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THE GEOGRAPHICAL VARIATION OF THE FULMAR (*FULMARUS GLACIALIS*) AND THE ZONES OF MARINE ENVIRONMENT IN THE NORTH ATLANTIC

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THE Fulmar was previously considered to form a single subspecies in its entire range in the North Atlantic area, but in a recent paper (Salomonsen, 1950: 100) I pointed out that the population of Admiralty Inlet, Baffin Island, belonged to a new subspecies characterized by a considerably shorter bill than the boreal form of Europe, and that the name *minor* (Kjaerbølling, 1852: 324) should be used for it. The exposed culmen of 21 adult males from Admiralty Inlet measured 33.2 to 39.0 mm (average 35.9), compared with 37.0 to 43.2 mm (average 40.4) in 16 adult males from the Faeroes and Iceland. The corresponding measurements of females were 32.3 to 34.0 mm (average 33.1) in 6 specimens from Admiralty Inlet, compared with 35.0 to 40.0 mm (average 37.4) in 19 females from the Faeroes and Iceland. In the present paper I have disregarded measurements of females throughout in order to save space, and for the same reason I have excluded measurements of wing, tail, and tarsus, which generally have been ignored by students of the Fulmar. A further difference between the two populations concerned the distribution of the dark phase, which is absent in the boreal European populations, but vastly predominates in the Baffin Island population.

The newly recognized form was at once accepted as valid by the A.O.U. Check-List Committee (1951: 367), and appears in the A.O.U. Check-List (fifth edition, 1957: see p. 12). It was fully described in the *Handbook of North American birds* (Palmer, 1962: 143). Meanwhile, Wynne-Edwards (1952: 105; 1952a: 84) discussed it and demonstrated that the breeding population of Cape Searle in southeastern Baffin Island belonged to *F. g. minor*. Subsequently, Watson (1957: 89) examined additional material from Cape Searle and furnished new evidence of the distinctness of *minor*. He also pointed out that *minor* dif-

fered from nominate *glacialis* in having, on the average, a lesser body weight.

In view of this wide support for the recognition of *minor*, I was surprised to read the following note (G. N., 1963: 250; "G. N." is undoubtedly Günther Niethammer):

> *Fulmarus glacialis minor* is not valid, as pointed out by Dr. Charles Vaurie in a discussion during his visit to Koenig Museum in Bonn. The variation in bill length in Greenland as well as in Spitsbergen and Bear Island is considerable and the measurements are everywhere almost identical. According to the measurements taken by Vaurie the bill length in birds from Spitsbergen (12 males) ranges from 36 to 39 mm, from Bear Island (28 males) 35 to 43.5 mm, and from Greenland (6 males) 36 to 42 mm. Twenty males in the Copenhagen Museum measured 33.5 to 41 (average 36) mm. . . . Consequently, *minor* designates merely the small specimens in the entire range of the Fulmar.[1]

This statement is not correct, however, and I find it necessary, therefore, to revert to the subject once more. I do so not so much from the desire to correct an error as to take this opportunity to discuss the zoogeography of the Fulmar. I have studied this species for years, almost as enthusiastically as James Fisher, its well known monographer. I wish here, especially, to point out the close correlation between the geographical variation of the Fulmar, as well as of other sea birds, and the zonal division of the North Atlantic based on the physical factors of the sea.

The Zones of Marine Environment in the North Atlantic

The zoogeographical division of the northern seas has been based mainly on the distributions of marine invertebrates, but also on those of fish and mammals (whales, seals), and closely follows the variation in important oceanographic factors like temperature, ice cover, salinity, etc. From a biological point of view the zonal division has proved to be of the utmost importance and is the guiding system even for the commercial fishery. Nevertheless, it has been grossly ignored by ornithologists. This is probably because sea birds, being dependent on the land for breeding, generally are looked upon as terrestrial organisms. This viewpoint is not correct, however. Sea birds are intimately attached to the marine environment and in their distribution are delimited by the physical factors of the sea, just as other marine groups of animals are. In the southern hemisphere the presence of distinct oceanic convergences makes the whole picture much clearer, and the connection between sea bird distribution and the oceanic zones has been well established, mainly by the excellent work of Murphy (1936: vol. 1, see pp. 59–110).

The zoogeography of the seas has been fully dealt with by Ekman

[1] Original in German; translated by me.

(1935), and more recently by Dunbar (1951 and 1953), as far as the northern seas are concerned. I have in various works (Salomonsen, 1950–51; Freuchen and Salomonsen, 1958; Salomonsen, 1963) adverted to the zonal distribution of the northern sea birds, but have never given a general description of the zones. I find it appropriate, therefore, to publish a brief description now, in connection with the discussion of the geographical variation of the Fulmar.

Animal distribution is more complicated at sea than on land, because it has a vertical dimension apart from the horizontal one. The following zonation is restricted, therefore, to the upper water layers, above a depth of roughly 25 meters. These are of primary significance for the distribution of birds.

For still other reasons it is much more difficult to delimit the regions of the sea than those of the land. From the tropics to the north a steady decrease in water temperature takes place. In some places there are fairly sharp limits between the cold polar water and the warm water from the tropics, but in other places the change is very gradual. In the Atlantic Ocean, where conditions are best known, the Atlantic drift called the Gulf Stream carries tropical water from the Gulf of Mexico to the north. Due to the rotation of the earth, the current is deflected to the east so that it crosses the North Atlantic diagonally, part of it running parallel with the Norwegian coast and even farther to the north. All the while the temperature of the water steadily decreases until the current finally disappears in the depths of the Arctic Ocean. The movements of the water in the northern hemisphere have a counter-clockwise direction, and the southward-moving cold currents in the Atlantic are found, therefore, in the western sector. Here the main currents that carry cold polar water to the south are the East Greenland Current and the Canadian Current (east of Baffin Island). The East Greenland Current turns to the north around Cape Farewell and follows the west coast of Greenland to the north, but part of it moves westward and in the southern Davis Strait joins the southgoing Canadian Current. These united currents, together with water masses coming from Hudson Bay and Foxe Basin, form the large and important Labrador Current, which carries polar water as far south as Newfoundland and the northern United States and makes the Gulf of Saint Lawrence an arctic water.

The boundary between the warm, and very salt, southern water masses and the cold, less saline, polar ones constitutes the limit between a northern *arctic* and a southern *boreal* region. But in the southern parts of the arctic seas there is a considerable mixture of polar and southern water, particularly in the eastern Atlantic, and it is thus not possible, when basing the division exclusively on hydrographical facts, to fix any exact

border between the arctic and boreal zones in the sea. It is necessary, therefore, to stress the distribution of certain key animals in order to get a usable delimitation.

In studying the animal life of the sea, it appears that there is a certain belt in which the ranges of a large number of representative northern (arctic) species attain their southern boundary and where, on the other hand, many "southern" (boreal) species reach their northern limit. This belt, in which there is a marked shift in the animal population, corresponds fairly well with upper water layers with a mean temperature for the warmest month (August) of 10°C, or with those which have an annual mean temperature of 5°C. This belt forms the southern boundary of the marine arctic region. The southern limit of the boreal region, where it borders the subtropical zone, is often drawn along the isotherm of 15°C (annual mean) of the upper water layers, and this has been done also in Figure 1, beyond. This line is somewhat arbitrary, and does not very well agree with the distribution of marine organisms. According to Ekman (1935: 144) the boreal fauna on the European side of the Atlantic reaches its southern limit off Brittany, and this corresponds very well with the situation in the sea birds. Farther west the boundary must pass somewhat north of the Azores, which are typically subtropical. On the American side the conditions cannot be compared with the European ones, and it is difficult to fix a definite boundary. Cape Cod, Massachusetts, forms a well known boundary region, even in birds, but various boreal inshore birds penetrate considerably farther south. In the open ocean the boreal/subtropical boundary is still more difficult to fix, but the southern limit of the Fulmar's range appears to be well suited to indicate the boundary between the two zones.

The marine arctic region is not uniform, but can be divided into two zones, the *higharctic* and *lowarctic* zones, which are rather sharply delimited. The marine higharctic zone covers those areas in which is found unmixed water of polar origin (from the upper layers of the Arctic Ocean), admixture of water of terrigeneous origin being ignored in this definition. The water of the lowarctic zone is composed of a mixture of polar and boreal water. The boundary of the two zones agrees fairly well with that separating the corresponding two zones on the land. It must again be emphasized that this marine delimitation holds good only for the surface water, not for the masses of deeper water or for the bottom of the sea, where conditions are different. The distribution of certain key animals helps in the delimitation of the two zones.

