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

C.M. PERRINS[1] & S.B. SMITH[2]

[1]*Edward Grey Institute of Field Ornithology, Department of Zoology, University of Zoology, South Parks Road, Oxford, OX1 3PS, England, U.K.;* [2]*Wildlife Trust West Wales, 7 Market Street, Haverfordwest, Pembrokeshire SA62 3BJ, Wales, U.K.*

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

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

INTRODUCTION

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

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

* Known as *Larus graelsii* on the Dutch list

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

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

SPECIES ACCOUNTS

Lesser Black-backed Gull

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

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

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

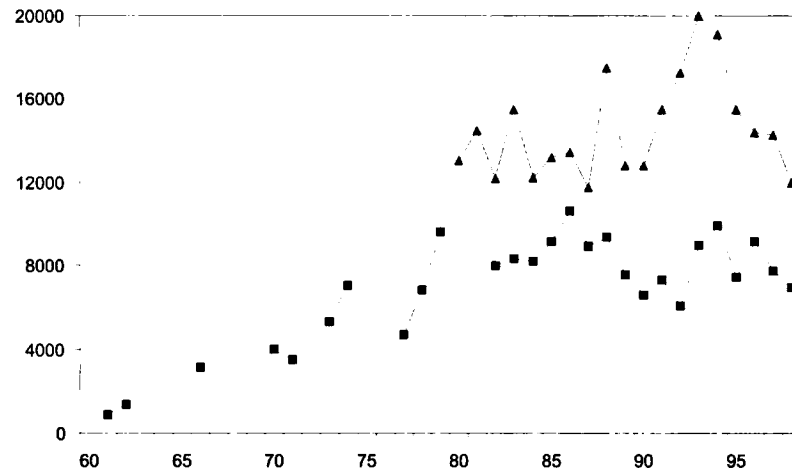

Figure 1. Lesser Black-backed Gull numbers on Skomer Island 1962-98. Squares show the "eye-counts" and triangles the numbers adjusted as a result of the "cane counts" (see text).

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

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

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

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

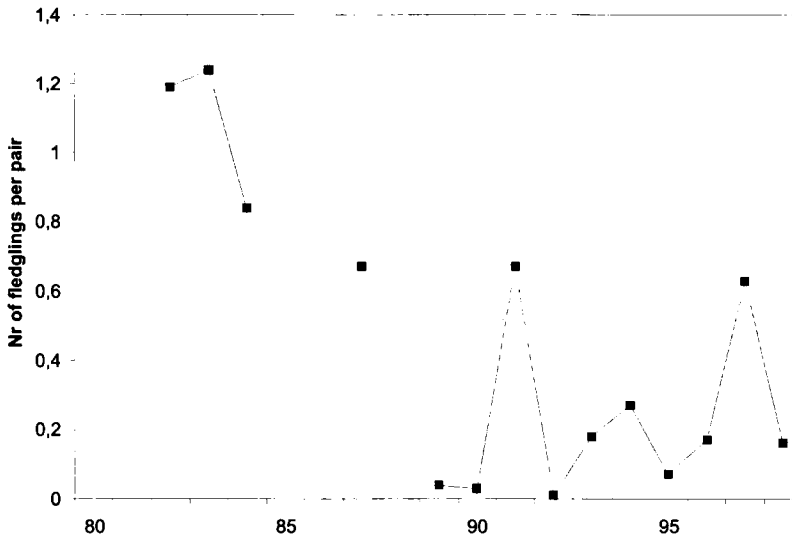

Figure 2. Lesser Black-backed Gull productivity on Skomer Island 1982-98 (estimated number of fledglings per breeding pair).

