ADULT SURVIVAL AND PRODUCTIVITY OF NORTHERN FULMARS IN ALASKA[1]

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Abstract. The population dynamics of Northern Fulmars (*Fulmarus glacialis*) were stud-
ied at the Semidi Islands in the western Gulf of Alaska. Fulmars occurred in a broad range
of color phases, and annual survival was estimated from the return of birds in the rarer
plumage classes. A raw estimate of mean annual survival over a 5-year period was 0.963,
but a removal experiment indicated the raw value was probably biased downward. The
estimate of annual survival adjusted accordingly was 0.969. Mortality during the breeding
season was less than 10% of the annual total, and postbreeding mortality of failed breeders
was three to four times higher than that of successful breeders. Breeding success averaged
41% over 9 years. About 5% of experienced birds failed to breed each year due to physical
destruction of their breeding sites, mate-loss, or other causes. An estimated 30% of the birds
near the colony in one year were of prebreeding age. A comparison of population parameters
in Pacific and Atlantic fulmars indicates that higher survival in the prebreeding years is the
likely basis for population growth in the northeastern Atlantic. The correlation of breeding
success and survival suggests both parameters may decline with age.

*Key words: Northern Fulmar; Fulmarus glacialis; Alaska; population dynamics; survival;
productivity; nonbreeding.*

INTRODUCTION

The Northern Fulmar (*Fulmarus glacialis*) has
been studied from the standpoint of population
dynamics and life history, but most available
information pertains to an expanding population
in the temperate northeastern Atlantic. Total
population in that region has increased at an an-
nual rate of 4 to 7% over a period of about 200
years (Fisher 1952, 1966; Cramp et al. 1974).
The attendant proliferation of colonies (e.g., for-
merly only one in Britain, now hundreds) con-
trasts sharply with the species' pattern of dis-
persion elsewhere. In arctic regions of Europe,
Greenland, and eastern Canada, as well as in

Alaska, fulmars tend to have relatively few
breeding places, but colonies often are exceed-
ingly large (Salomonsen 1965, Nettleship 1977,
Sowls et al. 1978).

Here I present information on adult survival
and annual productivity gathered over 11 years
at the Semidi Islands, one of four major breeding
areas of fulmars in the northeastern Pacific. The
purpose of this study was to estimate basic pop-
ulation parameters at the Semidis and provide
comparative information for assessing differ-
ences in population dynamics between Pacific
and Atlantic fulmars.

STUDY AREA AND METHODS

The Semidi Islands (56°N, 156°W) are located
about 80 km from the mainland in the western
Gulf of Alaska. An estimated 440,000 fulmars
bred throughout the Semidis, using about 65 km

[685]

of coastline on nine islands (Hatch and Hatch 1983). Sample plots and breeding sites were located on a 2-km stretch of cliffs on the west side of Chowiet Island, the largest island in the group (1,300 ha).

Estimates of adult survival and the most detailed data on productivity were obtained in a 6-year intensive study period from 1976 through 1981. I arrived in the study area between 31 March and 2 May and departed between 27 August and 9 September each year, except 1978, when I was present from 24 May through 29 June and on 2 days later in the season, 30 August and 8 September. In 1983, 1985, and 1986 I spent one to several days at the study site in late August to assess the annual production of young.

POPULATION STATUS AND PRODUCTIVITY

Fulmars bred mainly on the upper, vegetated portions of cliffs. Their breeding sites were in most cases permanent, easily recognizable features that persisted because of the digging and clearing that the birds engaged in each spring. In 1976 I established six permanent census plots comprising 500 to 600 apparent breeding sites and made daily attendance counts of the singles and pairs present (118 counts in 1976, 129 in 1977, 35 in 1978, 116 in 1979, 122 in 1980, 153 in 1981). Counts were generally made between 09:00 and 16:00, since day-long watches at one plot in 1977 showed that midday counts were little affected by diurnal variation in numbers (Hatch 1985). I selected 292 occupied sites for detailed observation in 1976, then increased the sample to 540 to 550 sites in later years. About half of those sites were on the census plots just described; the locations of all individually monitored sites were marked on photographs, and daily observations were made from a distance using binoculars or spotting scope to record attendance, egg dates, hatching, and the survival of young. Observations on the same sites were carried over between years, even after discontinued use by any particular pair of fulmars.

I use the term breeding success to mean the fraction of eggs laid that resulted in a fledged (or late stage) chick. Hatching success refers to the proportion of eggs laid that hatched; fledging success is the survival of chicks from hatched eggs. Hatchability is the proportion of eggs incubated to full-term that hatched. "Experienced" pairs were known to have produced an egg in a previous year. I use the term prebreeders to denote those birds believed to have no prior breeding experience, and the term nonbreeders to include prebreeders as well as experienced birds that skipped a breeding year.