The higharctic zone has a severe polar climate. The winters are long, cold, and often very windy, with temperatures practically always below freezing. The summers are short and cool, with a July mean (air tem-

perature) below 5°C. The coastal waters are usually blocked with ice, which does not scatter until July and August, and navigation is possible for only about six weeks, except for very powerful icebreakers. The tidal zone is completely lifeless.

In the lowarctic zone conditions are somewhat mitigated. The winters are not so cold and long, often showing alternating periods of thaw and freeze. The summers are more extended and milder, with a July mean (air temperature) between 5°C and 10°C. The coastal waters are ice-free for varying periods, which are everywhere much longer than in the higharctic zone. Protected bays and fjords are ice-covered even into the beginning of summer, but open coasts may in many areas be ice-free during the entire winter. The tidal zone is inhabited by a considerable number and variety of animals, including snails, mussels, worms, sea-anemones, sea-urchins, crustaceans, and many other forms. These organisms are very sensitive to the presence of boreal water, and their distribution, therefore, affords good clues as to the delimitation of the lowarctic zone. The distribution of the tidal animals has been studied by Madsen (1940: 1) in Greenland and by Ellis (1955: 224) in Baffin Island. Subsequent comments have been given by Barnes (1957: 1).

Maps showing the zones of the marine environment in the northern parts of the northern hemisphere have been published, e.g., by Dunbar (1953: 76) and Freuchen and Salomonsen (1958: 8).[1] The map (Figure 1) in the present paper gives the zones in the North Atlantic.

It should be mentioned here that Dunbar as well as most other American zoogeographers and ecologists use the terms "Arctic Zone" and "Subarctic Zone" for what is, by Ekman (1935: 254) and in the present paper, called higharctic ("hocharktisch") and lowarctic ("niederarktisch"), respectively.[2] This is unfortunate, because it does not correspond with the terminology of the terrestrial life-zones, of which the "arctic region" equals the marine region which is here called arctic, and not its higharctic subdivision alone. The subarctic zone of terrestrial zoogeography and ecology equals the zone which in America is called the "Hudsonian Zone" and in the Soviet is called "Ljesotundra." Consequently, it is more expedient to use the determinations higharctic and lowarctic also in marine zoogeography.

Organisms which are distributed in both the higharctic and lowarctic marine zone are generally called panarctic; those which are distributed in both the panarctic and the boreal zone are called boreo-panarctic; and,

[1] The legends to the figures on pp. 8 and 16 were unfortunately transposed in that book.

[2] Ekman (1935: 145) uses the term "subarctic" for an ill-defined boreo-arctic transitional zone in the North Atlantic.

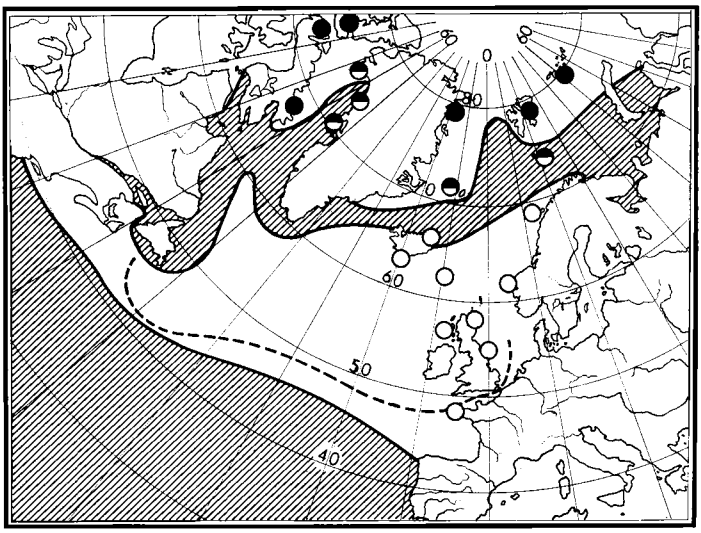

Figure 1. The zones of marine environment in the North Atlantic. From above: higharctic (unshaded), lowarctic (shaded), boreal (unshaded), subtropical (shaded). The breeding range of the Fulmar is shown by circles. Solid circles, small-billed populations; open circles, large-billed populations; half-solid circles, populations with intermediate bill length. The broken line indicates the southern limit of the regular occurrence in winter of the Fulmar.

finally, those which are distributed in both the boreal and the lowarctic zone are called boreo-lowarctic.

When an advanced draft of the present paper was already finished, a review of oceanic studies of sea birds was published by Bourne (1963: 831). In this very stimulating and informative paper, Bourne touches on many of the problems dealt with above, and even proposes a special zoogeographical system covering all oceans (*op. cit.*: 836), but differing somewhat in terminology from that usually adopted by marine biologists. His "Polar Communities" correspond to the higharctic ones, while his "Subpolar Communities" correspond mainly to the combined lowarctic and boreal ones (the boreo-lowarctic organisms).

The distribution of the North Atlantic sea birds is closely correlated with the marine zones, as defined above. This appears distinctly from the appended list (Table 1) of species and subspecies arranged in accordance with their breeding distribution.

THE GEOGRAPHICAL VARIATION OF THE FULMAR IN THE NORTH ATLANTIC

The geographical variation of the Fulmar in the North Atlantic involves two characters, bill length and dichromatism. While the differences

TABLE 1

DISTRIBUTION OF NORTH ATLANTIC SEA BIRDS IN RELATION TO MARINE ZONES

Boreo-panarctic	Lowarctic
Fulmarus glacialis	*Larus glaucoides: glaucoides* and *kumlieni*
Somateria mollissima	*Uria aalge hyperborea*
Stercorarius parasiticus	
Rissa tridactyla	Boreo-lowarctic
Sterna paradisaea	*Mergus serrator*
Cepphus grylle	*Phalacrocorax carbo carbo*
Fratercula arctica	*Larus marinus*
	Larus argentatus smithsonianus
Panarctic	*Alca torda*
Branta bernicla	*Uria aalge*
Stercorarius pomarinus	*Cepphus grylle: grylle* group
Stercorarius longicaudus	*Fratercula arctica arctica*
Larus hyperboreus	
Larus glaucoides	Boreal
Uria lomvia[1]	*Morus bassanus*
	Puffinus puffinus puffinus[6]
Higharctic	*Hydrobates pelagicus*[6]
Somateria spectabilis	*Oceanodroma leucorrhoa leucorrhoa*
Branta bernicla hrota	*Phalacrocorax aristotelis*[6, 7]
Pagophila eburnea	*Stercorarius skua skua*
Larus glaucoides thayeri	*Larus argentatus: argentatus* and *omissus*[8]
Xema sabini[2]	*Larus fuscus*[8]
Rhodostethia rosea[3]	*Larus canus canus*[8]
Cepphus grylle: mandti group[4]	*Sterna hirundo*[6]
Plotus alle[5]	*Pinguinus impennis* (extinct)
Fratercula arctica naumanni	*Fratercula arctica grabae*

[1] Locally breeding in boreal southern Iceland.
[2] In the Pacific also lowarctic.
[3] Not typical, breeding in a terrestrial habitat in the subarctic zone, but restricted to the higharctic zone for the remaining part of the life cycle.
[4] Breeding south to Bear Island, and to Upernavik District in northwestern Greenland.
[5] Breeding in the higharctic zone in millions, in the transitional area between the higharctic and lowarctic zones in thousands, and in the lowarctic zone proper in isolated pairs.
[6] Also subtropical.
[7] Slightly penetrating into the southern part of the lowarctic zone (northwestern Iceland, western Murman Coast).
[8] Extends into the lowarctic zone on Kola Peninsula.

in bill length cannot be observed in the field the light and dark phases can be easily distinguished.

The distribution of the two phases has been summarized by James Fisher in his excellent monograph of the Fulmar (1952: 266–325), but unfortunately he was unaware of the ecological zonation of the Atlantic. I pointed out to Fisher the connection between the dark phase and the higharctic zone, and he quotes our discussion fairly enough (p. 283), admitting that the correlation appears to be good, but he drew no conclusions from this fact. He went so far as to say that it was impossible to correlate the distribution of the Fulmar with any physical factor of the sea: "All such comparisons [with physical factors] have proved fruitless, for the Fulmar's distribution is controlled by the abundance of food, by its availability, by its accessibility, by the time the

Fulmar has to find it and gather it" (p. 325). This is true, of course, only with the reservation that the feeding habitat must be situated within the marine zone to the life conditions of which the Fulmar is adapted.

