M. J. HEUTS

A COMPARISON OF VARIATION, BEHAVIOR AND EVOLUTION IN THE SEA BIRD GENERA URIA AND CEPPHUS

BY

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BY

ROBERT W. STORER

(A contribution from the Museum of Vertebrate Zoölogy of the University of California)

INTRODUCTION

EVOLUTION is a process entailing so many diverse, yet interacting, factors that it is almost certain that the same factors have never been involved in an identical manner in the evolution of any two groups of organisms. The relative roles played by time, by changes of climate and physical barriers in the past, and by genetic mechanisms can only be surmised in analyzing the processes by which the patterns of speciation in most vertebrate groups have arisen. The influence of and the limitations set by such innate factors as structure and behavior, and through them, ecology, are somewhat more easy to discern. It was with a view to comparing the effects of such factors in the evolution of the several forms of two related genera that the present investigation was undertaken. The two genera selected—*Uria,* the murres, and *Cepphus,* the guillemots—are both members of the same family of sea birds, the Alcidae, and are similar in their basic structural and behavioral characteristics. Both have extensive and nearly congruent ranges in the colder parts of the Northern Hemisphere, and thus are, and probably have been in the past, subject to the same climatic factors and major physiographic barriers.

A study of the variation in these genera, including an analysis of "freak" specimens, may provide some clues to the mode of inheritance of a few genetic factors, but these birds are in general ill-adapted to genetic analysis and all but impossible as subjects of genetic experiments. The closeness of their relationship is the basis for assuming that the genetic mechanisms involved in the evolution of their several forms must be quite similar. The relative lengths of time during which these genera have evolved and become subdivided are, of course, unknown; and even with the increasing amount of paleontological material being uncovered, it seems doubtful that these time factors can ever be determined with even a fair degree of accuracy. On the other hand, the total number of forms of each genus and the similarity of the degrees of differentiation in the two genera suggest that they are of approximately the same age. This, of course, assumes that inherent evolutionary rates and the genetic mechanisms have been approximately the same in these related forms.

Although the birds of these genera are fairly closely related and therefore alike in their fundamental characters, they differ widely in their habits, ecology, and in minor anatomical features (Storer, 1945). The degree of relationship corresponds roughly to that of two tribes in the sense Delacour and Mayr (1945) used in subdividing the family Anatidae. Thus a murre and a guillemot differ from each other approximately as much as do a duck and a goose, and they are different enough in their ecological preferences so that intergeneric competition is negligible. Differences in the patterns of evolution of the forms of these two genera can thus be ascribed largely to inherent differences in structure and behavior and, through these, ecological preferences which in the last analysis are expressions of innate behavior.

FIELD WORK

The section on the behavior of the guillemots is based primarily on field work done at Point Lobos, Monterey County, California. The colony of pigeon guillemots, *Cepphus columba,* there was visited on fifteen days between late April (April 27, 1942) and late July (July 31, 1948), and a total of approximately forty hours was spent in observation. The period from July 5 to 25, 1946, was spent on Bonaventure Island, Gaspé County, Quebec, where considerable time was spent observing black guillemots, *Cepphus grylle.* Common murres, *Uria aalge,* were watched at Point Reyes, Marin County, California, where a total of 22 hours of observation was spent. The earliest visit was on February 13 (1949) and the latest, August 14 (1948). Both the common and the thick-billed murres, *Uria aalge* and *U. lomvia,* were observed on Bonaventure Island, but as most of them nested in dark crevices, conditions for observation were poor. Common murres were also seen on 22 trips out to sea off the coast of central California, and scattered short observations on both murres and guillemots were made at several points along the California coast.

ACKNOWLEDGMENTS

Museum specimens of murres and guillemots are so large that it is difficult to assemble extensive series. For this reason a five-week trip was made in January and February, 1948, to examine specimens in the following Eastern collections: the Chicago Natural History Museum, the University of Michigan Museum of Zoölogy, the Royal Ontario Museum of Zoölogy, the Canadian National Museum, the Museum of Comparative Zoölogy, the American Museum of Natural History, the Princeton Museum of Zoölogy, the Academy of Natural Sciences of Philadelphia, the United States National Museum, the Carnegie Museum, and the private collections of Max Minor Peet and T. T. McCabe. Other institutions were visited subsequently or specimens were borrowed from them. A total of 3,157 specimens was examined. Table 1 summarizes the number of specimens examined from each source. To the owners and curators of these collections I am deeply endebted for permission to use the materials as well as for their cordiality and help in many other ways.

The whole investigation has been carried out under the guidance of Dr. Alden H. Miller, whose help has been invaluable. Drs. Seth B. Benson, Charles L. Camp, Frank A. Pitelka, G. L. Stebbins, Jr., and J. Van Tyne have read the manuscript and offered many helpful suggestions. Drs. R. L. Bolin, P. R. Needham, and C. M. Yonge have checked the information on fish and invertebrates presented in the tables on food habits, and Dr. O. L. Austin, Jr., has contributed original notes on the habits of *Cepphus carbo.* Among others to whom I am endebted for assistance are Mr. and Mrs. L. O. Williams, Lois C. Taylor, T. R. Howell, P. S. Humphrey, R. R. Ronkin, N. Voge, A. O. Gross, and H. E. Winn.

METHODS OF TAKING DATA

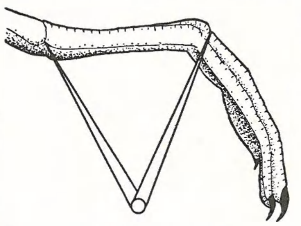
The analysis of geographic variation in the genera *Uria* and *Cepphus* is based primarily on four measurements: wing length, tarsal length, culmen length, and bill depth. A millimeter rule with a flange on the zero end was used to measure the wing length, the bend of the wing being held against the flange and the primaries straightened out along the scale. This method was used both because it is believed easiest to duplicate, especially with large birds, and because it forms a more valid basis for comparing the present data with those supplied by Salomonsen (1944), who used a similar method of measuring wing length (*in litt.*). In the absence of weights and of skeletal measurements, the length of the tarsus is probably the best indicator of body size. It was measured with dial calipers to the

TABLE 1

SOURCES OF SPECIMENS EXAMINED

Collection (with abbreviations used in text)	*Cepphus grylle*	*Cepphus columba*	*Cepphus carbo*	*Uria aalge*	*Uria lomvia*	Total
American Museum of Natural History (AMNH)	192	69	11	115	104	491
Museum of Comparative Zoölogy (MCZ)	155	60	6	131	104	456
California Academy of Sciences (CAS)	10	172	...	158	5	345
United States National Museum (USNM)	96	64	2	79	67	308
Canadian National Museum (CNM)	153	26	...	69	60	308
Museum of Vertebrate Zoölogy (MVZ)	19	94	...	82	39	234
Chicago Natural History Museum (CNHM)	61	28	...	51	56	196
Carnegie Museum (CM)	128	17	...	16	15	176
Royal Ontario Museum of Zoölogy (ROMZ)	61	8	...	29	57	155
University of Michigan Museum of Zoölogy (UMMZ)	58	8	...	10	23	99
Academy of Natural Sciences of Philadelphia (ANSP)	14	29	1	23	21	88
Collection of Max Minor Peet (MMP)	13	15	...	25	13	66
San Diego Museum (SD)	23	17	...	11	7	58
Donald R. Dickey Collection (Dickey)	3	12	...	16	3	34
Los Angeles County Museum of History, Science and Art (LACM)	4	7	...	13	3	27
Chicago Academy of Sciences (ChAc)	11	...	...	2	10	23
Bowdoin College (Bowdoin)	21	...	...	...	...	21
Washington State Museum (WSM)	...	9	...	6	...	15
Collection of Stanley G. Jewett (SGJ)	...	5	...	5	...	10
Collection of T. T. McCabe (TTMcC)	...	10	...	...	...	10
Princeton Museum of Zoölogy (PMZ)	7	...	...	...	2	9
University of Oregon Museum of Zoölogy (UOr)	...	3	...	4	...	7
Collection of Ralph Ellis (R. Ellis)	...	3	...	4	...	7
University of Kansas Museum of Natural History (KU)	2	...	...	...	4	6
Collection of Ed N. Harrison (ENH)	...	2	...	2	...	4
Pacific Union College (PUC)	...	1	...	2	...	3
Collection of John R. Arnold (JRA)	...	...	...	1	...	1
Totals	1031	659	20	854	593	3157

nearest tenth of a millimeter along the outer side of the foot, as shown in figure 1, and represents a close approximation of the length of the tarsometatarsus. The length of the exposed culmen (chord) was measured with dial calipers to the nearest tenth of a millimeter from the bases of the anteriormost feathers on the top of the bill to the tip of the maxilla. In the statistical treatment, measurements of the tarsus and culmen were rounded off to the nearest five-tenths of a millimeter. The bill depth was measured with dial calipers to the nearest tenth of a millimeter as the vertical depth of the closed bill at the level of the anteriormost feathers on the bill in the nostril region. This last measurement proved the least satisfactory, because it is difficult to duplicate results owing to the curvature of the bill, and because the bill is subject to considerable age, sexual, and even seasonal variation.



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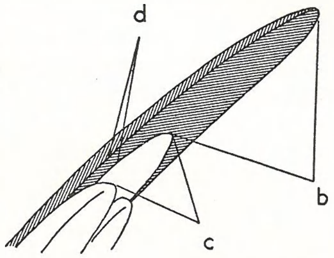

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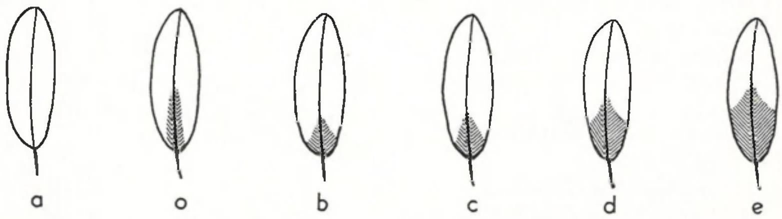

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Fig. 1. Method of measuring tarsus.
Fig. 2. Measurements of white in outermost primary; after Salomonsen (1944:62).
Fig. 3. Types of secondary coverts; after Austin (1929:3).

Where possible, several estimates of the amount of white on the wing were taken on guillemots. Two measurements of the white on the outermost primary, described by Salomonsen (1944:62) as "b" and "c," and shown in figure 2, were made; and the value $\frac{100c}{b+c}$ was calculated and used as a figure for comparing individuals and populations. Salomonsen's measurement "a" (*loc. cit.*)—the amount of white on the secondary coverts—was not taken; but the relative amounts of white and dark on these feathers were compared directly with a set of standards (fig. 3) which was taken from Austin (1929:3) and to which one further type (o) was added. Analysis of this character was made and is presented in tabular form.

The amount of white in the under wing coverts of the pigeon guillemots was likewise estimated as "none," "very little," "little," "moderate," or "much." Examples of the categories thus described are shown in figure 4. The under wing coverts of black guillemots are entirely white.

The colors of the head, neck, and back of individuals of various populations of murres were compared where possible; but extensive comparisons of this type were not possible, since most specimens were examined in the museums to which they belong and not gathered in one place. However, with the exception of *Uria aalge albionis* and possibly *U. a. spiloptera,* variation in the tone of color is not an important character. More extensive notes were taken on the amount of spotting on the under wing coverts. Notes and sketches were made on several aberrant specimens, and these are treated in a special section. All individuals of the races of the common murre (*U. aalge*) were noted as "ringed" or normal. These data cannot, however, be used to estimate the frequency of occurrence of the "ringed" mutant, because selective collecting is almost certainly involved. Several analyses of this frequency, based on field observations, have been made by British workers and will be discussed in a later section.

