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

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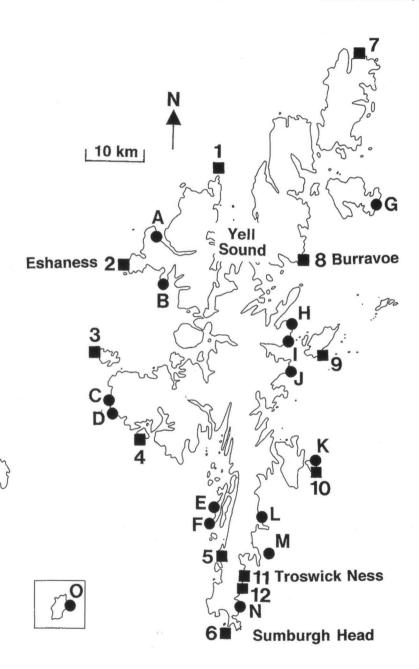
Kittiwake Rissa tridactyla numbers in Shetland, monitored by periodic nest counts at all colonies, declined from 54 600 pairs in 1981 to 23 000 pairs in 1998, probably due to low food availability and increased predation by Great Skuas Catharacta skua. Pre-breeding counts of Black Guillemots Cepphus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

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INTRODUCTION

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

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



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

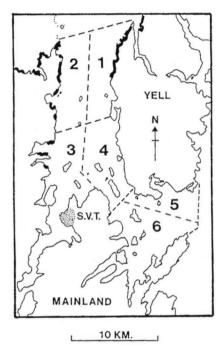


Figure 2. Map of Yell Sound showing the six monitoring areas for Black Guillemot, and the location of the Sullom Voe Terminal (S.V.T.). Cliff coastline over 50 m high is indicated by solid black.

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

METHODS

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

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

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

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

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

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

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

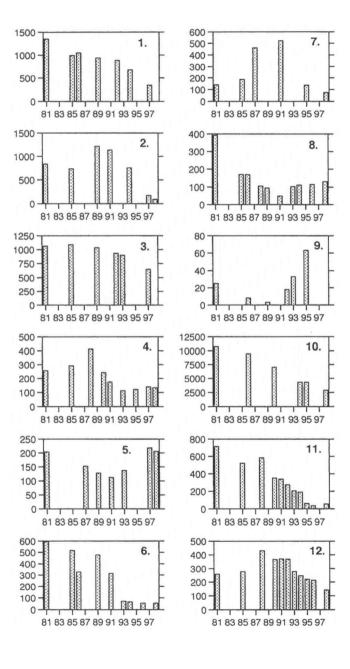
A complete survey of Yell Sound usually takes eight mornings so for recording purposes the coastline was divided into six areas, each differing considerably in the extent of suitable nesting habitat (Fig. 2). Where two surveys were made the higher count of each area was used to calculate an overall total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

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

RESULTS

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

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



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

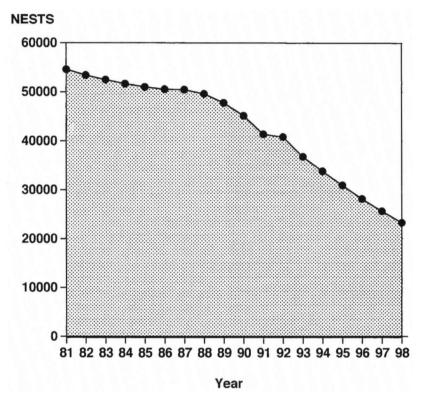


Figure 4. The estimated Shetland Kittiwake breeding population, 1981-98.

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

young fledged / nest

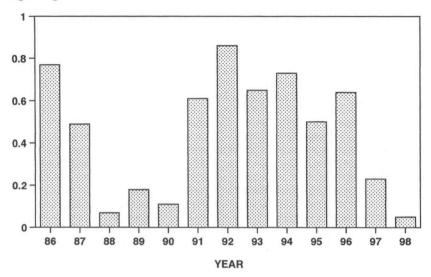


Figure 5. Mean annual Kittiwake breeding success (young fledged per nest at which eggs were seen or assumed to have been laid) at 5-10 monitored breeding stations