The fledging period of fulmars averages about 53 days (Mougin 1967). When I left the islands the youngest chicks were about 3 weeks old and the oldest were still 1 to 2 weeks from fledging. Estimates of fledging success were based on the number of young surviving when I departed, and must be considered maximal. Observations in 1978 spanned the entire egg-laying period, but breeding success was determined on two visits late in the season. Estimates of breeding success in 1983, 1985, and 1986 were the number of young surviving in August divided by the mean number of eggs laid in the same sites from 1976 to 1981.

ADULT SURVIVAL

The population of fulmars on the Semidi Islands included the full range of color phases found in this polymorphic species. The gradation from light to dark morphs was continuous, but for practical purposes I classified birds into four groups denoted LL, L, D, and DD, following Fisher (1952). The distribution in a sample of 4,642 birds was 1.8% LL, 13.0% L, 3.5% D, and 81.7% DD.

The estimation of survival was based on individual recognition of birds in the rarer color morphs. The sample included one bird from each of about 200 pairs and both birds from another 20 to 30 pairs that belonged to the LL, L, or D categories. I also included eight to 10 dark phase birds that had aberrant, nearly all-black culmens (possessed by less than 1% of the population of DD fulmars). The majority (72%) of individuals monitored for survival were of the L color phase, and although that category was the most common of the three morphs used, it was also the most variable. Consequently I had a greater knowledge of most birds as individuals than implied by a simple assignment to category, and this familiarity was reinforced through daily observation. I recorded on tape a detailed description of each bird, noting especially the relative degree of dark shading on the belly, breast, crown, and nape, and any other distinguishing features. I reviewed my recorded notes in cases of doubt about the identification of individuals between years. The sexes of birds in mixed pairs were determined by their position in copulation, and

the annual sample of birds at risk included only those known to have bred the preceding year.

REMOVAL EXPERIMENT

To assess the problem of birds changing breeding sites and thereby lowering the estimate of annual survival, I collected the dark member in each of 20 LL/DD, L/DD, or D/DD pairs in 1979, and made daily observations on the sites for the remainder of that season and in the next 2 years. If the surviving bird of each pair acquired a new mate and resumed breeding in the same site it would indicate that disuse of a site more likely resulted from a move than from the death of one member of a pair. I collected an additional 20 birds from mixed pairs in 1980, for which I obtained information spanning one succeeding year.

DATA ANALYSIS

I use the formula $(2 - m)/2m$ (Lack 1954) to calculate mean adult life expectancy from the mortality rate (m), an appropriate conversion if either of the following conditions is true: (1) mortality rate is independent of age, or (2) the population is at equilibrium and the sample used to estimate m is an unbiased cross-section of adult age structure. I assume that my sample of adults was essentially random and included age classes in proportion to their occurrence in the population.

For proportions that represent an annual rate of some event such as survival or hatching success, I first tested for significant heterogeneity among years using the G test statistic (Sokal and Rohlf 1981). If heterogeneity was nonsignificant, the mean I report is a pooled sample proportion: $\sum_{i=1}^{k} X_i / \sum_{i=1}^{k} n_i$, where k is the number of years sampled, n_i is the sample size in year i, and X_i is the number of occurrences of the event in year i. If there was heterogeneity among years, I report an arithmetic mean of proportions: $\sum_{i=1}^{k} P_i/k$, where P_i is the proportion observed in year i. In either case, I used Cochran's (1977) method of estimating the variance of a proportion from cluster sampling (clusters = years).

RESULTS

ADULT SURVIVAL

Five estimates of the annual survival rate varied from 0.922 to 0.979 (Table 1), but the observed heterogeneity among years was nonsignificant $(G = 6.53, df = 4, P > 0.1)$. Survival averaged 0.963 overall, indicating a mean adult life expectancy of 26.5 years. Considering the limitations of the method, that estimate of life expectancy is believed to be conservative (see Discussion).

Apparent overwinter mortality was four times higher among birds that had failed in their breeding attempt the preceding year than among successful breeders (Table 1). A high incidence of summer mortality and associated breeding failure could explain the difference, because some birds missing in spring would have failed to raise young the year before simply because they died in the attempt. Criteria for deciding that parental death was the cause, not the aftermath, of a breeding failure were: (1) that I never saw the known individual of a pair during the remainder of the season in which failure occurred, and (2) the attendance pattern of the survivor indicated the loss (e.g., an unusually long incubation shift preceding egg loss or lone attendance on a regular basis after failure). Only three of the 40 presumed mortalities in Table 1 met those criteria. Thus, adult mortality during the three summer months June to August was less than 10% of the annual total, and most of the apparent difference in survival between failed and successful breeders remains to be explained.