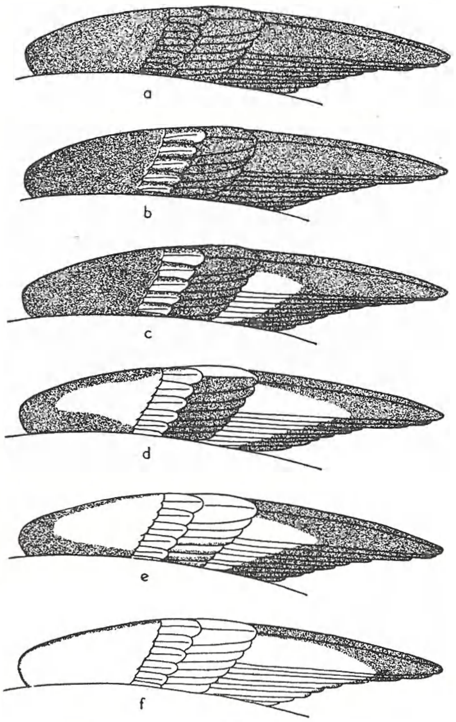

Fig. 4. Types of wing linings of guillemots. *a,* none; *b,* very little; *c,* little; *d,* moderate; *e,* much; *f,* all white (*Cepphus grylle*). *b,* MVZ, 17722; *c,* MVZ 17721; *d,* MVZ 31463; *e,* MVZ 60581; *f,* MVZ 45093.

DEGREE OF SEXUAL AND AGE VARIATION

The relatively small size of the population samples available and the fairly large proportion of unsexed specimens make it desirable to combine the measurements of the males with those of the females and those of the first-year birds with those of the adults wherever possible. In order to determine for which measurements this procedure is safe, the degree of significance of age and sexual variation has been estimated by means of the "t" test (Snedecor, 1940:56). These results are shown in tables 2 through 10. It is apparent that there is no significant sexual difference in wing and tarsal measurements. Both genera contain populations in which the mean wing length for the males is greater than that for the females and vice versa. The same is true for the tarsal measurements in *Cepphus*. In *Uria* the tarsi of the males average consistently longer than those of the females, but the difference is never statistically significant and is never more than 2 per cent of the total length. The same situation applies to the culmen measurements in *Cepphus*, and it seems best to combine data from the males with those from the females in the analyses of these measurements. The figures for culmen length in *Uria* and for bill depth in both genera are consistently greater in the males than in the females and corroborate the data for bill depth in murres given by Verwey (1922).

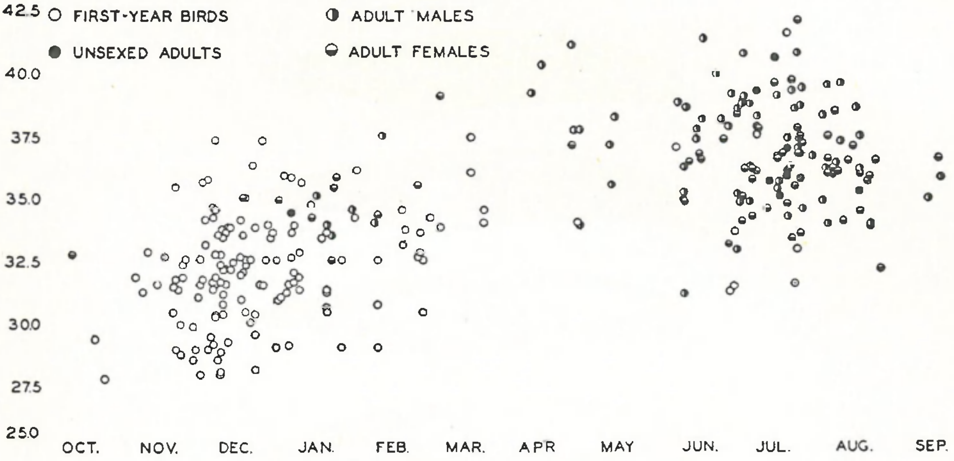

Fig. 5. Growth curve for culmen length in *Uria l. lomvia*.

Guillemots in first winter plumage are readily distinguishable from older birds by the dark tips to the secondary coverts, which give the specula of young birds a spotted appearance. In the northern populations the spotted speculum is retained in the first nuptial plumage, but the southern birds apparently molt the wing coverts in the prenuptial molt, after which these birds are not always distinguishable from older ones, although the lateness of the molt, shorter wing, smaller bill, and more faded remiges are indications of first-year birds. First-year murres are readily distinguished from adults as late as March or April by their small bills and later retention of the winter plumage, at least in the southern populations. As with the guillemots, incompleteness of the prenuptial molt, shorter, more faded wing, and smaller bill help segregate birds in their first summer plumage from older birds.

In making calculations of differences in size between first-year and adult birds, the former included those taken from November 1 of the birds' first winter through their first summer. Table 7 shows that in both genera there is a significant difference in wing length between first-year birds and adults. The only population which fails to show this difference is that from California, and, as is pointed out elsewhere (p. 158), the first-winter birds taken in California waters are probably migrants from Alaska. On the other hand, no population of either genus shows (table 8) a significant difference between the two age groups in tarsal length. A similar lack of significant difference is shown in the length of the culmen in *Cepphus* (table 9). The growth curve for culmen length in *Uria lomvia lomvia* (fig. 5) shows that the culmen length continues to increase through the first winter and spring, hence data from first-year birds have not been used in calculations of bill length in this genus. This figure also gives some indication that there may be a seasonal variation in culmen length as there is in bill depth.

I think that two or three independent sets of genetic factors control the white in the primaries of the guillemots; one controlling the extent of the white, one controlling the presence or absence of white, and probably another determining whether the white area is clear-cut or diffuse. For this reason the values for $\frac{100c}{b+c}$ were calculated for only those specimens with clear-cut white areas on the primaries. Tables 6 and 10 show that in at least some populations there are very significant sex and age variations in this character.

The results of the foregoing section have indicated in which characters it is safe to combine the measurements of males with those of females and those of adults with those of first-year birds. These conclusions are summarized in table 11. In actual practice, however, it has not often been practical to combine measurements of adult and young birds even where this analysis has indicated it feasible because of the tendency for the young to wander, or even perform long migrations, as do the Alaska murres.

MOLT

Cepphus

Salomonsen (1944) has given a detailed account of the molt of murres and guillemots. This account states that in the guillemots there is first a blackish-brown natal down, which is succeeded by the juvenal plumage; the latter is nearly complete at the time the young leave the nest. The primaries are the last feathers to finish growth; almost as soon as their growth has stopped, there is a complete molt of the body feathers and the first winter plumage is assumed. Another complete or nearly complete molt of the body feathers occurs in the spring, producing the first nuptial plumage. After the breeding season, there is the usual complete annual molt, during which the remiges are all shed at one time and the birds are flightless. The rectrices are also shed together shortly after the new remiges have begun to grow. The annual molt results in the adult winter plumage, which is replaced in winter (as early as November) or spring by a complete molt of the body·feathers, producing the adult nuptial plumage. The latter two molts are repeated annually thereafter throughout the life of the bird.

There is considerable geographic variation in the time of the prenuptial molt; birds inhabiting cold waters (*C. g. ultimus, mandtii,* and *grylle*) molt later in

TABLE 2
SEXUAL VARIATION IN WING LENGTH
(In millimeters)

Form and locality	Sex	No.	Range	σ	Mean$\pm\sigma_m$	t
Cepphus columba						
California	♂	70	196–176	4.40	187.1±0.5	1.56
	♀	88	197–179	3.68	188.1±0.4	
Cepphus grylle						
Alaska-Asia	♂	9	175–162	5.01	170.0±1.7	0.24
	♀	13	177–164	4.34	169.5±1.2	
South Baffinland	♂	16	173–160	4.21	167.8±1.1	0.15
	♀	10	180–162	5.37	168.1±1.7	
St. Lawrence	♂	17	170–161	2.74	164.5±0.7	1.13
	♀	29	173–158	4.25	165.7±0.8	
British Isles	♂	33	172–158	3.44	164.3±0.6	0.94
	♀	23	172–158	3.06	165.1±0.6	
Uria aalge						
California	♂	91	218–196	4.53	208.5±0.5	0.81
	♀	61	220–194	5.30	209.2±0.7	
British Columbia	♂	12	222–200	6.25	214.4±1.8	0.09
	♀	23	225–206	5.18	214.6±1.1	
Alaska	♂	45	230–207	5.73	217.8±0.9	0.87
	♀	25	225–207	4.29	216.7±0.9	
Eastern North America	♂	38	216–193	5.55	207.3±0.9	1.32
	♀	41	219–198	4.83	208.9±0.8	
Uria lomvia						
Atlantic	♂	67	227–201	5.74	216.1±0.7	0.59
	♀	69	234–204	6.92	216.7±0.8	
Pacific	♂	54	241–213	6.60	227.1±0.9	1.16
	♀	60	240–211	6.46	225.7±0.8	

TABLE 3
SEXUAL VARIATION IN TARSAL LENGTH
(In millimeters)

Form and locality	Sex	No.	Range	σ	Mean±σ_m	t
Cepphus columba						
California	♂	70	38.0–32.5	1.26	35.89±0.15	1.93
	♀	87	39.0–34.0	1.26	36.28±0.14	
Cepphus grylle						
Alaska-Asia	♂	13	33.5–30.5	0.85	31.65±0.24	2.14
	♀	19	32.0–29.5	0.70	31.03±0.16	
South Baffinland	♂	16	33.5–29.5	1.16	31.19±0.29	0.50
	♀	10	33.0–30.0	0.89	31.40±0.28	
St. Lawrence	♂	18	33.5–30.0	1.09	32.00±0.26	0.91
	♀	30	34.0–30.0	1.09	31.69±0.20	
British Isles	♂	28	33.5–28.0	1.31	31.38±0.25	0.95
	♀	24	33.5–29.5	1.03	31.69±0.21	
Uria aalge						
California	♂	122	41.5–35.0	1.28	38.27±0.12	2.58
	♀	66	41.0–35.5	1.28	37.77±0.16	
British Columbia	♂	15	40.5–36.0	1.16	38.90±0.30	1.33
	♀	28	40.5–36.0	1.00	38.43±0.19	
Alaska	♂	40	42.0–35.0	1.58	38.90±0.30	1.03
	♀	22	40.0–35.5	1.23	38.02±0.26	
Eastern North America	♂	38	41.5–35.5	1.38	38.42±0.22	1.77
	♀	41	40.5–35.0	1.28	37.89±0.20	
Uria lomvia						
Atlantic	♂	62	40.5–33.0	1.61	36.85±0.24	2.18
	♀	69	39.5–32.0	1.55	36.18±0.19	
Pacific	♂	53	40.5–35.0	1.27	37.76±0.17	2.81
	♀	57	40.0–33.5	1.51	37.02±0.20	

TABLE 4

Sexual Variation in Culmen Length

(In millimeters)

Form and locality	Sex	No.	Range	σ	Mean$\pm\sigma_m$	t
Cepphus columba						
California	♂	68	39.5–33.5	1.49	36.60±0.18	0.10
	♀	80	39.0–33.5	1.31	36.54±0.15	
Cepphus grylle						
Alaska-Asia	♂	13	34.0–30.0	1.31	31.54±0.36	0.94
	♀	14	33.5–28.0	1.70	31.00±0.45	
South Baffinland	♂	16	31.5–26.5	1.21	29.16±0.30	1.22
	♀	10	31.0–25.0	1.92	28.60±0.61	
St. Lawrence	♂	17	34.0–29.5	1.16	31.71±0.28	0.96
	♀	29	35.5–29.0	1.68	31.31±0.31	
British Isles	♂	26	37.5–29.5	1.98	33.33±0.39	0.20
	♀	24	36.5–31.0	1.58	33.23±0.32	
Uria aalge						
California	♂	117	53.5–43.0	2.05	49.23±0.19	6.06
	♀	62	52.0–41.5	2.25	47.13±0.29	
British Columbia	♂	15	51.5–45.5	1.78	49.00±0.46	3.10
	♀	24	51.5–43.5	2.04	47.02±0.42	
Alaska	♂	42	53.0–43.5	2.25	47.66±0.35	3.50
	♀	24	52.0–42.0	2.01	45.77±0.41	
Eastern North America	♂	36	48.0–41.5	1.74	44.58±0.29	2.86
	♀	39	51.5–39.0	2.40	43.21±0.38	
Uria lomvia						
Atlantic	♂	61	40.5–30.5	2.08	36.43±0.27	1.93
	♀	65	41.5–31.5	1.77	35.76±0.22	
Pacific	♂	52	47.0–35.0	2.99	41.07±0.41	3.27
	♀	58	44.5–35.0	2.41	39.37±0.32	

