1992 (Velando 1997). This is similar to the population increase reported elsewhere. On the island of Canna, west Scotland, there was an annual increase of 9% between 1974 and 1984, the nest count increasing from 856 to 1753 (Swann *et al.* 1994); on the Farne Islands, north-east England, an 11% annual increase has been recorded, the original 1890 count of 10 pairs rising to 1900 pairs in 1969 (Potts 1969); and on the Isle of May, east Scotland, the population increased from 1 pair in 1918 to 1916 pairs in 1987, representing an average annual rate of increase of 11% and a maximum growth rate of 15% until 1973 (Aebischer & Wanless 1992). The increase in the number of nest sites on the Cíes Islands between 1986 and 1992 may be related to the fact that these islands were declared a Natural Park in 1980, and since the establishment of the Wildlife Service in 1984 have been managed by the Autonomous Government (Xunta de Galicia). Seabird colonies on the island of Ons also receive special protection. The establishment of protected areas has had a notable effect. Traditional practices, such as the taking of eggs and chicks for human consumption have ceased, and there has been a reduction in human disturbance. A ban on hunting from boats and the enforcement of this ban in the 1980s has helped greatly in the conservation of this species. The cessation of these practices may also have contributed to the increase in the population on the Asturian coast. On the Farne Islands between 1890 and 1965, population growth was also related to habitat protection, the reduction of disturbance in the breeding colonies, and the cessation of human exploitation (Potts 1969).

The distribution of the European Shag on the Atlantic coast of the Iberian Peninsula is quite dispersed (Fig. 1), with 87 colonies scattered all along the coast. Of these, 87% have fewer than 20 pairs, 11% have between 20 and 60 pairs, and only two colonies contain more than 500 pairs, namely the island of Ons with 557 pairs and the Cíes Islands with 905 pairs. These islands, which are less than 15 km apart, hold approximately 2% of the world population of the European Shag. Along with the island of Foula, Shetland Islands (2400 pairs), the Shiant Islands, west Scotland (1776 pairs), Lambay Island, Ireland (1597 pairs), the Isle of May (1524 pairs), the Farne Islands (1248 pairs), Runde, Norway (2100 pairs), and Lille Kamøy, Norway (2400 pairs), they are among the largest colonies of this species (Røv 1990; Lloyd *et al.* 1991). Applying Lloyd's (1984) criteria, they must be accorded international importance, this having resulted in the designation of this area as an Important Bird Area by the Spanish and European authorities.

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SAMENVATTING

In dit artikel wordt een overzicht gegeven van alle kolonies Kuifaalscholvers Stictocarbo [Phalacrocorax] aristotelis langs de Atlantische kust van Spanje en Portugal. In totaal werden bij tellingen tussen 1990 en 1994 2239 broedparen aangetroffen, waarvan 66% op de Cies en Ons Eilanden voor de kust van Galicia (## 35 en 36, Fig. 1). Niet alle kolonies werden recentelijk onderzocht, maar over het algemeen lijkt de periode van groei (vooral op genoemde eilanden) tot staan gekomen te zijn. In Euskadia nam het bestand op vijf kolonies toe van 40-55 paren in 1990 tot 57-67 paren in 1994. Zeven kolonies in Cantabria werden alleen in 1992 onderzocht (36-41 paren). In Asturias werden in 1997 op tien kolonies 199-250 broedparen geteld (vgl. 98-124 paren in 1986). In Galicia werden 14 kolonies bekeken, sommige belangrijke om de vijf jaar (1976-94). Op de Cies en Ons Eilanden nam het bestand toe van 312 paren in 1976 via 485 in 1981, 703 in 1986 tot 1461 paren in 1994. De Portugese zuidwest kust werd sinds 1983 niet meer onderzocht, maar in Portugal lijkt de populatie gestabiliseerd te zijn op een niveau van ongeveer 130-150 paren.

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*Known as *Stictocarbo aristotelis* on the Dutch list (Ardea 87: 147)

REPRODUCTIVE SUCCESS IN THE GREAT CORMORANT *PHALACROCORAX CARBO CARBO* IN RELATION TO COLONY NEST POSITION AND TIMING OF NESTING

BROEDSUCCES BIJ DE AALSCHOLVER IN RELATIE MET DE POSITIE VAN HET NEST EN HET TIJDSTIP VAN BROEDEN

D.J. ANDREWS¹ & K.R. DAY²

¹The National Trust, Strangford Lough Wildlife Scheme, Rowallane, Saintfield, BT24 7LH, Northern Ireland, UK; ² Environment Research Group, University of Ulster, Coleraine BT52 1SA, Northern Ireland, UK.

Great Cormorant *Phalacrocorax carbo carbo* breeding success was studied at two colonies on small islands in Strangford Lough, Northern Ireland in 1993 and 1994. Mean clutch sizes were 3.71 on Bird Island and 3.76 on Black Rock in 1993, and 3.4 on Bird Island in 1994. Total productivity on Bird Island in 1993 was calculated as 1.79 young fledged per nesting attempt. Reproductive success was measured on Bird Island in 1993 using data collected from 121 marked nests, and included clutch size, the number of eggs hatched and the number of young fledged. These data were related to the timing of nesting and the position of the nest within the colony. Early nests tended to be located more centrally in the colony than later nests, which were progressively further from the centre. There was a progressive decline in mean values for each reproductive parameter between early and late nesting birds and with increasing distance from the colony centre.

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INTRODUCTION

Great Cormorant *Phalacrocorax carbo carbo* numbers in Ireland have increased significantly during the last thirty years as a result of a reduction in persecution and increases in carrying capacity (Macdonald 1987; Kennedy & Greer 1988; Warke *et al.* 1992). On Strangford Lough, Great Cormorants began breeding in 1980 at a time when numbers at the main colony in Northern Ireland (Sheep Island) had peaked. Since then, the colony, centred on two small islands, grew at a mean annual rate of 17% until 1994 before levelling off at a population of around 200 pairs between 1994 and 1998. The presence of this breeding population is of concern to local fishery managers and a clear understanding of

the processes involved in colony dynamics is therefore important to the conservation management of this species.

Cormorants, like other long lived seabirds, adopt a low risk reproductive strategy (Drent & Daan 1980). Variations in the number of eggs laid and hatched, and prolonged egg laying ensure asymmetric competition within and between broods (Williams & Cooper 1983; Shaw 1985), and together with constraints on fishing efforts by parents (Plateeuw *et al.* 1995) lead to differences in fledging rates among nests.

Many seabird studies have demonstrated that not only are there asymmetries in survival within a family but there is also asymmetry in reproductive performance within a colony. This may be related to the age and experience of nesting birds (Coulson 1968), the quality of the nest site (Potts *et al.* 1980), or the timing of nesting, with earlier arrivals to the colony occupying more central positions (Leger & McNeil 1987; Siegel-Causey & Hunt 1986). On Strangford Lough, the main Great Cormorant colony is on Bird Island, a low lying grassy island with a wide rocky intertidal fringe. Most of the nests are located on the upper shore grouped in a roughly circular pattern, thus providing an ideal opportunity to examine the spatial relationships between nests and their corresponding productivity. This paper describes asymmetries in reproductive performance related to spatial and temporal aspects of breeding.

METHODS

The main study was carried out on Bird Island, Strangford Lough between early March and mid-July 1993, when sixteen visits were made to mark nests and record details of clutch size, numbers of eggs hatched and number of young fledged. As young Great Cormorants tend to leave their nests, particularly when disturbed but also apparently naturally for a time before fledging (Cramp & Simmons 1977), an attempt was made to mark all young birds before they exhibited this behaviour. In practice, this involved ringing the pulli between the age of 10 and 18 days old and resulted in 187 young being ringed (83% of the estimated number of young fledged). This enabled the fate of the young to be determined after they left their nests and before fledging. As the island is also occupied by a Herring Gull *Larus argentatus* colony (31 pairs in 1993), care was taken not to cause opportunistic predation during visits to the colony; survey time was kept to a minimum and retreat was made to an appropriate distance on completion of the survey in order to allow the birds safe return to their nests. No predation was seen to take place during colony visits.

When the last young had left the colony, the positions of 121 nests were recorded using measurements taken from two fixed points. The flattened diameter of 12 nests selected at random was also measured. These data enabled

Table 1. Details of egg laying periods and of distance from colony centre categories.
Tabel 1. Perioden van eileg en afstandcategorieën naar het centrum van de kolonie.

period	date of first egg laid	category	distance from colony centre (m)
1	≤ 16 April	1	0 - 3.0
2	17 - 21 April	2	3.1 - 4.0
3	22 - 27 April	3	4.1 - 5.0
4	28 April - 4 May	4	5.1 - 6.0
5	≥ 5 May	5	6.1 - 7.0
		6	>7.1 m

a map of the colony to be drawn and the central point of the colony determined (by halving the distances along both the north-south and east-west axes). The distance between each nest and its nearest neighbour was calculated as well as the six nearest neighbours to a random selection of five nests.

The nesting data were analysed in their entirety and mean values calculated for clutch size, number of eggs hatched and number of young fledged per nest. Nests were also separated into groups corresponding to five egg laying periods determined by the appearance of the first eggs in the nest (Table 1). For the purposes of further analysis, nests were also divided into six categories determined by the distance of the nest from the centre of the colony (Table 1).

The reproductive parameters detailed above were examined for each data-set and differences in the calculated mean values were statistically tested using one-way analysis of variance.

Mean clutch size was also calculated on Black Rock, the other Strangford Lough colony, in 1993 and also on Bird Island in 1994.

RESULTS

The colony nest map (Fig. 1) illustrates that the Great Cormorant colony on Bird Island in 1993 was roughly circular in shape (diameters approximately 14.5 m east-west and 12.5 m north-south) with the majority of nests constructed on the shore (93%). The mean (\pm SD) diameter of the flattened nests was 0.58 ± 0.03 m, $n = 12$) and the mean distance between nearest neighbour nests (measured edge to edge) was calculated as 0.34 ± 0.24 m, $n = 118$, range zero (nests touching) to 2.12 m). The mean distance between five nests selected at random and their six nearest neighbours was 0.7 ± 0.2 m, $n = 30$, range = 0.42 to 1.13 m. These distances are much closer than those recorded by Debout (1988) at St. Marcouf, Normandy where nearest neighbour distances were around 1 m.