The 5-year total of 1,091 bird-years at risk (Table 1) was distributed between the sexes as follows: 589 bird-years for males, 449 bird-years for females, and 53 bird-years for individuals that died or were deleted from the sample before they were positively sexed. Thus, the composition of the sample was 56.7% males and 43.3% females. Similarly, among 32 birds of known sex that disappeared between breeding seasons, 18 (56.3%) were males and 14 (43.8%) were females. There was thus no evidence of a sex difference in the annual survival rate.

REMOVAL EXPERIMENT

Thirty-eight (95%) of the 40 survivors in the removal experiment continued to occupy their old breeding site in the season following the removal of their mates (Table 2). Thirty-six birds acquired new mates, and 20 of those newly formed pairs bred in their first year together. Thus, the usual pattern of site use after the death of one member of a pair was clear: the survivor acquired a new mate and resumed breeding at the same

TABLE 1. Adult survival rates of fulmars breeding on the Semidi Islands.

| Year i | Variable | Breeding attempt year $i - 1$ | | Total |
		Successful	Failed	
1977	Birds at risk	27	75	102
	Apparent deaths	2	6	8
	Survival	0.926	0.920	0.922
1978	Birds at risk	129	124	253
	Apparent deaths	2	9	11
	Survival	0.984	0.927	0.957
1979	Birds at risk	119	137	256
	Apparent deaths	0	7	7
	Survival	1.000	0.949	0.973
1980	Birds at risk	134	110	244
	Apparent deaths	1	8	9
	Survival	0.993	0.927	0.963
1981	Birds at risk	136	100	236
	Apparent deaths	3	2	5
	Survival	0.978	0.980	0.979
Total	Birds at risk	545	546	1,091
	Apparent deaths	8	32	40
	Survival ($\pm$SE)	0.985 $\pm$ 0.005	0.941 $\pm$ 0.010	0.963 $\pm$ 0.007
	$\bar{x}$ adult life (years)	66.2	16.4	26.5

nest site, sometimes after a delay of one or more years. The experiment detected no differences in those respects between males and females.

PRODUCTIVITY

Breeding success varied from about 7 to 72%, averaging 41% (Table 3). Hatching success was more variable than fledging success, but both rates varied significantly among years ($P < 0.001$, G-tests). Fulmars lay a single egg each season, and relaying after the loss of the first clutch is unknown.

Overall, about 75% of the observed prefledging mortality occurred during the egg stage, and those losses were concentrated in the first 2 weeks after laying (Fig. 1). Usually there was no sign of the mode of failure other than the disappearance of the egg or chick. However, most egg losses were believed to have resulted from opportunistic predation on unattended eggs by Glaucous-winged Gulls (*Larus glaucescens*) or Common Ravens (*Corvus corax*). Another period of relatively high mortality was the first 2 weeks after hatching, when chicks were rarely left unattended. Poor

TABLE 2. Breeding status of surviving fulmars one and two years after experimental removal of their mates.

| Status of survivor | Survivors, 1979 removal (8 males, 12 females) | | Survivors, 1980 removal (11 males, 9 females) |
	1980	1981	1981
Present, same site			
Males	8 (100%)	7 (88%)	11 (100%)
Females	10 (83%)	7 (70%)	9 (100%)
Sexes combined	18 (90%)[a]	14 (78%)[a]	20 (100%)[a]
Paired			
Males	8 (100%)	7 (88%)	10 (91%)
Females	10 (100%)	7 (70%)	8 (89%)
Sexes combined	18 (100%)[a]	14 (100%)[a]	18 (90%)[a]
Breeding			
Males	2 (25%)	4 (57%)	6 (60%)
Females	5 (50%)	5 (71%)	7 (88%)
Sexes combined	7 (39%)[b]	9 (64%)[b]	13 (72%)[b]

[a] Sex differences, if any, not significant ($0.2 < P < 0.9$) in G tests of two-way contingency tables.
[b] Sample sizes too small for contingency tests.

provisioning by the parents or inviability of some of the recently hatched young may have contributed to those losses. Chicks were constantly guarded by one or both parents for an average of 16 days, after which the nestlings appeared to be invulnerable to avian predators.

Essentially the same pattern of prefledging survivorship was observed every year, although the relative intensity of egg and chick losses in the two critical periods was variable (Fig. 1). Some of the losses depicted in Figure 1 for the post-hatching guard stage were actually of inviable, unhatched eggs. On average, 7% of fully incubated eggs failed to hatch, with little variation in hatchability among years (Table 1). Those failures amounted to 12% of total egg and chick mortality, and 16% of the losses occurring in the egg stage.