TABLE 5

SEXUAL VARIATION IN BILL DEPTH

(In millimeters)

Form and locality	Sex	No.	Range	σ	Mean±σ_m	t
Cepphus columba						
California	♂	61	11.6– 9.5	0.38	10.38±0.05	1.43
	♀	83	11.1– 8.8	0.45	10.06±0.05	
Cepphus grylle						
Alaska-Asia	♂	11	9.4– 7.9	0.50	8.69±0.15	2.24
	♀	16	9.2– 7.5	0.62	8.20±0.16	
South Baffinland	♂	16	9.0– 7.7	0.47	8.41±0.12	0.94
	♀	9	8.9– 7.6	0.45	8.23±0.15	
St. Lawrence	♂	16	9.7– 8.0	0.41	9.05±0.10	3.66
	♀	29	10.3– 7.5	0.42	8.55±0.08	
British Isles	♂	25	10.6– 9.1	0.43	9.80±0.09	2.73
	♀	22	10.7– 8.4	0.56	9.39±0.12	
Uria aalge						
California	♂	117	15.6–11.9	0.68	13.74±0.06	0.93
	♀	61	15.2–11.1	0.68	13.64±0.09	
British Columbia	♂	14	15.5–12.8	0.90	14.35±0.24	1.22
	♀	25	15.9–12.6	0.88	13.99±0.18	
Alaska	♂	42	16.6–12.9	0.87	14.52±0.13	5.43
	♀	19	15.0–12.4	0.67	13.59±0.15	
Eastern North America	♂	35	15.2–12.6	0.61	13.78±0.10	3.52
	♀	38	14.5–12.6	0.51	13.33±0.08	
Uria lomvia						
Atlantic	♂	58	15.6–12.2	0.78	14.01±0.10	4.35
	♀	64	15.8–12.0	0.58	13.48±0.07	
Pacific	♂	49	16.1–13.6	0.62	14.70±0.09	3.71
	♀	57	15.6–12.9	0.69	14.23±0.90	

TABLE 6

SEXUAL VARIATION IN WHITE ON OUTERMOST PRIMARY

(100c/b+c)

Form and locality	Sex	No.	Range	σ	Mean±σ_m	t
Cepphus grylle						
St. Lawrence	♂	19	30–12	5.65	20.8±1.3	0.33
	♀	29	48– 9	7.96	20.2±1.5	
Etah region	♂	23	46–25	6.15	37.9±1.5	1.81
	♀	17	52–28	7.53	42.5±1.8	
Sukkertoppen	♂	19	33– 6	6.60	20.5±1.5	0.52
	♀	16	33– 9	8.00	21.8±2.0	
East Hudson Bay	♂	17	46–22	6.03	35.6±1.5	1.94
	♀	10	52–31	6.61	40.6±2.1	
South Baffinland	♂	19	46–22	6.43	32.3±1.5	2.44
	♀	11	55–28	7.85	39.2±2.4	

TABLE 7

AGE VARIATION IN WING LENGTH

(In millimeters)

Form and locality	Age	No.	Range	σ	Mean±σ_m	t
Cepphus columba						
California	Ad.	158	197–176	4.04	187.46±0.32	7.07
	1st.	13	187–166	5.48	176.46±1.52	
Cepphus grylle						
South Baffinland	Ad.	58	180–158	4.51	167.41±0.59	5.23
	1st.	26	171–154	4.12	162.08±0.82	
Etah region	Ad.	43	174–156	3.62	164.58±0.55	6.60
	1st.	15	166–153	4.01	157.67±1.07	
Uria aalge						
Alaska	Ad.	70	230–207	5.35	217.4 ±0.6	7.58
	1st.	18	217–200	4.62	207.9 ±1.1	
Sweden	Ad.	27	208–192	4.42	202.1 ±0.9	5.20
	1st.	22	206–184	5.64	194.3 ±1.2	
British Columbia	Ad.	35	225–200	5.50	214.5 ±0.9	3.95
	1st.	27	221–194	7.98	207.6 ±1.5	
Uria lomvia						
Atlantic	Ad.	148	234–201	6.5	216.0 ±0.5	14.56
	1st.	204	222–194	5.66	206.7 ±0.4	

TABLE 8
Age Variation in Tarsal Length
(In millimeters)

Form and locality	Age	No.	Range	σ	Mean$\pm\sigma_m$	t
Cepphus columba						
California	Ad.	157	39.0–32.5	1.27	36.13±0.10	2.74
	1st.	11	36.5–33.5	1.08	35.18±0.33	
Cepphus grylle						
South Baffinland	Ad.	58	34.0–28.5	1.13	31.28±0.15	0.45
	1st.	27	34.0–29.0	1.28	31.15±0.25	
Etah region	Ad.	43	33.5–28.5	1.06	30.77±0.16	0.13
	1st.	15	32.0–30.0	0.68	30.80±0.55	
Uria aalge						
Alaska	Ad.	62	42.0–35.0	1.47	38.26±0.19	0.46
	1st.	12	40.5–35.5	1.52	38.04±0.44	
Uria lomvia						
Atlantic	Ad.	165	41.0–32.0	2.03	36.18±0.16	4.29
	1st.	205	40.5–31.5	1.42	35.37±0.10	

TABLE 9
Age Variation in Culmen Length
(In millimeters)

Form and locality	Age	No.	Range	σ	Mean$\pm\sigma_m$	t
Cepphus columba						
California	Ad.	148	39.5–33.5	1.40	36.57±0.12	0.71
	1st.	11	39.0–35.5	1.11	36.82±0.33	
Cepphus grylle						
South Baffinland	Ad.	57	32.0–25.0	1.34	28.64±0.18	2.96
	1st.	24	30.5–25.0	1.65	27.50±0.34	
Etah region	Ad.	38	32.5–26.5	1.16	29.38±0.19	0.74
	1st.	14	31.5–27.0	1.15	29.11±0.31	
Uria lomvia						
Atlantic	Ad.	162	41.5–30.5	2.03	36.00±0.16	18.63
	1st.	192	38.0–26.5	2.24	31.79±0.16	

the spring than *C. g. arcticus* and the southern populations of *C. columba.* Also, the prenuptial molt of first-year birds takes place later in the spring than that of adults, and that of the more southern populations apparently includes a molt of all the wing coverts, whereas in the north first-winter coverts are retained through the first nuptial plumage.

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The molt sequence of the murres differs from that of the guillemots in several ways. The natal down, which is dark above and light below, is succeeded by the juvenal plumage, which is complete except for the remiges; these are grown along with the first-winter plumage after the young have left the nesting colonies. The relatively late time of development of the remiges in both genera may account for the lack of difference in shape between the remiges of the young and adult birds. The prenuptial molt of murres is incomplete, involving only the feathers of the head and neck regions.

TABLE 10

AGE VARIATION IN WHITE ON OUTERMOST PRIMARY

(100c/b+c)

Form and locality	Age	No.	Range	σ	Mean ± σ_m	t
Cepphus grylle						
South Baffinland	Ad.	58	55–19	7.54	34.8±1.0	4.27
	1st.	28	58–25	9.21	43.6±1.8	
Etah region	Ad.	43	52–25	6.85	39.8±1.0	6.71
	1st.	14	67–46	7.04	54.2±1.9	

TABLE 11

SUMMARY OF CHARACTERS COMBINED FOR PURPOSES OF ANALYSIS

Character	Sexes combined	Sexes separate	Adults and first-year birds combined	Adults and first-year birds separate
Wing length	*Uria, Cepphus*			*Uria, Cepphus*
Tarsal length	*Uria, Cepphus*		*Uria, Cepphus*	
Culmen length	*Cepphus*	*Uria*	*Cepphus*	*Uria*
Bill depth		*Uria, Cepphus*		*Uria, Cepphus*
100c/b+c		*Cepphus*		*Cepphus*

Verwey (1922:100–102), aging birds by histological examination of the female reproductive tract, showed that the prenuptial molt of the first-year birds occurs later in the spring than that of second-year birds, which in turn takes place later than that of third-year and older birds. Verwey's data seem conclusive, but allowances must be made for the fact that in all probability he included in the data individuals of at least two geographic races (*U. a. albionis* and *U. a. aalge*) which may differ in the times at which they attain the nuptial plumage.

Many alcids, notably auklets and puffins, molt parts of the sheath of the bill after the breeding season. Although it appears likely that murres have a seasonal increase and decrease in the thickness of the bill, I know of no evidence that they actually shed part of the sheath.

ENVIRONMENT AND FEEDING BEHAVIOR

Typically, birds of the auk family, to which the murres and guillemots belong, are marine, spending the nonbreeding season in what Wynne-Edwards (1935: 241) characterizes as the "offshore" zone, which extends from four or five miles offshore to the edge of the continental shelf. The birds are primarily nektonic feeders, obtaining their food by "flying" under water, the wings bent at the carpal joint so that the primaries are pointed backward. The feet are also directed backward, and supplement the action of the short tail in steering as they do in aerial flight. Although these birds are not normally found in fresh water, some populations are found in bodies of brackish water, notably the Baltic Sea.

During the breeding season most alcids are colonial, resorting to islands or steep rocky headlands to nest. The adults frequent the nesting colonies for a considerable period before the nest sites are settled and the nesting cycle is begun. During this period the colony may be visited by the birds for only a few hours a day and may not be visited every day. It is as though the transition from the seagoing phase to the landbound phase of the birds' behavior, presumably brought about through the medium of endocrine changes, is a gradual one. In the far north where the nesting colonies are free of snow for only a short season, this period of prenesting visits to the colony is considerably reduced.

There is little sexual dimorphism in the species of this family, and this is largely confined to slight differences in bill size. Consequently, displays are largely mutual, and the bill, which in many species is laterally compressed and either ornamented or strikingly marked, or the lining of the mouth, which may be brightly colored, is a focal point of courtship activity.

The eggs, numbering one or two, are most frequently laid on bare ground or rock, usually under some sort of cover. The young are covered with down and may remain as long as a month and a half in the nest, where they are fed by both parents. After taking to the water, the young are led out to sea by the parents and may be convoyed for a month or more thereafter.

Two behaviorisms may be regarded as characteristic of the whole family and are undoubtedly connected with the birds' marine existence. One of these might be termed "head dipping." While swimming on the water, an alcid will often dip the bill and the anterior part of the head into the water in what appears to be a nervous manner (fig. 6, *a*). Many observations of this mannerism were made on birds which were not actively feeding; thus it is not, as several writers have indicated, a feeding action. Nor do I think it is a "false drink" action as Witherby *et al.* (1941: 162) characterize it. The frequency with which the birds use this mannerism increases when the birds are disturbed; so it seems likely that this is primarily a safety mechanism aimed at looking for underwater predators, although it also may have an important function in locating prey before diving.

The other mannerism is that of skittering across the water when alarmed. The wings are then bent back at the wrists, as they are when the birds "fly" under water, and are beaten while the feet paddle rapidly (fig. 6, *b*), the whole performance giving the impression of a deadlock between the impulse to fly and that to dive. In fact, the birds usually end by doing one or the other.

Although alcids as a group follow this general pattern of existence, there is considerable variation shown by the different genera, species, and even populations within a given species. In many ways the guillemots are the most generalized and consequently the most adaptable group. They have probably evolved as primarily littoral-benthic feeders, but their inherent behavior has remained sufficiently plastic to permit them to change their feeding habits when, as in the arctic winter, conditions prevent their feeding on the bottom, or where another food type has become abundantly available to them.