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

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

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

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

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

Area	1st/2nd	1st/2nd	1st/2nd	1st/2nd	1st/2nd
1	131/ -	202/145	264/ -	372/335	322/ -
	226/ -	226/231	247/275	254/262	291/288°
2 3	59/ -	89/82	117/ -	135/128	99*/-
4	35/ -	28/30	53/ -	61/58	54/ -
5	34/ -	41/41	72/ -	65/85	69/ -
6	70/ -	50/40	74/ -	69/65	89/ -
Total A	555/ -	636/569	827/ -	956/933	924*/-
Total B	555	643	855	984	924*
% change per annum		+ 7.6	+15.3	+15.1	
		1983-85	1985-87	1987-88	
	1991	1993	1996	1998	1983-98
Area	1st/2nd	1st/2nd	1st/2nd	1st/2nd	% change
1	422/ -	585/ -	652/499	697/738	+463
2	295/-	298/340	323/301	310/343	+52
2 3	155/ -	147/ -	144/ <i>141</i>	142/145	+146
4	72/ -	<i>50</i> /67	71/65	57/70	+100
5	65/ -	75/ -	<i>37</i> /48	47/56	+65
6	76/ -	61/-	52/83	64/57 [*]	-9
Total A	1085/ -	1216/ -	1279/1137	1317/1409	
Total B	1085	1275	1321	1416	+155
% change per annum	+ 3.3	+ 8.4	+ 1.2	+ 3.5	+ 6.4
	1988-91	1991-93	1993-96	1996-98	1983-98

incomplete coverage of the area

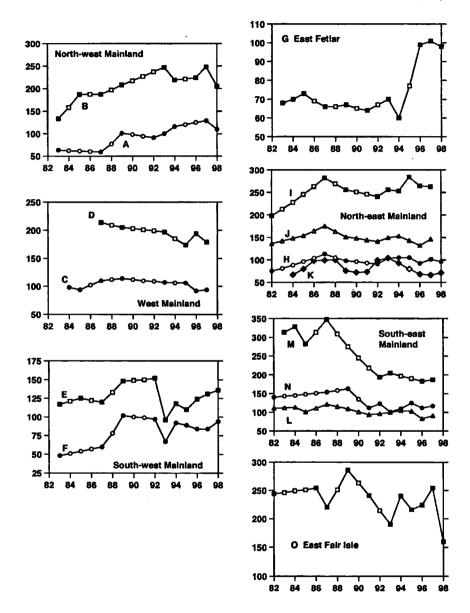


Figure 6. Counts of Black Guillemots at 15 monitoring sites, 1982-98. Solid symbols are actual counts, open symbols are estimates calculated by mean annual percentage change between actual counts. Letters denote site locations (see Fig. 1).

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

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

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

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

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

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

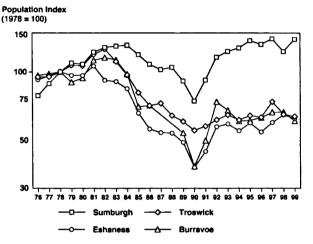


Figure 7. Indices (1978 = 100) of mean annual counts of Guillemots in study plots at four breeding colonies plotted on a log scale. Actual counts (1978): Sumburgh Head 1326; Troswick Ness 282; Eshaness 699; Burravoe 334. See Fig. 1. for colony locations.

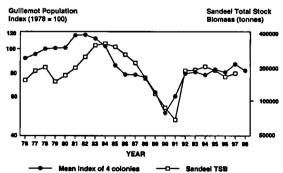


Figure 8. Mean annual index (1978 = 100) of Guillemots (*) in study plots at four breeding colonies, and estimates of total stock biomass (TSB) of sandeels (\(\sigma\)) at 1 July in the Shetland assessment area (1998 = 567 634 tonnes), plotted on a log scale. Sandeel data courtesy of the Scottish Executive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

Index / Number

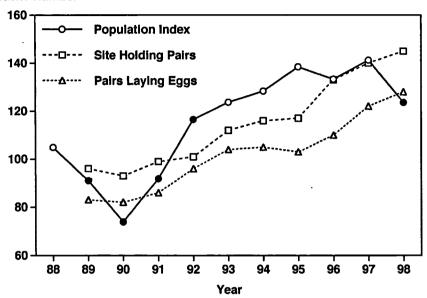


Figure 9. Mean annual index (1978 = 100) of Guillemot numbers in eight study plots at Sumburgh Head (solid symbols indicate a statistically significant change from the previous year; see text) and the actual number of site-holding and egg-laying pairs in a single breeding success study plot.

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

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SAMENVATTING

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

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

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

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