Nonbreeding among experienced breeders reduced slightly the potential production of young. Instances of failure to attempt to breed in any year could be ascribed to at least three causes. First, breeding sites were destroyed by physical processes (erosion, rockfalls, etc.) at an annual rate of about 1% (11 instances/983 site-years), which on average resulted in the loss of one breeding year for the affected pair (8 years missed by seven pairs in which the effect was known; range: 0–2 years missed). Second, in about half of the instances in which a bird died, there was a loss of at least one breeding year for the surviving member of the pair (Table 2). Finally, there were two instances of nonbreeding by experienced pairs in which both individuals were known (2.8% of 71 observations); these pairs failed to produce an egg for unknown, possibly physiological, reasons. Altogether, about 5% of experienced birds failed to breed in any year due to these factors.

SITE USE AND OCCURRENCE OF PREBREEDERS

A relatively constant fraction (87%) of the breeding sites observed were regularly attended by breeding or nonbreeding pairs (Table 4). On average, about 8% of the sites were vacant each year, and the remainder were used by an unpaired bird. Overall, the proportion of nonbreeders among site-holding pairs averaged about 15%. Including unpaired singles, the fraction of non-breeding birds in this sample averaged 17.3%.
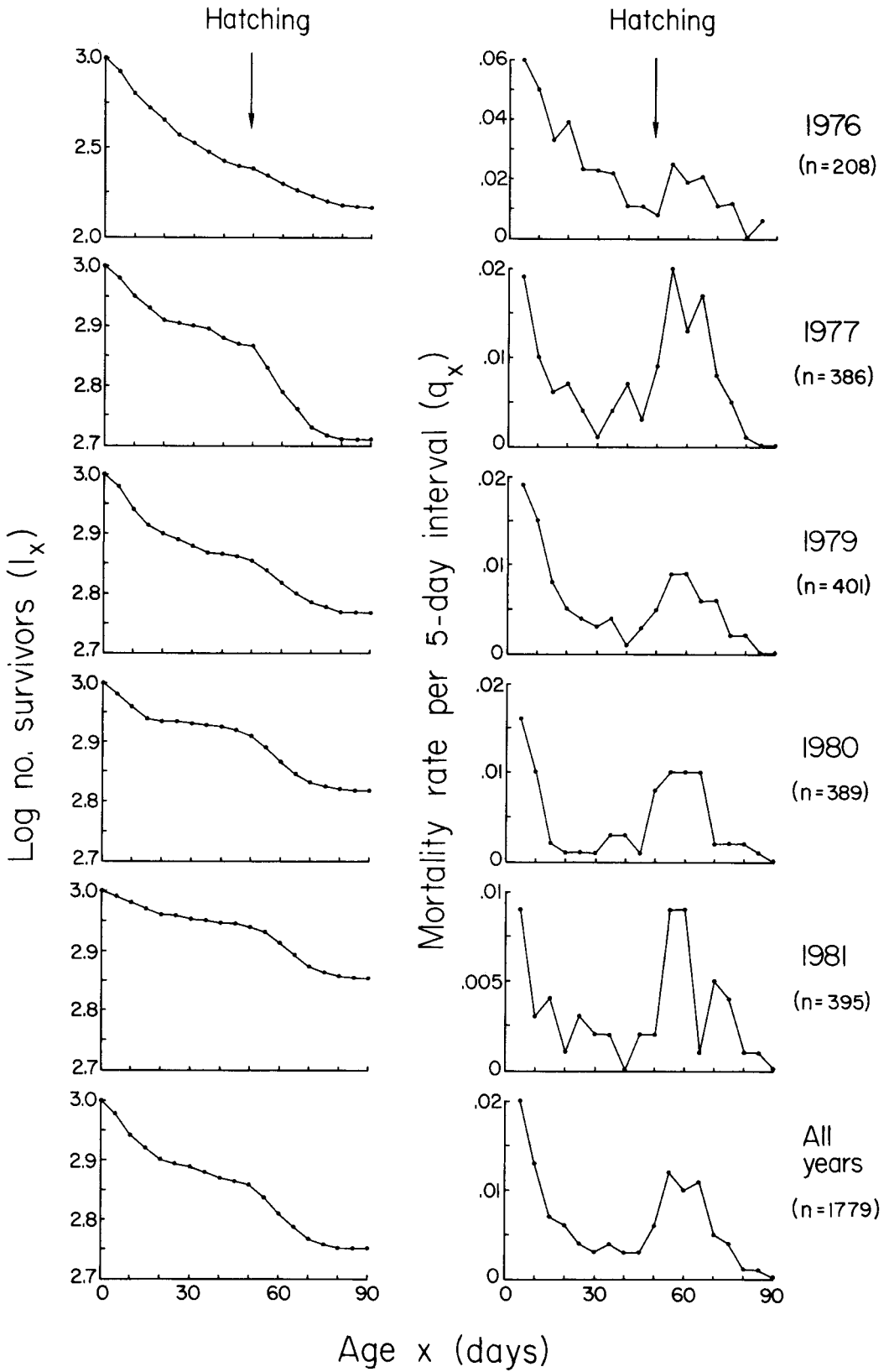
On certain days during the prelaying period nearly all of the pairs that produced eggs in a