The Fulmar is a typical boreo-panarctic sea bird. Even in winter it does not penetrate the subtropical zone (see Figure 1). The light phase is attached to the boreo-lowarctic waters and only sparingly breeds in the higharctic zone proper, where it constitutes, at most, 15 per cent of the breeding population, but usually much less. The dark phase (including the intermediate types) is restricted to the higharctic zone as a breeding bird, but in its distribution at sea it is indicative of arctic water generally. This means that both color phases occur in the lowarctic seas.

In winter the water temperature in the northernmost parts of the boreal zone is considerably lowered and the dark phase then penetrates slightly southward, dark birds occurring rather frequently in these areas. They may even be found, although irregularly and in small numbers only, on the Newfoundland Banks and off the Shetland Islands and the western coast of Norway. In summer, however, they withdraw to the north, and in the breeding season (i.e., May to August) only exceptionally do individuals occur south of the boreal-lowarctic convergence.

On the other hand, the dark phase can be observed almost immediately when one approaches from the south or crosses the boundary areas between the boreal and the lowarctic zones, the dark birds being unfailing indicators of the presence of arctic water. This can be seen in the areas north of Iceland, those between Norway and Bear Island, and in the offshore zone off Finmarken in northern Norway (see Fisher, 1952: 307–320). The percentage of the dark phase in the local feeding population may vary considerably in these waters, but the dark birds always constitute at least a few per cent of the feeding population.

A very high correlation between the appearance of the dark phase and the zonation of the sea is found in the waters between Greenland and Spitsbergen, according to the careful notes made by Manniche (1910: 124) during the Danmark Expedition in July 1906. The first dark birds were observed at 66° N lat. and 12° W long., i.e., when crossing the boreal-lowarctic convergence east of Iceland. The dark form began to predominate at about 74° 30′ N lat. and 3° W long., i.e., when passing from the lowarctic to the higharctic zone. Farther west, in the pack ice at 75° to 76° N, 75 to 100 per cent of the birds observed were dark.

The distribution of the two color phases has been most thoroughly studied in the approaches of Kap Farvel (Cape Farewell) in the northwestern Atlantic on the sailing route from Copenhagen to Greenland. This route, which is shown on the map (figure 1) given by Christensen (1937: 56), follows the latitude of approximately 60° to 61° N across

the Atlantic and transgresses the boreal-lowarctic convergence at about 38° to 40° W longitude in a rather sharply marked belt. On several voyages I have observed the occurrence of the two color phases of the Fulmar and also noted the water temperature. In the boreal zone, extending across the North Atlantic westward as far as about 38° W, the temperature of the upper water layers at about 60° N in May is 8° to 10°C, rising to 10° to 12°C by the end of June. In the area between 38° W and about 45° W the temperature drops abruptly to 3° to 5°C in May and to 4° to 7°C in late June. The dark phase is completely missing in the boreal waters east of 38° W at least in the period May–August, but promptly appears in the zone of cold water from about 38° W and westward. The occurrence of the dark birds always coincides with the appearance of small flocks of the Thick-billed Murre, *Uria lomvia*, another species belonging to the arctic zone and avoiding the boreal water masses. The result of three typical countings made by me during my voyages is given in Table 2.

Christensen (1937: 60) counted the number of the two color phases of the Fulmar observed on the sailing route to Greenland during 349 hours of observation. It appears from his diagram (figure 2) that the dark form rather suddenly increases in number when one proceeds west of 40° W longitude. The appearance of dark birds in the Kap Farvel waters is well known by the captains of the Greenland boats, who since the old days call them "Hukkens Maager" (= Kap Farvel Gulls).

The correlation between the presence of cold (arctic) water and the occurrence of the dark phase is clear enough, but it is noteworthy that this correlation has nothing to do with food resources. Jespersen (1954: 1) has demonstrated that a very pronounced concentration of macroplankton is to be found in the northwestern Atlantic between about 62° and 50° N and 25° and 38° W, i.e., a region which is steadily supplied with nutritive surface water originating from the mixing areas along East Greenland; see Nielsen (1935: 50), and Salomonsen (1955: 93). The dark Fulmars penetrate only into the northernmost parts of this area rich in food, which is utilized predominantly by the light form.

In the eastern, lowarctic parts of Davis Strait, on the fishing banks off the West Greenland coast, both color phases are found, just as in the Kap Farvel waters. The number of dark birds varies greatly, usually amounting to 10 to 20 per cent of the population, but sometimes up to 50 per cent, and once I have counted about 75 per cent (17 May 1960, south of Faeringehavn in southwestern Greenland). The dark birds belong, undoubtedly, to the breeding population of Baffin Island, but some may also originate from northeastern Greenland. The greater part of the light birds belong to the breeding population of northwestern

TABLE 2

THREE TRANSECTS OF THE NORTH ATLANTIC AT ABOUT 60° N LAT., SHOWING SURFACE WATER TEMPERATURE (IN °C) AND THE OCCURRENCE OF THE DARK PHASE OF THE FULMAR[1]

°W long.	*Dates of transects*					
	18–25 June 1946		*7–11 June 1954*		*12–16 May 1960*	
	Temp.	*Dark Fulmars*	*Temp.*	*Dark Fulmars*	*Temp.*	*Dark Fulmars*
0–29	9.1–11.8	—	9.8–11.0	—	8.0–10.0	—
30	—	—	9.2	—	8.2	—
31	8.8	—	—	—	—	—
32	—	—	8.0	—	8.4	—
33	—	—	—	—	—	—
34	8.9	2	8.0	—	8.2	—
35	—	—	—	—	—	—
36	—	—	8.0	1	7.2	—
37	—	—	—	—	5.8	*
38	7.4	15–20%[2]	7.6	1[2]	—	—
39	—	15–20%[2]	—	—	4.8	*
40	7.3	15–20%[2]	5.4	—	4.8	*
41	—	15–20%[2]	—	—	—	5–10%[2]
42	7.0	15–20%[2]	5.4	*	5.2	5–10%[2]
43	4.4	15–20%[2]	—	+10%[2]	—	5–10%[2]
44	6.4	15–20%[2]	5.8	+10%[2]	4.3	5–10%[2]
45	5.8	15–20%[2]	4.6	+10%[2]	—	5–10%[2]
46	5.8	15–20%[2]	—	+10%[2]	4.6	5–10%[2]
47	5.4	15–20%[2]	—	+10%[2]	—	25–50%[2]
48	1.6	15–20%[2]	5.4	+10%[2]	4.8	25–50%[2]
49	—	15–20%[2]	—	+10%[2]	3.4	25–50%[2]

[1] This table is based on observations made by the author on east to west voyages from Copenhagen to Greenland. Only the occurrences of *dark* Fulmars have been considered in the table (numbers when few, per cent of total when many), but it should be emphasized that light Fulmars were numerous on all days of observation. An asterisk (*) denotes that no observations were made at the longitude in question. A plus sign (+) indicates that *at least* 10 per cent of the Fulmars seen were dark.

[2] Various numbers of *Uria lomvia* also noted.

Greenland. In May the percentage of dark birds on the fishing banks decreases rapidly north of Godthaab and rarely amounts to more than 2 per cent of the population off the Sukkertoppen–Holsteinsborg districts. Farther north, in the Egedesminde District, only occasional dark birds are met with, because these waters are within the premises of the local breeding population of the Disko Bay colonies, which consist almost exclusively of light birds. In the summer (June–August), when many non-breeding birds return to sea from cliff-prospecting, the dark birds are met with farther north, and then the population may often consist of 10 to 20 per cent of dark birds, even in the waters north of Holsteinsborg. In the coastal waters north of Disko, right up to Melville Bay, dark birds are only exceptionally met with, but they appear in increasing numbers to the west, when one approaches the higharctic zone in the western part of Baffin Bay and Davis Strait. The description above of the status

of the two color phases in the waters off West Greenland is based on my own unpublished observations during many years.

The following review of the geographical variation in the breeding populations considers bill length as well as dimorphism. The populations are arranged according to the zonation of the North Atlantic as described above.

HIGHARCTIC POPULATIONS

The populations of the typical higharctic breeding places appear to be very similar. They consist almost exclusively of dark birds, only a very small percentage being light, and the bill length is small in all populations from which measurements have been taken.

