GEOGRAPHICAL VARIATION OF THE FULMAR *Fulmarus glacialis* IN THE NORTH ATLANTIC

JAN ANDRIES VAN FRANERK & JAN WATTEL

Institute for Taxonomic Zoology, University of Amsterdam, The Netherlands

Received 9 July 1980, Revised 8 January 1981

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1. INTRODUCTION

The Fulmar *Fulmarus glacialis* (Linnaeus, 1761) breeds in the northern part of the northern hemisphere and is, according to Vooos (1949), a pleistocene or earlier descendant of an antarctic Fulmar nowadays represented by *Fulmarus glacialisoides* (Smith, 1840). This antarctic Fulmar is supposed to have settled in the Bering Strait area during a cold period; later the North Atlantic would have been occupied from there through the Arctic Ocean. At present the Pacific and Atlantic Fulmars are separated by a wide distributional gap. The Pacific Fulmar has been described as *Fulmarus glacialis rodgersii* Cassin, 1862. The Atlantic Fulmar has been divided by Salomonsen (1965) into two subspecies on account of differences in coloration and bill-length, correlated with the zonation in the marine environment. The dark and small-billed high-arctic populations are called *F. g. glacialis* (Linnaeus, 1761); the light and long- or intermediate-billed boreal and low-arctic populations are called *F. g. auduboni* Bonaparte, 1857.

New material, collected by J. de Korte in East Spitsbergen and East Greenland for the Zoologisch Museum Amsterdam justifies a re-examination of the geographical variation of the Atlantic Fulmar. Valuable studies on this subject have been published already by Fisher (1952), Wynne-Edwards (1952a), Mathiasson (1963), and Salomonsen (1950, 1965).

This paper summarizes data on the geographical variation of the North Atlantic Fulmar and discusses the zoogeography of *Fulmarus glacialis* (L.).

2. METHODS

Like Salomonsen we have put the emphasis in this investigation on coloration and bill-length (from edge of feathers to the most distant part of the curve of the hook, this is normally the tip of the hook), but also other characters were considered: weight, and length of wing, tail, and tarsus. Measurements of study skins were taken according to the methods outlined by Cramp et al. (1977). Abbreviations of the names of the museums to which our material belonged are given in Table 1.

Measurements for males and females are considered separately because of the difference in size between the sexes. For each sample of measurements the following parameters are given: mean, standard deviation, number of specimens, and range. These parameters are presented graphically. When figures are needed in the discussion, they are given in the form used by Cramp et al. (1977), which implies that weights are in g and lengths in mm.

Concerning coloration, the literature is very confusing because many authors use the descriptions "light" and "dark" without stating what exactly they mean. Variation in colour is continuous; countless intermediate types between the extremes exist. Fisher (1952: 267—268) defined four colour-phases on which our survey of the colour variation is based. In order to make our allocation of birds as stable as possible, we chose four standard specimens from a series of 120 study skins, each representing one of these colour-phases. In addition three specimens were selected exemplifying borderlines between the colour classes (Fig. 1). The colour-phases can be described as follows:

Table 1. Abbreviated and full names of the museums to which the studied material belongs

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Full Name</th>
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<tbody>
<tr>
<td>BM</td>
<td>British Museum (Natural History), Tring</td>
</tr>
<tr>
<td>RMNH</td>
<td>Rijksmuseum van Natuurlijke Historie, Leiden</td>
</tr>
<tr>
<td>RSM</td>
<td>Royal Scottish Museum, Edinburgh</td>
</tr>
<tr>
<td>UA</td>
<td>Department of Zoology, University of Aberdeen</td>
</tr>
<tr>
<td>ZMA</td>
<td>Zoölogisch Museum, Amsterdam</td>
</tr>
<tr>
<td>ZFMK</td>
<td>Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn</td>
</tr>
<tr>
<td>ZMK</td>
<td>Zoologisk Museum, Kopenhagen</td>
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Ardea 70 (1982): 31—44
LL (double light) — head, neck and underparts white, except for dark eye-mark. The white may be tinged yellow (standard specimen ZMA nr. 28.492).

L (light) — crown of head, nape, and hindneck grey, grading into grey of mantle. Breast white, rest of underparts may be white, light grey, or flecked with grey (standard specimen ZMA nr. 20.057).

D (dark) — head, neck, and underparts light or medium grey; breast in most cases lighter, but never white (standard specimen ZMA nr. 27.006).

DD (double dark) — almost uniformly dark or very dark grey; wings almost as dark as their tips (standard specimen ZMA nr. 27.099).

The borders between the colour-phases are arbitrary, but to divide the whole range of variation into a number of distinct groups is the only way to analyze the variability of a series of populations. The colour-phases may be combined in two ways, viz white (LL) as opposed to coloured (L, D, DD) or light (LL, L) as opposed to dark (D, DD).

3. THE NORTH ATLANTIC FULMAR-POPULATIONS

In this chapter we discuss colour-phases and measurements in North Atlantic Fulmar-populations, arranged geographically as in Salomonsen (1965). Where our findings correspond with his, we have endeavoured to be brief, but where our data or our interpretation differ, a fuller treatment seemed justified. Information on coloration and measurements is summarized in Figs. 3 and 4. The basic data on which these diagrams are based are kept at the Zoologisch Museum Amsterdam (available on request). In constructing the figures we also used data from the literature in order to obtain a picture of geographical variation as complete as possible. Sources are mentioned in text and figures.