TABLE 3. Breeding performance of fulmars in 9 years at the Semidi Islands.

Variable	1976	1977	1978	1979	1980	1981	1983	1985	1986	All years[a]
Eggs laid	208	386	397	400	389	395	370[b]	393[b]	393[b]	3,331
Eggs hatched	47	267	—	270	300	312	—	—	—	—
Inviable eggs	4	18	—	19	19	32	—	—	—	—
Chicks fledged	31	197	183	238	256	283	136	26	75	1,422
Hatchability	0.922	0.937	—	0.934	0.940	0.907	—	—	—	0.929 ± 0.0076
Hatching success	0.226	0.692	—	0.675	0.771	0.790	—	—	—	0.631 ± 0.0768*
Fledging success	0.660	0.738	—	0.881	0.853	0.907	—	—	—	0.808 ± 0.0411*
Breeding success	0.149	0.510	0.461	0.595	0.658	0.716	0.368	0.066	0.191	0.413 ± 0.0920*

[a] Asterisks indicate significant between-year variation ($P < 0.001$).
[b] Mean number of eggs laid in previous years on plots checked in August.

Hatching

Hatching

1976
(n=208)

1977
(n=386)

1979
(n=401)

1980
(n=389)

1981
(n=395)

All
years
(n=1779)

Log no. survivors (l_x)

Mortality rate per 5-day interval (q_x)

Age x (days)

given season were present at their breeding sites. On 19 April 1981, for instance, 378 of 396 known breeding pairs were present, and another nine breeding birds were present as singles. Plot counts that day totaled 511 pairs and 176 singles. Applying ratios of breeding and nonbreeding birds present in individual breeding sites to the plot counts, I estimated that 257 (21.8%) of the 1,178 birds on the study plots were nonbreeders. That estimate is larger than the 17.3% indicated above because it includes nonbreeders observed on land early in the season that did not use established, recognizable sites.

Since the large majority of birds that eventually bred in 1981 were on their breeding sites when the count was made on 19 April, it follows that birds in the air or on the water at that time were mostly nonbreeders. A total of 7,000 birds were estimated to be either flying (2,000) or sitting on the water (5,000) adjacent to the 2-km expanse of cliffs that constituted the main study area. A census in 1976 had indicated a total of about 40,000 birds on land in the area (Hatch 1979). Thus the best estimate of the nonbreeding portion of the population is 34%: 22% of 40,000 birds on land plus 7,000 birds on the wing or resting on the water. Since only about 5% of experienced birds failed to breed each year, birds of prebreeding age constituted about 30% of the population on or near the colony in 1981.

POPULATION STATUS AND TRENDS

Population stability seemed to be indicated by the relative constancy of site use and egg production from year to year (Table 4). Daily attendance counts on study plots were also intended as an indicator of annual changes in population, but the counts varied greatly depending on the stage of the breeding cycle. Attendance was so variable before egg laying that counts made then were poorly suited to the purpose; the smallest variances over any 30-day period were obtained during early to mid-incubation. The means of those counts showed an obvious upward trend over 6 years (Fig. 2). As it happened, however, breeding success also increased almost monotonically over the study period (Table 3), so plot counts in the early years reflected, at least in part,
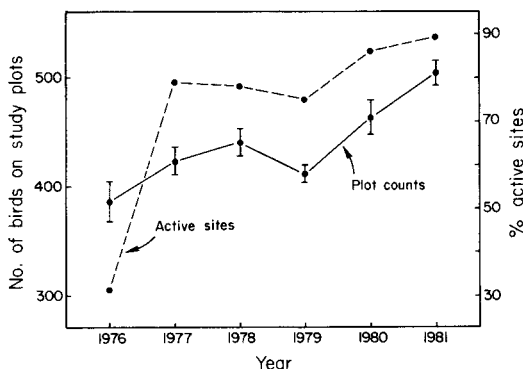

FIGURE 2. Number of birds (mean ± SE) on six study plots over the period from 11 to 40 days after egg laying began in 6 years ($n = 30$ counts for all years except 1978, for which $n = 21$). The plot of active sites is the percentage of eggs surviving on the last day of the counting period.

the lower attendance by failed birds. A regression of mean plot counts and the percentage of active sites ($r = 0.74$, $P < 0.05$) left no significant trend that would indicate an increase in population. Finally, there was no trend in the maximum count obtained on any single day in May in 4 years: 1,152 in 1977, 1,093 in 1979, 1,095 in 1980, and 1,228 in 1981.