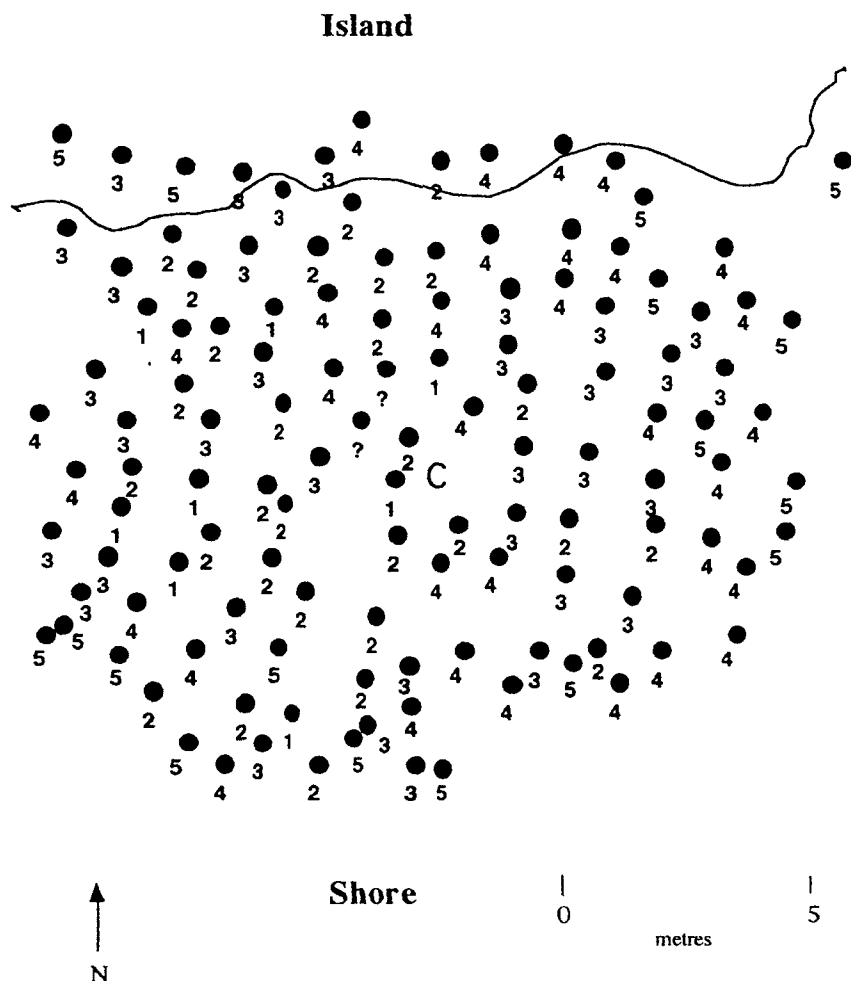


Figure 1. Locations of nests in the Great Cormorant colony on Bird Island, indicating egg laying periods (cf. Table 1). C = the centre of the colony.

Figuur 1. Posities van aalscholvernesten op Bird Island onder vermelding van de periode van eileg (zie Tabel 1). C = is het midden van de kolonie.

Table 2 shows the mean clutch size for nests on Bird Island in 1993 and 1994 and for Black Rock in 1993. There was little difference in clutch size in 1993 (3.71 on Bird Island and 3.76 on Black Rock) and a small decrease to

Table 2. The total number of nests, mean clutch sizes and relative frequency of number of eggs in completed clutches on Bird Island and Black Rock Great Cormorant colonies in 1993 and 1994. Productivity (number of young fledged per successful nest) of the Bird Island colony in 1993 is also presented.

Tabel 2. Aantal nesten, legselgrootte en frequentie (%) van gecompleteerde nesten met verschillende legselgroottes op Bird Island and Black Rock in 1993 en 1994. Het broedsucces van de kolonie op Bird Island (aantal uitgevlogen jongen per succesvol nest) is eveneens gegeven.

	Bird Island 1993	Bird Island 1994	Black Rock 1993
Total number of nests	126	58	58
Mean (\pm SD) clutch size	3.71 ± 0.74	3.40 ± 0.76	3.76 ± 0.82
% with 1 egg	0	1.7	1.7
% with 2 eggs	6.3	8.6	3.4
% with 3 eggs	24.6	41.4	25.9
% with 4 eggs	60.3	41.4	56.9
% with 5 eggs	8.7	6.9	10.3
% with 6 eggs	0	0	1.7
Mean (\pm SD) number of young fledged	2.16 ± 0.83	-	-

3.4 on Bird Island in 1994. Three nests with no eggs were recorded on Bird Island in 1993; taking these into account reduces the mean clutch size for all nests to 3.62.

The number of eggs recorded in completed clutches on Bird Island and Black Rock is also shown in Table 2. On Bird Island in 1993, nests with four eggs accounted for 60.3% of clutches and nests containing three or four eggs accounted for 84.9% of clutches. On Bird Island in 1994, nests with four eggs accounted for 41.4% of clutches and nests with three or four eggs accounted for 82.8%. On Black Rock in 1993, nests with four eggs accounted for 56.9% of clutches and nests containing three or four eggs accounted for 82.8% of clutches. Total productivity for the colony in 1993 was estimated at 225 young fledged from 126 nests, a mean of 1.79 young fledged per nesting attempt. In those nests from which young fledged, the mean number fledged was 2.16 ± 0.83 , $n = 92$). This represents a nesting success of 73%, while 27% of birds failed to rear any young.

Egg laying periods The location of nests with respect to each egg laying period is shown in Fig. 1. Period 1 included eight nests; period 2, 30 nests; period 3, 36 nests; period 4, 34 nests; and period 5, 18 nests. The mean distance of nests from the colony centre within each egg laying period is shown in Fig. 2. The pattern that emerges is one with new nests in each successive period being situated further from the colony centre (the mean distance from the centre for

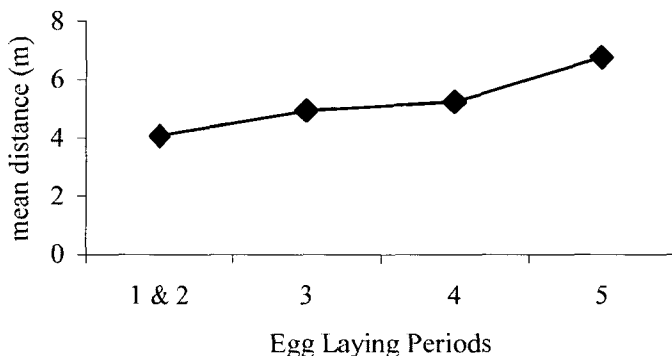


Figure 2. The mean distance from the colony centre for nests in each egg laying period.
 Figuur 2. Gemiddelde afstand tot het koloniemiddelpunt voor elke eilegperiode.

nests in periods 1 and 2 combined is 4.05 m and in period 5 is 6.75 m). This was not an entirely orderly process in concentric circles from the centre out; nests were sometimes built at some distance to others within the same period, the gaps then being available for nests in later egg laying periods.

The mean completed clutch size, mean number of eggs hatched and young fledged for nests in each egg laying period are shown in Fig. 3. With the exception of mean clutch size and mean number of eggs for period 2, there is a clear pattern of progressively smaller mean values between periods 1 and 5 (mean clutch size decreasing from 3.75 to 3.11; mean number of eggs hatched decreasing from 2.67 to 0.89; and the mean number of young fledged per nest decreasing from 2.62 to 0.44). These differences are statistically significant (one-way ANOVA): mean clutch size ($F_{4, 121} = 3.59$, $P < 0.05$); mean number of eggs hatched ($F_{4, 120} = 8.97$, $P < 0.01$); and mean number of young fledged ($F_{4, 119} = 9.43$, $P < 0.01$).

The relationship between egg laying period and nest outcome is further illustrated in Figs 4a and 4b. Fig. 4a shows the marked decrease in eggs hatched as a percentage of eggs laid from 70% in period 1 to 18% in period 5. Again, in Fig. 4b there is a progressive decrease in both young fledged as a percentage of eggs laid (from 70% in period 1 to 14% in period 5), and young fledged as a percentage of eggs hatched (from 100% in period 1 to 50% in period 5).

Distance from colony centre For nests in each of the six distance from colony centre categories, the mean values for completed clutch size, number of eggs

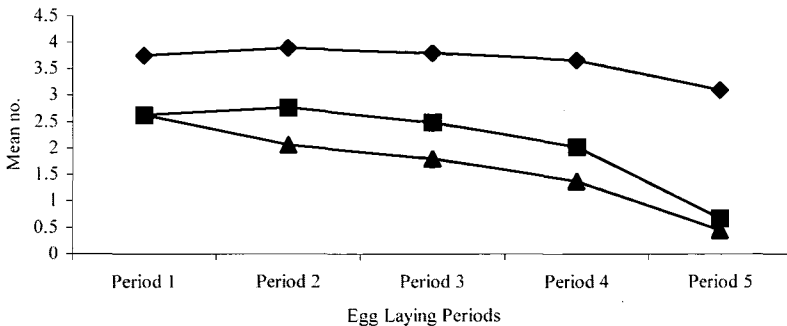


Figure 3. The mean completed clutch size (◆), the mean number of eggs hatched (■) and the mean number of young fledged (▲) for nests in each egg laying period.
 Figuur 3. Gemiddelde, gecompleteerde legselgrootte (◆), gemiddeld aantal uitkomende eieren (■) en gemiddeld aantal uitgevlogen jongen (▲) voor elke eilegperiode.

hatched and number of young fledged are shown in Fig. 5. This shows a progressive decrease in mean values for each reproductive parameter between central nests and those successively further from the colony centre: mean clutch size decreases from 4.1 to 3.4; mean number of eggs hatched from 2.9 to 1.5; and mean number of young fledged decreases from 2.6 to 1.2. These differences are statistically significant (one-way ANOVA) for completed clutch size ($F_{5, 113} = 7.60$, $P < 0.05$) and for the number of young fledged ($F_{5, 115} = 2.50$, $P < 0.01$).

The progressive decline in reproductive success with increasing nest distance from the colony centre is further illustrated in Figs 6a and 6b. The number of eggs hatched as a percentage of eggs laid (Fig. 6a) decreases from 71.8% in the most central category to 37.8% in the outermost, with only the next nearest to the most central category deviating from the trend (73.4%). Both the number of young fledged as a percentage of eggs hatched and the number of young fledged as a percentage of eggs laid show a similar trend (Fig. 6b), decreasing from the central to the outer category from 89.3% to 64.3% and 64.1% to 24.3% respectively; both data-sets indicate that nests in the fourth category (5.1 to 6.0 m from the centre) fare better than predicted.

Fig. 7 shows the locations of the 22 nests that failed at the egg stage, all of which were on the periphery of the colony and presumably more vulnerable to predation. Eggs in most of these nests ($n = 16$, 72.7%) were laid in egg laying periods 4 and 5. Predated Great Cormorant eggs were occasionally found away from the colony, possibly taken by Herring Gulls or Hooded Crows *Corvus corone* [cornix] which were frequently seen in the vicinity of the colony.

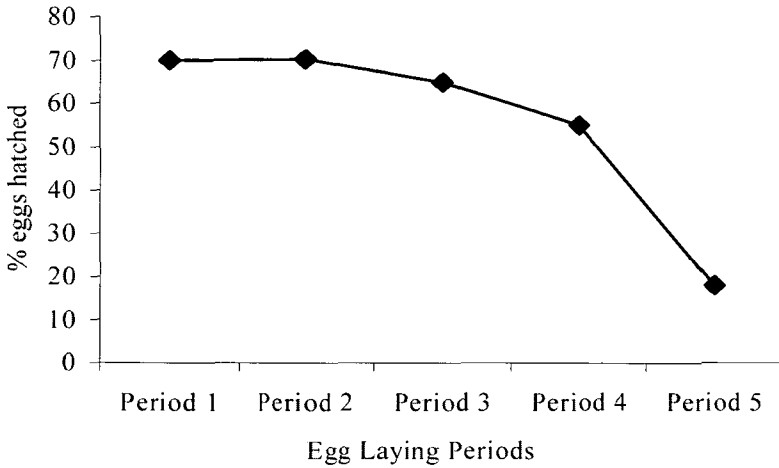


Figure 4a. The proportion of eggs laid that hatched in each egg laying period.
Figuur 4a. Percentage uitkomende eieren voor elk van de perioden van eileg.