3.1. HIGH-ARCTIC POPULATIONS

3.1.1. The Canadian Arctic

Distribution. Several large colonies are present at the east and north coast of Baffin Island, at Devon Island, and at Prince Leopold Island. Breeding is suspected at Coburg Island and Hantch Island (Brown et al. 1975).

Material. Baffin Island: South-East 3 ♂♂, 5 ♀♀ (UA); Arctic Bay 1 ♀ (BM).

Colour. L-2 ♀♀; D-1 ♀; DD-3 ♂♂, 3 ♀♀. According to Wynne-Edwards (1952b), at Cape Searle about one bird in eight is of the typical light phase, about the same proportion is extremely dark, and the remaining 75% is intermediate. Assuming that birds of the “typical
light phase" are LL, this works out at LL:L and D:DD = 1:6:1. So, in our material dark birds are over-represented, which may be due to selective collecting of birds.

Fisher (1952) thought that in North Baffin Island dark birds (D+DD) were more predominant (95%) than in the south-east. However, from more recent sources (Brown et al. 1975) it may be concluded that the northernmost colonies contain a larger proportion of light birds than was formerly supposed. A recent motion picture of the birds of Prince Leopold Island by Dr. D.N. Nettleship showed Fulmars varying from LL to D; most birds were L with some grey on the sides. Exact figures on the northernmost Canadian colonies are not available but the majority of the birds is coloured and among these birds of the L type are predominant.

Measurements. Measurements of wing, tail, and tarsus are presented in Fig. 4B, D, and E. Our measurements of birds of South-East Baffin Island gave bill-length in δ δ 36.5 (1.25; 3) 35.5—37.9 and in ♂ ♀ 33.4 (0.82; 5) 32.8—34.8. Wynne-Edwards (1952a) combined data from Salomonsen (1950) from Admiralty Inlet with his own measurements from Devon Island and gave as bill-length: δ δ 36.2 (33) 33.2—39.0 and ♂ ♀ 33.1 (9) 31.0—35.5. Our data, despite the small numbers, show sufficient similarity to these figures for the northern colonies to conclude that all populations in the Canadian Arctic are small-billed. In Fig. 4A Wynne-Edwards' figures are used. Concerning weights there are two literature sources (Wynne-Edwards 1952a, Watson 1957) which show sufficient similarity to our data (4 birds) to combine the figures. The result, δ δ 725 (8) 710—740 and ♂ ♀ 582 (10) 565—625, is used in Fig. 4C.

3.1.2. East Greenland

Distribution. Three colonies of considerable size are known at the north-east point of Greenland: Mallemukfjældet, Cape Jungersen, and Mt. Magefjældet (Salomonsen 1950—51). Far more to the south there are three small colonies near Scoresbysund at Rathbone Island, Raffles Island, and Kap Brewster (Meltzoff 1976, J. de Korte, pers. comm.).

Material. North-East Greenland: none. Rathbone Island: 14 δ δ, 26 ♂ ♀ (collected for ZMA by J. de Korte in the period May—August 1973; as far as we know this is the first collection of breeding Fulmars from East Greenland).

Colour. In the northernmost colonies almost exclusively dark birds have been seen (Manniche 1910). Probably the situation is similar to Spitsbergen. Rathbone Island collection: LL-6 δ δ, 15 ♂ ♀; L-1 δ δ, 3 ♂ ♀; D-5 δ δ, 5 ♂ ♀, DD-2 δ δ, 3 ♂ ♀. Proportionally there are even more white birds in the population since some selective shooting has been done on coloured ones. The best estimate is that 70% to 80% of the birds is LL and that most of the other birds are dark (D+DD) while intermediate L birds are less frequent: the colonies at Raffles Island and Kap Brewster show a similar trend of a majority of light birds, but since these colonies are hard to approach this is not exactly known (J. de Korte, pers. comm.).

Measurements. North-East Greenland unknown. Measurements of the birds from Rathbone Island are given in Fig. 4. Mathiasson (1963) gave for the Scoresbysund area: δ δ 38.5 (11) 37.8—40.0; ♂ ♀ 36.4 (3) 34.7—37.9. These figures are rather different from ours. Salomonsen (1965) already mentioned the possibility that Mathiasson's material contained visitors from other breeding areas. In 1973 J. de Korte collected some birds (1 δ δ and 10 ♂ ♀) at Kap Tobin, Scoresbysund Outlet. There is no breeding-colony at Kap Tobin and 8 of the 10 females collected are young (oviduct straight and thin) with new or not quite full-grown primaries. This indicates that the Scoresbysund area may be an assembling place of young birds and failed breeders from different origins (Meltzoff 1976 mentioned increasing numbers during summer). Measurements show that these birds are larger than the birds from Rathbone Island and since they were all LL it is well possible that they were partly visitors from more southern origin. Therefore they were not used in this study. The fact that the Kap Tobin females have a bill-length (36.5 (10) 35.5—39.8) very similar to Mathiasson's data may indicate that his material also contained such visitors.