DISCUSSION

RELIABILITY OF SURVIVAL ESTIMATES

There are advantages and pitfalls in using natural markings to identify individual animals in the field (Pennycuick 1978). The system used in the present study could not easily have been shared by two observers working independently, nor would I have attempted to estimate survival had observations been limited to one brief period each year. However, the frequency and duration of observations promoted a familiarity with many individuals and their behavior patterns that would be difficult to duplicate or record by any other means. The method avoided one problem encountered in banding studies; namely, the disturbance associated with capture and handling that can influence chances for resighting (e.g., Birkhead and Hudson 1977, Dunnet and Ollason 1978a). However, since the birds were not band-

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FIGURE 1. Survivorship curves and age-specific mortality rates of Northern Fulmar eggs and chicks in 5 years on the Semidi Islands.

TABLE 4. Occupation of potential breeding sites[a] and the breeding status of pairs in 6 years.

Year	No. sites observed	Pairs[b] No.	Pairs[b] %	Breeding pairs No.	Breeding pairs %	Unpaired singles[c] No.	Unpaired singles[c] %	Empty sites[d] No.	Empty sites[d] %
1976	217	187	86.2	150	80.2	16	7.4	14	6.4
1977	425	378	88.9	312	82.5	26	6.1	21	5.0
1978	424	340	80.2	321	94.4	29	6.8	55	13.0
1979	426	369	86.6	321	87.0	26	6.1	31	7.3
1980	423	361	85.3	314	87.0	19	4.5	43	10.2
1981	422	363	86.0	317	87.3	16	3.8	43	10.2
Mean[e]	383	332	86.7	283	85.3	21	5.4	30	7.9
SE$_{mean}$			0.67		1.22		0.58		1.11

[a] Potential breeding sites defined as sites regularly occupied by a single bird or pair in at least one season.
[b] Pair present at site on three consecutive days or on 5 of any 15 consecutive days during season.
[c] Above criteria (in [b]) met by a single bird only.
[d] Sites at which neither of the above conditions ([b] or [c]) was true.
[e] Data for 1978 biased relative to other years because no observations made in the prenesting period; 1978 data excluded from means.

ed, there was no guarantee against possible mistakes in identification.

Despite the absence of banded birds, two checks on the reliability of the data are available. First, if the estimate of survival shown in Table 1 is accepted as an approximation (0.963), it can be calculated from the frequency distribution of color phases that 3.1 substitutions within categories (LL for LL, L for L, or D for D) were expected to occur during the study. In fact, two such changes that I detected are included in the total of 40 mortalities. Expected and observed frequencies did not differ in this instance (G = 0.20, df = 1, P > 0.5), although an expected value greater than 5 is the conventional requirement for such a test (Sokal and Rohlf 1981).

Another check on the reliability of the whole sample is the apparent survival of the rarest morphs. If mistakes were made in identifying individuals, the resulting bias would be in the direction of overestimating survival. However, the error would be greater among L birds (13% of the population) than among LL birds (1.8%), for instance, because the likelihood of undetected replacements occurring in the latter group was lower. The annual survival rate estimated for LL, D, and black-billed birds was 0.974, based on 306 bird-years of observations (Table 5), compared with 0.959 annual survival estimated for L birds. The direction of the difference was opposite to that predicted if mistakes in identification were occurring, but nonsignificant in any case (G = 1.42, df = 1, P > 0.2).

Also of concern is the possibility of an opposite bias introduced by undetected changes of breeding site. Pairs that changed breeding sites often sat alternately at the old and new site, both of which became known to me, over a period of days or weeks in the season before the change. Lacking such information, however, changes of breeding site were liable to be recorded as mortalities, resulting in an underestimate of survival.

The removal experiment provided a control. Its implications for survival estimates are seen by comparing site use after experimental and presumed natural mortalities (Table 6). The higher incidence of empty, unused sites associated with the presumed natural deaths suggests that in most of those instances the event was not mortality but an undetected change of breeding site. In particular, the removal experiment indicated that about six of the presumed mortalities in Table

TABLE 5. Survival estimates based on returns of the rarest morphs.

