

SURVIVAL AND AGE AT FIRST BREEDING IN THE RAZORBILL (*Alca torda*)

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INTRODUCTION

The breeding biology of several of the Atlantic auk species is now fairly well known. In particular there have been studies of the Razorbill, *Alca torda* (Paludan, 1947; Bédard, 1969; Lloyd, 1976a), of the Common Murre, *Uria aalge* (Tschanz, 1959; Tuck, 1960; Birkhead, 1976) and of the Common Puffin, *Fratercula arctica* (Myrberget, 1962; Nettleship, 1972; Ashcroft, 1976). All three species have been studied on both sides of the Atlantic Ocean. Most studies have either been short-term, lasting two or three years, or have not involved many banded adult birds so that relatively little has been concluded about the age of first breeding or annual survival. Adult survival rates have been calculated from band recoveries for these species (Birkhead, 1974a; Lloyd, 1974; Mead, 1974); however, such data depend on birds washed ashore dead, and band recoveries do not always give survival rates similar to those found in more detailed studies of marked populations (Grosskopf, 1964; Perrins, 1971).

The Razorbill breeds in the low arctic marine zone of the North Atlantic (Voous, 1960), and at least 70% of the total world population breeds in Britain and Ireland (Lloyd, 1976b). Razorbills only come to land to breed (from March or April until July or August); for the rest of the year they remain at sea, usually in coastal waters. Young birds from European colonies are migratory; recoveries of birds banded on Skokholm have been reported from as far south as Morocco and as far east as Genoa, Italy. The birds do not normally return to the breeding colonies in their first summer of life. Older birds disperse away from the colony during winter and are therefore not truly migratory (Lloyd, 1974).

This paper describes findings based on a breeding population of Razorbills on Skokholm Island in Pembrokeshire (Dyfed, Wales), with some additional data from the adjacent island of Skomer. With the exception of the war years (1940-45), the island has been manned by ornithologists every summer since 1928, and 8,581 Razorbills have been banded in the years 1936-1973 inclusive. There has probably been a small decline in the Razorbill population on Skokholm during the last 25 years, but changes in numbers have been somewhat erratic. The situation is unclear because the birds are difficult to count accurately. Not all census information seems equally reliable, and a small (but variable) proportion of the adult birds may not breed. During the years 1963-73, on which these findings are based, the population remained roughly stable, and during the main years of study (1970-73) about 470 pairs bred.

A second feature that makes these birds difficult to study is that they shuffle along the rock on their tarsi, an action which leads to considerable band wear. The pre-war bands (aluminum) lasted barely two years, and hence we have no records of Razorbills

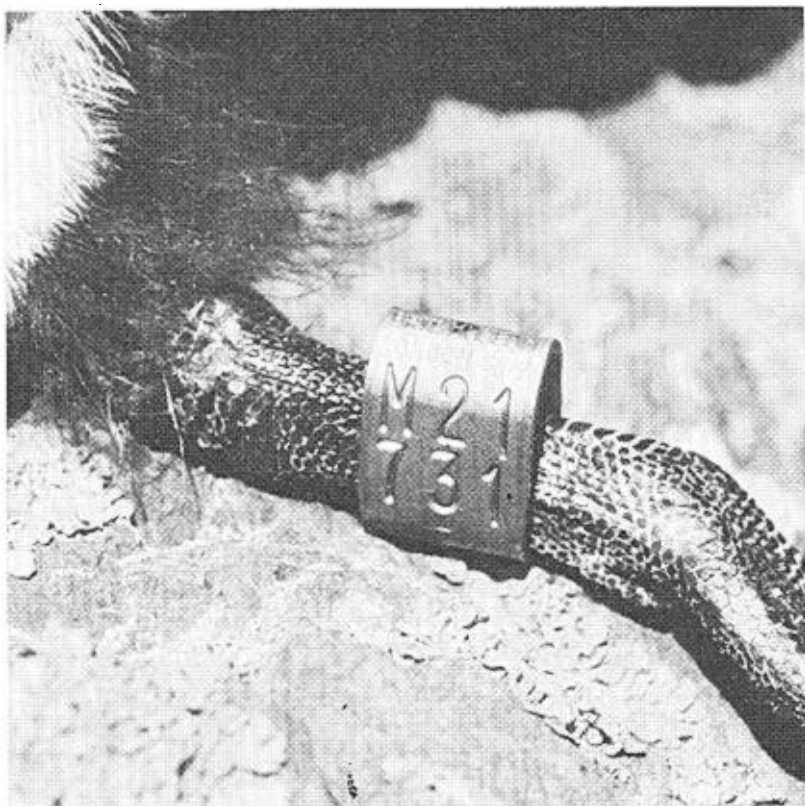


FIGURE 1. Incoloy band used on Razorbills since 1973. Unlike their earlier counterparts, these permit the whole band number to be read from one side; the reporting address is given on the upper side.