3.1.3. Spitsbergen

Distribution. The Fulmar breeds in most parts of Spitsbergen, but the majority of the colonies
is situated along the west coast (Fisher 1952, Løvenskiold 1964).

*Material.* Edgeøya, South-East Spitsbergen, 8 \( \delta \delta \), 14 \( \varphi \varphi \); from different localities along the west coast 9 \( \delta \delta \), 11 \( \varphi \varphi \) (ZMA, ZFMK, BM, UA). Data on the specimens in the ZMA have been published by De Korte (1972), who collected the Edgeøya-material. For the present study the ZMA material was re-examined.

*Colour.* LL-2 \( \delta \delta \); L-8 \( \delta \delta \), 9 \( \varphi \varphi \); D-6 \( \delta \delta \), 14 \( \varphi \varphi \); DD-1 \( \delta \). The LL/L and D/DD borderline-specimens mentioned in chapter 2 were from Spitsbergen and are not included in these figures. Several birds in the ZMA-collection described as D by De Korte (1972) were re-examined and judged to be L. The Edgeøya-collection reflects the actual variation in coloration of the Edgeøya population (De Korte 1972) and from our judgement of the birds (1 LL/L, 8 L, 11 D, 1 D/DD, 1 DD) one may conclude that the Edgeøya-population is coloured for almost 100\%, while about 65\% is dark (D+DD). Comparing the Edgeøya specimens with those from West Spitsbergen the latter seem to be slightly lighter (Edgeøya 35\% light, 65\% dark; West Spitsbergen 55\% light, 45\% dark), a phenomenon already commented upon by Fisher (1952), Salomonsen (1965), and De Korte (1972). However, the West Spitsbergen specimens may not be representative; Pennycuick & Webbe (1959) reported from a colony at Tempelfjord 0.5\% LL, 5% L, 85% D, and 10% DD. The alleged difference between west and east clearly needs more detailed study. Nevertheless, there can exist no doubt that by far the majority of the Spitsbergen Fulmars has an intermediate colour-shade (L+D) while the extremes LL and DD constitute only a small proportion. According to Salomonsen (1965) over 99\% of the birds is dark; this clearly has to be interpreted as over 99\% coloured.

*Measurements.* Statistical tests revealed no significant differences between birds from West and East Spitsbergen; so data for all birds have been pooled in Fig. 4. The result for bill-length in males (37.6) is intermediate between the values given in the literature: Vaurie (1965) gave an average of 36.5 mm for 14 males, while Mathiasson (1963) measured 38.4 in 11 males. In our females the bill is somewhat smaller than given by Mathiasson (1963).

### 3.1.4. Franz Joseph Land

*Distribution.* Most of the Fulmar colonies are in the south: (Prince George Island); only two of them are situated more to the north (Salisbury Island and Rudolf Island) (Fisher 1952).

*Material.* None.

*Colour.* According to Nansen & Collett (1899) most of the birds belong to the dark variety and the same is said by Dement’ev et al. (1951). Probably the birds are much like the Spitsbergen Fulmars.

*Measurements.* Unknown.

### 3.1.5. Novaya Zemlya

*Distribution.* Dement’ev et al. (1951) mentioned three breeding-localities on the northern island of Novaya Zemlya but Fisher (1952) said that there is only one certain colony at William Island on the west coast.

*Material.* None.

*Colour.* According to Dement’ev et al. (1951) light birds are prevalent at Novaya Zemlya, but since he does not particularly speak about breeding birds and does not mean LL by “light” (light is described with axillaries and under wing-covers light grey, so it probably means an L-like coloration) the meaning of this statement is questionable. Maybe a large part of the population is only weakly coloured (L).

*Measurements.* Unknown.

### 3.2. LOW-ARCTIC POPULATIONS

#### 3.2.1. North-West Greenland

*Distribution.* Four main groups of colonies are found in North-West Greenland: Disko Bay, Umanak Fjord, Upernavik District, and Thule District (Salomonsen 1950—’51).

*Material.* None. Some specimens were measured, but these may have been visitors since they were not captured near any colony.

*Colour.* In all colonies the light phase vastly predominates: in southern colonies dark birds only constitute 0.1\%, in the northern colonies 1\% of the population (Salomonsen 1965). Dr. F. Salomonsen kindly informed us that “light” means mainly LL and that lighter grey birds (L)
do occur among the white ones, but do not form any great percentage of the breeding population.

**Measurements.** Salomonsen (1965) refrained from publishing measurements because few birds had been collected at breeding-localities. He concluded: “Although not satisfactory, the measurements show that the West Greenland populations are intermediate as far as bill-length is concerned; the smallest measurements of _minor_ as well as the largest ones of _glacialis_ are missing.” In our opinion the absence of very large or very small measurements indicates that few or no visitors from elsewhere were included in his material. In Fig. 4A, we have included Mathiasson’s data (1963), in which extremes are also absent. We consider these as a fair representation of the bill-length of the West Greenland population. The range is quite normal; when also visitors would have been measured a much larger range would have been expected. The West Greenland birds, then, are not intermediate, but rather small-billed.