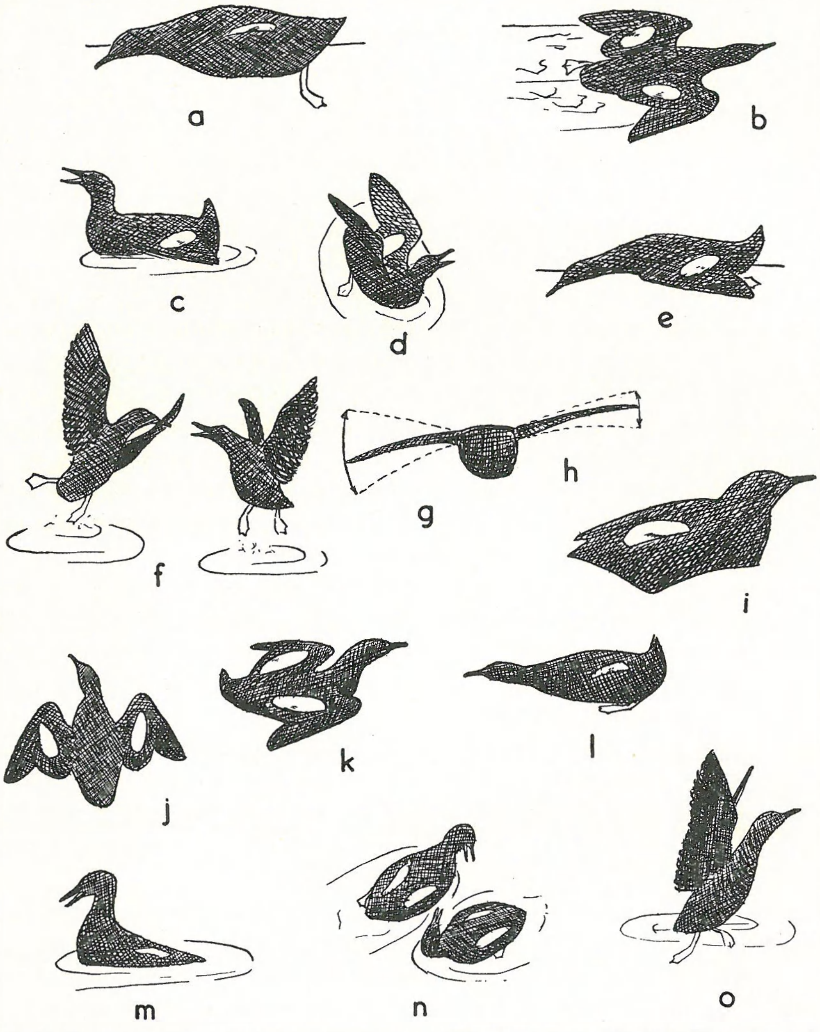


Fig. 6. Guillemot postures. *a–l*, and *o*, pigeon guillemots; *m–n*, black guillemots. *a*, head dipping; *b*, skittering; *c*, *d*, *e*, *j*, *k*, and *l*. displaying; *f*, fighting; *g*, steady flight; *h*, slowing up; *i*, resting; *m* and *n*, circling on the water; *o*, treading water.

The feeding behavior of the black guillemots, *Cepphus grylle,* of Bonaventure

Island in the Gulf of St. Lawrence appears to be characteristic of birds of the genus *Cepphus* throughout most of their range. The two following extracts from my field notes for July 13 and 14, 1946, show the extremes in feeding behavior which I observed there. "8:30 to 8:45 P.M.—after sunset but still fairly light, saw two birds on the water 100′ ± off the point [The feeding bird appeared to be working along a reef extending out from the point.].... One bird cruised along bill-dipping, the other was diving—evidently for food. I timed five successive dives which lasted 45, 40, 40, 45, and 48 seconds. Between each two dives the bird sat on the water, first dipping bill in water with a side-to-side motion different from the ordinary type of bill dipping, the former [sideways motion] giving the impression that the bird was worrying a fish, but I saw no fish in the bird's bill." At this time most guillemots had young in the nest, and this latter behavior was probably connected with the process of killing the fish before it is presented to the young. This is corroborated in the second excerpt from my notes. "After supper watched a guillemot feeding very near shore, diving to rock weed on side of rock often in water less than a foot or 18″ deep. Even in this case the wings were used. The dives were of less than five seconds duration, with correspondingly short periods between. On one dive it went between two rocks about one foot apart and came up with a fish about five inches long and quite wide. At this point someone frightened it, and it swam a couple of hundred feet out. Then it would drop the fish and dive after it, come up with it and dabble or worry it. Finally after several minutes it flew off with the fish in its bill."

Furthermore, the islanders say that the black guillemots remain around Bonaventure Island all winter and, ice conditions permitting, forage in the same manner at that season. In New England waters, guillemots frequent offshore reefs and steep rocky shores in winter. Since actual written reports of foraging behavior and of areas utilized are scarce, these can perhaps best be inferred from the data available on food habits. These are summarized in table 12.

In the arctic regions, guillemots which may feed near shore in summer, winter near the edge of the ice pack, apparently without regard for the depth of the water, and feed on the abundant swimming crustacean fauna (Austin, 1932; Soper, 1946). The guillemots of the Faeroes are not infrequently observed some distance from land in winter (August to January) (Salomonsen, 1935: 116); and Hantzsch (1905:112) states that birds of the Iceland population are seldom seen near land during the autumn and winter months.

A particularly striking contrast is evident between the black guillemots which nest on Bonaventure Island and the pigeon guillemots, *Cepphus columba*, which breed along the California coast. Whereas the former regularly forage near shore, I have never, in many hours of observation on the California coast, observed a guillemot foraging near shore. At Point Lobos, Monterey County, these birds appear to fish the deep waters of Carmel Bay and are often to be seen bringing fish to the young from the bay. The adults spend much time on the water near the nesting colony, but I have never seen one foraging there. I have also watched guillemots flying seaward from the Farallones and Point Reyes, apparently bent on foraging expeditions. A discussion of the significance of this difference in behavior is reserved for a later section (p. 188). Where most of the California

TABLE 12

FOOD HABITS OF GUILLEMOTS

Authority	Locality	Number examined	Food items
Cepphus grylle			
Eifrig (1905)	Hudson Bay	8	Crustaceans and fish
Soper (1928)	S. Baffinland	..	Crustaceans and small cusks
Hantzsch (1928)	N. E. Labrador	6	4 fish, 1 crustaceans, 1 *Gammarus,*[a] 1 small snail
Austin (1932)	Labrador	..	Capelin,[b] carrying lance[c]
Dutcher (1904)	Maine	..	Rock eel (*Gunnellus gunnellus*)[d] for young
Sutton (1932)	Southampton Id.	17+	Feb. 24 (15 ex.) "sea louse, a pink crustacean = the kingook of the eskimo."[a] May 15, sea louse and mollusc shells. Sept. 8, crustaceans
Bent (1919)	Maine	..	Largely *Gunnellus gunnellus*[d] also mussels and other molluscs, sea insects, marine worms, shrimp, small crabs and other crustaceans
Turner in Bent (1919)	Ungava	svl.	*Mysis mixta*[e] and all manner of crustacea
Manniche (1910)	N. E. Greenland	svl.	Remnants of crustaceans and in one case chaetopods (= polychaets)
Salomonsen (1935)	Faeroes	..	Almost exclusively *Centronotus gunnellus*[d] + some molluscs and crustacea
Bird and Bird (1935)	Jan Mayen	8	Amphipods[a] (*Gammarus locusta* and *Amathilla homari*)
Oldham (1930)	Cornwall	..	Sight record—probably crabs
Van Oordt (1921)	Spitsbergen	..	Crustaceans and a few molluscs
Montague (1926)	Spitsbergen	..	Principally fish—also takes pteropod (*Clio*)[f]
Gorbunow (1932)	Franz Josef Land	1	*Gadus saida*[g]
Nelson (1883)	N. Pacific and Arctic oceans		Reported feeding on small arctic tomcod[g]
Patten (1906)	Ireland	4	Several *Portunus arcuatus,*[h] 10–17 mm., *Pagurus bernardus*[i] and other Paguridae,[i] *Porcellana longicornus,*[j] *Galathea squamifera,*[j] and other unidentified crustacea, "Litho-thamnia"[k]
Walter (1890)	Spitsbergen	1	1 amphipod,[a] 1 *Clio borealis,*[f] masses of annelid setae and jaws
Koenig (1911)	Spitsbergen	22	Empty (2); pebbles (5); crustaceans (amphipods and gammarids) (12); mollusc shells (*Margarita helicina* and *Natica affinis*) (10); fish (5); and annelids (2)
Romer and Schaudinn (1900)	Spitsbergen	..	Observed to eat *Clio,*[f] *Beroë,*[l] worms and crustaceans; found fish bones in stomach
Witherby, *et al.* (1941)	Great Britain	..	Fish (*Gunnellus gunnellus*);[d] crustacea [small crabs, shrimps, prawns, and hermit crabs (*Eupagurus*)]; mollusca (mussels; gastropoda); annelida (polychaeta) and seaweed; accidentally drowned insects (Tipulidae)

TABLE 12—*Continued*

Authority	Locality	Number examined	Food items
			Cepphus columba
Dixon (Mus. Vert. Zool. Field Notes, 1908:45)	Alaska	1	Long yellow marine worm brought to young
Shortt (1939)	Yakutat Bay	..	For young—kelp with small molluscs and crustaceans, long marine worms
Preble and McAtee (1923)	Pribilof Is.	..	Amphipods......56.8% Spider and hermit crabs......20.8 Isopods......17.2 Fish...... 4.0 Univalves...... 0.2 Fragments of marine worm and 1 pycnogonid
Storer (obs.)	California	..	Brought to young—fish sp.?

[a] Gammarus and most other amphipods are benthic.
[b] Capelin, *Mallotus villosus*, a fish of the high seas, coming to shallow water near shore to spawn.
[c] Lance, lant, *Ammodytes americanus*, burrow in sand in shallow water, apparently move to deeper water in winter.
[d] Rock eel, *Pholis* (=*Gunnellus*, =*Centronotus*) *gunnellus*, Blenniidae, confined to rocky bottoms, 2 to 15 fathoms.
[e] Mysids may be either benthic or free-swimming. Some come near the surface by night and descend by day.
[f] Pelagic forms.
[g] The cods are pelagic when young and primarily bottom feeders when over 3–4 cm. in length.
[h] *Portunus arcuatus*, a swimming crab.
[i] Paguridae (hermit crabs), bottom-living forms.
[j] Anomurans living in shallow water on rocky coasts.
[k] Litho-thamnia = coralline algae.
[l] *Beroë*, a pelagic ctenophore.

population winters is not known, but the chances are good that the wintering grounds will be found in the belt of cold water off the coast.

To the north, the pigeon guillemots appear to utilize the littoral-benthic zone in their foraging. This is apparently true for the population on Forrester Island off southern Alaska (Willett, 1915: 299) and the birds wintering near the Pribilof Islands (Preble and McAtee, 1923: 25).

Dr. O. L. Austin, Jr., visited the breeding colony of the spectacled guillemot, *Cepphus carbo,* on Teure-jima off the northwestern coast of Hokkaido, Japan, in June, 1949, and reports (*in litt.*) the following concerning the habits of this little-known species: "The entire time I was on Teure-jima little groups of birds idled about just off shore, acting just like *grylle* under the circumstances, bobbing about with occasional nervous jerks of the head. But there was no food available close to the rookery, and they were getting their supply from a tide rip between the two islands, several miles away. A steady stream of birds kept moving all day between the rookery and this feeding ground, practically every incoming bird carrying a fish in its bill. The fish were thin minnows 3″–6″ long, probably lance. I never observed so marked a 'ferry service' in *grylle,* but don't recall any similar set of circumstances in Labrador, where there was obviously no food close to shore near the rookery."

Off central California, and presumably other coastal areas, common murres, *Uria aalge,* frequent the deeper waters of the continental shelf. From November, 1944, to July, 1945, I made eighteen trips out of San Francisco. These trips followed roughly the course shown on the map (fig. 7), with the exception of one trip (April 27, 1945) when a distance of eighty miles southwest of the Farallones was reached. By noting our position with respect to buoys, I was able to plot crudely the locations of the murres seen. Observations of 583 murres so plotted follow. (Because the amount of time during which observations were made, and consequently the mileage traversed in each of the categories listed below, was not continuous, these data cannot be compared accurately, and the numbers of murres for each area represent only crude estimates of relative abundance.)