Canada.—The Baffin Island breeding places (Cape Searle and Admiralty Inlet) have been well studied. In 37 males measured by me (Salomonsen, 1950: 100), Wynne-Edwards (1952a: 91), and Watson (1957: 90) bill length ranges from 33.2 to 39.0 mm (average 36.2); the birds are small-billed. Dr. Charles Vaurie has kindly given me access to his unpublished measurements of Fulmars taken from material in various museums. Dr. Vaurie gives the bill length in seven males from "Baffin Island and northwestern Greenland" as 34.5 to 38.5 mm (average 36.6), which corresponds with the measurements taken by the above-mentioned students. Part of Dr. Vaurie's material may, however, belong to Greenland populations and not to Baffin Island ones.

The dark phase (including specimens of intermediate color shades) is by far predominant, constituting about 85 per cent of the population according to Wynne-Edwards (*loc. cit.*) and Watson (*loc. cit.*).

The population of the rookery on Devon Island, at Jones Sound, consists also of small-billed birds. Wynne-Edwards (*loc. cit.*) gives the bill length in five males as 35.5 to 37.5 (average 36.6) mm. The dark phase is predominant, constituting at least 90 per cent of the population according to Duvall (Fisher, 1952: 281).

Northeastern Greenland.—The big colony on Mallemukfjaeldet (80° 12′ N) consists "almost exclusively of dark birds," according to the explorers Koch and Bertelsen (Manniche, 1910: 123). No measurements have been taken of northeastern Greenland breeding birds. The few specimens which have been measured have been collected at sea, at some distance from land, and may as well belong to the Jan Mayen population or even to other populations still farther removed. It may here be repeated that birds collected on the sea are almost useless when the problem is to analyze a breeding population. The birds must be collected in the immediate vicinity of the breeding place. Manniche (1910: 125) gives the bill length of three males collected on 31 July 1906, in the pack ice at 75° N and 8° W, as 39, 41, and 42 mm. These birds were all light, which indicates that they could probably not have come from the northeastern Greenland breeding places. The collecting place is not far from the boundary between the higharctic and lowarctic zone (see Figure 1). Three dark females collected at the same place are all small-billed. Wynne-Edwards (1952a: 91) gives the bill length of 2 males from East Greenland as 38 and 40 mm. Mathiasson (1963: 274–276) gives the bill length of 11 males from East Greenland as 37.8 to 40.0 mm (average 38.5), and Vaurie (*in litt.*) gives for 7 males the measurements 36 to 42 mm (average 38.6). All these

birds, most of them from the vaguely defined locality "East Greenland" have rather big bills, approaching in size those of the boreal birds, although on the average somewhat smaller. As said already, they may be birds from Jan Mayen or from northern Iceland. According to the map in Mathiasson (*loc. cit.*), his East Greenland material originated from the Scoresby Sound region, which is far removed from the higharctic Fulmar colonies in northeastern Greenland and where the visitors for the greater part probably are Jan Mayen birds.

We know practically nothing about the small population breeding on Raffles Island off the Liverpool coast. The population consists of both light and dark birds, but the percentage of each is not stated, and no specimens have been collected. Even at the outlet of nearby Scoresby Sound, where the Fulmar does not breed, both color phases are met with, apparently in almost equal numbers, although the composition of the feeding population occurring there appears to be subject to much variation. Farther to the south along the coast, when one approaches and enters the lowarctic zone the percentage of the light birds increases gradually.

Jan Mayen.—See below, under the lowarctic populations.

Spitsbergen.—All observers agree that the dark form vastly predominates; there are a good many intermediate individuals, but very few light ones. Although very few exact countings have been made, there can be no doubt that the light birds constitute less than one per cent of the population. In the northern and eastern parts of Spitsbergen, in which the higharctic regime is more pronounced, light birds are virtually non-existent (Løvenskiold, 1964: 76).

Until quite recently no bill measurements of Spitsbergen birds have been published. Vaurie (*in litt.*) gives the bill length of 14 males as 34 to 39 mm (average 36.5), which shows that this population has small bills as does that of Baffin Island. Wynne-Edwards (1952a: 91) gives the bill length of 3 males as 37.2, 38.3, and 39.7 mm. Recently Mathiasson (1963: 274–276) gave the bill length of 11 Spitsbergen males as 36.5 to 40.0 mm (average 38.4), which shows somewhat higher values than those stated by Dr. Vaurie. This may be due either to differences in the way of measuring, or it may, rather, indicate that the material comprises stragglers from Bear Island, the population of which on the average has longer bills.

Franz Joseph Land.—The composition of the breeding population is, apparently, very similar to the situation on Spitsbergen. By far the majority of the birds are dark, but no specimens have been examined and nothing is known about the bill length.[1]

LOWARCTIC POPULATIONS

The breeding populations of the lowarctic zone hold an intermediate position between the higharctic and the boreal ones. They are not uniform, however, but differ in accordance with their different origin.

In all lowarctic populations the bill length is intermediate between that of the higharctic ones and that of the boreal ones, thus demonstrating a close correlation with the environmental factors. The light color phase is vastly predominating in most breeding colonies, but there is in all localities a slight admixture of dark birds. The percentage of these appears

[1] I cannot say anything about the Fulmars breeding on Nowaya Zemlya.

to increase slightly to the north, indicating either gene flow from high-arctic populations or, more likely, an increased selective advantage of the individuals with dark coloration.

Populations of the composition and appearance described above are not typically lowarctic, but inhabit the transitory belt between the low-arctic and higharctic zone, covering the cooler (northernmost) parts of the lowarctic zone and the neighboring (southernmost) parts of the high-arctic zone. In West Greenland Fulmars of this type breed in a number of huge colonies in the lowarctic zone from Disko Bay north to Upernavik District and in a single, rather small colony in the adjacent higharctic Thule District. In addition, this type of Fulmar breeds on Jan Mayen, which is situated almost on the border line between the higharctic and the lowarctic zone, but on the higharctic side. There are no Fulmars breeding in the lowarctic zone of the American mainland, in the southern parts of lowarctic Greenland, or in the lowarctic parts of Norway and the Russian Murman Coast.

The Fulmars breeding on Bear Island differ remarkably in coloration from the other lowarctic populations in the Atlantic. This locality is very far removed from the other lowarctic breeding places, but is situated rather close to the higharctic Spitsbergen. The Fulmar population of Bear Island, like that of Spitsbergen, consists predominantly of dark birds, although the percentage is lower than in Spitsbergen. Evidently, this indicates increased survival value of the genes for light coloration in the lowarctic environment of Bear Island. The Fulmar colony of Bear Island is, obviously, an offshoot from the nearby Spitsbergen population. Probably the colonization of Bear Island took place in a period when the climate was more severe than at present, approaching higharctic conditions. During the subsequent gradual climatic change the Bear Island population became adapted to milder life conditions, under which a selective premium was paid for greater bill length and probably also for lighter coloration. As is shown below, there is strong evidence for the assumption that an increase in the percentage of light birds has taken place on Bear Island during the present climatic amelioration.

Contrary to the other dimorphic sea birds in the North Atlantic, the Fulmar does not in its dimorphism demonstrate any clinal variation. In the Fulmar two sharply different groups of populations are separated by a wide morphological gap. The first group consists primarily of dark birds,[1] constituting 85 to 100 per cent of the population, and the second group consists almost or exclusively of light birds, which constitute 99 to 100 per cent of the population. The first group is adapted to the higharctic environment, the second group to the lowarctic environment,

[1] Including intermediate color shades.

but, as shown above, there is a slight overlap in the ecological tolerance of the two groups. Both groups may just cross the boundary between the lowarctic and the higharctic zone and settle beyond it. The higharctic group has made this crossing on Bear Island, while the lowarctic group has made it in Thule District and on Jan Mayen. These expansions have caused only very insignificant changes, if any, in the ratio of the two color phases in the populations. This demonstrates that the difference between the two groups in the ratio of light to dark birds is not simply a result of an adaptation to different environments, but that the two groups represent different genetical systems. The genetic differences between them must have been brought about through reproductive isolation. The groups must some time in the past long have been mutually isolated, one in a higharctic, the other in a lowarctic environment. It is not possible to say where and when this isolation took place, but it may very well have happened in the last glacial period. The present distribution of the two groups corresponds with that of the two subspecies groups of the Black Guillemot (*Cepphus grylle*), of which the *mandti* group is restricted to the higharctic zone and the *grylle* group to the boreo-lowarctic zone. It is noteworthy that in the Black Guillemot, as in the Fulmar, the higharctic form inhabits Bear Island, whereas the populations of all other species of widely distributed sea birds breeding on this island belong to lowarctic subspecies. Probably this is because the greater part of the sea bird species inhabiting Bear Island are migratory, while the Black Guillemot and the Fulmar are resident in the surrounding lowarctic waters. There, as far as wintering is concerned, the higharctic form undoubtedly is the superior. The migratory habits and the wintering conditions, therefore, must be considered also when analyzing the breeding ranges of the different forms of sea birds. It is very likely that adaptation to the winter environment was decisive in determining whether the higharctic or lowarctic form of the Fulmar and the Black Guillemot got a foothold on Bear Island and was superior in its colonization.