### 3.2.2. Jan Mayen

**Material.** 5♂♂, 12 ♀♀, 1 of unknown sex (BM; collection made in 1934 by C. G. & E. G. Bird).

**Colour.** LL-1 ♂ (approaching L); L-3 ♂♂, 4 ♀♀; D-1 ♂, 8 ♀♀, 1 of unknown sex. Bird & Bird (1935) said about the Jan Mayen population and their collection: “The dark and intermediate forms were very rare; we estimated them at only 0.5%. We obtained a large series showing every gradation in colour”. In fact, the skins show every gradation between our standards L and D, except for one LL bird, approaching LL/L. The literature is almost unanimous that the Jan Mayen population is very largely Light (Fisher 1952, B. Løppenthin _in litt._). So, Bird & Bird may have made efforts to collect dark and intermediate birds from the small proportion thus coloured. Considering the evidence we tentatively conclude that “over 99% light” (Fisher 1952) means, that the majority of the Jan Mayen population is L and that the D and DD part of the population is less than 1%, but obviously this population deserves further investigation.

**Measurements.** Measurements are given in

Fig. 4. One specimen, labelled as a female, was left out of the calculations because of the extremely large measurements (bill 41.8, tarsus 59 mm, even outside the range for males). Mathiasson’s (1963) figures for bill-length average somewhat higher than ours (3 ♂♂ 39.8; 9 ♀♀ 36.8), but considering the small numbers this may easily be due to chance.

### 3.2.3. Bear Island

**Material.** 32 ♂♂, 13 ♀♀ (ZFMK, BM, UA, RMNH).

**Colour.** LL-5 ♂♂, 5 ♀♀; L-11 ♂♂, 3 ♀♀; D-11 ♂♂, 4 ♀♀; DD-5 ♂♂, 1 ♀♀. These figures, however, are not representative for the population. An accurate description was given by Duffey & Sergeart (1950); 10% LL, 75% intermediate, and 15% DD. Salomonsen (1965) compared these data with the figures given by Kohlhoff in 1898 (fide Fisher 1952: 274) who mentioned less than 0.1% LL birds (“with a pure white head and throat”). Salomonsen concluded that there had been an increase in the percentage of light birds since about 1920. However, Koenig & Le Roi, who visited the island in 1907—'08, made a statement similar to Kohlhoff’s (fide Fisher 1952), but collected at the same time 34 Fulmars (ZMFK) of which 9 were LL and 9 L. Of course, this may not agree with the actual proportions in the population, but it does indicate that LL was not all that rare. We therefore doubt the hundredfold increase of “light” (LL) birds suggested in the literature. Nevertheless, it is possible that there has been some change in coloration. Nyholm (1971) estimated the proportion of the light phase at 17%, but it is not clear whether “light” means exclusively LL. Salomonsen (1965) thought of an increased survival value for genes of light coloration in an ameliorating climate. We tentatively interpret the increase of the proportion of LL birds as the consequence of an influx of birds from the expansive boreal populations (see also 3.2.4.).

**Measurements.** Our data are shown in Fig. 4. The figures on bill-length are virtually the same as given by Vaurie (1965) and Mathiasson (1963). No data on weight are known except for an extremely heavy male of 1200 grammes, mentioned by Bourne (1974). This bird, which
is not a recently fledged young (captured at 3 July), is even out of the range of British Fulmars (max. 957 gr.). We doubt whether this weight was taken correctly; otherwise the bird may have been abnormal.

3.2.4. Recent Low-Arctic Settlements

Recently new settlements were reported from South-West Greenland (less than 140 nest-sites) by Salomonsen (1974, 1979) and from Newfoundland (6 pairs) and probably Labrador by Brown et al. (1975). Not much is known about these birds, but Salomonsen (1979) argued that the new Greenland birds are from boreal and not from arctic origin. Considering the enormous expansion of the boreal Fulmar and the fact that many young go to the waters near Newfoundland and South-West Greenland this is well possible. Many British and some Norwegian Fulmars have been recovered in these areas (MacDonald 1977, Haftorn 1971).

If it is true that boreal Fulmars have recently established themselves in the Low-Arctic, this may strengthen our assumption that the alleged increase of the proportion of light birds on Bear Island could also be due to an influx of boreal birds in the population. The island is within the pelagic range of these birds as several immatures as well as adults, that had been ringed in Britain, were recovered off the Norwegian coast and in the Barents Sea (MacDonald 1977).

3.3. BOREAL POPULATIONS

3.3.1. The British Isles

Distribution. Breeding of the Fulmar in Britain, except for St. Kilda, was first proved in 1879 on Foula, Shetland. Nowadays Fulmars can be found breeding along almost all British coasts, but they are most numerous in the Shetlands, the Orkneys, and the North. The census of 1969—’70 revealed over 300,000 breeding-sites in the British Isles (Fisher 1952, 1966, Cramp et al. 1974).

Material. 26 δ δ, 22 φ φ (mainly from the Shetlands, Orkneys and northern Scotland; 6 δ δ and 1 φ from St. Kilda) (RSM, UA, BM, ZMA).