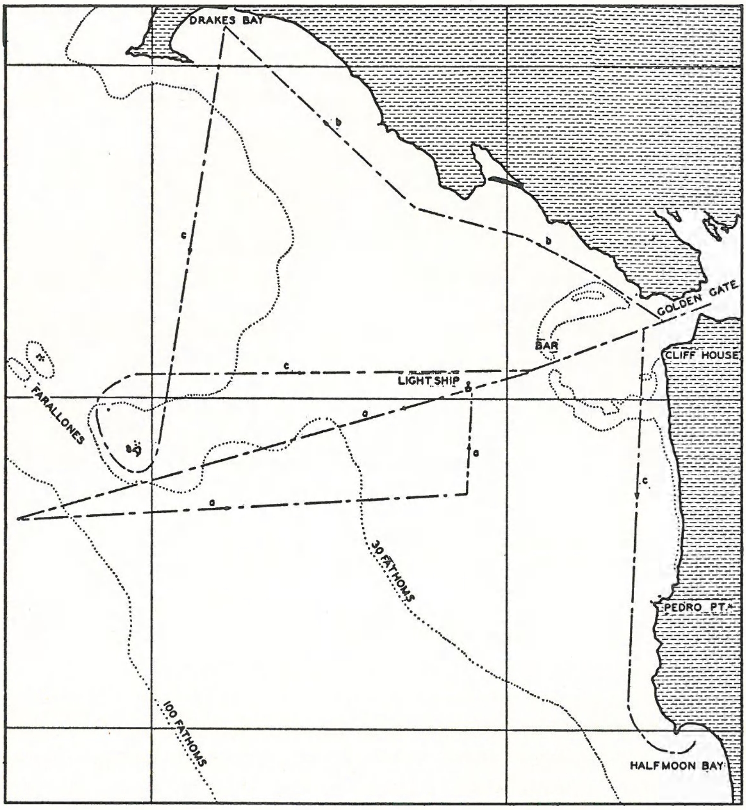


Fig. 7. Map of sea trips off San Francisco; from U.S. C. and G. S. Chart 5402. *a,* 18 trips, November, 1944, to July, 1945; b, August 27, 1948; c, August 29, 1948.

Area	*Number of murres*
Golden Gate to bar	35
Bar to 30-fathom curve	145
30-fathom curve to Farallones	223
0 to 10 miles west of Farallones	180

On a trip from August 27 to 29, 1948 (also charted on fig. 7), the murres seen were distributed according to table 13.

These data indicate that murres are widely and rather evenly distributed on waters of moderate depth off the California coast between Point Reyes and Half Moon Bay. Murres are less abundant in the turbid water which flows out of the Golden Gate. The birds' scarcity here is probably correlated with their need to see their prey while pursuing it. Their scarcity inside the bar is well indicated by the data of 1944–1945. The relatively large number of murres seen east of the bar on August 29, 1948, may be explained by the tidal conditions on that date. Low water occurred at the Golden Gate at 12:18 P.M. (3.4 feet), which represented a drop of only 0.6 feet from the previous high water; hence there was relatively little turbid water from San Francisco Bay inside the bar at that time.

The only guillemots observed on any of these trips were seen on May 29 and June 12, 1945, when we were respectively four to five and five to ten miles southwest of the Farallones. In each instance two birds were seen flying to the southwest away from the islands, presumably to feed. On the Atlantic coast, guillemots have not to my knowledge been reported so far from land, except near ledges and along the edge of the pack ice.

TABLE 13

DISTRIBUTION OF MURRES OFF SAN FRANCISCO, AUGUST 27–29, 1948
(see fig. 7 for routes)

Route	Date	Time	Miles traversed	Number of murres
Golden Gate to Drake's Bay......	Aug. 27, 1948	1:33–3:15 P.M.	28	104
4 mi. NE to 5 mi. E of the Farallones (including circuit of the islands)	Aug. 29, 1948	8:08–8:45 A.M.	20±	36
1–2 mi. E lightship to bar.........	Aug. 29, 1948	11:55 A.M.–12:03 P.M.	3	33
Bar to 4 mi. E bar................	Aug. 29, 1948	12:03–12:15 P.M.	4	39
Cliff House to Pedro Point (2–5 mi. offshore)......................	Aug. 29, 1948	1:34–2:18 P.M.	9	43
Pedro Point to Half Moon Bay (2–5 mi. offshore)...................	Aug. 29, 1948	2:18–2:45 P.M.	4.5	39

Except when feeding in groups, the California murres are relatively solitary. After the breeding season they are to be seen in family groups of three—two parents and one young—until about late August, after which time the young is usually convoyed by one parent. After the young become independent, murres are most frequently found singly, as is well shown in table 14. The figures for late August, based on 322 birds seen, represent the season when the young are dependent upon their parents; and the April data, based on 74 birds, the season when the young are independent. It is interesting to note the relatively few pairs of birds observed together on the water in April. At this season there is much courtship activity at the breeding colonies, but evidently the bond between the members of a pair does not hold while the birds are away from the colony, even before the egg is laid.

In the far north, where the populations of murres are much denser, the birds go about in flocks to and from the feeding grounds and may be seen in great numbers on the water. Salomonsen (*in litt.*) thinks that large flocks participate in seasonal migrations which are carried out by swimming. This apparent discrepancy in flock size in various parts of the range of the genus requires a detailed statistical analysis of much additional field data before adequately supported conclusions can be reached.

As would be inferred from their more pelagic habitat, murres differ rather strongly from most guillemots in their feeding habits, usually preying on nektonic organisms. Murres often gather in mixed flocks with cormorants, shearwaters, and gulls to feed, pursuing schools of small fish. Although Couch (1847: 192) describes the circling of the murres around a school of mullet, they more frequently must follow schools of fish in a line, as Batholomew (1942) has described for the double-crested cormorant. I have had verbal reports of groups of murres foraging in lines, and their tendency to form lines when loafing on the water near the breeding colonies seems related to the same behavioral mechanism. Either type of behavior would tend to concentrate the fish into compact schools, and this might have a definite selective advantage for the birds. There is also some evidence that the fish come to the surface when pursued; but whether this is the normal pattern of behavior of the fish or whether it is induced by special behaviorisms of the murres is not clear. This behavior is advantageous to gulls (Norris-Elye, 1945: 174) and other birds, such as shearwaters, which are probably not capable of obtaining fish far below the surface. Murres occasionally take benthic

TABLE 14

SEASONAL VARIATION IN GROUP SIZE OF THE COMMON MURRE OFF CENTRAL CALIFORNIA

	August 27–30, 1948			April 20, 1945		
A	B	C	D	B	C	D
Number of birds in group	No. of groups	A times B	Per cent of total birds in group	No. of groups	A times B	Per cent of total birds in group
1	36	36	11.2	32	32	43.2
2	74	148	46.0	4	8	10.8
3	13	39	12.1	2	6	8.1
4	5	20	6.2	1	4	5.4
5	3	15	4.7	1	5	6.8
6	3	18	5.6	..	..	....
7	1	7	2.2	..	..	....
8	..	..	....	..	..	....
9	..	..	....	1	9	12.2
10	..	..	....	1	10	13.5
11	..	..	....	..	..	....
12	1	12	3.7	..	..	....
13	1	13	4.0	..	..	....
14	1	14	4.3	..	..	....
Total	138	322	100	42	74	100

forms (see table 15), but this is apparently the exception rather than the rule. Gurney (1913: 410–411) reports murres' being caught in nets set at depths of from 120 to 180 feet, but the accuracy of such records is usually open to question.

Hartley (1935: 203–210) has described flights of murres and other sea birds off the Cornwall coast during the spring and summer months; he thinks that these are daily movements to and from the feeding grounds. More than ten miles from the nesting colony on the Farallones, I observed a murre carrying a fish toward the colony. Little attention has been paid to the problem of how far from the breeding grounds these birds go to look for food, a matter which merits further study.

In places where both species of murres nest, there seems to be some ecological segregation of the two species. The food listed for the common murre on the Pribilof Islands by Preble and McAtee (1923: 27–28, and see table 15) consists largely of littoral-benthic forms, whereas that for the thick-billed murre at the same place (*op. cit.:* 29) is represented largely by pelagic forms. Guillemots are not known to nest on these islands, and the common murre has taken over the guillemots' feeding grounds. In winter the thick-billed murres tend to leave the vicinity of the islands, and the common murres tend to remain. At this season the pigeon guillemots also occur about the islands and have a diet similar to that of the common murres. Evidently the competition for food is sufficiently critical only during the breeding season to force the guillemots to go elsewhere.

Preble and McAtee also noted a tendency for the two species to be segregated on the nesting cliffs; Bertram and Lack (1933: 299), reporting on the mixed colonies of Bear Island, state that *aalge* is more numerous on the large flat areas and *lomvia* on the cliff ledges, although the two species frequently nest side by side, and one may even adopt the egg or young of the other species. Morrison (1938: 135–136) reports an essentially similar segregation on an island off Iceland. There are also reports (Lockley, 1936: 716; and Krasovski, 1937: 73) that the colonies of the common murre more frequently face south, whereas those of the thick-billed murre tend to face north; but much more evidence is needed before we are justified in accepting this suggestion. Certainly a comparative study of these two species both from an ecological and behavioral point of view would be most rewarding.

There is not enough information on food habits available to discuss regional differences in them; and these differences, insofar as they may exist, probably are due to variations in the abundance of the various prey species rather than to regional differences in the birds' food preferences. In any event, it is apparent that in the main the littoral-benthic feeding grounds of the guillemots and the pelagic ones of the murres prevent extensive intergeneric competition.

BREEDING BEHAVIOR

A detailed account of the breeding behavior of murres and guillemots would not be appropriate here, even if sufficient material were available. A brief picture of the principal contrasts in behavior between these two groups is, however, in order.

In many ways the guillemots seem closest to the ancestral stock of the family. This is perhaps most striking in the latitude of their choice of nesting sites. The

TABLE 15

FOOD HABITS OF MURRES

Authority	Locality	Number examined	Food items
			Uria lomvia
Trevor-Battye (1897)	Spitsbergen	..	Arctic cod (*Boreogadus fabricii*)[a] 5″ long
Montague (1926)	Spitsbergen	..	Fish only
Krasovski (1937)	Novaya Zemlya	..	Food for young—fish *Gadus callarius*[a]. . . . . .58.0% *Boreogadus saida*[a]. . . . . .16.1 *Mallotus villosus*[b]. . . . . .11.3 *Ammodytes tobianus*[c]. . . . . 9.7 *Aspidophoroides alrickii*[d]. 4.9
Gross (1937)	Labrador	..	Fish and shrimps
Sutton (1932)	Southampton Id.	..	Fish
Fleming (1907)	Eastern North America	2	1—fresh water fish 1—25 *Goliosoma bosci* + 2 *Menida* not to be regarded as normal diet
Wynne-Edwards (1933)	Quebec	2	6 sp. fresh water fish
Gorbunow (1932)	Franz Josef Land	22	Small fish (*Gadus saida?*)[a] and *Amphioda* and *Sclerocrangon*
Grinnell (1900)	Kotzebue Sound	..	Small crustaceans[e]
Preble and McAtee (1923)	Pribilof Is.	..	Fish. . . . . .48.75% Squid[f]. . . . . .26.25 Crustaceans. . . 25.00 (*Spirontocaris polaris*)[g]
Palmer (1899)	Pribilof Is.	..	Tufted blenny (*Bryostemma arctocephalus*)[h] lying beside young
Walter (1890)	Spitsbergen	3	Many *Gammarus* (*locusta*); many (243+) amphipods of three or four species including *Gammarus locusta*, 1 *Hippolyte;* many (319+) amphipods and 1 *Hyppolyte*
Witherby *et al.* (1941)	?	..	*Clupea harengus*,[f] *Mallotus villosus*,[b] *Leptoclinus maculatus*,[i] Crustacea (prawns —*Spirontocaris*,[j] *Hippolyte;*[k] amphipods —Gammaridae; Euphausiacea—*Thysanoessa;*[f] Copepoda,[f] Cephalopoda[f]

principal requirement appears to be a roof over their heads, and this can be anything from a boulder on a talus slope or a cave in a cliff to a thatch of grass or a horizontal tunnel in a vertical clay bank. The latter type of nest is excavated by the guillemots themselves, using both bill and feet "with no little exertion and infinitely less grace than . . . a Bank Swallow" (Dawson and Bowles, 1909: 927). It has been reported only in the Puget Sound area, where it is in some places the usual type of nesting place for birds of this genus. In that area the versatility of the guillemots is most in evidence. The same authors also mention (*op. cit.:* 926) guillemots laying their eggs "in quite open situations upon ledges and the like,"