which have survived from before the war, as their bands would have fallen off even had the birds themselves survived. Nor do we have many records of birds banded prior to 1959 surviving for long periods, since they had to be caught at least every two years for the records to be maintained. The oldest known birds on Skokholm are two individuals banded when full grown and both last recaptured 19 years later; as we shall show, these two birds must have been more than 20 years old. Even when Monel bands were introduced (around 1960), the inscription often became illegible through wear within about two years. Recently, bands have been made of still harder material, Incoloy (Fig. 1). In addition, the inscription has been placed so that it does not wear off so easily and so that it can be read with a telescope (Lloyd, 1975a), a feature which increases the number of birds re-sighted in later years.

Most of the banding from which the data are derived dates from 1963, when an intensive campaign of banding nestlings was started. From 1968 onwards, all nestlings have been given a colored plastic

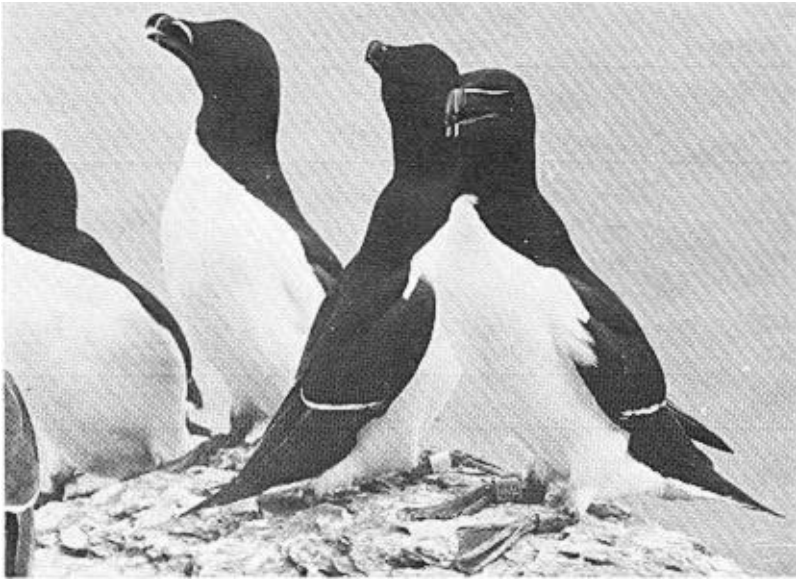


FIGURE 2. Color-banded Razorbills on Skokholm. The bird in the foreground, bearing a plastic band on its right leg and monel band on its left leg, was banded as an adult. The bird behind, with a white plastic band on its right leg, was banded as a pullus in 1968.

band denoting their year class so that the age of the birds could be determined from subsequent sight records (Fig. 2). The plastic bands, like their metal counterparts, suffered from wear but provided valuable information on the return of young birds to the colony. Finally, beginning in 1970, full grown birds have been given a laminated plastic band on which large numbers were inscribed, enabling the individuals to be identified at considerable distances in the field. (Table 1).

Observations of banded birds on Skokholm were made during daily visits to the cliffs between mid-March and mid-August (1971-73), and the work was continued by the staff of the Bird Observatory in 1974. In one study colony, The Bluffs, visited daily throughout the season, the birds became tame, and there was a high probability of identifying all color-banded birds present. Only two records (out of a possible 86) relate to birds that were missed in one year but seen in the next (2%), compared with 19 out of 226 (8%) for the other colonies on Skokholm and 31 out of 118 (26%) for the study colony on Skomer.

RESULTS

Fidelity to Natal Colony

Nearly all Razorbills return to their natal colonies to breed. Out of 477 banded birds retrapped on Skokholm, only three (0.6%) had been banded elsewhere. Two birds, aged two and seven years, had been banded on Skomer only three km away, and the other bird,

TABLE 1.
Number of Razorbills color-banded on Skokholm and Skomer 1968-73.