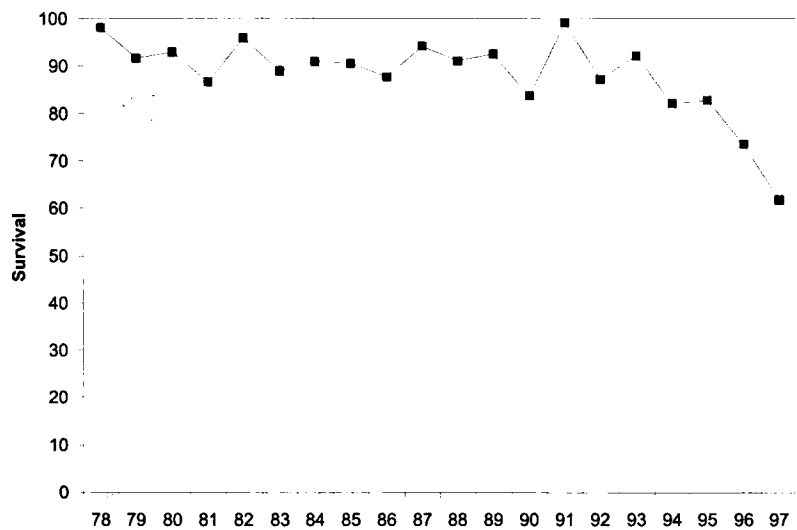

Figure 3. Lesser Black-backed Gull annual adult survival on Skomer Island 1978-97.

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

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

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

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

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

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

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

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

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

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

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

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

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

Herring Gull

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

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

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

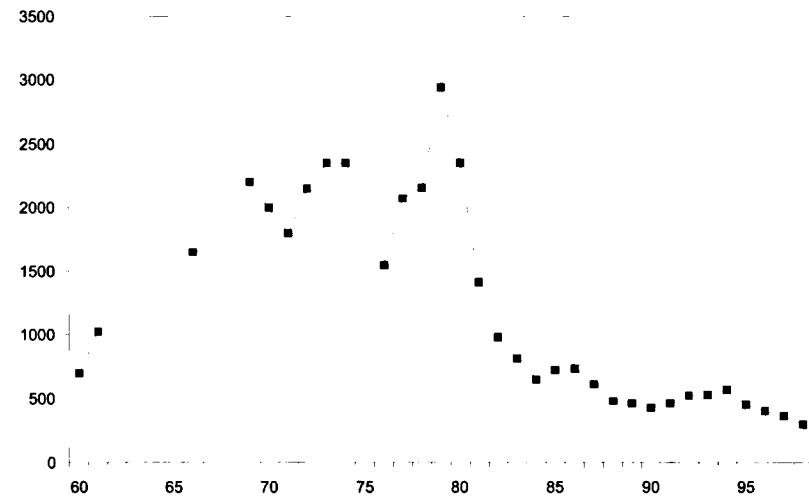

Figure 4. Herring Gull numbers on Skomer Island 1962-98.

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

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

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

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

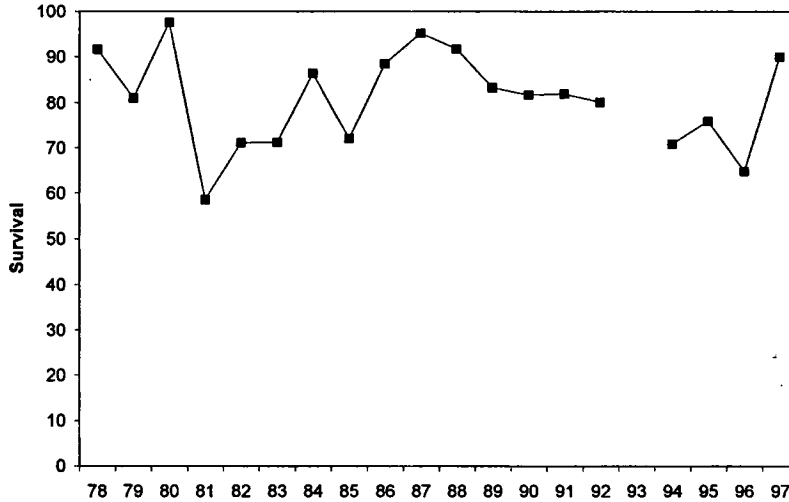

Figure 5. Herring Gull annual adult survival on Skomer Island 1978-97. The survival for 1993 was high, but can not be estimated accurately.