TABLE 15—*Continued*

Authority	Locality	Number examined	Food items
		Uria aalge	
Preble and McAtee (1923)	Pribilof Is.	..	Largely amphipods—some cottids[j]
Heath (1915)	Forrester Id.	..	Almost wholly sea launce,[c] varied by an occasional amphipod[e] or shrimp[e]
Bent (1919)	Eastern North America, etc.	..	Lant,[c] capelin,[b] and other small fishes. Also shrimps, crustacea, etc.
Storer	California	1	2 scorpaenids,[l] young (2–3″ long)
Salomonsen (1935)	Faeroes	..	Small fish in shoals (*Clupea sprattus*)[f] which they also feed young
Tåning *fide* Salomonsen (1935)	Iceland	..	Fry of *Gadus callarius,*[a] *G. aeglefinus,*[a] *G. merlingus,*[a] *Onos* sp., and *Mallotus villosus,*[b] (preferably the first two species
Witherby *et al.* (1941)	Great Britain	98	Fish............................51.6% (including *Ammodytes*[c]) Roe............................0.06 Crustacea and annelida..........35.52 Mollusca.........................10.19 Algae.......................... 2.63

[a] The cods are pelagic when young and primarily bottom feeders when over 3–4 cm. in length.
[b] Capelin, *Mallotus villosus*, a fish of the high seas, coming into shallow water near shore to spawn.
[c] Lant, launce, *Ammodytes tobianus*, burrow in sand in shallow water, apparently move to deeper water in winter.
[d] The related species, the alligator fish (*Aspidophoriodes monopterygius*), is a bottom fish, found at depths of 15 to 100 fathoms. Young up to 29 mm. are pelagic (have been taken in tow nets).
[e] May be either benthic or pelagic.
[f] Primarily pelagic forms.
[g] A prawn—possibly pelagic.
[h] Like *Pholis*, a bottom fish of shallow water.
[i] *Leptoclinus maculatus*, a blenny, is a bottom fish of fairly deep water, coming to shallow water to spawn.
[j] Primarily benthic forms.
[k] Benthic by day, may be pelagic by night.
[l] Members of the Scorpaenidae are pelagic when young and bottom feeders when adult.

in abandoned puffin burrows, and even on the ground in thick grass—thus running the gamut of types of nest sites used by all members of the family Alcidae. From such a species with wide tolerances for nesting requirements it is easy to visualize how radiation in nest types has arisen.

According to Austin (*in litt.*), nesting spectacled guillemots, *Cepphus carbo,* on Teure-jima "were scattered all over the colony. I first looked for the nests of *carbo* where I'd expect to find those of *grylle,* under the rocks of the talus slope along the shore at the base of the cliff, and I found plenty of them there. . . . I was surprised, however, to find *carbo* nesting just as thickly in cracks and crevices all the way up the cliff. There were numbers of them at the very crest about 400 feet above the water, where the rocks gave way to steep banks of volcanic soil in which the Horned Puffins dig their burrows."

In other areas guillemots are much less plastic in their choice of nesting sites. Soper (1940: 17) states that the Mandt guillemots in the eastern Canadian arctic "resort to very barren and precipitous islands of Pre-Cambrian rocks on which to breed. An indispensable feature is the presence of talus slides at the base of cliffs near the sea where the nests are hidden away among the boulders. This imposes a highly restraining influence on general distribution." This is probably an extreme example, for Van Oordt (1921: 163) records *mandtii* nesting high above the loomery on Mount Congress, Spitsbergen; and Workman (1913: 202) and others have reported black guillemots nesting in holes in harbor walls in Ireland.

The murres' habit of nesting on open ledges was probably developed through nesting in large caves and was evolved along with, and in turn made possible by, the murres' extremely colonial breeding habits. In fact, these colonial habits are the key to the murres' behavior patterns (and even some of their minor morphological features). As the density of the populations on the nesting ledges increased and the nest "territories" became crowded together, many of the ancestral behaviorisms likewise became compressed or lost, and the upright posture may have developed through this type of pressure. The large colonies of birds, located on isolated cliff ledges and islands, suffered less predation and hence had high nesting success. This made it possible for the species to maintain itself by each pair's producing but a single egg per season. The single egg can be rested across the tarsi, incubated in this position, and even carried short distances by the shuffling adult. Finally, the push given the egg as the parent departs hurriedly from the ledge, lunges at a potential predator, or fights with a neighbor was probably the selective factor responsible for the evolution of the extreme pearlike form of the egg. This in turn has made possible the successful nesting of murres on narrow ledges.

The activities of nesting guillemots may be exemplified by a group of approximately twenty pairs using a small rocky islet off the north shore of Point Lobos, Monterey County, California. This islet, figured by Grinnell and Linsdale (1936: pl. 22., fig. B), is roughly 70 feet high, 250 feet long, and 150 feet wide, and is separated from the mainland by a narrow channel fifteen to twenty feet across. To the north is Carmel Bay, and to the east is a small cove, known as Bluefish Cove. Western gulls nest on the flattish top of the rock, pelagic cormorants on small ledges on the nearly vertical south face, and the guillemots utilize crevices in the rocks of both the islet and the point opposite.

The guillemots' nesting season here is a long one, although a month or more shorter than that of the California murres. This long season is made possible in part by the mild climate. The adults arrive in March and may be seen bringing food to the young as late as mid-August. Early in the breeding cycle, before incubation starts, the birds spend the morning on or near the rock, and leave, flying out to sea or to the deep waters of Carmel Bay, about noon.

The rocks, air, and water around the nesting area are the scenes of much varied activity. Almost always when birds are present here, one can see groups of guillemots resting on the water nearby. These birds, which may number as many as twenty in a group, move about slowly on the water, forming and reforming lines and arcs. In these maneuvers much of the group appears to be subdivided into twos, probably pairs, but the maneuvers are performed primarily by the group as a whole. (Coues, writing of the black guillemot, states [1861: 256] that on sunny days the adults leave the eggs and young, both members of the pair joining in the communal swimming activities; and he checked this point by looking into a number of nests.) The birds call frequently, and in doing so display the red linings of their mouths. The birds may also use a more intense form of display, the tails cocked and the wings partly spread and held out to the side (fig. 6, *c*) or raised (fig. 6, *d*). This is frequently followed by head dipping (fig. 6, *e*) and a chase, either flying, skittering, or submarine, but most often the latter. Often the whole group of birds will dive at once, sometimes just milling about or occasionally dividing into several bona fide chases. I have seen as many as nine birds in such a mass dive. The following is an extract from my field notes for June 12, 1948: "Six birds on the water of the channel all dive and fly under water apparently at random—*not* chasing each other, but for the most part remaining within a fifteen foot diameter circle. Same thing seen later . . . [performed] by four birds."

Underwater chases indulged in by two birds may result in a fight if the pursued turns to meet the pursuer. On May 21, 1945, an apparently unmated bird "dives . . . flying under water to another pair. As he approaches, one bird . . . dips head, turns and dives to meet him. Both birds burst from the water and fly up a couple of feet fighting" (fig. 6, *f*). Aerial chases may be climaxed by both birds' meeting face to face in midair and tumbling to the water, fighting like two passerines. In other instances fights may start on land. For instance, on May 26, 1946: "One bird climbs low rock and settles down. Second bird starts up rock (3′ × 8′) and is attacked by first which grabs (second's) lower back feathers. Both flop off rock and swim under water thirty feet and come up, first still holding second by back feathers." Certainly most of this fighting is not territorial, but rather results from a response to a behavior pattern of another bird *without regard to where the birds are.* As such, this may be the forerunner of typical territorial behavior.

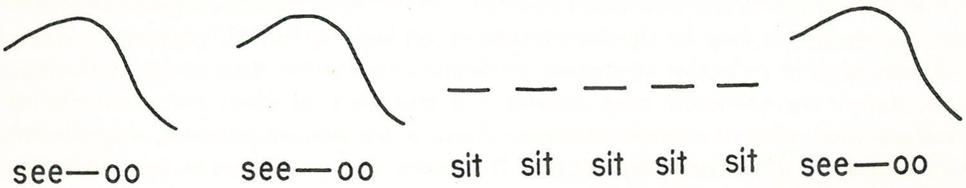
In reacting to potential predators, guillemots may either dive or fly. A western gull, flying low overhead, may stimulate a guillemot to dive; and a low-flying airplane may elicit the same response. When a sea lion approaches, a guillemot will first head dip several times; and if the sea lion continues to approach, the bird will either dive or take flight.

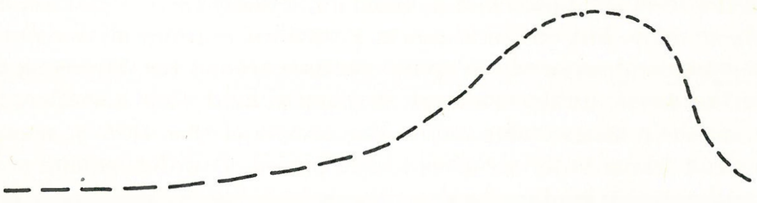
Short circling flights over the cove or around the island were frequently observed, the birds starting from the water, the nest site, or the rocks and making one or more circles from 300 to 400 feet in diameter. Usually these flights are made by single birds or pairs, but on one occasion I watched a group of twelve birds circle the island once and seven of the group continue around for the second time. In landing on the water, guillemots most frequently land with a shallow dive, continuing to use their wings under water. The reverse of this, that is, emerging from the water and taking to the air after a brief period of skittering, also occurs. Sometimes a guillemot will land on the water like a duck, "stop-flapping" (Hankin, 1913: 157) and braking with the feet just before alighting. During the course of steady flight the wings are beaten through a short arc (fig. 6, *g*); and when slowing up, this arc is shortened further (fig. 6, *h*). Sometimes the birds even glide for short distances. Most flights are at low elevations—only a few feet above the water—so that when coming to the nest, the birds arrive with an upward swoop which must be of assistance in checking speed.

While on the nesting grounds, guillemots spend much time on the flat or rounded tops of rocks or ledges. The lowest of these may be reached by a bird's swimming up to the rock, waiting for a wave to lift it part way up, and half running, half flying the rest of the way. Most loafing spots, however, are reached by flight. Much of the time is spent resting (fig. 6, *i*) singly, in pairs, or in small groups. This resting is interspersed with periods of various activities.

There are two types of display which might be termed aggressive. In the first, already described, the wings are partly spread and held horizontally and the tail is cocked (figs. 6, *j*, 6, *k*, and 6, *c*). In the second, the tail is also cocked but the wings are folded, and the head is held low and directed toward the bird threatened (fig. 6, *l*). The first type is used both in the vicinity of the nest and also on loafing areas and on the water. The second was observed only once when two birds were on a loafing place, and may precede actual pecking.

In much of the courtship activity the bill and the red lining of the mouth are focal points, and the display of the latter is usually accompanied by vocalizations. The voice of pigeon guillemots is high-pitched and thin, reminiscent of that of young birds. The principal components of their vocalizations are a single sibilant, slow note: *see oo* with first a slight rising in pitch followed by a longer falling in pitch, and a second simple note, also sibilant: *tsit*. These may be combined variously or the second type may be expanded into a trill, accelerated like the trill of a male wren tit, *Chamaea*, but higher in pitch throughout, rising and then falling near the maximum acceleration. One frequently used combination of the two notes and the trill are indicated diagrammatically below. The trill may be succeeded by one or two *see oo* notes, and may frequently be heard issuing from the nesting crevices, presumably given by incubating or brooding adults. It is also given by birds on the loafing grounds or the water and seems to indicate a higher emotional pitch than the single notes. The latter are used more often than the trill on the loafing grounds and the water. On one occasion, May 21, 1945, when two birds were calling, I noted what I thought to be a sexual difference in the single notes of the birds, one being higher-pitched than the other. Calling and the display of the red lining of the





mouth may be accompanied by fencing or billing and sometimes a slow shaking of the head from side to side.