Category	Bird-years at risk	Apparent deaths	Annual survival
Black culmen (DD)[a]	23	1	0.957
White (LL)	165	4	0.976
Gray (D)	118	3	0.975
Total	306	8	0.974

[a] All birds with black bills were dark phase (DD) birds.

TABLE 6. Breeding site status after natural and experimental mortalities.

Status	Natural (n = 40)	Experimental (n = 40)
New partner, breeding	20 (50%)	20 (50%)
New partner, nonbreeding	10 (25%)	16 (40%)
No partner, same site	2 (5%)	2 (5%)
Site empty	8 (20%)[a]	2 (5%)[a]

[a] Percentages differ significantly (G = 4.14, df = 1, P < 0.05).

1 probably did not occur. An adjusted estimate of annual survival that is consistent with the results of the removal experiment is 0.969.

Accuracy in estimating prefledging survival is also important when considering the life table of this population. Although losses were practically nil during the last 2 weeks of observation each year (Fig. 1), it is possible that chick mortality increased again before fledging. For example, late-hatched fulmars often died shortly before fledging due to the onset of winter and inclement conditions in a high arctic colony (D. N. Nettleship, pers. comm.). Comparable mortality in the relatively temperate conditions around the Semidi Islands seems unlikely, but events during the latest stages of the breeding cycle were not observed.

COMPARISON OF PACIFIC AND ATLANTIC COLONIES

Adult survival estimates obtained in this study were similar to those reported from colonies in Britain: 0.984 (Macdonald 1977), 0.943 (Dunnet and Ollason 1978a), 0.968 (Buckland 1982, from a reanalysis of Dunnet and Ollason's data). Estimates of annual productivity averaging 0.36 young per pair are available from 27 colony-years of observation in the same region (Mougin 1967, Macdonald 1975, Dunnet 1975, Dunnet et al. 1979). Annual productivity in both regions tends to be highly variable, and my estimate of 0.41 young per pair ($n = 9$ years) does not differ significantly from the British value. Colonies in the British Isles have increased rapidly in recent years, whereas no evidence of population change was found in the present study.

No one has directly measured the prebreeding survival of Northern Fulmars, but the mean expected in British colonies was calculated by Dunnet and Ollason (1978b) to be 0.884 per year, given a 4% annual increase in population, or 0.934 per year, given a 7% annual increase. Those rates correspond to 33 to 54% of fledged young surviving to breed at age 9 years, the mean age of first breeding (Ollason and Dunnet 1978). Assuming the same age of first breeding applies also to birds on the Semidis, the calculated mean annual survival rate of prebreeders at equilibrium is 0.814 (substituting 0.969 for annual survival). That is, as few as 15% of the young fledged on the Semidis may survive to breed. My unadjusted estimate of adult survival (0.963, Table 1) corresponds to eventual recruitment of only 18% of fledged young. These comparisons suggest that the fulmar population of the Semidi Islands and the expanding boreal Atlantic colonies differ primarily in the magnitude of prebreeding mortality. The results of a simulation model developed by Ollason and Dunnet (1983) also emphasized the need for more information on the fate of prebreeding fulmars.

PREBREEDING AND POPULATION STATUS

About one-third of the birds present at the colony before egg laying in 1981 were nonbreeders, and most of those apparently were prebreeders. The occurrence of large numbers of nonbreeders in the prelaying period has also been reported from other colonies. For example, Coulson and Horobin (1972) noted that over half of the potential breeding sites in one British colony were occupied by nonbreeders in winter; the proportion of nonbreeders present at another colony was estimated to be in the range of 18 to 50% (Macdonald 1980).

There is some question, however, whether the estimate of 30% prebreeders can be reconciled with the assumption of equilibrium in the Semidi Islands population. The number of animals of breeding age or older in a stationary population is given by the annual rate of recruitment divided by the adult mortality rate. Thus, in a population of fulmars with 3% annual adult mortality and first reproduction at age 9 years, there are 3,333 adults for every 100 birds recruited at age 9 years (100/0.03). If prebreeding survival were constant at 81% per year (the mean calculated above), the total of birds 1 to 8 years old would make up 41% of the population (Table 7). It is generally thought, however, that juvenile mortality in seabirds is concentrated in the first year or two of life, after which the survival rate may approximate that of adults (Lack 1966, Nelson 1966, Fisher 1975, Potts et al. 1980). Furthermore, young fulmars apparently do not return to the colony for several years after fledging (Fisher 1952; G. M. Dunnet, pers. comm.). Under more realistic assumptions, then, birds aged 3 to 8 years would make up only 17% of the total (Table 7). Clearly, more information is needed on the age at which fulmars return to the colony, and the stability of prebreeding age structure needs to be assessed. It is possible, for instance, that my estimate of prebreeders in 1981 included one or more uncommonly large year classes.