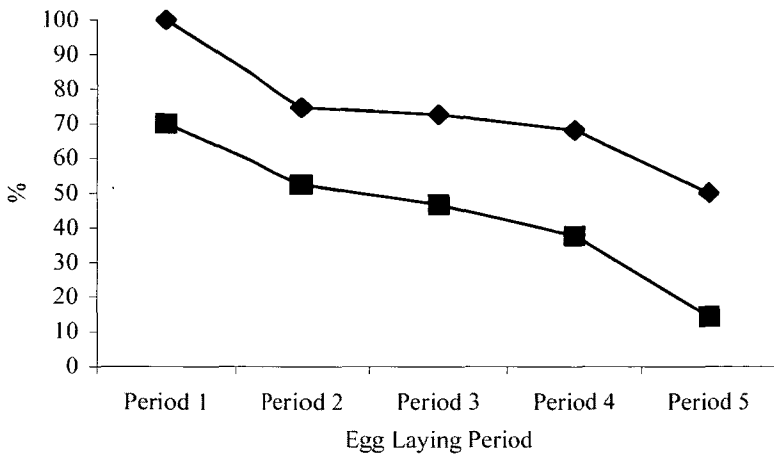


Figure 4b. The proportions of eggs laid (■) and hatched (◆) that fledged young in each egg laying period.
Figuur 4b. Percentage gelegde eieren (■) en uitkomende eieren (◆) met uitvliegende jongen in elke eilegperiode.

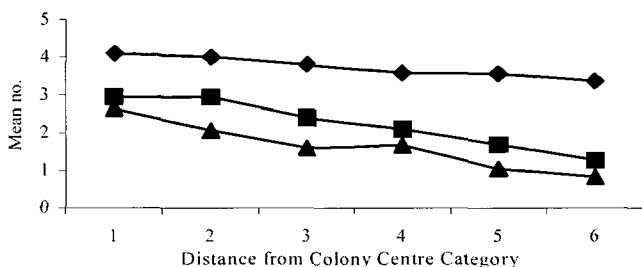


Figure 5. The mean completed clutch size (◆), the mean number of eggs hatched (■) and the mean number of young fledged (▲) for nests in each distance from colony centre categories.

Figuur 5. Gemiddelde legselgrootte (◆), gemiddeld aantal uitkomende eieren (■) en het gemiddeld uitvliegende aantal jongen (▲) voor nesten in elk van de afstandscategorieën naar het midden van de kolonie.

DISCUSSION

The Great Cormorant breeding biology data gathered for this study are similar to those described in other studies. The mean clutch size on Bird Island was 3.71 in 1993 and 3.4 in 1994, and 3.76 on Black Rock in 1993. These values are higher than those recorded for Sheep Island, County Antrim (N. Ireland) where the mean completed clutch size recorded between 1988 and 1993 was 3.13 including nests in which no eggs were laid (Warke 1994). Data collected at two Great Cormorant colonies in England and Wales indicate a range of clutch sizes in these areas between 2.6 and 3.7; at St. Margaret's Island in Wales, mean clutch sizes of 3.1 in 1989, 2.6 in 1990, 2.7 in 1992, and 3.7 in 1996 were reported (Debout *et al.* 1995; Sellers & Hughes 1996), and at Grune Point, England, Carrier & Baker (1991) recorded mean clutch sizes of 3.2 and 3.6 in 1983 and 1984 respectively. In colonies in Norway, Røv (1984) recorded mean clutch sizes of 3.2 and 3.6 in 1983 and 1984 respectively.

Nests containing three or four eggs accounted for 84.9% and 82.8% of clutches on Bird Island in 1993 and 1994 respectively, and 82.8% of clutches on Black Rock in 1993. Warke (1994) found similar clutch sizes in 1991 when 80.5% of nests on Sheep Island contained 3 or 4 eggs, although in both 1992 and 1993 this figure was reduced to 54.8% and 54.6% respectively, with nests containing 2 eggs accounting for proportionately more.

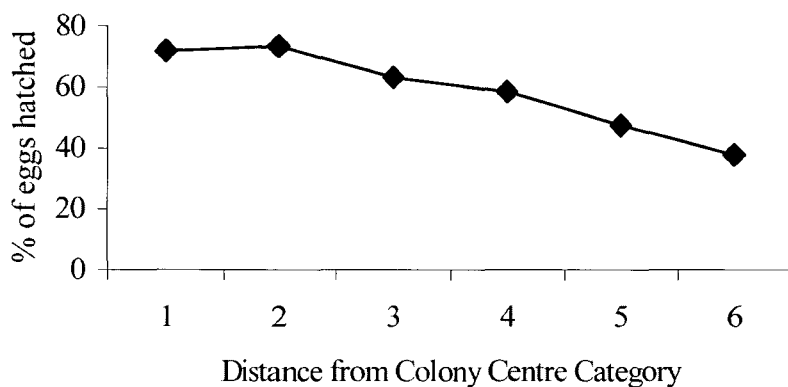


Figure 6a. The proportion of eggs laid that hatched in relation to distance from colony centre.

Figuur 6a. Het percentage uitkomende eieren in relatie tot de afstand tot de kolonie.

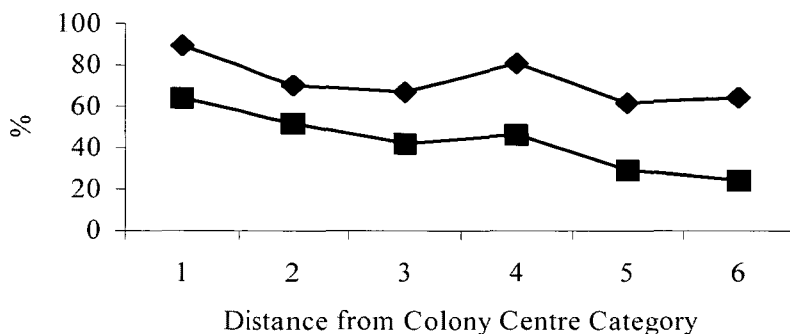


Figure 6b. The proportions of eggs laid (■) and hatched (◆) that fledged young in relation to distance from colony centre.

Figuur 6b. Percentage gelegde eieren (■) en uitkomende eieren (◆) met uitvliegende jongen in relatie tot de afstand naar het midden van de kolonie.

The nesting success of the Bird Island colony of 74% in 1993 was higher than that reported by Sellers & Hughes (1996) for colonies in Wales in 1996 where nesting success was 65% at St. Margaret's Island and 69% at Blockhouse Stack.

The reproductive success of breeding Great Cormorants on Bird Island, Strangford Lough has been shown to be related to the location of the nest within the colony and the timing of breeding. The mean completed clutch size, mean number of eggs hatched and the mean number of young fledged declined progressively from the colony centre to the colony edge and between early and late season. There was also a relationship between the timing of nesting and nest site selection with, in general, earlier nesting birds adopting more central nest sites and later nests being more peripheral within the colony.

Such asymmetry in reproductive success has been explained by a number of factors including the relative age of breeding birds and the effects of predation. Relatively poor breeding performances of young birds have been established in virtually every species studied (Potts *et al.* 1980) including the Great Cormorant (Kortlandt 1942). Other studies have shown that for some species, centre nesting birds are generally older, more experienced birds, whereas young and inexperienced birds are more likely to be found at the edge of the colony (Kharitonov 1971; Veen 1977; Siegel-Causey & Hunt 1986). Peripheral nests may also be subject to greater predation pressure (Leger & McNeil 1987), and may contain fewer eggs or young than central nests (DesGrange & Reed 1981). Lower reproductive effort may be an adaptation whereby young birds gain valuable breeding experience without incurring the higher cost of a large brood which may jeopardise future chances of reproduction (Aebischer & Coulson 1990).

Wooller *et al.* (1989) argue that reproductive success depends on the fitness of the breeding birds and the quality of nest site. Coulson (1968) suggested that the intense pressure for central nests sites in the Kittiwake *Rissa tridactyla* results in very high selection for vigorous males with less severe selection towards the colony edge.

Fretwell & Lucas (1970) proposed a mechanism by which colonial birds could assess and choose optimal breeding sites from among a range of choices. They suggested that as nest density in the optimal nesting habitat increases a density dependent factor such as neighbour conflict or predator awareness results in a decrease in the expected breeding success. At a certain density, reproductive success in the optimal habitat will equal that in an unoccupied but suboptimal habitat. New, incoming birds should then occupy both habitats at an equivalent rate rather than saturate the optimal habitat. This model was tested by Siegel-Causey & Hunt (1986) for a colony of Double-crested Cormorants *P. auritus*. They selected nest sites as predicted, although it

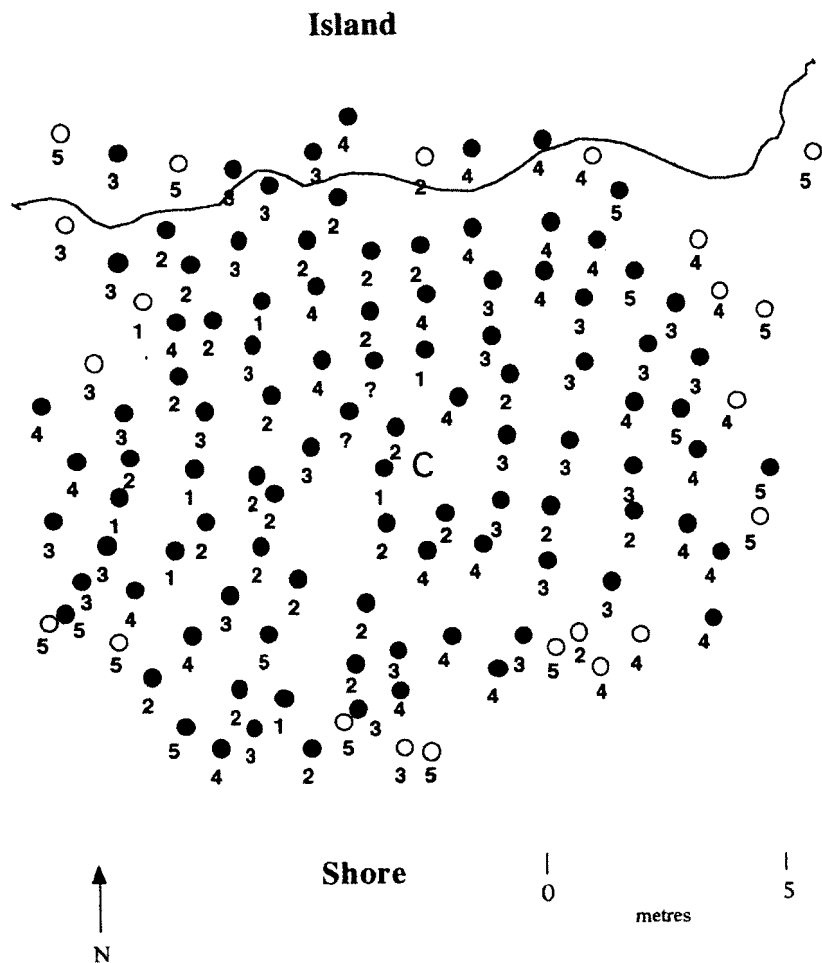


Figure 7. Nest map of the Great Cormorant colony on Bird Island. Circles indicate those nests that failed during the egg stage.