Colour. All the birds examined belong to the colour-phase LL. Coloured birds are extremely rare in Britain though birds with some grey on the head (L) are somewhat more often seen than really dark birds (Fisher 1952).

Measurements. Measurements are given in Fig. 4. An extremely large φ, probably a mis-sexed δ, was left out of the calculations. Literature data on the length of the bill (Wyne-Edwards 1952a, Dunnet & Anderson 1961, Vaurie 1965, Mougin 1967) concur with our results, though our males average slightly smaller than given in some sources. In Wyne-Edwards’ data (1952a) the St. Kilda Fulmars appeared to have smaller bills than the other British Fulmars (St. Kilda 7 δ δ, 40.2; Scotland 10 δ δ, 41.3). Our data also point in this direction (St. Kilda 6 δ δ, 39.7; rest of Britain 20 δ δ, 40.7) but we cannot jump to conclusions since the number of birds measured is too small and since we might have measured the same birds as Wyne-Edwards. However, it is possible that the old St. Kilda population is different from the recently founded other British populations. A comparison of a longer series of St. Kilda Fulmars with other British specimens (and of Grimsey birds with the other Icelandic Fulmars) may give the answer to the problem where the Fulmar’s spread in the boreal zone has started (Fisher 1952, Salomonsen 1965). However, since data are too scarce, the British Fulmar population was considered homogeneous in this study; our data in Fig. 4 include the St. Kilda birds.

Dunnet & Anderson (1961) found a significantly larger wing for British males (18 δ δ, 340 mm) than we did (22 δ δ, 332 mm), while our figures for females are almost identical. Mougin’s measurements (1967) are intermediate. Mougin’s figures for tarsus (6 δ δ, 54.9 mm; 3 φ φ, 52.2 mm) and tail (6 δ δ, 122 mm; 3 φ φ, 119 mm) show good correspondence with our results. In this study no data on weight could be obtained and therefore the figures given by Dunnet & Anderson (1961) and Mougin (1967) are shown in Fig. 4C.

3.3.2. Iceland and the Faeroes

Distribution. Before 1753 the only certainly known colony was on Grimsey, north of Iceland; since then the whole of Iceland and the Faeroes has been colonized (Fisher 1952).

Material. 29 Icelandic birds have been examined on their coloration only (ZMK).
Colour. All of the Icelandic birds were LL, though some of them approached L. According to Fisher (1952) more than half of the Icelandic breeding birds belong to colour-phase L, while the rest of the birds is LL (except for a very small percentage D). At the Faeroes most of the birds would be LL, maybe partly L. Generally in the literature the Icelandic birds are considered like the other boreal populations (almost 100% LL) and considering the ZMK collection we agree. Fisher must have used a different border between LL and L (Chapter 2). If there is a certain percentage of L birds in Iceland or the Faeroes it must consist of birds very close to the LL type.

No measurements were taken of birds from the Faeroes of Iceland. In literature, several authors supply data on bill-length (Salomonsen 1950, Wynne-Edwards 1952a, Mathiasson 1963, Vaurie 1965). Their averages for Iceland vary between 40.4 and 40.9 mm for males and 37.3 and 37.7 for females. For the Faeroes these figures are 39.7—40.7 mm and 38.2—38.5 respectively. In Fig. 4A Mathiasson’s data are used since his figures contain the largest number of birds for the separate localities (a combination of his own measurements and data from Wynne-Edwards 1952b). Timmermann (1949) mentioned the weight of two males from Iceland; both 830 g.

From these data it is apparent that the Icelandic and Faeroese Fulmars are very similar to the British (probably also in characters on which no data are available.

3.3.3. Norway

Distribution. The first breeding Fulmars in Norway were found in 1920 at Rundøy; in 1976 there were about 1700—2000 nest-sites in this area (Folkestad 1978). Røst (Lofoten) was colonized in about 1940 and had about 50 nest-sites in 1963, not including some very small colonies in the neighbourhood (Haftrøm 1971).

Material. None.

Colour. The Norwegian Fulmars are probably all LL; Fisher (1952) gives light (= LL+L) but probably alleged L birds are much like his L birds from Iceland, which, in our opinion, are LL.

Measurements. Mathiasson (1963) gives for bill of ♂♂ from Røst 39.1 (3) 38.6—39.8 and for ♀♀ 37.2 (4) 36.5—37.6. These figures are somewhat lower than the figures for other boreal populations but the sample is very small; probably the Norwegian Fulmars are like the British-Icelandic Fulmars, of which they are undoubtedly an offshoot.

3.3.4. Recent Boreal Settlements

In France the first Fulmars were found breeding on the Sept Isles in 1960. At present there are several small colonies in Brittany and Normandy; Yetman (1976) gave less than 40 breeding pairs in France, of which 25 on the Sept Isles.

Since 1969 regularly 1 to 3 pairs of Fulmars were observed at Heligoland. Breeding was first proved in 1972 and in 1973 there were at least two breeding pairs (Berndt & Drenckhahn 1974). Both the French and German Fulmars undoubtedly will prove to be of the boreal type.