	Adults		Color	Pulli ¹	
	Skokholm	Skomer		Skokholm	Skomer
1968	—	—	White	236	—
1969	—	—	Red	302	—
1970	85	17	Yellow	275	188
1971	61	27	Green	271	188
1972	51	26	Blue	215	272
1973	36	11	Orange	223	68
Total	233	81		1522	716

¹Excluding those that died or lost their color band before fledging. After 1970 chicks on Skomer were color-banded on the right leg and those on Skokholm on the left so that the natal colony was known at subsequent sightings.

banded as a pullus on the Calf of Man (265 km north), was re-trapped breeding on Skokholm in 1970 and recorded in all subsequent years of the study. One Razorbill color-banded as a pullus on Skokholm in 1969 was found breeding on St. Margaret's Island off Tenby (38 km east) in 1974.

A total of 22 birds banded as pulli on Skokholm were positively identified on Skomer up to 1974 (Table 2); no sightings of Skomer-banded birds were made on Skokholm. Two of the Skokholm color-banded birds eventually bred on Skomer. Hence there is some permanent emigration from the colony. Presumably this usually

TABLE 2.
Details of 22 color-banded Razorbills that were banded as pulli on Skokholm and were known to have visited Skomer in their prebreeding years.¹

Year of banding	Year of sighting	Number of sightings
1968	1972	9 (26%) ²
1968	1973	1 (5%)
1968	1974	1 (10%)
1971	1973	0 (10%)
1971	1974	10 (42%)
1972	1974	1 (33%)

¹No pulli were color-banded on Skomer in 1968 (or 1969). Therefore all 1968 class bands were of Skokholm origin; no 1969 class birds were seen on Skomer. The natal colony of birds color-banded in 1970 was not distinguishable (Table 1). Most 1974 records were supplied by T. R. Birkhead.

²The number of sightings on Skomer are given in parentheses expressed as a percentage of the annual total of sightings (*not* corrected for band loss) of birds in that age class.

occurs before breeding age; we have no records of birds moving to another colony once they have started to breed. On the other hand, not all immature birds that visit other colonies necessarily breed there; we think that many may, after visiting another colony, eventually return to their natal colonies to breed. The sharp drop in older birds banded on Skokholm and sighted on Skomer may be explained in this way.

Return of Young Birds to the Breeding Colony

Young Razorbills can be distinguished from adults by plumage characteristics until the second autumn of life (Salomonsen, 1944). In this study, two-year-old birds could also sometimes be recognized by the lack of a white bill stripe. In some individuals the stripe was incomplete or faint (Chambers, 1971), but this character was not a reliable age indicator. Further, the bill of many two-year-old birds may still be noticeably shorter, less deep, and less ridged than that of older birds. In late July, some of the immature birds started the autumn body molt, and white feathers appeared on the throat, giving the plumage a speckled appearance.

The calculations in this and succeeding sections are complicated by unusual events in two years of the study. First, in 1969 a larger than usual number of banded fledgling Razorbills from Skokholm were recovered shortly after leaving the island (see below) and therefore fewer must have survived to reach breeding age than in other years. Secondly, the return of birds in the spring of 1972 was disrupted by almost continuous rough weather (Lloyd, 1973). Possibly as a result of this, laying was delayed by 14 days (compared with 1971), and there may also have been a higher mortality of both adults and immatures (Lloyd, 1976a).

No color-banded, one-year-old birds were recorded on land in the present study, and there were only three sightings of first year birds in the rafts of auks below the colonies, confirming that Razorbills rarely return to the breeding colony when one year old (Lloyd, 1974). Even the number of two-year-old birds coming to land was small (compared with the number that later bred). For each cohort of young, more birds returned to the colony each year from age 2 to age 5 (Tables 3 and 4).

As mentioned, the survival of birds banded as chicks in 1969 was especially low, possibly due to the heavy mortality of Razorbills in a "wreck" during the autumn (NERC, 1971) when 10 (an unusually high number) Skokholm-banded pulli were recovered within a few weeks of fledging. Sightings in 1974 were probably biased by a change in observers, as few of the 1968 or 1969 banded birds (which were almost certainly still alive) were reported. Excluding these observations, the average numbers of birds returning to the colony at successive ages are shown in Table 4. Once the birds started breeding, loss of the color bands increased (presumably because the birds spent more time on the ledges, thus wearing the bands more than if they were at sea). In 1973, at least three 1968 young lost their bands during the breeding season. Band loss must

TABLE 3.