Figuur 7. Nestenkaart van Aalscholvers op Bird Island. Cirkels geven de in de eifase mislukte nesten weer.

was not clear by which mechanism new arrivals were able to assess the suitability of a particular habitat. A similar mechanism may be applicable to the Bird Island data, which show that the colony did not develop from the centre outwards in a progressive manner but that new nests continued to appear in the central (optimal) area up until the fourth egg laying period.

On Bird Island, nests are usually completely washed away during the winter and although the colony is in a similar location each year, it is not known if birds return to occupy the same area on the ground. It is evident, however, that whereas the timing of breeding is in the control of the individual bird, the relative position of the nest in the colony is, to some extent, a matter of chance unless the dynamics of colony formation determine that earlier nesting birds will ultimately also be in the centre of the colony.

Birds that return early to the colony are likely to be experienced males which therefore establish their nest sites first, later arrivals perhaps selecting their nests sites in response to stimuli provided by those nesting birds already present. This may explain why the colony on Bird Island assumes a roughly circular shape. This process is clearly dependent on the topography of the colony location but may also be affected by the proximity of available nests sites to the land or to the sea, as the perceived predator threat from the former and safety provided by the latter are likely to be strong factors in nest site selection; otherwise the entire colony would move landward where it would be at least safe from the effects of high tides.

The relatively high density of nests (compared with Debout 1988) may also be a direct response to a perceived threat from the adjacent Herring Gull colony. It is clear that neither timing of nesting nor position of nest site within the colony were the sole factors determining breeding success. Nor is it clear which is the more powerful influence, but it is likely that both act in combination with a number of environmental factors to result in earlier, more centrally nesting birds being more successful than later, more peripherally nesting birds.

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SAMENVATTING

*Het broedsucces van de Aalscholver *Phalacrocorax carbo* werd onderzocht op twee kleine eilandjes in Strangford Lough, Noord-Ierland, in 1993 en 1994. De gemiddelde legselgrootte was 3.71 op Bird Island en 3.76 op Black Rock in 1993 en 3.4 op Bird Island in 1994. Het broedsucces op Bird Island werd geschat op 1.79 uitgevlogen jongen per broedpoging. Het broedsucces werd bepaald in 121 gemerkte nesten en kon vervolgens worden gerelateerd aan het tijdstip van nestbouw en eileg en aan de positie in de kolonie. 'Vroege' legfels werden vooral in de buurt van het centrum van de kolonie aangetroffen, latere legfels vooral aan de randen. Berekend vanuit het centrum van de kolonie werd een gestage afname in broedsucces gevonden bij een toenemende afstand tot het centrum van de kolonie.*

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COMPARATIVE BREEDING BIOLOGY
OF GUILLEMOTS *URIA* SPP. AND
RAZORBILLS *ALCA TORDA* AT A COLONY
IN THE NORTHWEST ATLANTIC
*VERGELIJKENDE BROEDBIOLOGIE VAN ZEEKOETEN EN
ALKEN OP EEN KOLONIE
IN HET NOORWESTELIJKE ATLANTISCHE GEBIED*

J. MARK HIPFNER & RACHEL BRYANT

Biopsychology Programme, Memorial University of Newfoundland
St. John's, NF, Canada A1B 3X9 e-mail: d66jmh@morgan.ucs.mun.ca

We compared various aspects of the breeding biology of Razorbills, Common Guillemots, and Brünnich's Guillemots (the "intermediate" auks) at the Gannet Islands, Labrador, Canada, in 1997. In all three species, laying followed a strongly right-skewed pattern, with median laying dates falling within a narrow window between 27-29 June. In comparison to previous years, laying was late, and relatively synchronous among species. Incubation periods were 2 days longer in Razorbills (median 35 days) than in either guillemot species (33 days), whereas Common Guillemots had longer nestling periods (mean 24 days) than Razorbills (19 days) or Brünnich's Guillemots (20 days). In all species, there was a tendency for late-laying pairs to contract their breeding periods, mainly by reducing the duration of the nestling period. Breeding success was high in Razorbills (73%) and Common Guillemots (85%), but low in Brünnich's Guillemots (51%), largely due to low hatching success. Late-breeding Brünnich's Guillemots were more likely to fail than were early pairs, but there was little indication of this in the other two species. Seasonal patterns of colony attendance suggested that there were many young, pre-breeding Brünnich's Guillemots and Razorbills present; populations of these species appear to be faring well at this colony. Despite a major shift in chick diets since the early 1980's, caused by a decline in the availability of capelin in Labrador, chicks of all three species grew relatively quickly and departed the colony at normal masses.

Hipfner J.M. & Bryant R. 1999. Comparative breeding biology of Guillemots *Uria* spp. and Razorbills *Alca torda* at a colony in the Northwest Atlantic. *Atlantic Seabirds* 1(3): 121-134.

INTRODUCTION

The diversity of nestling developmental strategies found within the Alcidae (the auks) is unmatched by any other bird family (Sealy 1973). Three species, Razorbill *Alca torda*, Common Guillemot *Uria aalge*, and Brünnich's Guillemot *Uria lomvia*, employ a unique strategy that is 'intermediate' between the precocial and semi-precocial developmental modes of other auks. In the

intermediate auks, the single chick is fed by both parents at the nest site for 15–30 days, leaves the colony at less than 30% of adult mass and covered in a transitional, mesoptile plumage, and subsequently is cared for at sea by its male parent for several weeks. Not surprisingly, there are broad ecological similarities between the three species, but they differ in important respects in morphology, feeding behaviour, nesting habitat, and distribution. Razorbills and Common Guillemots are mainly boreal and low-Arctic species, while Brünnich's Guillemot is an Arctic-nesting species (Gaston & Jones 1998). The breeding biology of these three species has rarely been studied at one time and place, in large part because there are few colonies where all three breed and are accessible. In this paper, we compare: (1) the timing of breeding; (2) the duration of incubation, nestling, and breeding periods; (3) seasonal trends in reproductive success; (4) seasonal patterns of colony attendance; and (5) egg size and chick growth, of the three intermediate auks breeding at the Gannet Islands, Labrador, Canada.

METHODS

The Gannet Islands (53°57'N 56°31'W) support the largest Razorbill colony in North America, with *c.* 10 000 pairs, as well as *c.* 50 000 pairs of Common Guillemots and *c.* 3000 pairs of Brünnich's Guillemots (Lock *et al.* 1994; Chapdelaine *et al.* 1999; G.J. Robertson unpubl. data). Lying in the path of the Labrador current, the colony is part of a low-Arctic marine ecosystem (Nettleship & Evans 1985). All observations were made between mid-June and early September in 1997 on 'GC4', one of seven small islands comprising the Gannet Clusters (see Birkhead & Nettleship 1987a).

We used the Type I methods of Birkhead & Nettleship (1980) to monitor breeding chronology and breeding success. Common Guillemot pairs were observed from a blind situated 5 m above a 15 m² plot on which they nested densely on a gently sloping, boulder-strewn rock face, 5 m above sea level and 20 m from the sea. Razorbills and Brünnich's Guillemots occupied nest sites on narrow cliff ledges and steep rocky slopes, most of them > 10 m above sea level, and were monitored from a blind at distances of 5–30 m. Many Razorbill pairs also nested in crevices among boulders, but these birds could not be monitored without causing excessive disturbance. We included only sites for which we knew laying, hatching, and nest departure dates to within one day. Chicks were considered to have survived to departure if they were at least 15 days of age when last seen.

Numbers of adults present were counted on five plots at 1600 h every two to three days. The count plots included those plots that we monitored for breeding chronology and success. Prior to hatching, length and maximum breadth (\pm 0.1 mm, with dial callipers) of eggs laid by all three species were

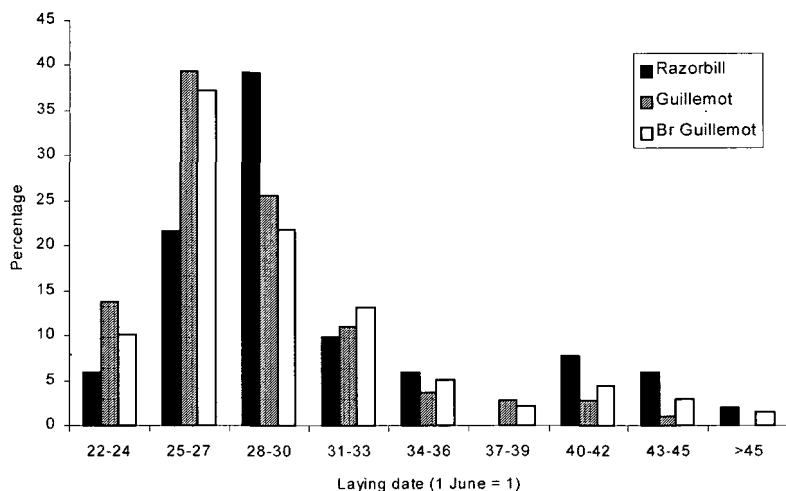


Figure 1. Laying dates of Razorbills ($n = 51$), Common Guillemots ($n = 109$) and Brünnich's Guillemots ($n = 137$) at the Gannet Islands in 1997.

Figuur 1. Legdata van Alken ($n = 51$), Zeekoeten ($n = 109$) en Dikbekzeekoeten ($n = 137$) op de Gannet Islands in 1997.

measured. An egg volume index (length \times breadth²) that has a strong linear relationship with fresh egg mass in all three species (Birkhead & Nettleship 1984) was used as a measure of egg size. We measured mass (± 1 g, with a 300 g Pesola) and wing length (maximum flattened cord excluding down tips, ± 1 mm, with a ruler) of the chicks that hatched from these eggs at two- or occasionally three-day intervals between hatching and nest departure. Chicks were assumed to have hatched on the day between consecutive checks, unless they were still wet after hatching or their down was still matted. For identification, chicks were marked with a binary code of nail clipping when first found, and banded when large enough, always within one week of hatching.

Data were analysed using SPSS (version 7.5) statistical software. Parametric statistics were used where residuals fit the assumptions of normality and equality of variances, otherwise non-parametric statistics were used. We used Tukey's tests to make pair-wise, multiple comparisons following significant ANOVAs, and non-parametric multiple comparisons following significant Kruskal-Wallis tests. A significance level of $\alpha_{crit} = 0.05$ was used for all statistical tests.

RESULTS

Breeding chronology Timing of laying differed among species (Kruskal-Wallis test, $H_2 = 8.1$, $P = 0.02$), but median laying dates for all three species fell between 27-29 June, and none of the pairwise comparisons were significant (Fig. 1). Timing of laying of first eggs followed a right-skewed pattern in all three species, with a sharp peak in the last week of June, and laying continued until mid-July (Fig. 1). Incubation periods differed among species (Kruskal-Wallis test, $H_2 = 63.6$, $P < 0.001$), being shorter in both guillemot species (medians = 33 days) than in Razorbills (median = 35 days).