4. THE ZOO GEOGRAPHY OF THE FULMAR IN THE NORTH ATLANTIC

4.1. PRESENT DISTRIBUTION

The distribution of breeding localities and the approximate number of nest-sites (breeding pairs) of the Fulmar in the North Atlantic are shown in Fig. 2. This map is based on data given by the authors mentioned under the captions "Distribution" in the previous chapter; for Bear Island the census figures by Williams (1971) were used. Some doubtful breeding localities, not indicated on the map, are Melville Island and Victoria Island in the Canadian Arctic, and Lonely Island in the Kara Sea. Fisher (1952) thoroughly investigated the literature on this subject and considered breeding in these localities highly improbable.

The size of some of the northernmost colonies in Atlantic is poorly known. Fisher (1952) thought that these were rather small, but Salomonsen (1950—51) mentioned colonies of considerable size in Holms Land and Amdrups Land (North-East Greenland), and according to Dementjev (1951) the Fulmar is common in Novaya Zemlya and common or numerous in Franz Joseph Land.
4.2. THE PATTERN OF VARIATION.

4.2.1. Colour

From the data given for the separate populations a picture emerges of the geographical variation of the Fulmar in the North Atlantic. The most important and conspicuous variation concerns colour. The proportions of the different colour-phases in each population are shown in Fig. 3, in which also the zonation of the marine environment is indicated (Salomonsen 1972). The diagrams reflect our personal opinion and no exact literature data from different sources. Several populations are poorly known and different observers delimit the colour-phases differently. In most populations the percentage of white birds as opposed to the percentage of coloured birds is reasonably known, but not the proportion of L, D, or DD separately. The proportions of the colour-phases in the Nowaya Zemlya population are entirely unknown (also the LL part). The distribution of the light and dark morphs in the North Pacific is derived from Fisher (1952: 280).

From the map it is clear that, in general, in the North Atlantic, coloured populations occur in high-arctic environments and white populations in boreal low-arctic environments. According to Salomonsen (1965) there is a strong discontinuity between light and dark populations, correlated with the zonation of the marine environment. In our opinion neither the discontinuity nor the environmental correlation is as strong as Salomonsen suggested. The colour differences are not a case of simple dimorphism. In the Pacific, where the majority of the birds is either very dark (darker than DD) or light (LL and L), a dimorphism is recognizable. In the Atlantic, however, is a continuous variation in pigmentation. The boreal populations, resulting from a recent expansion of one or two colonies, are virtually monomorphic LL, but in the low-arctic and high-arctic populations we find a great variation in the proportions of the different colour-phases. Salomonsen (1965) exaggerated the discontinuity in writing about "a sudden drop in the percentage of dark birds"
from 90–100% to less than 1%, when moving from the high-arctic to the low-arctic populations”. The new data on the decidedly high-arctic populations near the entrance of Scoresbysund are incompatible with this generalization. It had already the inherent weakness that the light-grey birds (L) in light populations (West Greenland) had to be counted as light (“over 99% light”), but in the darker populations (Bear Island) as dark (“90% dark”). Nevertheless, there is a tendency for local populations to be either mainly (over 70% coloured (L, D, and DD) or white (LL). The extreme admixture of coloured birds in a white population is found near Scoresbysund, the extreme of white birds in a coloured population may be found in Bear Island or in the northernmost Canadian populations. It is striking, that really dark (DD) birds everywhere constitute a small minority. Two “centres of darkness” are present, one in southern Baffin Land, the other in North-East Greenland and Spitsbergen. At the same time,
West Greenland and the European populations form two "centres of lightness", one low- to high-arctic, the other boreal, which was earlier pointed out by Salomonsen himself (1950—'51).

4.2.2. Measurements

Other characters showing geographical variation are the size of the bill and the length of the tarsus. The variation in length of bill is summarized in Fig. 4A. In this figure the populations are arranged according to the April—September temperatures of air and water in their breeding haunts. Particularly in July, West Greenland may be warmer than Jan Mayen and Bear Island. However, looking at the entire period during which Fulmars have to be present at the breeding colonies, West Greenland averages colder since it lacks the moderating influence of the Gulf Stream. In addition, within a single area the temperature may vary within limits, e.g. northern and southern West Greenland, West and East Spitsbergen. This makes it impossible to analyse the variation of bill size with temperature mathematically. In any case, a decrease of bill towards colder environment is apparent. Salomonsen (1965) expressed this as follows: "The bill-length is precisely adjusted to the present environment, the variation forming a gradient with decreasing length closely correlated with decreasing water (and air) temperature". Our data show a general correspondence of bill-size and temperature, but there are deviations in detail. All boreal populations have rather uniform bills, in spite of the increasing temperatures from Iceland to the British Isles, but this may be explained by the recent history of the distribution in this area. In West Greenland and the Canadian Arctic, however, Fulmars have bills that are smaller than those in localities with comparable temperatures (Jan Mayen/Bear Island and East Greenland respectively). Apparently, within the general trend of smaller bills towards colder regions, not all the differences may be attributed exclusively to different temperatures. Assuming that bill-length in the Fulmar is more or less correlated with environmental temperatures, it may be expected that the birds of Nowaya Zemlya and Franz Joseph Land have small bills.