Color-banded birds of known age seen after banding, expressed as percentage of those banded (corrected for band loss).¹

Year of banding as pullus	Year of sighting			
	1970	1971	1972	1973
1968	3 (6)	11 (23)	18 (35)	12 (22) ²
1969		1 (3)	5 (14)	13 (33)
1970			3 (8)	11 (29)
1971				4 (11)

¹Band loss progressed linearly - after 3 years: 7%; 4 years: 12%; 5 years: 28%; and (predicted) 6 years: 40%. It was not always possible to be sure that some of the color-banded birds in a colony were not omitted or counted twice in these records (and those in Table 2), since several different color-banded birds in each age class were often present on land or in flight at the same time.

²Actual numbers seen are given in parentheses.

TABLE 4.

Average (%) return to colony by birds in their second, third, and fourth years of life.

Age (years)	Excluding 1969 pulli	1969 pulli alone
Two	3.2	1.0
Three	11.0	5.0
Four	17.8	12.9

partly account for the relatively small number of sightings of birds of breeding age.

Records of known nonbreeders (identified by color band and metal band number) on successive days throughout the season, permitted an estimate of the amount of the season these individuals spent on land (measured by the difference between the earliest and latest records of individuals in different seasons). Generally, the youngest birds were on land for the shortest time, and the oldest birds for the most time, although the difference between three- and four-year-old birds was not significant (Table 5). Birds aged four years or older and known to be breeding are omitted from this table.

The timing of the breeding season was different in the different years. The dates upon which individual color-banded birds were first seen on land in successive years were corrected for these differences so that data for all years could be compared (Fig. 3). The scale therefore gives the relative stage in the breeding season for the return of young birds. The mean dates of return to the colony (given on the same scale in Figure 3) show that the youngest birds tended not to come to land until the nestling period; these birds remained in the colony for about two weeks and left as the chicks started to fledge. The three-year-old birds first returned at the end

TABLE 5.
Average duration of visit to land during prebreeding years
(days \pm 1 standard deviation)

Age (years)	Length of stay	n	t	P
Two	12.6 \pm 5.5	3	9.3	0.001
Three	21.4 \pm 5.5	7		
Four	21.0 \pm 3.5	11	25.0	0.001
Five	33.0 \pm 7.3	4		

of the incubation period, on the average one week earlier than the two-year-olds, but their departure also coincided with that of the fledging chicks. The four- and five-year-old birds returned even earlier in the breeding season and at least some were present on the island throughout the incubation period; again their departure coincided with the start of fledging.

Age at First Breeding

Before color-banding began at the Skokholm colonies in 1968, few Razorbills under the age of six years were caught as breeding birds (Table 6), although a few birds bred at four years of age. Most birds were caught on the nest, and the youngest breeding birds were nervous and therefore unlikely to be trapped.

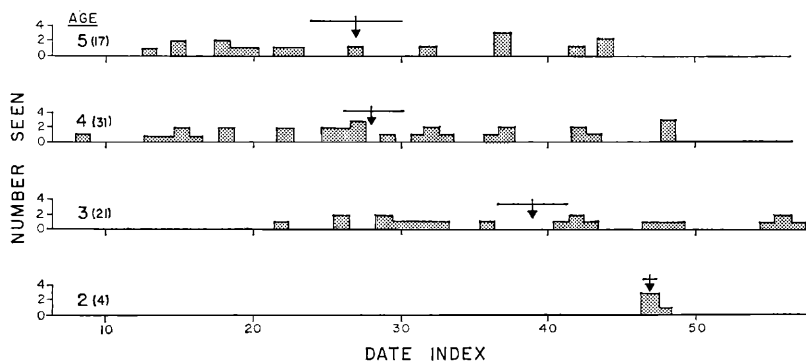


FIGURE 3. Comparison of dates of first sighting on land of immature birds of different ages. Data are corrected for differences in laying date between years. Date Index 25 = approximately the middle of the laying period; arrows mark mean date of return with 1 standard error either side; ages are given in years with sample sizes in parentheses. The significance of differences in mean arrival dates in successive ages is as follows: 2-3 years $d = 3.08$, $P = 0.01$ with 21 d.f.; 3-4 years $t = 3.45$, $P = 0.002$; 4-5 years $t = 0.29$, $P = 0.05$.