Northwestern Greenland.—The percentage of the two color phases is well documented in all populations of northwestern Greenland. The Fulmar breeds along the coast from Disko Bay northwards to Thule District. The light phase vastly predominates in all populations. The dark birds constitute about 0.1 per cent of the populations in Disko Bay and Umanak District and about 1.0 per cent of those in Upernavik and Thule districts. I have personally investigated all known colonies (Salomonsen, 1950–51: 32–33).

The bill length of the West Greenland breeding birds is not known with certainty. When I studied these birds I refrained from publishing measurements, because very few specimens were collected at the breeding places proper and very few were properly sexed. It is well known that Fulmars from many populations are found off the West Greenland coasts. It has been pointed out above that dark birds from higharctic breeding places are common there in summer. Banding has demonstrated

that individuals even from British breeding places occur there. My West Greenland material comprised both short-billed and long-billed specimens (Salomonsen, 1950: 103), but I could not distinguish breeding birds from visitors. When Niethammer (1963: 250) states that the bills of 20 males measure 33.5 to 41.0 mm (average 36) it does not, consequently, mean very much. Mathiasson (1963: 274–276) gives for 15 males a bill length of 35 to 39 mm (average 37.2), but these measurements seem too small to be representative; I have measured males from West Greenland with a bill length of 39.8 mm and, as stated above, Niethammer has measured birds with a bill length of 41 mm. 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.

Jan Mayen.—The breeding population consists almost exclusively of light birds, the dark ones constituting only about 0.4 per cent of the population (see Fisher, 1952: 274). The composition of the population is, thus, virtually identical with that of the West Greenland populations. Measurements of bill length have been given by two students, but the total number of measured birds is small. Wynne-Edwards (1952a: 91) gives the bill lengths of two males as 39 and 39.5 mm and Mathiasson (1963: 274–276) gives those of three males as 39 to 41 mm (average 39.8). This tends to show that the bills of the Jan Mayen birds are intermediate in length, but on the average slightly longer than those of the West Greenland populations.

Bear Island.—As in nearby Spitsbergen, the dark phase vastly predominates. According to the newest census (1948), only 10 per cent of the birds are light, while of the remaining 90 per cent, 15 are dark and 75 are intermediates of various color shades (Fisher, 1952: 275). The number of intermediate individuals appears to be greater than in Spitsbergen, but there the estimates have been based usually on observation rather than on collected material, and it is thus difficult to make an exact comparison of the figures. It is evident, however, that the percentage of light birds is greater than in Spitsbergen. In the summer of 1958 Løvenskiold (1964: 76) observed "a relatively large number of light birds on Bear Island." Apparently, the percentage of light birds has increased on Bear Island since about 1920, in correlation with the recent amelioration of the climate. Kolthoff, who was a well known zoologist and an excellent observer, visited the island in 1898 and stated that only about 0.1 per cent were light birds. A similar statement was made by Le Roi, who visited Bear Island in 1907 and 1908 and also was a keen observer (see Fisher, *loc. cit.*).

Wynne-Edwards (1952a: 91) gives the bill length of two males from Bear Island as 38.6 and 40.6 mm and Mathiasson (1963: 274–276) that of three males as 37.0 to 40.6 mm (average 38.7). Vaurie (*in litt.*) has examined no less than 31 males and gives the bill length as 35 to 43.5 mm (average 38.6). These measurements are intermediate between those of the short-billed and of the long-billed type. The measurements given by Vaurie indicate that there is a considerable individual variation in bill length in the Bear Island population.

BOREAL POPULATIONS

During less than 200 years the Fulmar has spread over great parts of the boreal zone, having originated from a single center. The increase in number and the spread of the species took place with unbelievable rapidity.

This tends to show that selection pressures of either the physical or biotic environment must have been negligible during the expansion. It is very unlikely, therefore, that any genetic differences should have developed between the populations of the boreal zone. Moreover, any development of genetic differences would imply an almost unprecedented speed in evolutionary rate owing to the rapidity of the expansion, and even this fact speaks in favor of the homogeneity of the boreal populations. A study of the morphological characters bears out the assumption. The boreal populations are virtually identical. All consist exclusively of light birds, but odd individuals of an intermediate color type may occasionally, or even regularly, be found among the breeding birds. The order of magnitude in which they occur in the populations is so minute, about 0.001 per cent, that it may be permissible to ignore them.

The only area in which the expanding Fulmars have occupied breeding places outside the boreal zone is in northern Iceland, where they have settled in the southern part of the lowarctic zone. Even there the populations consist exclusively of light birds. The population inhabiting the island of Grimsey may form an exception. Unlike other northern Iceland populations the Grimsey colony has been known from ancient time, hence its presence there is unrelated to the recent expansion. The evidence concerning the ratio of the two color phases on Grimsey is conflicting. According to the summary given by Fisher (1952: 273) there were 0.1 per cent dark birds present about 1850, while all visitors after 1900 have failed to observe any dark birds. Saemundsson (1936: 481) states, however, that there are 2 per cent dark birds. This conflicts with the results of all other observers and may result from counting dark birds occurring in the surrounding seas but originating from northern breeding places. As noted above, dark birds from higharctic breeding places occur as common summer visitors in lowarctic waters, and they occur regularly and in some numbers off northern Iceland at some distance from land.

All boreal populations have a long bill. The bill lengths of 9 males from British breeding places were given by Witherby *et al.* (1940: 80) as 38 to 43 mm, and those of 16 males from Iceland and the Faeroes by me (Salomonsen, 1950: 102) as 37 to 43.2 mm (average 40.4); 6 further males (skulls only) had bill lengths of 39 to 43 mm (average 41.3). Wynne-Edwards (1952a: 93) gives the following measurements (all of males): 10, Scotland, 39.0–43.6 mm (average, 41.3); 7, St. Kilda, 37.6–42.3 (40.2); 7, the Faeroes, 39.0–43.0 (40.7); 10, Iceland, 39.0–43.0 (40.9). Combined; 34, 37.6–43.6 (40.83).

Mathiasson (1963: 274–276) quotes the measurements given by Wynne-Edwards, adding a few from Iceland and the Faeroes, giving the average bill length in males from these two localities as 40.4 and 40.1 mm, respectively. The smallest measurement in the Iceland series is 35 mm, but this may result from the presence of northern visitors obtained at sea. Vaurie (*in litt.*) has taken the following measure-

ments (males): 11, British Isles, 35.0–42.5 mm (average 39.1); 7, the Faeroes, 36.0–43.0 (39.7); 9, Iceland, 37.0–43.0 (40.6).

The small extreme among the British birds may result either from exceptions or, more probably, from visitors from lowarctic populations. Birds banded in northwestern Greenland have been recovered as far away as western France and, naturally, Greenland birds occur also off the coasts of the British Isles. Wynne-Edwards (1952a: 97) has already paid attention to such small-billed specimens of northern origin, from the British Isles, and similar individuals have turned up in German and Swedish waters.

Mathiasson (1963: 277) gives the bill length of three males from one of the breeding places in Norway as 38.6 to 39.8 mm (average 39.1), which is smaller than that expected although within the range of variation of the other boreal populations. The sample is too small, however, to be of decisive value. Four females from the same locality measure 36.5 to 37.6 mm (average 37.2), which is quite typical for boreal populations.

CONCLUDING REMARKS ON GEOGRAPHICAL VARIATION

The description of the different populations has shown that the northern ones are small-billed and consist of dark birds, whereas the southern ones are large-billed and consist of light birds. The two variable characters are not correlated, however; the geographical variation in dimorphism and that in bill length do not coincide.

As far as dimorphism is concerned it is possible to distinguish between two groups:

(1) Populations consisting of dark birds, with an admixture of at most 10 to 15 per cent light birds: all higharctic populations (northeastern Canada, northeastern Greenland[1]), Spitsbergen, Franz Joseph Land, and Bear Island.