The spread in incubation periods was similar in all species at 4-5 days (Fig. 2). Nestling periods also differed among species (ANOVA, $F_{2,154} = 89.5$, $P < 0.001$), and all pair-wise comparisons were significant: Razorbills had the shortest nestling periods (mean ± 1 SD = 18.9 ± 1.6 days), followed by Brünnich's Guillemots (20.0 ± 2.0 days), and Common Guillemots (23.5 ± 1.6 days). The spread in nestling periods was similar in all species at 8-10 days (Fig. 2). Breeding periods (i.e. incubation + nestling periods) also differed (Kruskal-Wallis test, $H_2 = 56.1$, $P < 0.001$), being similar in Razorbills and Brünnich's Guillemots (medians = 54 and 53 days, respectively), but longer in Common Guillemots (median = 56 days). Again, the spread in breeding periods was similar among species, at 8-10 days (Fig. 2).

The duration of incubation showed little relationship with laying date in Razorbills or Common Guillemots, but declined significantly with date in Brünnich's Guillemots (Table 1; see Hipfner *et al.* in press). Nestling periods declined with hatching date in both guillemot species, and showed a similar, but non-significant, decline in Razorbills. Overall, breeding periods were negatively related to laying date in all species, although the decline was not significant in Razorbills (Table 1).

Breeding success Reproductive success (i.e. the proportion of eggs laid that produced chicks that survived to 15 days of age) differed among species, being lower in Brünnich's Guillemots than in either Razorbills ($\chi^2_{1df} = 6.3$, $P = 0.01$) or Common Guillemots ($\chi^2_{1df} = 29.3$, $P < 0.001$; Table 2). This was mainly due to lower hatching success (the proportion of eggs laid that hatched) in Brünnich's Guillemots than in the other two species (both $P \leq 0.05$). Nestling success (the proportion of eggs that hatched that produced chicks that survived to 15 days) was high in all three species.

Whereas reproductive success varied little with timing of breeding in Razorbills or Common Guillemots, both hatching and reproductive success declined with date among Brünnich's Guillemots (Table 2).

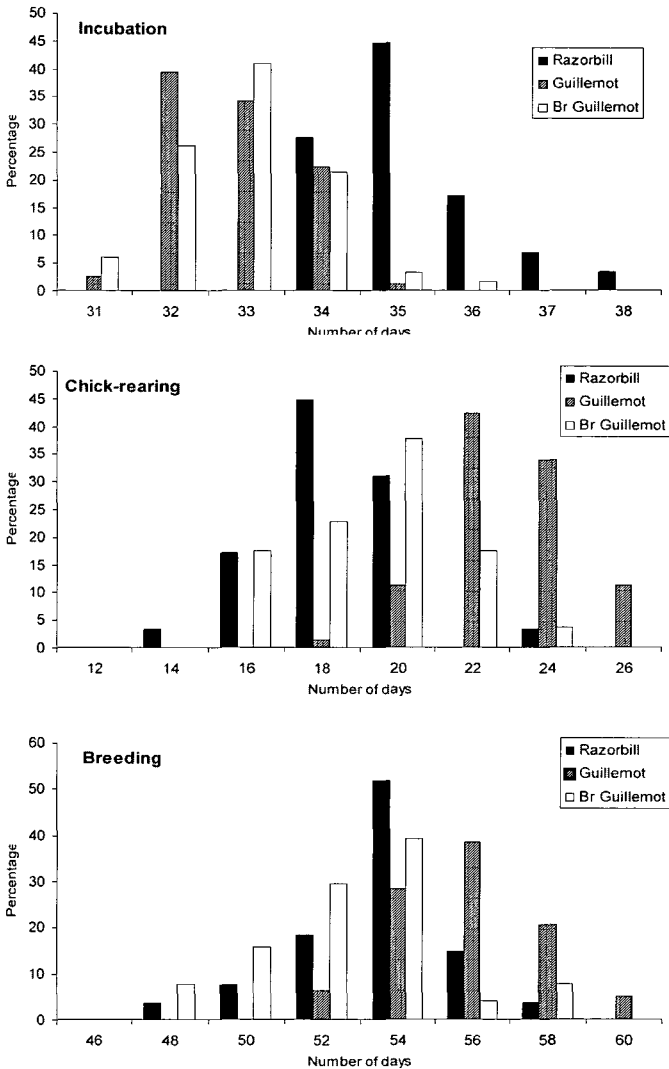


Figure 2. Duration of incubation, nestling and breeding periods of Razorbills ($n = 29$, 29, and 27 respectively), Common Guillemots ($n = 80$, 71, 77), and Brännich's Guillemots ($n = 61$, 57, and 51) at the Gannet Islands in 1997.

Figuur 2. Tijdsduur van broeden, kuikenfase en broedperiode van Alken ($n = 29$, 29, en 27), Zeekoeten ($n = 80$, 71, 77) en Dikbekzeekoeten ($n = 61$, 57 en 51) op de Gannet Islands in 1997

Table 1: Linear regressions showing seasonal trends in duration of incubation (inc), nestling (nest), and total breeding periods (tot) for auks at the Gannet Islands in 1997.

Tabel 1. Resultaten van lineaire regressie analyse ter illustratie van trends in de duur van het bebroeden van het ei (inc), de kuikenfase (nest) en van de totale broedduur (tot) voor alkachtigen op de Gannet Islands in 1997.

Parameter	<i>Alca torda</i>			<i>Uria aalge</i>			<i>Uria lomvia</i>		
	inc	nest	tot.	inc	nest	tot.	inc	nest	tot
<i>n</i> =	29	29	27	80	71	77	61	57	51
<i>R</i> ² =	0.002	0.09	0.07	0.003	0.19	0.40	0.10	0.30	0.37
<i>P</i> =	0.81	0.12	0.20	0.61	<0.001	<0.001	0.02	<0.001	<0.001
Slope	0.05	-0.30	-0.26	-0.06	-0.34	-0.52	-0.08	-0.23	-0.35

Table 2: Logistic regressions showing seasonal trends in hatching (hatch), nestling (nestl), and reproductive success (repr) for auks at the Gannet Islands in 1997.

Tabel 2. Resultaten van logistische regressie ter illustratie van seizoenpatronen in het uitkomen van de eieren (hatch), de overleving van nestjongen (nestl) en van het totale broedsucces (repr) voor alkachtigen op de Gannet Islands in 1997.

Parameter	<i>Alca torda</i>			<i>Uria aalge</i>			<i>Uria lomvia</i>		
	hatch	nestl	repr	hatch	nestl	repr	hatch	nestl	repr
<i>n</i> =	51	37	51	108	79	102	136	67	136
success (%)	75	97	73	87	98	85	57	89	51
Wald χ^2	0.26	0.92	1.02	0.007	0.57	0.67	8.40	0.51	6.51
<i>P</i> =	0.61	0.34	0.31	0.93	0.45	0.41	0.004	0.48	0.01
Slope	-0.02	-0.05	-0.05	-0.005	0.38	-0.06	-0.10	0.06	-0.09

Colony attendance Numbers of Razorbills attending the colony were high during the pre- and early-laying period, then declined sharply after median laying (Fig. 3). Numbers then built up to a peak in early-to-mid chick-rearing, before dropping off late in the season. Common Guillemot attendance was low during pre- and early-laying, then increased after median laying. Numbers were more or less stable through the incubation period, with a small peak in early chick-rearing, then dropped off late in the season. Brünnich's Guillemot numbers increased steadily between pre-laying and late incubation/early chick-rearing, then doubled to mid chick-rearing, before dropping off (Fig. 3).

Chick growth and development The smallest of the three species, the Razorbill, laid smaller eggs than either guillemot species; as a result, 2 day old Razorbill chicks were lighter in mass (Table 3). Razorbill chicks also gained

Table 3. (A) Growth parameters (mean \pm SD) for auks. % values are percentages of adult measurements taken during incubation. (B) Post-hoc comparisons that are the results of Tukey's tests at $P = 0.05$ following ANOVAs on measurements as absolute values, and as percentages of adult measurements (% adult). Values that are not significantly different are underlined together.

Table 3. (A) Groeivariabelen (gemiddelde \pm SD) voor alkachtigen. De getallen tussen haakjes zijn percentages van maten van adulte vogels genomen in de broedtijd. (B) Post-hoc vergelijkingen als resultaten van Tukey's test bij $P = 0.05$ op grond van ANOVAs op biometrische gegevens als absolute getallen en als percentage van afmetingen bij adulte vogels (% adult). Resultaten die niet significant verschillen zijn door onderstreping verbonden.

(A)	Parameter	Species (n)					
		<i>Alca torda</i> (14)		<i>Uria aalge</i> (8)		<i>Uria lomvia</i> (8)	
		(%)		(%)		(%)	
	Egg volume index (cm ³)	185.1 ± 15.7		198.0 ± 16.0		201.7 ± 12.9	
	Two day mass (g)	72.0 ± 7.2	10.0	84.4 ± 6.4	8.6	83.0 ± 9.4	8.3
	Growth 2-14 d:						
	mass (g)	103.1 ± 15.5	14.3	125.3 ± 16.0	12.8	130.0 ± 34.6	13.0
	wing (mm)	34.9 ± 4.5	16.8	20.9 ± 6.3	9.8	30.3 ± 7.2	13.0
	Departure mass (g)	186.7 ± 19.8	25.9	223.1 ± 20.8	22.8	221.1 ± 25.1	23.0
	Departure wing (mm)	72.5 ± 8.0	34.8	62.4 ± 4.4	29.4	72.8 ± 33.3	33.0

(B)	Post-hoc comparisons					
	Absolute			% Adult		
	RZ	G	BG			
	RZ	BG	G	G	BG	R
	RZ	G	BG		n.s.	
	G	BG	RZ	G	BG	R
	RZ	BG	G		G	BG
	G	RZ	BG	G	BG	R

mass more slowly than guillemot chicks, and were less heavy at nest departure (Table 3, Fig. 4). Chicks of the two guillemot species gained mass at similar rates, and departed to sea at similar masses. Conversely, the rate of wing growth did not differ between Razorbill and Brünnich's Guillemot chicks, but Common Guillemot chicks grew their wings more slowly. Razorbill and Brünnich's Guillemot chicks departed with wings of similar length, and longer than those of Common Guillemots.

In relation to adult masses during incubation in 1997, Razorbill chicks actually were heavier at 2 days of age than were chicks of either guillemot species (Table 3), presumably because Razorbill eggs are c. 2% heavier as a proportion of adult mass (M. Hipfner unpubl. data). The three species differed

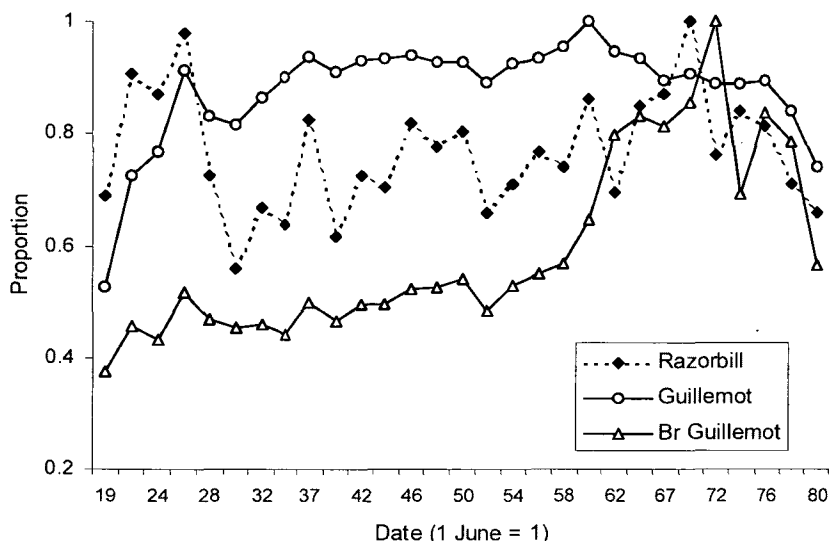


Figure 3. Colony attendance of Razorbills, Common Guillemots, and Brünnich's Guillemots at the Gannet Islands in 1997. Values are proportions of the single highest count.