TABLE 6.

Number of retraps of known age breeding birds 1963-1970. Birds are included at first recapture only.

Age in years	Number of retraps
Four	7
Five	12
Six	10
Seven	8
Eight	7
Nine	8
Ten	5
Eleven	1

Although the same problems in trapping young breeding birds existed in the present study, the necessary information was obtained mostly from observations of color-banded breeding birds that could be identified without being caught. Twenty individuals of known age were recorded breeding for the first time in the three main years of the study (Table 7). These showed that just over one third of the birds breeding for the first time were four years old and most of the rest were five. There was no evidence that males and females bred for the first time at different ages, as has been reported in other seabirds (Richdale, 1952; 1957; Coulson & White, 1956). The age of first breeding may vary in different colonies; preliminary results of a study at Clo Mor, Sutherland (Highland, Scotland), have shown that some Razorbills breed at

TABLE 7.

Age (years) at first breeding.

Age	1971	1972	1973	Total
Four	3	1 ¹	4	7
Five	2	3	7	12
Six			1	1

¹Skomer breeding bird - see text.

three (J.L.F. Parslow, pers. comm.). There was evidence in the banding data from Skokholm that relatively few young birds bred for the first time in 1972 (the year in which breeding was delayed by bad weather). Although at least 18% of the chicks banded in 1968 were present at the colony in 1972, no color-banded four-year-old birds bred on Skokholm. In 1973, however, despite the poor survival of the 1969 chicks which resulted in only 14% of them returning to the colony, four four-year-old birds bred.

Survival of Adult Birds

Sightings of individually color-banded adult Razorbills provided the following estimates of annual survival:

	% Mean survival	Standard deviation
All birds color-banded on Skokholm	80.7 ±	2.8
Birds color-banded in The Bluffs study colony, Skokholm	89.0 ±	6.1
Birds color-banded in the Inner Basin study colony, Skomer	92.1 ±	4.7

The differences in estimates of survival between all the birds and the two small groups were significant ($t = 3.09$, $P = 0.01$, and $t = 5.10$, $P < 0.001$ for The Bluffs and Skomer birds, respectively) but survival of birds on The Bluffs was similar to that on Skomer ($t = 1.05$, $P > 0.05$).

Sightings in 1974 were used to correct records for birds missed in previous years. Otherwise only the 1974 sightings for The Bluffs are included in the estimates of mean survival, as the change in observers (after 1973) meant that many birds were missed outside The Bluffs in 1974. On Skokholm the highest annual survival rate was recorded on The Bluffs where nearly 90% of the adults survive each year. On Skomer the estimate was higher than this (92%). Estimates based on banding recoveries of birds banded throughout Britain and Ireland between 1960 and 1970 gave an annual survival figure of $89.0 \pm 1.1\%$ (Lloyd, 1974). This agrees closely with the 89 to 92% annual survival of color-banded birds on Skokholm and Skomer and with Mead's (1974) analysis of banding records, using only those birds ". . . recovered after the heavy mortality and before ring loss has started," which gave $91.4 \pm 4.0\%$ annual survival.

Life Table for the Skokholm Razorbills

Using the data presented in this paper and other material on the breeding success (Lloyd, 1976a), it is possible to construct a rough life table for the Razorbill on Skokholm. There is no firm evidence that pairs failed to lay in certain years, although it is possible some adults that lose their mates fail to remate in time to breed. Considering a population of 100 pairs, 100 eggs are laid and produce 66 fledged young. However, one fourth of the pairs that lose their eggs (the majority of the failures are as a result of egg loss) lay a replacement. Such eggs have a slightly lower overall success (63%) than the first clutches, but about five replacement chicks are raised by each 100 pairs. Hence, 100 pairs of birds might be expected to raise 71 ($66 + 5$) young each year.