Immigration and emigration are often over-

TABLE 7. The proportion of prebreeders in a stationary population of Northern Fulmars under two assumptions about prebreeding survivorship.

Age, x	Juvenile survival 0.81 year^{-1} (ages 0–8)				Juvenile survival 0.97 year^{-1} (ages 3–8)			
	No. birds age x[a]	Total birds in population ≥x years old	No. birds ages x to 8	% of population ages x to 8	No. birds age x[a]	Total birds in population ≥x years old	No. birds ages x to 8	% of population ages x to 8
0	666	6,316	2,983	47.2	—	—	—	—
1	540	5,646	2,313	41.0	—	—	—	—
2	437	5,106	1,773	34.7	—	—	—	—
3	354	4,669	1,336	28.6	119	3,998	665	16.6
4	287	4,315	982	22.8	116	3,879	546	14.1
5	232	4,028	695	17.3	112	3,763	430	11.4
6	188	3,796	463	12.2	109	3,651	318	8.7
7	152	3,608	275	7.6	106	3,542	209	5.9
8	123	3,456	123	3.6	103	3,436	103	3.0
9	100	3,333	—	—	100	3,333	—	—

[a] Age structures calculated relative to a cohort of 100 birds recruited to the breeding population at age 9 years (e.g., 100/0.81 = 123; 123/0.81 = 152; etc.).

looked factors that may influence the population dynamics of seabird colonies. Dunnet and Ollason (1978b) estimated that more than 90% of the young raised in one colony in Orkney emigrated to other colonies to breed. This behavior may be associated with the rapid and sustained increase in the boreal Atlantic population. It is unlikely that any comparable movements are now occurring in Alaska. More than 99% of the total population of fulmars in Alaska is contained in four widely-separated colonies. The Semidi Islands are the only breeding place of fulmars in the Gulf of Alaska, except for two small colonies more than 400 km east. The nearest large colony containing any dark phase birds lies 1,000 km to the west (Sowls et al. 1978). That colony is located on Chagulak Island in the Aleutians (52°N, 171°W), where more than 99% of the several hundred thousand birds present are DD (Hatch, unpubl. data). The nearest large colony to Chagulak is located on the Pribilof Islands (57°N, 170°W), 500 km north, where less than 1% of the estimated 80,000 resident birds are D or DD (Craighead and Oppenheim 1982). These observations suggest there is little gene flow among the major Alaskan colonies at the present time, and that the Semidi Islands may host an essentially closed population.

BREEDING SUCCESS AND SURVIVAL

Birds that failed to raise a chick appeared to have a higher mortality than those that succeeded (Table 1). Some of the difference was likely due to the tendency of fulmars to change breeding sites in the year following an unsuccessful breeding attempt (Macdonald 1977, Ollason and Dunnet 1978, Hatch 1985). Knowing that, one would tend to place more confidence in the survival estimate for successful birds (0.985), but the adult life expectancy projected for that group (66 years) seems an improbably high value for the population as a whole. This suggests that much of the apparent difference in survival between the two groups was real.

Two factors that could partially account for the difference in rates of disappearance of failed and successful breeders have already been mentioned: changes of breeding site and mortality during the breeding season. Thus, a conservative test of association between breeding success and survival reduces the total of mortalities among failed birds by six to account for probable changes of breeding site, and by three to account for deaths linked to breeding failure in the same season (see above). The adjusted totals are eight overwinter mortalities among successful birds and 23 overwinter mortalities among failed birds, giving respective mortality rates of 1.47% and 4.28% per year. The three-fold difference remains highly significant (G = 7.63, df = 1, P < 0.01).

One might expect a relationship opposite to what I found if the parental investment required to complete the breeding cycle has lasting effects on the birds' condition (Williams 1966, Goodman 1974, Wooller and Coulson 1977, Hunt 1980, Curio 1983). In a long-lived species such as the Northern Fulmar, however, a more important factor may be senescence, affecting both winter survival and the ability to breed successfully. A long-term study of fulmars in Orkney

has in fact revealed a decline of breeding success in old females (Ollason and Dunnet 1978). The same study has shown no increase in mortality associated with advancing age (Buckland 1982), but may yet do so as birds banded as chicks or young breeders approach and exceed the mean span of adult life.

ACKNOWLEDGMENTS

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