Figuur 3. Aanwezigheid op de kolonie door Alken, Zeekoeten en Dikbekzeekoeten op de Gannet Islands in 1997. De gepresenteerde waarden zijn proportioneel ten opzichte van de hoogste waargenomen presentie.

little in the relative rate at which they gained mass, but Razorbill chicks were somewhat heavier than Common Guillemot chicks at departure. Relative to adult wing lengths, neither rates of wing growth nor wing lengths at nest departure differed between Razorbills and Brünnich's Guillemots, but both were greater in these species than in Common Guillemots (Table 3).

DISCUSSION

Breeding chronology Both the timing and the pattern of laying by Razorbills, Common Guillemots, and Brünnich's Guillemots were quite similar at the Gannet Islands in 1997. The right-skewed laying pattern is typical for these species, and in Brünnich's Guillemots occurs mainly because older, more experienced females lay early, while young, inexperienced females continue to lay for extended periods after the peak (de Forest & Gaston 1996; Hipfner *et al.* 1997). Common Guillemots laid 3-12 days later in 1997 than they had in 1981-1983, while Brünnich's Guillemots laid 2-9 days later (cf. Birkhead &

Nettleship 1987a). In Birkhead and Nettleship's study, delayed and synchronous laying by the two guillemot species in one year (1982) were attributed to heavy spring ice cover in waters around the Gannet Islands. Ice conditions are known to affect timing of laying by Brünnich's Guillemots (Gaston & Hipfner 1998), but ice maps obtained from Environment Canada (and our own observations) showed that there was little sea ice around the Gannet Islands during early June of 1997. We can only speculate on what other factors might have caused the late and synchronous laying. Total breeding failure by Black-legged Kittiwakes *Rissa tridactyla* at the Gannet Islands in 1997, due mainly to failure to lay eggs (pers. obs.), suggests that food availability was low early in the season. This might have been caused by the recent, anomalously cold oceanographic conditions in the Northwest Atlantic (Drinkwater 1996).

Incubation and nestling periods of Razorbills and Brünnich's Guillemots were similar to those reported previously at this colony (Birkhead & Nettleship 1987a), and at others (Lloyd 1979; Harris & Wanless 1989). Common Guillemot incubation periods also were typical, but their nestling periods were long compared to other colonies (cf. Murphy & Schauer 1994). As growth rates of Common Guillemot chicks appeared normal, it seems unlikely that the long nestling periods were consequences of developmental constraints; they may have been due to low predation pressure that would select for rapid departure of young from the nest site (Ydenberg 1989).

There was a tendency in all species for late-laying birds to contract their breeding seasons, mainly by reducing the nestling period (cf. Murphy 1995). Seasonal declines in departure age increase the colony-wide synchrony of nest departure, which reduces the predation risk for individual departing chicks (Daan & Tinbergen 1979), and they lessen the predation risk for late-hatched young at the colony (Hatchwell 1991). On GC4, Herring Gulls *Larus argentatus* and Great Black-backed Gulls *L. marinus* preyed heavily on departing chicks, but we saw few predation attempts on nestlings.

Breeding success Despite a decrease in capelin availability to marine birds at the Gannet Islands, reproductive success of both guillemots in 1997 was similar to that in the early 1980s (Bryant *et al.* 1999). Common Guillemots had higher success than Brünnich's Guillemots, and their breeding success at the Gannet Islands (85%) was high compared to that at other Atlantic colonies (70-80% is typical, Gaston & Jones 1998). Conversely, success of Brünnich's Guillemots (51%) was at the low end of the range compared to other colonies (48-82%; Gaston *et al.* 1994). Reproductive success of Razorbills (73%) was similar to that at other colonies (70-76%; Gaston & Jones 1998), even though all monitored pairs laid on exposed ledges, habitats where success is sometimes low (Hudson 1982).

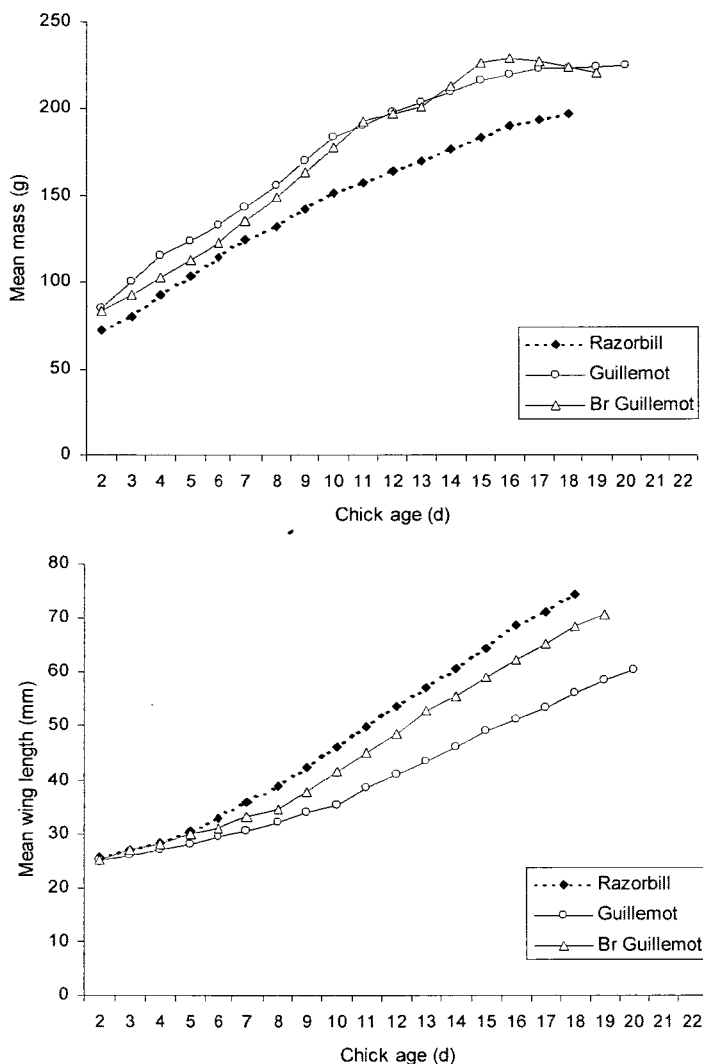


Figure 4. Growth in mass and wing length of Razorbill ($n = 14$), Guillemot ($n = 8$), and Brünnich's Guillemot ($n = 8$) chicks at the Gannet Islands in 1997.

Figuur 4. Groei in massa en vleugellengte van Alk, Zeekoet en Dikbekzeekoetkuikens op de Gannet Islands in 1997.



Guillemot and chick shortly prior to fledging *Zeekeet met jong, kort voor het 'uitvliegen'* (C.J. Camphuysen)

Reproductive success of Brünnich's Guillemots declined with date, due mainly to a seasonal decline in hatching success. However, early-laying pairs that were induced to lay replacement eggs bred as successfully as unmanipulated early-laying pairs, suggesting that the population-wide declines were not caused by seasonal environmental effects (Hipfner *et al.* 1999). At another Brünnich's Guillemot colony, such declines were caused by late laying of young, inexperienced pairs (de Forest & Gaston 1996), and this seems a likely explanation for the observed declines at the Gannet Islands. Seasonal declines in success are often reported for Razorbills and Common Guillemots as well (Lloyd 1979; Hatchwell 1991); it is not apparent to us why this did not occur at our study colony.

Colony attendance The seasonal patterns of colony attendance by Razorbills and Common Guillemots were generally similar to other published observations (Lloyd 1975; Birkhead & Nettleship 1987a), but attendance by Brünnich's Guillemots was unusual in showing a very marked increase late in incubation. Peaks in numbers of birds attending the colony occur then mainly because this is when many non-breeding birds begin to visit (Bédard 1969; Gaston & Nettleship 1982), and probably young, pre-breeding birds in particular (Halley *et al.* 1995). The peak was pronounced in Razorbills, and very pronounced in Brünnich's Guillemots, consistent with recent surveys that indicate that populations of these species are increasing at the Gannet Islands (Bryant *et al.* 1999; Chapdelaine *et al.* 1999).

Chick growth and development The diets of guillemot chicks included lower proportions of capelin and higher proportions of benthic fish (especially daubed shanny *Lumpenus maculatus*) in 1997 than in 1981-1983; however, this appeared to have little effect on growth rates and departure masses (Bryant *et al.* 1999). Razorbills chicks also grew normally compared to other colonies (Bédard 1969; Lloyd 1979). After controlling for variation in adult mass, the three species gained mass at similar rates, but Razorbills and Brünnich's Guillemots grew their wings more quickly (see also Barrett *et al.* 1997). As wing growth mainly measures growth of the primary coverts, this suggests that Razorbill and Brünnich's Guillemot chicks grew their wing feathers more quickly than did Common Guillemot chicks. This was seen in growth of the contour feathers as well, because Common Guillemot chicks retained natal down longer than Razorbills or Brünnich's Guillemots. The cliff-nesting habit of and Razorbills may place an evolutionary premium on wing feather growth, because success at departure may depend on the chick's ability to glide a long distance (Gilchrist & Gaston 1997; Hipfner & Gaston 1999). At many colonies, including the Gannet Islands, many Common Guillemot chicks simply walk from the nest site to sea. An evaluation of how chick development varies at colonies where ecological

conditions differ (e.g. where most guillemots nest on cliffs) might be enlightening.

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SAMENVATTING

Verschillende aspecten van de broedbiologie van Alk *Alca torda*, Zeekoet *Uria aalge* en Dikbekzeekoet *U. lomvia* werden onderzocht in een vergelijkende studie op de Gannet Islands in Labrador (Canada) in 1997. De mediaan van de eileg voor elk van deze soorten viel in een opmerkelijk korte periode, tussen 27 en 29 juni, en kon worden gekarakteriseerd als 'laat' in vergelijking tot eerdere jaren van onderzoek. Vermoedelijk als gevolg van deze uitgestelde eileg was de broedsynchronisatie tussen de onderzochte soorten erg groot. Alken bebroedden de eieren iets langer (mediaan 35 dagen) dan de beide zeekoeten (33 dagen), terwijl de Zeekoet de jongen het langst op het nest hield (gemiddeld 24 dagen, tegen gemiddeld 19 dagen bij de Alk en 20 dagen bij de Dikbekzeekoet). Bij alle soorten werd van relatief 'late' broedvogels de neiging waargenomen om de nestperiode te bekorten, door eerder met het kuiken naar zee te vertrekken. Het broedsucces was hoog bij de Alk (73%) en de Zeekoet (85%), maar laag bij de Dikbekzeekoet (51%), vooral als gevolg van een laag percentage uitkomende eieren. Ondanks een belangrijke verschuiving in het voedsel van de kuikens sinds het begin van de jaren tachtig, hoofdzakelijk veroorzaakt door een afgenomen aanbod van Lodde *Mallotus villosus* in Labrador, groeiden de kuikens bij alle soorten relatief snel en verlieten de kuikens de kolonie met een normaal gewicht.