About 18% of the young birds may survive to breeding age (4 or 5 years) (Table 4). Hence, only about 13 young per 100 pairs (18% of 71) are likely to reach breeding age each year. This figure is a minimum since interchange between colonies is assumed to be negligible, although we know that a few Skokholm birds finally

breed on Skomer. Nevertheless, if the population is to remain stable, recruitment seems insufficient in view of the data on adult survival. An annual mortality of 8 to 10% yields 16 to 20 adults dying per 100 pairs per year.

Apart from the errors already discussed, there are other difficulties in accepting these findings. On Skokholm, an estimated 62% of the eggs lost before hatching (19% of all those laid) were probably taken by Jackdaws (*Corvus monedula*) (Lloyd, 1976a). This is a relatively new source of mortality; only three pairs of Jackdaws bred on Skokholm in 1965 although there were at least 70 pairs by 1974. Comparable figures for Skomer are about 20 pairs in 1946 (Buxton and Lockley, 1950) and about 200 pairs in 1964 with little change since then (Birkhead, 1974b). Moreover, one of the main years for which adult survival was calculated (1972) was unusual in that the breeding season was late and there was some indication of higher than usual mortality among the adults before the breeding season. The little evidence available suggests that survival of adults may exceed 90-92% in some years, but is less in other years. In order to obtain more accurate estimates, and hence a more reliable average figure, longer-term study would be necessary. Continuing studies of Razorbills at Clo Mor have shown that annual survival of adults can be as high as 96% (J.L.F. Parslow, pers. comm.).

DISCUSSION

To summarize, color-banding on Skokholm showed that most Razorbills return to their natal colony to breed. There was no interchange of adult birds between colonies, but some young birds from Skokholm were seen on Skomer, and at least one remained there to breed. Other banding records suggest that there is little permanent immigration or emigration at the Skokholm colonies. Similar studies of the Manx Shearwater (*Puffinus puffinus*) on Skokholm (Harris, 1972) have shown that even short-distance movements (to Skomer) are uncommon (0.15%) and very few birds (0.06%) move away from Skokholm to breed. Like Razorbills, young shearwaters may visit other colonies during their pre-breeding years but eventually return to breed on Skokholm.

Few young Razorbills returned to the colony before their third and fourth year of life. The return of nonbreeding birds followed a similar pattern to that described for other seabirds. Perrins et al. (1973) found that the youngest immature Manx Shearwaters (two years old) returned to the colony latest in the season and stayed the shortest time, while the older immature birds returned progressively earlier each year and remained at the colony for increasing lengths of time. As many as 30% of the shearwater chicks banded each year returned to the colony in prebreeding years. Comparable figures for other species of seabirds studied are 38% for the Short-tailed Shearwater (*Puffinus tenuirostris*) (Serventy, 1967) and 64% for the Waved Albatross (*Diomedea irrorata*) (Harris, 1973). Compared with these, the 18% return of Razorbill chicks up to the age of four is low.

Studies of attendance at breeding colonies throughout the season in the Razorbill on Skokholm (Lloyd, 1973; Lloyd, 1976a) and elsewhere (Lloyd, 1975b) have shown that the number of birds in a colony increases gradually to a peak in the nestling period. Color-banding of Razorbills on Skokholm has shown that this is due to the return of nonbreeding birds that are present in greatest numbers about the time of the nestling period. As soon as the chicks start to fledge, attendance at the colony decreases and becomes more variable, and this coincides with the exodus of immature birds from the colony.

TABLE 8.
The age at first breeding (years) of some seabird species.

Species	Age	Reference
Waved Albatross (<i>Diomedea irrorata</i>)	6	Harris, 1969
Laysan Albatross (<i>D. immutabilis</i>)	7	Rice and Kenyon, 1962
Black-footed Albatross (<i>D. nigripes</i>)	5	Rice and Kenyon, 1962
Royal Albatross (<i>D. epomophora</i>)	♀, 9 ♂, 8 or 11	Richdale, 1952
Manx Shearwater (<i>Puffinus puffinus</i>)	5 or 6 8 or 9	Perrins et al., 1973 Brooke, 1974
Sooty Shearwater (<i>P. griseus</i>)	6	Richdale, 1963
Short-tailed Shearwater (<i>P. tenuirostris</i>)	♀, 5 or 6 ♂, 6 or 7	Serventy, 1967
Storm Petrel (<i>Hydrobates pelagicus</i>)	4 or 5	Scott, 1970
Leach's Petrel (<i>Oceanodroma leucorhoa</i>)	4 or 5	Huntington and Burt, 1972
Gannet (<i>Morus bassanus</i>)	5 or 6	Nelson, 1966
Lesser Black-backed Gull (<i>Larus fuscus</i>)	4 or 5	Harris, 1970
Herring Gull (<i>L. argentatus</i>)	4 or 5	Harris, 1970
Black-legged Kittiwake (<i>Rissa tridactyla</i>)	♀, 3 or 4 ♂, 4 or 5	Coulson and White, 1956
Arctic Tern (<i>Sterna paradisaea</i>)	4	Coulson and Horobin, 1976
Razorbill (<i>Alca torda</i>)	4 or 5	Lloyd, 1976a
Common Murre (<i>Uria aalge</i>)	3	Southern et al., 1965
Common Puffin (<i>Fratercula arctica</i>)	5	Ashcroft, 1976