(2) Populations consisting exclusively of light birds: all boreal populations (Iceland, the Faeroes, British Isles, Brittany, Norway), or with a slight admixture of dark birds, amounting at most to 1 per cent of the population: lowarctic populations in Greenland (including Thule District) and Jan Mayen.

Bill length is directly correlated with the zonation of the sea, as has been stressed already. It is possible to distinguish three groups:

(1) Small-billed, with average bill length in adult males less than 37 mm: all higharctic populations investigated.

(2) Intermediate, with average bill length in adult males 38 to 39 mm: lowarctic populations (including Jan Mayen).

(3) Large-billed, with average bill length in adult males more than 40 mm: boreal populations.

[1] The colony on Raffles Island may have a greater percentage of light birds, but needs further examination.

The two variable characters have a different origin and a different biological significance. The dark color, which is very predominant among the birds in the higharctic populations and suddenly disappears in the lowarctic ones (except in Bear Island) is, probably, due to a pleiotropic effect of a gene or gene combination, with strong survival value in a high-arctic environment. The sudden drop in the percentage of dark birds from 90 to 100, to less than 1, when moving from the higharctic to the lowarctic populations is not in conformity with the gradual change from a higharctic to a lowarctic environment and must be due to historical causes, i.e., a long period of isolation of two populations, of which the first became adapted to higharctic, the other to lowarctic life conditions.

The variation in bill length is superimposed on the much more ancient variation in dimorphism. Contrary to the latter 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. This demonstrates a strong susceptibility of the bill structure to the influences of environmental factors. Variation in bill length is a direct response to extrinsic influences, resulting from selection of genes producing a phenotype optimally adapted to the local environment. The variation in bill length in the Fulmar is an example of the so-called Allen's rule, which is demonstrated by many arctic birds (see Freuchen and Salomonsen, 1958: 62–64). Allen's rule states that there is a strong tendency in populations of warm-blooded animals inhabiting regions with low temperatures to reduce projecting body parts, such as ears, tail, snout or bill, and feet, which are subject to a disproportionate loss of heat.

As noted above, it is possible to divide Fulmar populations into three groups based on variation in bill length. A similar division has been proposed by Wynne-Edwards (1952a: 91–97) and followed by Mathiasson (1963: 275–277). This division corresponds generally to that proposed above, but differs in various details. The long-billed group of both authors comprises the same populations as in my division, i.e., the boreal ones. The small-billed group of Wynne-Edwards comprises the typical *minor* from Baffin Island and Devon Island, but Mathiasson adds the northwestern Greenland populations. As demonstrated above, however, this is not correct, since these populations, although imperfectly known, definitely appear to have bills of the intermediate type. The third group of both authors, containing birds with bills of intermediate length, comprises the populations of Jan Mayen, East Greenland, Spitsbergen, and Bear Island. These areas form a circumscribed geographical region but belong to different ecological zones. Of these four areas, Jan Mayen and Bear Island are inhabited by birds with intermediate bills. Spitsbergen is inhabited by small-billed birds, as evidenced by the measurements taken

by Dr. Vaurie. East Greenland, finally, is *probably* inhabited by small-billed birds, but all East Greenland specimens examined are visitors captured at sea, often far from land, and probably for the greater part belonging to other populations. Not a single specimen has ever been taken at or in proximity to the higharctic northeastern Greenland colonies.

It is noteworthy that Wynne-Edwards (*loc. cit.*), in his excellent treatise on the variation in the Fulmar, approaches the viewpoints which have been advocated in the present paper. When discussing the variation in bill length and the division of the populations into the three groups mentioned above he adds (*op. cit.*, pp. 94–95):

> There appears to be no reason therefore to doubt the reality of the differences between these three regional groups. It is of value to note that colour-variability follows a similar distribution. The European type is almost 100 per cent light-phased, and the rare "non-white" birds are quite pale; whereas in *minor* dark and intermediate birds predominate . . . . It is worth remarking also that the European group have their breeding habitat in a temperate or merely boreal climate, contrasting sharply with the rigorous arctic environment of the Spitsbergen group and *minor*.

THE SPREAD OF THE FULMAR

The present investigation may throw some light on the remarkable expansion of the Fulmar in recent time and may alter some of the viewpoints generally given as explanation for this spectacular phenomenon. Among the populations of the three marine zones only those of the boreal zone are involved. The arctic breeding populations appear to have been static. It is unknown, to be sure, whether they have increased or decreased, but it is quite certain that they have not spread to new breeding places or extended their breeding range. Almost everywhere in the arctic region the Fulmar breeds in huge colonies situated on precipitous promontories of special configuration, usually on lofty heights, and consisting of 10,000 to 100,000 pairs. The number of these rookeries and their situations are well known. They appear to be fixed. This is true at least in West Greenland, where the present colonies have been known for almost 200 years (since 1768). There is in northwestern Greenland, on Arveprinsen Island in Disko Bay, a steep promontory called Qaqugdlugssuit (meaning the big breeding place of Fulmars) where the Fulmar does not breed today. The inhabitants do not know that it has ever bred there, and there is no tradition that it did so in former days. Nevertheless, the name, as well as the special structure of the cliff, suggests that this locality forms a deserted breeding place. It is, however, situated within the present breeding range, and there is no evidence for the assumption that the Fulmar has changed its breeding range in Greenland in historic time. There are also in Baffin Island some place names containing the word

"Qaqugdluq" (i.e., Fulmar), indicating that these localities were previously tenanted by Fulmars (see Fisher, 1952: 76).

If anything, then, the Fulmars of the Baffin Bay–Davis Strait area may have decreased in number and deserted a few breeding places, and this phenomenon may have some connection with the decline in whaling in these waters, as suggested by Fisher (*loc. cit.*).

The spread of the Fulmar in the European boreal area has been thoroughly dealt with by Fisher (1952). Unlike the arctic colonies, the boreal ones are often quite small, numbering only a few birds. The ability to carry out successful breeding in very small communities was a necessary prerequisite for the expansion.

Fisher thinks the expansion is a product of the increasing whaling and fishing industry in European waters in recent time, insofar as the offal and waste of this industry furnish the Fulmar with a surplus of food that formerly was nonexistent. Probably the modern fishing industry has furthered and accelerated the process by producing additional food for the Fulmar, but it has not given rise to the expansion and does not explain its origin.

When the expansion started, about 1750, only one boreal breeding place existed, namely St. Kilda off western Scotland. It consisted of at least 40,000 breeding pairs and remained stable for centuries, even though the human inhabitants took a considerable harvest of young birds annually for food. In the lowarctic zone of Europe there were in those days only two Fulmar colonies, one on Bear Island, consisting mainly of dark birds; and one on Grimsey, north of Iceland, consisting of light birds. It is possible, however, that there were a few other breeding places on the north coast of Iceland, and I have especially Latrabjarg in mind. This is the northwestern point of Iceland and, as noted by Fisher in detail, Fr. Faber discovered there a large Fulmar colony as early as 1821.

Fisher (*op. cit.*) thinks that no breeding place in Iceland in the 18th century would have remained unnoticed and unreported somewhere in print. However, the 18th century was one of the dark periods in the history of Iceland, during which the literary activity was at a minimum. It is very probable, therefore, that breeding places on the remote north coast could have existed without being known by the few chroniclers of this period.

It is quite certain that the first step in the expansion of the Fulmar took place in the years previous to 1750, when the Vestmanna Islands south of Iceland were colonized. A few years later the Fulmar was noted on the islands off Reykjanes. Some years before 1821, the mainland of Iceland was invaded, while at the same time the population of the Vestmanna Islands had enormously increased. It is obvious that this develop-

ment took place independently of any human activity, since there was no increase in fishing or whaling activity in Iceland waters in those days.

In the early 19th century, at least before 1840, Fulmars from the Vestmanna Islands settled on Suduroy, the southernmost of the Faeroes. By 1870 they had gradually colonized all the bigger islands in the group, apart from the northernmost ones. About 1900 all the Faeroes were inhabited. Even this development, however, could not have anything to do with an increase in fishing activity. The utilization of the great fishing banks in the western North Sea and in the waters south of Iceland did not start until the latter half of the 19th century. In 1878 the Fulmar had spread to the Shetlands, and from then on it rapidly expanded in the British Isles, where there are now hundreds of colonies (in 1950 about 70,000 pairs). In 1921 the Fulmar invaded western Norway and in 1960 Brittany.