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THE STATUS OF ARCTIC TERNS *STERNA*
PARADISAEA
 AT SHETLAND AND ORKNEY IN 1994
 DE AANTALLEN NOORDSE STERNS OP DE ORKNEY
 EN SHETLAND EILANDEN IN 1994

E. BRINDLEY¹, G. MUDGE², N. DYMOND³, C. LODGE⁴, B. RIBBANDS⁵,
 D. STEELE⁶, P. ELLIS⁷, E. MEEK⁸, D. SUDDABY⁹ & N. RATCLIFFE^{1*}

¹The Royal Society for the Protection of Birds (RSPB), The Lodge, Sandy, Bedfordshire, SG19 2PL, England, U.K.; ²Scottish Natural Heritage, 2, Anderson Place, Edinburgh, Scotland, U.K.; ³South Punds, Levenwick, Shetland, Scotland U.K.; ⁴23 New Road, Broomfield, Chelmsford, Essex, CM1 5AN, England, U.K.; ⁵Queenamidda, Rendall, Orkney, Scotland U.K.; ⁶93 Slaughter Road, Ballymena, Co. Antrim, BT42 2JJ, N. Ireland, U.K.; ⁷RSPB, Seaview, Sandwick, Shetland ZE2 9HP, Scotland, U.K.; ⁸RSPB, Smyril, Stenness, Stromness, Orkney KW16 3JY, Scotland U.K.; ⁹RSPB, Ouse Washes Reserve, Welches Dam, Manea, Cambs. PE15 0NF, England, U.K.;
 *Corresponding author

A census of Arctic Terns was carried out in Orkney and Shetland in 1994. The results indicated that the population in the Northern Isles as a whole was 32 400 (95% CI = 26 600-39 000), a decline of 27% (95% CI = 12-40%) since 1989. A population model indicated that this decline could be explained by poor natal recruitment following breeding failures on Shetland between 1985 and 1990 (Table 1). Within the two archipelagos, numbers declined by 47.5% in Orkney to approximately 15 600 birds, while in Shetland the population remained stable at 16 800 birds (95% CI = 11 400-23 800 birds). This is contrary to the predictions of the population model, which suggested a large decline in Shetland and a slight decline on Orkney. The best explanation for this discrepancy is that between 9000 and 10 000 Arctic Terns migrated from Orkney to Shetland, probably to exploit the increase in sandeel abundance there. The tern populations on Shetland and Orkney can therefore be regarded as components of a larger metapopulation.

Brindley E., G. Mudge, N. Dymond, C. Lodge, B. Ribbands, D. Steele, P. Ellis, E. Meek, D. Suddaby & N. Ratcliffe 1999. The status of Arctic terns *Sterna paradisaea* at Shetland and Orkney in 1994. *Atlantic Seabirds* 1(3): 135-143.

INTRODUCTION

Arctic Terns *Sterna paradisaea* have a circumpolar breeding distribution, with Great Britain and Ireland hosting approximately 10% of the global and 45% of the European population (Avery 1991a). The majority of the British Arctic Tern

population breeds on Orkney and Shetland where a survey in 1980 estimated a total of approximately 83 200 birds (Bullock & Gomersall 1981). By 1989 the population had fallen to 44 500 birds (Avery *et al.* 1993).

Sandeels *Ammodytes* spp. are the only small, energy-dense and abundant fish that Arctic Terns can exploit around the Northern Isles (i.e. the Orkney and Shetland Islands), and their reproductive success is dependent on availability of 0-group and 1-group fish (Monaghan *et al.* 1989, 1992; Suddaby & Ratcliffe 1997). Low recruitment of sandeels into the Shetland stock during the late 1980s and 1990 led to complete breeding failures of Arctic Terns on Shetland (Monaghan *et al.* 1989, 1992, Suddaby & Ratcliffe 1997). However, poor productivity alone was not sufficient to explain the rate of decline in the Arctic Tern population on the Northern Isles between 1980 and 1989, suggesting that rates of either adult mortality, non-breeding or emigration increased as well over the same period (Avery *et al.* 1993).

The Arctic Tern is recognised as being of conservation importance by its inclusion in the 'amber' list of Birds of Conservation Concern in the UK (Gibbons *et al.* 1996) and is also listed in Annex 1 of the European Community 'Birds Directive'. In view of the population declines through the 1980s and the poor productivity during this period, regular monitoring of breeding numbers is essential to determine current population trends. This paper presents the results of a census in 1994 and a population model that tests whether the trends in the population can be explained by lack of productivity on Shetland during the late 1980s and 1990.

METHODS

In 1989, all known Arctic Tern colonies in Orkney and Shetland were visited once between 25 May and 12 July (Avery *et al.* 1993). The numbers of birds were expected to vary through the season, so each colony was randomly assigned to be counted in one of three time periods; period 1 (25 May-10 June), period 2 (11-28 June) and period 3 (29 June-12 July). This method ensured that the three groups were similar in all respects so that comparisons could be made between counts at different stages of the breeding season (Avery *et al.* 1993). Although the count methods were identical in the two island groups during 1994, the selection of colonies to be counted differed. In Orkney it was possible to census all colonies at some time during the season and sum the number of birds at them to arrive at a total population figure. However, towards the end of the season, counts are thought to become less reliable (Avery 1991b), so a second population estimate was made using trends at those colonies visited during periods 1 and 2 in both the 1989 and 1994 surveys ($n = 140$). In Shetland, 500 colonies were visited in 1989, 378 of which were visited in

periods 1 and 2. Of the latter, a sample of 172 colonies was randomly selected for counting during 1994.

Observers estimated the number of adults attending colonies using flush counts as in previous surveys (Bullock & Gomersall 1981, Avery *et al.* 1993). Three estimates were obtained within three minutes of flushing the birds and the mean of these was then taken as the number of birds present at the colony. All results refer to numbers of adult birds flushed and not pairs. The majority of counts were carried out between 08.00 and 18.00 h GMT, and this was comparable with the 1989 survey. At each colony we also recorded altitude, distance from the sea, habitat type and land use.

Counts made in periods 1 and 2 in both years were used in matched comparisons between years (1989 and 1994). For both Orkney and Shetland, only 1994 counts falling within 14 days of those in 1989 were used in calculations in order to minimise seasonal variations in colony attendance. This gave a matched sample of 140 colonies in Orkney and 172 in Shetland. In some cases, there was more than one count in both years that would have been suitable for comparison, so those closest in date were used for analysis. The mean ratio (1994:1989) of birds at individual colonies and 95% confidence intervals were calculated by bootstrapping (Manly 1991). In order to calculate overall numbers in Shetland, the mean ratios and confidence intervals were applied to the total count in 1989. The final population estimates were rounded to the nearest 100 birds.

In Orkney, survey coverage of the islands was complete and so all new colonies established since 1989 were counted. However, in Shetland, the survey was based on counts of a sample of colonies known to have been in existence in 1980 or 1989, so we allowed for the possibility that new colonies could have been established in the intervening years. The area of land in Shetland that was potentially suitable for breeding terns was first estimated. The suitability of 1-km squares in Shetland was determined by assessing the altitude and distance from the sea of all colonies present during 1980 and 1989. Of the colonies present in Shetland in either 1989 or 1980, 86% ($n = 500$) were within 800 m of the sea and at an altitude of 50 m or less. Only 1-km squares containing land that fulfilled these criteria ($n = 1278$) were assumed to be potentially suitable for breeding terns in further analysis.

In 1994, a survey of Red-throated Divers *Gavia stellata* was undertaken in Shetland (Gibbons *et al.* 1997). As part of this survey work, all 5-km squares with standing freshwater were surveyed in late May or June, at the time of the optimum Arctic Tern survey period. During this survey, all previously unknown Arctic Tern colonies were counted using identical methods to the main survey. However, not all ground within the 5-km squares had been searched with equal effort so the survey data were broken down by 1-km square.

Only those squares that had received at least 50% coverage and contained land suitable for breeding terns were included in the analysis ($n = 62$). The bootstrapped mean number of Arctic Terns at new colonies per 1-km square was thus obtained and this figure was multiplied by the number of suitable squares on the whole of Shetland to obtain a total estimate of the number of birds at new colonies.

A simple deterministic population model was used to test whether the observed population trends can be explained by low Arctic Tern recruitment. The model used estimates of mortality and recruitment rates to predict the size of the breeding population in 1994. The annual adult survival rate of Arctic Terns on the Farne Islands was 88%, survival to recruitment 53% and modal age of first breeding four years (Coulson & Horobin 1976). These were used in conjunction with population and productivity estimates from Shetland and Orkney as parameters in the model. Population figures for the Northern Isles Arctic Tern surveys are based on counts of the number of birds, while the model requires knowledge of the number of pairs in order to estimate the number of chicks fledged. A correction factor of 1.5 birds to one pair was used to estimate the number of pairs (Bullock & Gomersall 1981).

In Shetland, productivity was zero from 1985 to 1990 (Monaghan *et al.* 1989, 1992; Walsh *et al.* 1990) and so no recruitment was expected to occur between 1989 and 1994 given the recruitment age of four years (Coulson & Horobin, 1976). Thus, population size was expected to decline by 12% per annum due to adult mortality. For Orkney, the prediction of the population in 1994 was more complicated and involved more assumptions. Productivity was higher in Orkney during the 1980s than on Shetland, but it was not accurately quantified. Calculating recruitment between 1989 to 1994 therefore demands estimation of the population size and productivity from 1985 to 1990. Population status figures in these years were estimated by calculating the annual rate of population decline between 1980 and 1989 and then using this rate to calculate the population size in each successive year. The average productivity recorded from 1990 to 1997 (0.31 chicks per pair) was used as the value for productivity during 1986-1989, after which observed values for each year were used. This technique assumes that the annual rate of decline between 1980 and 1989 was constant and that average productivity during 1985 to 1989 on Orkney was similar to that between 1990 and 1997. The parameters described above were substituted into the following equation (Croxall & Rothery 1991) to predict the population size in terms of the number of pairs:

$$N_{t+1} = S_A N_t + f S_i N_{(t+1-k)}$$

N_t = Number of females in year t , f = productivity (female chicks per pair), S_A = Adult survival rate, k = recruitment age, S_I = Immature survival rate. The number of pairs was converted back into the number of individual birds using the 1.5 birds to pairs correction factor and compared with the observed number of birds from the 1994 survey.

RESULTS

Orkney The total number of Arctic Terns at all colonies on Orkney during 1994 was 15,600 birds (Table 1). This compares with a total of 29,700 birds in 1989, representing an overall decline of 47.5%. The analysis of trends at individual colonies for the 140 colonies covered in either period 1 or 2 in both 1989 and 1994 showed that numbers fell by 47.8% between 1989 and 1994, which was similar to the percentage change derived from the analysis of all counts combined.

Shetland The rate of change between 1989 and 1994 at the sample of colonies censused in periods 1 and 2 at Shetland did not differ significantly (Period 1: mean 1.588, 95% Confidence Interval, CI = 0.992 - 2.563; Period 2: mean 0.867, 95% CI = 0.498 - 1.422) and therefore all ratios were pooled. The overall ratio between 1994 and 1989 was 1.102 (95% CI = 0.772-1.505) indicating that the population size had not changed significantly on Shetland. Multiplying these ratios by the population estimate from the complete count in 1989 gives a population estimate for Shetland of 16 200 (95% CI = 11 400-22 200) without allowing for the formation of new colonies between the two count periods.