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

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

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

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

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

Great Black-backed Gull

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

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

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

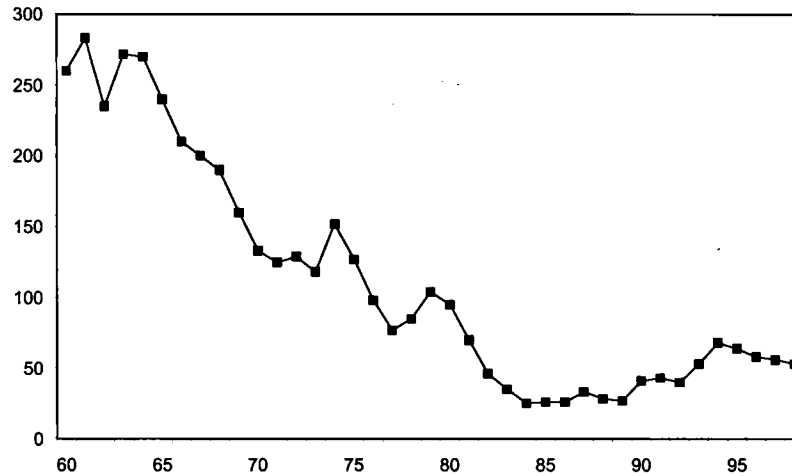

Figure 6. Great Black-backed Gull numbers on Skomer Island 1962-98.

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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

ACKNOWLEDGEMENTS

Valuable comments on the manuscript were received from S.J Sutcliffe and two referees. Thanks are due to all the people who have counted and caught gulls on Skomer, especially the Seabird Field Assistants of the EGI and WTWW. During the population counts the wardens of recent years have been greatly helped in particular by the assistance of Mike Wallen and Jim Poole who have ensured high levels of consistency and accuracy. The work reported in this paper was carried out as part of

an integrated seabird monitoring programme on Skomer Island NNR funded by the Wildlife Trust, West Wales, the Countryside Council for Wales and the Joint Nature Conservation Committee.

SAMENVATTING

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

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

REFERENCES

Alexander M. & Perrins C.M. 1980. A report on crop contents of Lesser Black-backed Gull chicks with recommendations for future research. Unpublished report to West Wales Trust for Nature Conservation Skokholm & Skomer Management Committee.

Alexander M.A. 1981. The diet of Lesser Black-backed Gull chicks on Skomer. Unpublished report to West Wales Trust for Nature Conservation.

Bradbury R. & Griffiths R. 1999. Sex-biased nestling mortality is influenced by hatching asynchrony in the Lesser Black-backed Gull *Larus fuscus*. J. Avian Biology 30: 316-322.

Calladine J. & Harris M.P. 1997. Intermittent breeding in the Herring Gull *Larus argentatus* and the Lesser Black-backed Gull *Larus fuscus*. Ibis 139, 259-263.

Chabrzyk G. & Coulson, J.C. 1976. Survival and recruitment in the Herring Gull *Larus argentatus*. J. Anim. Ecol. 45: 187-203.

Corkhill P. 1973. The diet of Great Black-backed Gulls on Skomer. Internal report to west Wales Trust for Nature Conservation.

Cramp S. & Simmons K.E.L. 1983. The Birds of the Western Palearctic, 3. Oxford University Press, Oxford.

Davies N. 1994. A comparison of the growth and survival of *Larus fuscus* and *Larus argentatus* pulli on Skomer Island. HND work placement, Pembrokeshire College.

Davis J.W.F. 1973. Aspects of the breeding ecology and feeding of certain gulls. Unpublished D.Phil thesis, Oxford University.

Donovan J.W.D. 1973. *Larus* Gulls and the Pembrokeshire islands. Unpublished report to West Wales Naturalists Trust.

Dunn E. 1993. Skomer and Skokholm Islands (West Wales): History of a gull colony deprived of discards. In unpublished report on seabirds and fisheries to RSPB.