Considering the Atlantic populations as a whole, dark birds have on average shorter bills than light ones. A comparison of the LL and L birds with the D and DD birds of Spitsbergen, Bear Island and Rathbone Island shows that there is no such correlation within local populations (Table 2). The differences between the bills of light and dark birds are not significant (analysis of variance, F = 0.75, P > 25%).

Data on length of tarsus are incomplete (Fig. 4B), but show the same general trend as length of bill. If tarsus-length is considered to be a measure of body-size, the figures indicate that the Fulmars of the British Isles, Faeroes, Iceland, Bear Island, and Jan Mayen are large, those of Spitsbergen, East Greenland, and Baffin Island small. Birds of Bear Island and Jan Mayen have short bills relative to their size. In the boreal populations the bills are relatively long.
Table 2. Average length of bill in light and dark specimens of *Fulmarus glacialis* from some Arctic breeding localities

<table>
<thead>
<tr>
<th></th>
<th>LL+L</th>
<th>D+DD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bear Island</td>
<td>38.7 (16)</td>
<td>39.0 (13)</td>
</tr>
<tr>
<td>Spitsbergen</td>
<td>37.4 (4)</td>
<td>38.5 (4)</td>
</tr>
<tr>
<td>Rathbone</td>
<td>38.2 (7)</td>
<td>36.9 (9)</td>
</tr>
</tbody>
</table>

ed as an additional indication of their large size, but the differences are small. In males the wing in Bear Island averages significantly longer than in Great Britain (t = 2.64), but for females the difference is not significant (t = 1.19).

4.3. SUBSPECIES IN THE FULMAR?

Interpreting the variation of the Fulmar in the North Atlantic, Salomonsen (1965) concluded that two subspecies may be recognized. We agree that birds of known sex may be identified with some confidence as either belonging to boreal (LL and large) or high-arctic populations (L to DD and small). However, smaller LL specimens are problematical since they may belong to both the high-arctic form *F. glacialis glacialis* or the boreal-low-arctic *F. g. auduboni*; e.g. most West Greenland *auduboni* are inseparable from light specimens of *glacialis*. It is even more difficult to allocate the birds from Scoresby Sund: if one wants to recognize the subspecies as morphological units, they may be called *auduboni* since the majority of the birds are white, but Salomonsen (1979) includes them in *glacialis*. The population of Jan Mayen can hardly be identified subspecifically, but appears closer to *glacialis*. In choosing this approach, we consider size as a relatively unimportant character as far as identification of subspecies goes.

5. A HYPOTHESIS ON THE ORIGIN OF THE VARIATION IN THE FULMAR

Perhaps more interesting than the amount of morphological difference between the subspecies is Salomonsen’s interpretation of his findings as evidence for the existence of two isolated populations of *F. glacialis* during the last glacial period. We feel that this interpretation is stretching the facts. As indicated before, it is as well possible to discern four groups as two: in
the L.I. populations the large birds of Iceland and Europe are rather different from the smaller West Greenland birds and in the coloured populations there is a morphological and distributional difference between the medium-sized Fulmars from Spitsbergen (and probably North-East Greenland) and the small Fulmars from southern Baffin Island. The populations of Bear Island, Jan Mayen, East Greenland, and the northern Canadian Arctic appear intermediate in some respect. In our opinion, there is no room for two refugia, a boreal-low-arctic and a high-arctic one. Recent studies (MacIntyre 1976) have indicated that during the Weichselian period the ice cover of the North Atlantic did not permit seabird refugia that were sufficiently isolated to cause the present differentiation of the Fulmar.

In addition, an important aspect of Salomonson's reconstruction of the biogeographical history of the Fulmar does not seem very convincing. He supposed that the dark colour in high-arctic environments was due to the pleiotropic effect of a gene or combination of genes with strong survival value in the High-Arctic. The main problem with this explanation is, that in the Pacific the dark Fulmars are found to the south of the whites. It appears very unlikely that dark coloration should be caused by two completely different factors in two oceans. Also in the Atlantic, survival in the High-Arctic is not inseparably linked with dark colour as is shown by the white birds in East and West Greenland and in small percentages in almost all other high-arctic populations.

This leaves us with the problem of why some Atlantic Fulmars are dark and others light. Our data are certainly insufficient for a satisfactory answer to this question. However, it is striking that the large numbers of intermediate birds, so characteristic for the North Atlantic populations, are apparently lacking in the North Pacific. Combining this with the fact that almost all predominantly light colonies in the Pacific are found in the high North, it is tempting to speculate that the colour types arose in different oceans. Some time during the Pleistocene, all Pacific Fulmars may have been of a very dark colour type, whereas the Atlantic was inhabited by light birds. Warm interglacials may have facilitated exchange of individuals by way of the Arctic Ocean. The great variation of most Atlantic high-arctic colonies may have arisen from introgression of genes for dark coloration in these populations for a long period. Similarly, the colonies of light birds in the North Pacific could have been recently founded by Fulmars originating from the Atlantic (West Greenland).

In this connection the question of recognition of subspecies arises again. Nowhere in the literature we could find good evidence that all Pacific Fulmars are different from the Atlantic ones. Voous (1949) described some differences in shape and colour of the bill, but probably he examined dark birds only and paid no attention to variation within the Pacific (light versus dark).