In the 62 suitable 1-km squares that were searched for new colonies, two new colonies holding a total of 27 birds were found, a mean of 0.44 birds per square (95% range 0-1.24). The total number of birds at new colonies in Shetland was estimated to be 562 birds (95% CI = 0-1585 birds), which is very small compared with the confidence intervals around the estimate from established colonies. This was added to the sample census estimate to give a total Shetland population estimate of 16 800 birds (95% CI = 11 400-23 800) which is not significantly different from the estimate for 1989 (Table 1).

Northern Isles total The number of Arctic Terns on the Northern Isles as a whole in 1994 can be estimated by summing the Shetland and Orkney estimates, giving a total of 32 400 (95% CI = 26 600-39 000, Table 1). This represents a population decline of 27% (CI = 12-40%) from 1989 to 1994.

Modelling population size The total number of Arctic terns predicted to occur in the Northern Isles by the population model was 33 100 and is well within the sampling error of the observed population estimate (Table 1). This suggests that

Table 1. Total numbers of breeding Arctic Terns counted in Orkney and Shetland between 1980 and 1994 and predicted values from the population model.

Tabel 1. Aantallen broedende Noordse Sterns op Orkney en Shetland tussen 1980 en 1994 en de voorspelde aantallen op grond van een populatie-model.

	Shetland	Orkney	Total
1980	40 800	42 400	83 200
1989	14 700	29 700	44 400
1994 (Observed)	*16 800	15 600	32 400
1994 (Predicted)	7800	25 300	33 100

*95% Confidence Interval of count: 11 400-23 800 birds

the low recruitment due to breeding failures on Shetland from 1985 to 1990 might explain the observed population decline on the Northern Isles. However, the number of birds observed on Shetland was far higher than predicted, while the numbers on Orkney were much lower than predicted. This finding is best explained by 9000-10 000 Arctic Terns emigrating from Orkney to Shetland between 1989 and 1994, although there are insufficient data from ringing studies to confirm this.

DISCUSSION

The Arctic Tern population in the Northern Isles halved between 1980 and 1989 (Bullock & Gomersall 1981, Avery *et al.* 1993). The results of the 1994 census show a further decline of approximately 27% since 1989. The population trends of Arctic Terns on the Northern Isles are closely mirrored by long-term trends of the sandeel stocks in Shetland waters. This would be expected since sandeels are the only suitable prey species for terns around Shetland and Orkney and productivity is strongly related to their availability (Monaghan *et al.* 1989, 1992; Suddaby & Ratcliffe 1997). The recruitment and spawning stock of sandeels in Shetland waters increased dramatically through the late 1970s and peaked in the early 1980s before declining due to low recruitment rates between the mid 1980s and 1990 (Wright & Bailey 1993).

The decline in sandeel availability was associated with poor reproductive success of Arctic Terns on Shetland during 1983 and 1984 (Ewins 1985) and complete breeding failures between 1985 and 1991 (Walsh *et al.* 1990). However, at the same time, Arctic Terns on Orkney were provisioning their chicks with sandeels and no widespread breeding failures were evident (Monaghan *et al.* 1992), suggesting that stocks around the two archipelagos may fluctuate independently. The rate of decline in the Arctic Tern population between 1980 and 1989 could only partially be explained by poor productivity,

and so it appears likely that adult mortality, emigration or non-breeding rates must also have increased during this period (Avery *et al.* 1993).

Sandeel abundance in Shetland waters increased dramatically during 1991 due to larval advection from Orkney, and this was associated with increased Arctic Tern productivity. However, the results of the 1994 Arctic Tern survey indicate that the population in the Northern Isles has undergone further declines since 1989 at a rate of 6% per annum. However, since the modal age of first breeding is 4 years old (Coulson & Horobin 1976), the chicks fledged on Shetland during 1991 would not have recruited by 1994. Modelling of expected population trends suggested that the results of the census in the Northern Isles could be adequately explained by natal recruitment being insufficient to balance losses due to adult mortality.

Population trends within Orkney and Shetland between 1989 and 1994 were very different from one another. The Orcadian population declined by 48% between 1989 and 1994 while that on Shetland did not change significantly. This is contrary to the trends predicted from the model, which suggested that the population on Shetland should have almost halved due to a lack of recruitment, while that on Orkney should have declined only slightly. The best explanation for this discrepancy is that between 9000 and 10 000 Arctic Terns emigrated from Orkney to Shetland between 1989 and 1994, probably to exploit the massive increase in sandeel abundance around Shetland following the high recruitment during 1991 (Wright & Bailey 1993). The Arctic Tern populations on Orkney and Shetland therefore appear to form components of a metapopulation, with birds moving among the archipelagos in response to changes in food availability.

Between 1990 and 1998, Arctic Tern productivity on Orkney and Shetland has fluctuated considerably (Ratcliffe *et al.* 1996; Thompson *et al.* 1997, 1998). The level of productivity required to maintain a stable population is 0.49 chicks per pair, but the 9 yr means on Shetland and Orkney were 0.32 and 0.30 respectively. It is therefore likely that further declines of Arctic Terns will occur and it is important that monitoring continues to examine whether this prediction is accurate. A complete census of Arctic Terns during the year 2000 should be a high priority. We would also advocate complete censuses of the Northern Isles in the future to ensure that precise population trends are obtained. The 1994 census on Shetland demonstrated that sample counts offer poor precision, as the low site fidelity of Arctic Terns results in high variance in the trends at individual colonies.

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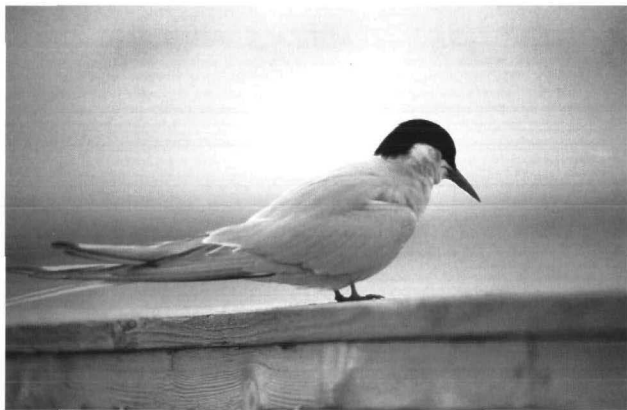
SAMENVATTING

Op de Orkney en Shetland Eilanden werd in 1994 het aantal broedende Noordse Sterns *Sterna paradisaea* geteld. In totaal werden 32 400 (95% CI = 26 600-39 000) paren geteld, hetgeen een afname van 27% (95% CI = 12-40%) sinds 1989 betekende. Een populatiemodel liet zien dat de afname veroorzaakt zou kunnen zijn door een geringe rekrutering in de populatie van jonge vogels na de teleurstellende broedresultaten tussen 1985 en 1990, als gevolg van voedselgebrek nadat de populatie zandspiering in dit gebied was ingestort (Tabel 1). Op de Orkney Eilanden nam de populatie af met 47.5% tot ongeveer 15 600 vogels, terwijl de stand op Shetland min of meer gelijk bleef op 16 800 (95% CI = 11 400-23 800). Dit resultaat is in precies het tegendeel van wat het populatiemodel zou hebben voorspeld: een grote afname in Shetland en een gering verschil op Orkney. De aangedragen verklaring is, dat tussen 9000 en 10 000 Noordse Sterns van Orkney naar Shetland zijn verhuisd, misschien als reactie op de snel herstellende voorraad zandspiering in die omgeving. Als dat juist is, dan zouden de sterns op Orkney en Shetland tot één en dezelfde metapopulatie gerekend kunnen worden.

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Arctic Tern *Noordse Stern* (C.J. Camphuysen)

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Greenstreet S.P.R. & M.L. Tasker (eds) 1996. Aquatic predators and their prey. Fishing News Books, Oxford.

Van Eerden M.R. & B. Voslamber 1995. Mass fishing by Cormorants *Phalacrocorax carbo sinensis* at lake IJsselmeer, The Netherlands: a recent and successful adaptation to a turbid environment. *Ardea* 83: 199-212.

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Atlantic Seabirds web page: <http://home.planet.nl/~camphuys/AS.html>

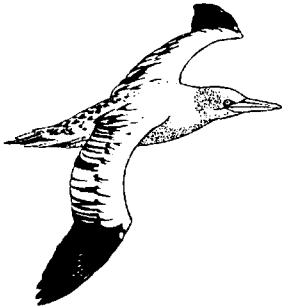
the Seabird Group

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 Ornithologists' 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. Four issues of *Atlantic Seabirds* and three Newsletters are circulated to members each year.

Current Executive Committee Chair S. Wanless, Secretary J. Uttley, Treasurer J.C. Davies, Membership Secretary S. Russell, Editor of *Atlantic Seabirds* J.B. Reid, Newsletter editor M.L. Tasker, also A. Douse, J.D. Okill, E.K. Dunn and S. Sutcliffe.



Nederlandse Zeevogelgroep (NZG)

(Dutch Seabird Group), een sectie van de Nederlandse Ornithologische Unie, werd opgericht op 1 januari 1991, als voortzetting van de Club van Zeetrekwaarnemers (1972-1990) en het Nederlands Stookolieslachtoffer-Onderzoek (1977-1990). De Nederlandse Zeevogelgroep stelt zich tot doel: (1) het stimuleren van zeevogelonderzoek in en vanuit Nederland en (2) het uitwisselen van informatie met de uitgave van het tijdschrift, aanvankelijk *Sula*, vanaf 1999 *Atlantic Seabirds*.

Voor zover samenvallend met onderzoek aan zeevogels worden activiteiten aan zeezoogdieren mede in de doelstelling betrokken. Door een viertal werkgroepen wordt onderzoek gestimuleerd naar broedende zeevogels, de verspreiding van vogels en zoogdieren op open zee (offshore), strandingen, zeetrek en de gevolgen van olievervuiling. De contributie van de NZG bedraagt f25 per jaar.

Dagelijks bestuur Voorzitter en Nieuwsbrief redacteur M.F. Leopold, Secretaris J.A. van Franeker, Penningmeester Y. Hermes, Eindredacteur *Atlantic Seabirds* C.J. Camphuysen, en verder A.J. van Dijk, E.W.M. Stienen en C.J.N. Winter.

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vol 1 no. 3 (1999)

CONTENTS

- 97 The status of the European Shag *Phalacrocorax aristotelis* population on the Atlantic coast of the Iberian peninsula - by *Alberto Velando, Franciso Docampo & David Alvarez*
- 107 Reproductive success in the Great Cormorant *Phalacrocorax carbo carbo* in relation to colony nest position and timing of nesting - by *D.J. Andrews & K.R. Day*
- 121 Comparative breeding biology of Guillemots *Uria* spp. and Razorbills *Alca torda* at a colony in the Northwest Atlantic - by *J. Mark Hipfner & Rachel Bryant*
- 135 The status of Arctic terns *Sterna paradisaea* at Shetland and Orkney in 1994 - by *Emma Brindley, G. Mudge, N. Dymond, C. Lodge, B. Ribbands, D. Steele, P. Ellis, E. Meek, D. Suddaby & N. Ratcliffe*
- 144 Guidelines for contributors to *Atlantic seabirds*

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