Harris M.P. 1962. The *Larus* gulls breeding on Skomer, Skokholm and Grassholm islands. Nature in Wales 8: 2.

Harris M.P. 1964. Aspects of the breeding biology of the gull *Larus argentatus*. Ibis 106: 432-456.

Harris M.P. 1965. The food of some *Larus* gulls. Ibis 107: 43-53.

Harris M.P. 1970. Rates and causes of increase in some British gull populations. Bird Study 17: 325-335.

Lebreton J.-D., Burnham K.P., Clobert J. & Anderson D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62: 67-118.

Lloyd C,. Tasker M.L. & Partridge K. 1991. The status of seabirds in Britain and Ireland. T & A.D. Poyser, London.

Mylne C.K. 1960. Predation of Manx Shearwaters by Great Black-backed Gulls on Skomer. Bird Notes 29: 73-76

O'Connell M.J., Coulson J.C., Raven S. & Joyce S. 1997. Nonbreeding and nests without eggs in the Lesser Black-backed Gull *Larus fuscus*. Ibis 139: 252-258.

Orsman C. & Sutcliffe, S.J. 1990. Seabird studies on Skomer Island 1989 and 1990. Nature Conservancy Council CSD Report No. 1165.

Perrins C.M. 1991. Lesser Black-backed Gulls: Skomer 1990. Unpublished report to Dyfed Wildlife Trust Skokholm & Skomer Management Committee.

Perrins C.M. 1992. Lesser Black-backed Gulls:Skomer 1991. Unpublished report to Dyfed Wildlife Trust Skokholm & Skomer Management Committee.

Poole J. 1995. Changes in the diet of Great Black-backed Gull *Larus marinus* on Skomer 1958-1992 Seabird 17: 50-55

Poole J. & Smith S.B., 1998. Seabird monitoring on Skomer Island 1997/98. JNCC Report. Report to JNCC by the Wildlife Trust, West Wales.

Ratcliffe D. 1993. The peregrine falcon 2nd edition. T. & A.D. Poyser, London.

Smith S.B. 1998a. Skomer Island NNR Bibliography, Part 2: Birds (1) Island Naturalist 35 pp 48-52.

Smith S.B. 1998b. Skomer Island NNR Bibliography, Part 3: Birds (2) Island Naturalist 36 pp 37-43.

Southwood, T.R.E. 1978. Ecological Methods 2nd edition. Chapman & Hall, London.

Stone CJ., Webb A. & Carter I.C. 1992. Lesser Black-backed Gull distribution at trawlers and food availability in the Celtic Sea, 1991. JNCC Report No. 106.

Sutcliffe S.J. 1986. Changes in the gull populations of SW Wales. Bird Study 33: 91-97.

Sutcliffe S.J. 1991. Lesser black-backed gulls on Skomer and Skokholm. Unpublished report to Dyfed Wildife Trust, Skomer and Skokholm Management Committee.

Sutcliffe S.J. 1992. Population trends of the *Larus* gulls breeding on Skomer Island NNR 1960-92. Report by Dyfed Wildlife Trust to CCW.

Sutcliffe S.J. 1997. Populations of breeding *Larus* gulls on Welsh islands. In: Rhind P.M., T.H. Blackstock & S.J. Parr (eds) Welsh islands: ecology, conservation and land use. CCW, Bangor pp 92-97.

Thompson L.F. 1995. The breeding ecology of the Lesser Black-backed Gull *Larus fuscus*: a comparative study of the populations of Skomer and Cardigan Islands. MSc Ecology dissertation, University of Wales, Bangor.

Todd P.R. 1986. Gull populations on Skomer. A report to the Dyfed Wildlife Trust Skokholm & Skomer Management Committee.

Todd P.R. 1987. The population dynamics and feeding ecology of the Herring Gull (*Larus argentatus*) and Lesser Black-backed Gull (*Larus fuscus*). Report to NERC.

de Wijs W.J.R. 1982. Research on gulls and some other species of seabirds on Skomer 1982. Report to the Edward Grey Institute of Field Ornithology, Oxford.

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