That guillemots appear to lack an alarm note was brought out sharply in 1948. That season a pair of black oyster-catchers nested on the islet and heralded my approach with their loud piping alarm notes. The guillemots' lack of a comparable note is a reflection of the fact that the young guillemots remain alone in the comparative safety of the nest cavities. On the other hand, the young oyster-catchers wander about in the open but always under the watchful eye of one parent, whose alarm note elicits a freezing reaction.

The circling performance which I have described and figured earlier (1945: 447–448) normally occurs before copulation. In this performance the two birds walk around in a small circle giving single call notes and at the same time displaying the red linings of their mouths. After circling, the leading bird stops and the other either mounts or else starts circling in the opposite direction as the leader or the same bird may continue leading in the same direction. The stimulus for mounting appears to be the stopping of the leading bird, but often, especially late in the season when one or both birds are not in the proper physiological condition to respond, mounting is not effected and often the birds merely stop and preen, which in this case could be classed as "substitute preening" as described by Tinbergen (1939: 225–226). Another example of "substitute preening" was observed when after a short period of billing, one member of the pair suddenly stopped billing and preened.

A type of circling also takes place on the water, the two birds swimming around each other in a circle, one or both calling and occasionally one displaying by raising the wings (fig. 6, *d*). This circling on the water is used more frequently by the black guillemots. As late as mid-July, 1946, I watched this procedure on Bonaventure Island, Quebec. Here one bird appeared to take the initiative, raising the neck and anterior part of the body, directing the bill downward toward the other bird, calling and at the same time displaying the red lining of the mouth (figs. 6, *m,* and 6, *n*). The other bird held the head low with the bill directed up toward the first. According to Witherby *et al.* (1941: 162), the two roles in this ceremony may be reversed as they are in the circling on land in the pigeon guillemots.

In all the forms of display which I have witnessed, the white wing patches stand out sharply and very probably play a part in the series of stimuli which set off these chains of behavior. I think, however, that their part in this is subordinate to those of the red feet and the lining of the mouth, because the white patches have been entirely lost in *Cepphus carbo* and nearly so in *Cepphus columba snowi,* whereas both of these forms have retained the red feet and probably also the red mouth.

A considerable change in daily rhythm occurs throughout the breeding season. During the early weeks the birds are in the vicinity of the breeding site for only a few hours each morning; but later, when the young are being fed, there are adult birds present throughout the day. Indeed, to judge by the great amount of time spent loafing near the nests, guillemots must be extremely efficient at their food getting.

A bird leaving the nest site, apparently after incubating, flew down to the water nearby and almost immediately began to bathe—"bill-dipping" throughout the process. Bathing was performed, as by most other birds, by dipping the head, partly spreading the wings, and shaking as the head was raised and the water came down over the back. After bathing, the bird "treaded water," flapping the wings vigorously (fig. 6, *o*). Bathing in salt water rather than visiting bodies of fresh water for this purpose is an indication of the strictly marine habits of these birds.

The location and nature of the nest cavities usually make it difficult to describe what goes on inside them. There is, however, some information available on the nesting activities of the black guillemot. According to Winn (1950:480), the two eggs are laid two to four days apart. Incubation starts from one to five days after the second egg is laid, and lasts approximately twenty-eight days. The young remain in the nest for about thirty-four to forty days after hatching and are nearly able to take care of themselves by the time they leave the nest.

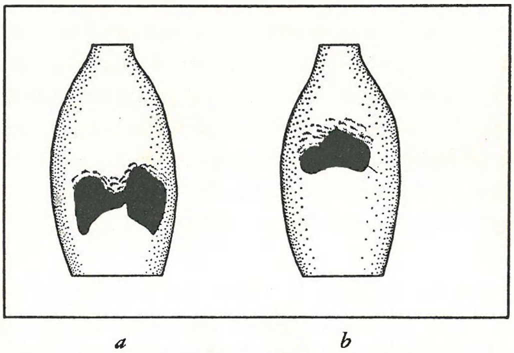


Fig. 8. Brood patches of a guillemot (*a*) and a murre (*b*). Guillemot, from CAS 10079; murre after Gurney (1913:354).

Hantzsch's studies in Iceland (1905: 111) show further that the nest cavity may be lined with small, broken stones or occasionally grass or moss. Both sexes possess the bilobed brood patch (fig. 8, *a*), and the males incubate through the night and the females by day. This last statement was checked by dissection in several instances ("verschiedenen Fällen"). The young are convoyed by the parents for a short period after leaving the nest.

At Point Lobos I watched one adult feed its well-grown young near the mouth of the vertical crevice where it was raised. The adult flew to the nest with a fish held crosswise in its bill, and the young took the fish from the adult without any ceremony. Most such feeding visits are brief, the adult entering the nest cavity and leaving within a period of fifteen seconds or less, at least when the young are fairly well grown. The fish are normally carried one at a time, are held crosswise, and, as mentioned earlier, are often killed before they are presented to the young.

On the basis of my observations, I would say that territorial behavior in guillemots is weakly developed except possibly in the immediate vicinity of the nest. Communal activity, on the other hand, is well marked, as shown by the communal "quadrilles" and diving and by the birds' nesting in groups. The closeness of one nest to another is determined in the main by the spacing of suitable nest sites. It is possible that this communal activity may not be necessary for successful nesting, that is, an isolated pair of guillemots might breed successfully, whereas a lone pair of murres would almost certainly not.

At the Point Reyes murre colony, the strong fishy odor, the continuous activity, and the muffled vocalizations of five thousand densely packed birds blend with the almost invariably on-shore wind, the ceaseless motion of the waves, and the low roar of the surf. Compared with the pastoral aspect of a group of breeding guillemots, the large "loomery" has the appearance of a city street during the rush hour. The principal colony at Point Reyes is on a rock off the windward (northwest) end of the point. The rock is approximately 250 feet long, 50 feet wide, and 35 feet high. The birds are concentrated on the top of the rock, on ledges on the leeward face, and on the east end that projects toward the point. The colonized rock is protected from the heavy surf by a second, somewhat higher rock to windward and separated from it by a narrow channel about twenty feet

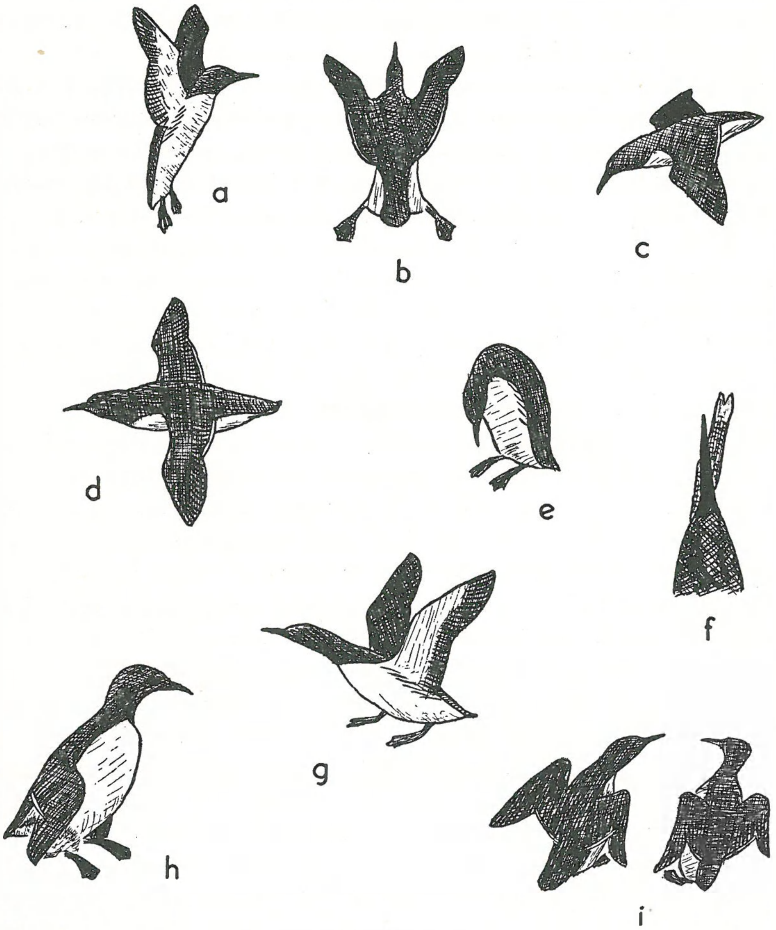


Fig. 9. Murre postures based on field sketches of the common murre. *a* and *b*, alighting; *c*, leaving cliff; *d*, steady flight; *e*, bowing; *f*, method of carrying fish; *g*, post-landing posture; *h*, tending young; *i*, fencing.

wide. At times when a heavy surf is running, waves break over the outer rock, thus making it an unsatisfactory site for a bird colony. However, its presence as a breakwater makes possible the colonization of the inner rock.

Murre colonies are most often located on high cliffs, where a downward drop at the time of taking off provides the birds with enough headway for direct flight. The lowness of the Point Reyes colony may be compensated for by its position on the windward side of the point, a situation which permits the birds of this colony to take off into the wind.

At the colony, birds are continually coming and going. The birds coming in from the sea fly southeast past the tip of the point and, if a moderate to strong northwest wind is blowing, go straight to the colony. In landing, they spread their legs and webbed feet far to the side (figs. 9, *a,* and 9, *b*), adding a considerable braking surface to that of the ridiculously small tail, and stop-flap furiously as they drop to the rock. At best they are clumsy in alighting, not infrequently landing on an incubating bird or skidding as a foot hits a slippery spot. Often a landing murre will change its mind, turn into the wind, and circle once or twice around the outer rock or farther before finally alighting. On June 23, 1948, when a southwest wind was blowing, the murres returning to the colony turned in a wide arc to the northeast and landed into the wind.

At the Point Reyes colony, murres usually take off into the wind and immediately start beating the wings rapidly. However, on Bonaventure Island, where they nest on ledges high on the cliffs, the birds gain momentum by a downward flight, the head and neck arched (fig. 9, *c*) and the wings beaten slowly in a manner quite different from the usual type of flight.

The flight of murres is direct and rapid. The head and neck are telescoped and the feet "shipped" partly under the under tail coverts (fig. 9, *d*); the wings appear long and narrow in contrast to the dumpy body. Before alighting and for a short time after the take-off, the feet are carried fanned out in a plane with the tail and are used as accessory steering organs as they are in diving. Compared with the flight of guillemots, that of murres is more direct and appears to be more rapid. And whereas guillemots almost invariably fly low over the water, usually within five feet of the surface, murres tend to fly higher than this.

A murre colony has a definite structure, as has been worked out by Johnson (1941:154–155). The activities of the birds at the nesting colony center in three areas: the nesting group, the loafing area, and the water near the colony. The first area is occupied by mated birds which are arranged in concentric formation, the birds in the center being those farthest along in the nesting cycle. In this area the birds are strongly territorial, defending their square foot or less of territory with vigor, although where territories have become settled, the murres' instinct to crowd together against a vertical rock as well as against one another virtually amounts to thigmotaxis. The crowding of nest territories has a definite selective advantage for birds nesting in the open in that predation on eggs and young can normally take place only along the margin of a nesting group. Even so, the birds of a tightly knit group, each with its sharp beak pointed outward, present a formidable array of weapons to a marauding gull or raven. Under normal circumstances a raven probably obtains eggs principally when rushed at by an overanxious murre which in so doing rolls the egg off its tarsi. At this point too the selective advantage of the shape of the egg, which rolls in a seven- to ten-inch diameter circle, becomes apparent. Also of survival value and directly correlated with this crowding together are the great variation in color and markings of the eggs and the parent's ability (as shown by Johnson, 1941:156–157) to recognize its own egg.