The expansion and increase since the latter part of the 19th century may very well have been influenced by the growing trawling industry in the North Atlantic and the North Sea, just as has been the case in certain species of gulls, but the early stages of the Fulmar expansion must definitely have been independent of this factor. Indeed, it seems unnecessary to invoke a human factor to explain how the food requirements of the boreal Fulmars are satisfied. These birds exploit an enormous expanse of sea, extending from northern Iceland south to Brittany and east to Norway, but the breeding population which utilizes this area (less than 400,000 pairs) is not larger than that of Spitsbergen and Bear Island combined, or than that of Davis Strait and Baffin Bay, which can subsist without human aid. The whole population in the British Isles contains fewer birds than the single colony on Cape Searle in Baffin Island .

When Fisher put forward his theory he overlooked the genetic aspect of the problem. He failed to note that Fulmars, like many other colonially nesting sea birds, show a strong adherence to the place where they were hatched. This can be followed closely in Greenland. During the peak years of whaling in Davis Strait, from 1780 to 1820, the Fulmar bred in exactly the same localities as in the present day and did not found new colonies.[1] It is probable that the number of breeding birds was greater than today's in the whaling period, judging from the amazing numbers reported in those days. If they were more numerous, however, it resulted only in an increase in size of the known colonies, not in the foundation of new ones. In the same way, the present large scale trawling activity in the Davis Strait has not changed the breeding range of the Fulmar at all. The trawling started about 1920, simultaneously with the northward ex-

[1] See, however, the note on Qaqugdlugssuit above.

pansion of cod due to the climatic amelioration, and has steadily increased to the present day when literally hundreds of vessels participate. The fishing grounds stretch from Frederikshaab District northwards almost to Disko Bay, and the Fulmar is numerous everywhere on the fishing banks. Nevertheless, it has not settled anywhere on the coast, which extends for almost 1,000 km (640 miles) along the fishing banks and possesses many cliffs suitable as breeding places. This demonstrates that an extensive fishing industry does not necessarily induce the Fulmar to any range expansions.

The Fulmar was originally an arctic bird, with primarily higharctic breeding range, extending southwards only into the northern parts of the lowarctic zone. It was missing in the southern parts of the lowarctic zone, apart from Grimsey and perhaps a few other localities in northern Iceland. The first condition for colonizing the boreal zone must have been the development of a population which was adapted to the boreal environment. Such a population existed already on St. Kilda. How and when the Fulmar settled there is completely unknown. The population of St. Kilda probably represents the result of an earlier expansion, emanating from the lowarctic zone, and perhaps taking place during a climatic pessimum, when life conditions approached those of the lowarctic zone, undoubtedly in prehistoric time. When the climate gradually changed the St. Kilda birds were able to adapt themselves to the new conditions and continued to breed there, now forming a relict population.

If this population should acquire the ability to spread and settle in other places the strong adherence to the breeding place must be broken. This process must involve at least three phenomena if the spread should be successful: (1) The strong instinct to return to the place of hatching must be abandoned; (2) the ability must be developed to settle and breed successfully in single pairs or in small bands, independently of the large rookeries in which the individuals usually gather; (3) the ecological tolerance must be widened or at least altered.

Such a profound change is thinkable only by assuming that genetic alterations have taken place. When discussing the spread of the Fulmar, as early as 1935, I made the following statement (Salomonsen, 1935: 251–252):

> The great impulse of expansion in the North European *Fulmarus glacialis* forms a striking contrast to the behaviour in other sea-birds, and more particularly the Tubinares, which persistently adhere to their old nesting-grounds, to which they are so attached that they often will not breed, if their nesting-grounds have been disturbed at their return in the spring. A development from this behaviour to that in *Fulmarus* (and also in certain *Larus*-species) which have become entirely independent of the old nesting-sites, can in my opinion only be affected through a mutation which changes certain individuals

> in a population in such a way that they lose their instinct of adhering to the old breeding-ground which is otherwise present in the species. The same must be the case with other species which suddenly extend their breeding range.

I am still in favor of this view, although I would now be inclined to change the wording somewhat. Nobody had taken up this thought in the 30 years which have passed since I published it, but recently Mayr (1963: 564) touches the subject when discussing the genetic changes in similarly expanding species (*Streptopelia decaocto* and *Serinus serinus*):

> Occasionally a species starts to expand its range explosively and advances in the course of this movement far into areas which only a few years previously had seemed totally unsuitable for the species . . . . In such cases one must suspect that some genotypic change occurred in a peripheral population which permitted the precipitant expansion. The genotypic change resulted in a change in climatic or habitat tolerance that permitted the subtropical species to enter the temperate zone.

I am quite certain that the Fulmar represents a parallel case. The genotypical changes which had the above-mentioned effects on the phenotype must have had a considerable selective advantage, because the new variants could utilize feeding areas which previously were not exploited by Fulmars. A successful spread could not be effected, however, until the pioneering individuals were so numerous that during their prospecting in scattered and often remote places they had a fair chance to find each other and begin pair formation. When this stage was reached the way was paved for the expanse and the increase in number.

The way in which a new locality is colonized has been observed a number of times in the British Isles, and the first colonization, that of the Vestmanna Islands in the 18th century, undoubtedly took place in the same way. In the first year only one bird or a pair settles for a short while on the potential breeding cliff. In subsequent years the pioneers are followed by a few more prospecting individuals. Finally, after a number of years, when the party has risen to 10 to 15 pairs the first two or three pairs begin egg laying. In the following years newcomers settle in the small colony, attracted by the breeding birds, and in this way the colony gradually grows. The young birds hatched in the colony do not always return to breed there, but may search for new breeding places, in accordance with their mutant characters.

The main reason for the success of the expansion was the fact that the Fulmar found an empty food niche. To be sure, there are other sea birds in the boreal zone feeding on macroplankton, but the Fulmar differs markedly from them in ecology. The species which may compete with the Fulmar for food are mostly migratory and leave the boreal waters in winter. Only the Black-legged Kittiwake remains, but it is rare near

the coasts in winter. The nonbreeding Fulmars as well as the winter visitors from the lowarctic zone scatter over the ocean, as the kittiwakes do, being truly pelagic, but the breeding Fulmars usually gather in the vicinity of the breeding places in October or November, after having withdrawn from them in August and September. Consequently, they frequent offshore habitats for the greater part of the year.

A comparison of the annual cycle of all sea birds breeding in the Faeroe Islands demonstrates that no two species are exactly similar, and that the Fulmar differs widely from the rest (see Salomonsen, 1955: 92). Probably food in summer is superabundant and competition, consequently, negligible. It is significant, however, that the Fulmar is the only species which utilizes the macroplankton of the offshore waters in winter, however modest the food resources then may be. This constitutes, therefore, the empty food niche which the Fulmar discovered and utilized.

Fisher, who so carefully described the complicated spread of the Fulmar, did not attempt to state where the expansion started. Where did the birds originate which colonized the Vestmanna Islands in the 18th century? There are two alternatives, Grimsey and St. Kilda. The former island is much nearer to the Vestmanna Islands than is St. Kilda. Nevertheless, I am satisfied that the spread started from St. Kilda, as stressed already. Grimsey is situated in the lowarctic zone, while both St. Kilda and the Vestmanna Islands are in the boreal zone. A colonization by St. Kilda birds is, therefore, the most likely alternative, because the colonists would be faced with much smaller environmental and ecological differences than if they came from lowarctic Grimsey.

The assumption that the colonists were of boreal, not of lowarctic, origin is borne out by the fact that the expanding birds remained within the boreal zone. Only in one place did the expansion cross the boundary towards the lowarctic region, namely in northern Iceland, but this happened at a very advanced stage of the expansion, i.e., about 1900, after a few forerunners had appeared in northwestern Iceland in the latter half of the 19th century, and their descendants still comprise less than 4 per cent of the Iceland population. This colonization of the southernmost fringe of the lowarctic zone by a boreal bird in a recent period may be related to the present climatic amelioration. At any rate, the same development has taken place in two other boreal birds, the Gannet (*Morus bassanus*) and the Skua (*Catharacta skua*), which both are expanding in this century and have settled in lowarctic northern Iceland, although in much more modest numbers than the Fulmar.

Fisher thinks the colonization of northern Iceland emanated from Grimsey, whereas the spread elsewhere in Iceland originated from the Vestmanna Islands, i.e., originally from St. Kilda. I find this theory

unsatisfactory, because it implies not only that the St. Kilda population was subject to genotypical changes, but that the Grimsey birds also began to undergo similar changes at the proper moment, i.e., in the period when the wave of expansion was about to reach northern Iceland.