In common with a number of seabirds (Table 8), the Razorbill does not breed during the first few years of life. Deferment of maturity was considered by Wynne-Edwards (1955) to be one of the ways in which the reproductive rate of a long-lived species is kept low in order to avoid over-population. If this were the main function of deferred maturity, in the absence of the threat of over-population, one would expect the age of first breeding to decrease; this has been reported in some expanding gull populations (Davis, 1975).

Deferment of maturity may also be a method whereby the younger birds of the population can avoid the strain of breeding until they reach an age at which the extra effort is justified by the probability of producing young (Lack, 1966). As with most other seabirds studied, Razorbills breeding for the first time produce fewer young than older birds (Lloyd, 1976a), possibly due to lack of experience in young birds, which leads to a breakdown of the behavior necessary for the care of egg or chick.

During the last years of this study (1971-73) the Razorbill population on Skokholm remained stable. Theoretically, in such a population with negligible emigration and immigration, recruitment should balance mortality each year. Recruitment depends not only on breeding production but also on the survival of the young to breeding age and, in a species showing a deferment of maturity, the latter is especially important.

Change in either of the two population parameters can be expected to affect the size of the breeding population. A slight increase in adult mortality has a significant effect on the breeding population. For example, in a species with 10% adult mortality, if five "extra" birds die per 100 adults, the annual mortality increases by 50% and the life expectancy falls from about 9½ years to about 6 years. This makes the breeding population especially vulnerable to the slightest variation in mortality. Breeding success also affects population size. Estimates of breeding success (percentage of eggs laid producing fledged young) in previous years on Skokholm (61% Brun, 1959; 52% Harris, 1965; 53% Plumb, 1965) indicate that breeding success was relatively high in the years of the present study. Our findings suggest, however, that the Skokholm Razorbills may be barely able to maintain their numbers and that they may not have the reproductive capacity to increase once numbers have been reduced as a result of a sudden temporary increase in adult mortality or decrease in breeding success.

SUMMARY

The paper is based on banding data from Skokholm and Skomer Islands (Dyfed, Wales) where 8,581 Razorbills have been banded since 1936. Color-banding was carried out between 1968 and 1974 in order to identify age classes among the young birds or individuals among the adult birds.

Most birds return to the breeding colony from the age of two years onwards. Some birds banded on Skokholm visited Skomer as immatures, although most birds finally bred in the natal colony. Immature birds returned progressively earlier each season and stayed correspondingly longer in the colony as they became older. Just over one third of the color-banded birds breeding for the first time were four years old, and most of the rest were five. This is similar to a number of other seabird species.

Adult annual survival was 90-92%; this compares well with similar estimates of survival in Razorbills using national band recoveries. An estimated 13 young per 100 pairs survive to breeding age to balance the 16 or 20 adults (per 100 pairs) that die annually;

thus the Razorbill on Skokholm may not be able to maintain its numbers. A relatively new source of mortality is egg predation by the island's increasing Jackdaw population.

ACKNOWLEDGMENTS

Clare Lloyd was supported by a Natural Environment Research Council grant from 1971 to 1973. We should like to thank all those who long-sufferingly helped trap Razorbills, especially the staff of Skokholm Bird Observatory and of the Edward Grey Institute, Oxford. The West Wales Naturalists' Trust allowed the study to be carried out on Skokholm and Skomer. Dr. M. P. Harris provided useful comments on the manuscript.

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