Our hypothesis of the history of the Fulmar will be strengthened if more characters are found in which white Fulmars of both oceans (West Greenland and North Pacific) agree. It will be falsified if differently coloured Fulmars from the same ocean are more similar in all other characters than similarly coloured Fulmars from different oceans. The rarity of intermediate individuals in the North Pacific might be explained by a recent arrival of white birds in this ocean. It could also be that white and coloured Fulmars in the Pacific show a rather strong reproductive isolation. This again is a point that may be tested by further studies.

Further analysis of the geographical variation of the Fulmar might start with the study of the West Greenland, Canadian, and North Pacific populations. It would be important to increase the number of characters. The main problem for such a research program will be the difficulty of obtaining sufficient material of breeding birds from the various colonies. The purpose of this paper was primarily to furnish a basis for further comparison of the colour-phases and to show that much of the infraspecific variation of the Fulmar is still unexplained. It seems as if we had to step backwards, rather than advance beyond earlier theories.

6. SUMMARY AND CONCLUSIONS

The geographical variation in the Fulmar was re-examined when new collections, especially material from Rathbone Island, East Greenland, became available in the Zoologisch Museum Amsterdam. Coloration, length of bill and
tarsus, weight, and length of wing and tail of the North Atlantic Fulmar populations were studied from skins and from the literature.

A clinal decrease in bill-length and probably also in tar-
sus-length and weight is found from warmer to colder re-
gions; deviations from the clinal pattern are too small, or in-
sufficiently known, to show historical instead of environ-
mental influences. Variation in length of wing and tail is small and erratic. See Fig. 4.

Variation in coloration is clearly not simply clinal, the lar-
ge majority of each population being either coloured (L, D, 
DD) or white (LL). See Fig. 1 and 3. The differences be-
tween the populations, though not as strong as assumed by
Salomonsen (1965), may be considered sufficiently pro-
nounced in coloration and size to maintain a purely morpho-
logical separation in *F. g. glacialis* and *F. g. auduboni*. It is argu-
d that these morphologically different forms can hardly be con-
sidered evolutionary units. A hypothesis of the his-
ory of *F. glacialis* is presented, in which close relationships are
suggested between similarly colored populations in the
Pacific and Atlantic, in order to stimulate further research
into the evolutionary meaning of the currently recognized
subspecies in the Fulmar.

7. ACKNOWLEDGEMENTS

In completing this study we wish to thank Dr. W. R. P.
Bourne, Dr. J. Fjeldså, Dr. I. C. J. Galbraith, Mr. I. H. J.
Lyster, Dr. G. F. Mees, Dr. D. W. Snow, and Dr. H. E.
Wolters for the opportunity to study material under their
care. We are grateful to Dr. F. Salomonsen for his lively in-
terest in our work, though this does not imply that he shares
our conclusions. Dr. B. Loppenthin and Drs. J. de Korte
supplied information concerning their field observations of
the Fulmar. With Mr. P. Hope Jones we discussed the prob-
lems of recognition of the colour-phases. Prof. Dr. K. H.
Vouos commented on earlier drafts of this paper. Tineke
Prins expertly typed the manuscript. To all of them we ex-
tend our sincere thanks.

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9. SAMENVATTING
Salomonsen (1965) heeft een uitvoerig bericht gegeven van de geografische variatie van de Noordse Stormvogel Fulmarus glacialis in het Noorden van de Atlantische Oceaan. Hij ontwierp een tweedeling in hoog-arctische, overwegend donker gekleurde en kortsnavelige populaties (subspecies glacialis) en lichtgekleurde, meestal langsnavelige boreo-laag-arctische populaties (subspecies auduboni). Een serie vogels van een broedplaats in het hoog-arctische gebied rondom Scoresbysund (Oost Groenland) leek niet in dit beeld te passen. Er komen daar naar verhouding teveel witte individuen voor. Dit was een reden om de opvatting van Salomonsen kritisch te toetsen, met name ook zijn veronderstelling dat de verdeling in twee groepen zou rusten op een verdeling over twee refugia gedurende de ijstijden. Hierin hebben wij eerst de door Fisher (1952) beschreven kleurfasen opnieuw gedefinieerd (Fig. 1) en vervolgens de geografische variatie beschreven (Hoofdstuk 3, Fig. 3 en 4).

Vastgesteld kon worden dat van een eenvoudige verdeling in twee groepen van populaties nauwelijks sprake is. Het is duidelijk dat de snavelen in de koude gebieden korter zijn dan in warmere, maar de verdeling van de kleurfasen loopt daarmee niet parallel. Eerder lijkt het alsof er vier groepen te onderscheiden zijn met daartussen overgangen: lichte en langsnavelige populaties in het boreale gebied, lichte en kortsnavelige in West Groenland, overwegend donker gekleurde met middelmatig lange snavel in Spitsbergen en donkere en kortsnavelige in Baffin Island (Canada). Een verklaring voor deze verdeling van de kleurfasen wordt gezocht in mogelijke herhaalde wederzijdse kolonisaties tussen de gebieden van de noordelijke Atlantische en Stille Oceaan in diverse stadia van het Pleistoceen.

Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Postbus 20125, 1000 HC Amsterdam