NOMENCLATURE

It is perhaps of minor interest whether the Atlantic Fulmar should be regarded as one form or should be divided into two subspecies. The morphological difference between the extremes, i.e., the higharctic and the boreal populations, is sufficiently pronounced to separate them as two subspecies. When combining the two variable characters (dimorphism and bill length) almost 100 per cent of the higharctic birds can be separated from all the boreal ones. The fact that the lowarctic populations are intermediate is no objection to the nomenclatural recognition. The presence of intermediate populations is a common phenomenon in polytypic species. The strong correlation between the geographical variation in the Fulmar and the zonation of the North Atlantic makes it in my opinion convenient to recognize two subspecies.

When discussing the variation in bill length of the Atlantic Fulmar I separated the small-billed Baffin Island form as *minor* (Kjaerbølling, 1852), considering that the nominate form inhabited the remaining breeding range (Salomonsen, 1950: 104). I added, however, that "the birds from Spitsbergen and northeastern Greenland may possibly tend to have smaller bills" (p. 105). I believed that the type locality of *Procellaria glacialis* of Linnaeus was Sweden, because this bird was described in *Fauna Suecica*, but unfortunately I overlooked the fact that Mathews (1934: 173) restricted the type locality to Spitsbergen after the first quotation given by Linnaeus. As Spitsbergen birds now have turned out to be similar to the small-billed and dark form of Baffin Island, the designation *glacialis* must be transferred to these higharctic populations. This leaves the southern, boreal populations without a name. Mathews (*loc. cit.*) has enumerated all names given to the Fulmar, quoting the original references.[1] Most of them are renamings of *glacialis* or were given to stragglers of unknown origin and so vaguely described that they may represent any population. The only name which definitely was given to the southern form is *Fulmarus auduboni* of Bonaparte (1857: 187). He described stragglers from Newfoundland and expressly stated that: "*Rostro majore, robusto, parum compresso; tubo nasali dorso carinato depresso. Specimina Terrae novae rostro gaudent etiam robustiore.*" This means that the bills of Newfoundland specimens were extraordinarily

[1] Mathews does not give the correct reference to *minor* Kjaerbølling (see Salomonsen, 1950: 100).

large, compared with the normal size in the Fulmar, and the specimens in question must, therefore, have belonged to the boreal form.

The delimitation of the breeding range may give rise to some discussion owing to the fact that the two geographically varying characters do not exactly coincide and that the lowarctic populations are intermediate. I find it most natural to put the emphasis on the dimorphism, which is a more fundamental character than bill length, and propose the following division:

Fulmarus glacialis glacialis (Linnaeus 1761). Type locality: Spitsbergen, restricted by Mathews (1934: 173). Higharctic North Atlantic area, including Baffin Island north to North Devon, northeastern Greenland, Spitsbergen, Franz Joseph Land; also Bear Island where approaching *auduboni*; probably this is the form that breeds on Nowaya Zemlya. Outside the breeding season frequents mainly the lowarctic parts of the Atlantic, occasionally straggling into the northern parts of the boreal zone.

Fulmarus glacialis auduboni Bonaparte 1857. Type locality: Newfoundland, designated by Bonaparte 1857, formerly restricted here. Mainly lowarctic and boreal North Atlantic area, including northwestern Greenland from Disko Bay north to Thule District, Jan Mayen, Iceland, Faeroes, British Isles, Brittany, and western Norway; in northwestern Greenland and Jan Mayen approaching nominate *glacialis*. Outside the breeding season frequents lowarctic and boreal parts of the Atlantic.

SUMMARY

The distribution and the geographical variation of the Fulmar as well as of other North Atlantic sea birds is closely correlated with the zonal division of the sea based on physical factors like temperature, ice-cover, salinity, etc. The three zones of marine environment in the North Atlantic are here recognized and described: higharctic, lowarctic, and boreal. All North Atlantic sea bird species are listed in accordance with their breeding distributions within these zones. The Fulmar is a typical boreo-panarctic sea bird, and even in winter does not enter the subtropical zone.

Geographical variation of the Fulmar in the North Atlantic involves dichromatism and bill length, which are not correlated. This variation is described for all breeding colonies in the zones recognized. The higharctic populations are small-billed and consist of dark birds; boreal ones, large-billed, light birds; lowarctic ones, intermediate.

Considering *dimorphism*, two groups are distinguished. (1) Populations chiefly of dark birds, with at most 10 to 15 per cent light birds: all higharctic populations and lowarctic Bear Island. (2) Populations exclusively of light birds: all boreal populations. Or populations with a slight admixture of dark birds (at most 1 per cent): lowarctic populations in West Greenland (including higharctic Thule District) and higharctic Jan Mayen. (Bear Island, as well as Thule and Jan Mayen, are situated near the boundary between the higharctic and lowarctic zones;

Bear Island is on the lowarctic side, Thule and Jan Mayen are on the higharctic side.)

The biological advantage of the dark phase, which is very predominant among the birds in the higharctic populations and suddenly disappears in the lowarctic ones (except in Bear Island), probably results from a pleiotropic effect of a gene with strong survival value in a high-arctic environment. The great difference in the percentage of dark birds (90 to 100 against less than 1) between the higharctic and lowarctic populations contrasts with the gradual change from higharctic to lowarctic environments. It must be due to former separation of two groups of populations, which were adapted separately to higharctic and lowarctic conditions. The groups show a slight overlap in ecological tolerance (Bear Island, Thule, and Jan Mayen).

Bill length (all measurements averages in adult males) is directly correlated with the zonation of the sea. Three groups can be distinguished: (1) small-billed (less than 37 mm): all higharctic populations investigated. (2) Intermediate (38–39 mm): lowarctic populations (including Jan Mayen and Thule). (3) Large-billed (more than 40 mm): boreal populations. Variation in bill length is superimposed on the more fundamental and more ancient variation in dimorphism. Unlike the latter, bill length is precisely adjusted to the present environment, decrease in length being closely and evenly correlated with decrease in water (and air) temperature. It results from a direct response to extrinsic influences, being the result of a selection of genes producing a phenotype optimally adapted to the local environment, and follows Allen's rule.

In distribution, dark-plumaged non-breeding birds at sea are closely correlated with the presence of arctic water masses.

During less than 200 years the Fulmar has spread over large parts of the boreal zone, in which zone it was formerly unknown as a breeding bird apart from the isolated, probably relict colony on St. Kilda off western Scotland. The increase in number and the spread of the species occurred very rapidly. A theory that the expansion resulted from the increasing whaling and fishing industry in European waters in recent times has been generally accepted, but historical evidence suggests that expansion occurred independently of human activity, since there was no increase in the fishing and whaling industry in north European waters in the early phases of the expansion. Modern large-scale trawling did not start until about 1880, after which it may well have had some effect.

The expansion involved the populations of the boreal zone only. The arctic populations appear to have been static. Even 40 years of extensive modern fishing activity on lowarctic fishing grounds off West Greenland has not caused any range expansions. The spread cannot, therefore, be

explained as a consequence of increasing fishing activity, but must be due to the appearance of new genotypes with strong selective advantage. This advantage may have been connected with the exploitation of a new food niche, the macroplankton of offshore habitats in the boreal waters, which were previously not utilized by sea birds in winter. In order to make the spread successful, the genotypical alterations must have involved at least: (1) the abandonment of strong homing instincts; (2) the ability to settle and breed successfully in single pairs or in small bands; (3) the broadening of ecological tolerance.

The expansion must have started from one center only; it is not likely that similar genotypical changes should occur almost simultaneously in two or more populations. Generally speaking, the spread remained within the boreal zone. Undoubtedly, therefore, St. Kilda formed the center of origin for the expansion. Arguments are given against Grimsey, the only likely alternative, as the center.

The boreal populations are virtually identical morphologically. This homogeneity is a logical consequence of the rapidity of the expansion.

When dimorphism and bill length are combined, almost 100 per cent of the higharctic birds can be separated from the boreal ones, while the lowarctic ones are intermediate. It is convenient, therefore, to recognize two subspecies in the North Atlantic area: the nominate *Fulmarus glacialis glacialis* (Linnaeus) (type locality, Spitsbergen) breeding in the higharctic zone (including Bear Island); and *Fulmarus glacialis auduboni* Bonaparte (type locality, Newfoundland) breeding in the boreal and lowarctic zones.

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