Loafing areas are used primarily by unmated birds, although they are also used as landing fields by some birds returning to their nest sites.

All day there are also groups of birds to be found bathing or loafing on the water near the colony. These groups, like those of the guillemots, tend to form lines. But unlike those of guillemots, loafing groups of murres on the water indulge in little or no diving, chasing, or display. This may be because of the fact that, at least after the egg is laid, it (and later the chick) is always attended by one parent. Thus pairs of murres are seldom present in these groups. However, Loomis (1896*a*:20) records a group of murres "having a clamorous concert several miles out on the ocean." The loafing groups also more often contain individuals of other species. I have observed razorbills, puffins, guillemots, surf scoters, and cormorants in these groups.

The social activities of guillemots, which nest in small, dark cavities, are carried out on the water and on rocks near the nest sites, whereas those of murres are carried out on the nest site proper. The crowding of murres on the nesting areas has resulted in a compressing of the breeding behavior. There is nothing in the behavior patterns of murres to correspond with the precopulatory circling of guillemots—there is no room for it. This pattern has been lost (if murres ever possessed it) along with the comparable circling on the water. Furthermore, the bright color of the feet which is so conspicuous in guillemots and which appears to be important in the circling is not generally evident in murres. However, it is of interest to note that an albinistic common murre has been reported by Newton (1877:2) to have had yellow legs, and three albinistic thick-billed murres in the collection of the American Museum show a reduction or absence of melanins in the legs and evidence of yellow or orange lipochromelike color. It is not unlikely, therefore, that murres are descended from ancestors with brightly colored feet. The color of the feet of guillemots appears to be solely of sexual significance. The color of the feet of murres seems to have lost its significance; but many nibbling, vestigial nest-building and feeding actions are still directed toward the general region of the feet.

The most frequently observed mannerism of murres at the colony is bowing (fig. 9, *e*), the bird standing nearly upright, lowering the head until the closed bill points directly downward in the general direction of the feet, and then raising the head until the bill is in a nearly horizontal position. Often this is followed by shaking the head several times from side to side. Bowing is an indication of excitement. The approach of a person to the colony usually starts a wave of bowings through the colony. This may be followed by wing flapping, which is an indication of greater excitement and usually precedes the departure of some individuals from the group, the birds on the loafing areas being the first to go. Both actions have the definite effect of group stimulation. Bowing, mixed with billing and display of the buccal lining, is also used by members of a pair after copulation and at other times; and occasionally birds will nibble small pebbles or other objects as though they were nesting material. The bowing ceremony most probably derives from that of feeding the young, which is accomplished in the same way, one parent holding a fish in its bill (see fig. 9, *f*) and both parents bowing their heads toward the chick. This fish-presentation ceremony is performed before the egg hatches and also by birds which have lost their egg or chick. Similar actions are used by an incubating bird in tucking the egg under it or attempting to do likewise with the young. On one occasion, March 11, 1945, a murre started to bow and, while its head was down, began to preen, possibly another example of substitute preening.

Murres share with guillemots three types of behavior: billing, fencing, and displaying the brightly colored lining of the mouth, the latter usually accompanying the two former actions. Fencing is merely an intensified type of billing; and, in fact, no sharp distinction can be drawn between them. At least in the murres, billing also grades into nibbling of the feathers of the mate's head and neck.

Murres also seem to differ from guillemots in lacking a threat display involving partly spreading the wings and cocking the tail. Murres do, however, often partly open the wings while fencing (fig. 9, *i*) or billing, but in this instance, I think, merely for balancing. On the other hand, murres have a display not shared by guillemots. In this display (fig. 9, *g*) the head and neck are extended forward at an angle of from 45 to 70 degrees from the horizontal and the wings are held nearly straight out and partly raised. In a variation of this posture the wings are folded. This display is used immediately on landing, while going through a nesting group to a mate, or, less often, before taking off. This last use parallels a well-known display of the gannet, another highly colonial species. The significance of this display of the murre is not clear, but it may indicate that the bird using it is mated and established in the group.

Murres are more noisy than guillemots, and their voices are lower in pitch. At Point Reyes it was impossible to separate the individual calls from the combined roar of the birds and the surf. Perry (1940:155–182), however, has described a considerable variety of notes and the circumstances under which they are used. Perhaps the larger vocabulary of the murres makes up in part for the fewer types of display.

Murres fight even more fiercely than guillemots, but the fighting occurs most frequently on the loafing grounds or in the nesting groups and seldom if ever on the water. Two fighting murres with locked bills may struggle over a group of incubating birds and may even knock other birds off the ledges. According to Perry (1940), most of this fighting results, at least in the later part of the nesting season, from unmated birds' interloping in a settled nesting group of mated birds.

Copulation in murres usually occurs at the nest site, and, as far as I can determine, without preliminaries. Attempts at copulation, most often made by unmated young males (Perry, 1940), occur on the loafing grounds as well as in the nesting groups as late in the season as the birds are at the colonies. In species like the guillemots, which have well-defined precopulatory behavior patterns, failure of one or both birds to be in the proper physiological and psychological state usually results in the breaking of the chain of reactions well before mounting is attempted. I think the lack of this type of behavior pattern explains the frequent attempts in murre colonies. Again there seems to be a definite connection between behavior patterns and the crowding of the nesting groups, because if the spacing of incubating birds were more open, unmated males would cause much more disturbance than they do.

During copulation the female's body is in a nearly horizontal position whereas the male stands nearly upright and, unlike the male guillemot, balances by resting his wing tips on the ground.

The incubation period of the common murre is highly variable, apparently owing to a corresponding variation in attentiveness shown by the incubating parents. Murre eggs have been hatched in an incubator in from 30 to 32 days, and Witherby *et al* (1941:155) give 28 to 37 days as the incubation period in nature. Perry (1940:202–203) watched the incubation of three murre eggs, which hatched on the 34th, 44th, and 49th days of incubation. Both parents share in incubation and later in brooding the young. Three pairs which Perry watched were "mixed" pairs, that is, one bird of each pair was a ringed "mutant" and the other was normal. In these three pairs Perry found considerable variation in the relative amount of time spent by the male and the female at the nest.

Incubation is performed with the egg resting across the parent's tarsi or on the webs of the feet, and the brood patch (fig. 8, *b*) is lowered over it.

After the egg hatches, the young is brooded constantly by one or both parents—in contrast with the guillemots, which leave their young in the nests for considerable periods of time. Nest relief usually follows a feeding of the young by the returning parent, but both parents enter into the ceremony as described previously. After the feeding there is usually a period of several minutes during which billing, display of the lining of the mouth, and preening may occur. The actual change-over is made while both parents droop their wings in a tentlike manner over the chick (fig. 9, *h*). As the chick grows older it spends less time under its parents and walks about on its toes, often exercising its wings. At an age of from 20 to 22 days it flies down to the water and is convoyed out to sea by its parents. These flights to the water are usually made late in the day, after gulls have gone to roost. At this age the young are perhaps half-grown; and, because the remiges are only partly grown, the greater wing coverts act as flight feathers both for this flight and for "flying" under water (Johnson, 1938:529–530). As stated earlier, both parents convoy the young for a short time, after which one takes over these duties. A single parent attending a young on Monterey Bay was shot by Loomis (1895:212) and proved to be a male. However, since there is apparently considerable variation in attentiveness at the nest shown by different birds regardless of sex, the convoying of young birds late in the season by the male may prove not to be the rule.

In attempting to get at the roots of differences in behavior between the murres and the guillemots, the observer repeatedly comes back to the crowding together of murres in the nesting colonies and in general to the gregariousness of these birds. Guillemots show strong tendencies to nest in groups, but spacing of the nests is determined by the distribution of suitable sites for individual nests. The murres' urge to crowd together may very well be another manifestation of the same urge which impels guillemots to nest under something. However, a world of difference has resulted from the murres' change in choice of type of nest site.

The number of suitable nest sites is probably the limiting factor for the size of the guillemot population of most areas. The largest nesting group of black or pigeon guillemots of which I have knowledge is one recorded by Gross (1937:34) at Perret Island, Labrador, where more than two thousand pairs nest. However, Austin (*in litt.*) estimated the size of the spectacled guillemot colony on Teurejima to be 5,000 pairs. In contrast, Krasovski (1937:66–71) estimated the total murre population of Nameless Bay, Novaya Zemlya, to be more than 1,600,000. The murre population of the coast of central California can be estimated in tens of thousands, whereas that of the guillemots is only a few hundred.

Large populations of murres concentrated in small areas fall heir to the usual advantages and disadvantages of coloniality. Group activity synchronizes breeding activity, and this in turn increases nesting success by reducing the total amount of time during which the colony contains eggs and young, which are most vulnerable to predators. The presence of other murres nearby is an important factor in preventing an alarmed murre from deserting its egg or young. However, when one bird is frightened to the point of leaving the group, all the other birds usually follow suit. There is generally a direct proportion between the size of a colony and the magnitude of the stimulus necessary to cause the birds to leave. Murres have become so dependent upon the presence of neighboring birds to prevent desertion of the egg when the birds are alarmed that it is doubtful whether a group of a few pairs could nest successfully. The immense numbers on the breeding colonies mean that a very small proportion will normally be taken by predators; yet one man, merely by scaring the birds away several times in a season, could cause the desertion of a large colony and consequently the failure of the colony to produce young. Finally, large populations of colonial species like murres are more seriously affected by epidemic diseases, locally adverse climatic conditions, and failures of the food supply; hence their numbers tend to fluctuate more than those of small, diffuse populations like those of the guillemots.

MIGRATION AND DISPERSAL

It is necessary to determine the extent of interchange between populations before estimating the degree of genetic isolation of the populations. At present there is little information of this nature available for murres and guillemots. One thing, however, is apparent. Murres have a strong tendency to nest year after year in the same place. Table 16, compiled from data in the files of the United States Fish and Wildlife Service, shows the numbers of common murres recaptured at the place of banding in Saguenay County, Quebec. I know of no record of a murre's or guillemot's having been banded at one breeding colony and being recovered at another.

Further evidence that murres return to the same nesting ledge is presented by Aspden (1928:50–56), who mapped the locations of ten murre eggs of uncommon color types in 1925 and, returning in 1926, found six of these types duplicated (presumably by the same birds) within 18 inches of the positions of the same types of eggs the previous year. In 1927 he found five of the types reduplicated. In 1926 he further found three eggs of one of the types where there was only one in 1925. This suggested to Aspden that the young may return to nest on the ledge where they were raised and that egg color is inherited.

Perry (1940:196) watched "ringed" murres on the Isle of Lundy, where the ringed birds make up approximately 1 per cent of the murre population. One ringed murre was said to have nested by a cable on the cliff ledge for more than twenty years. There is a good chance that this was the same bird or one of its descendants. Certainly mapping of the ringed murres in a colony such as this would lead to valuable information on the birds' returning year after year to the same nesting place.

TABLE 16

NUMBER OF COMMON MURRES BANDED AT BREEDING COLONIES IN SAGUENAY COUNTY, QUEBEC, AND RECAPTURED WHERE BANDED

Age when banded	Number of years between banding and recapturing:									
	1	2	3	4	5	6	7	8	9	10
Adult	99	49	39	31	17	14	6	6	3	1
Age?	21	16	9	4	1	1	..	..	..	..
Juvenile	..	2	..	..	..	..	..	..	..	..
Totals	120	67	48	35	18	15	6	6	3	1

Number of times recaptured	Number of individuals	Number of recaptures
Once	254	254
Twice	29	58
Three times	3	9
Total	287	321

Note: Band loss in this species is very great due to abrasion against the rocks at the nest sites as the birds move about and rest with the tarsometatarsus flat on the substrate.

Most recoveries of murres banded as young are made within a few months after the young take to the water; but there are at least three records of young being recaptured at the place of banding: two listed on table 16, and one bird banded at Skokholm, Pembrokeshire, Wales, July 22, 1937, and recovered where banded July 1, 1938 (Leach, 1939:365).

There is much evidence that murres, especially young birds, disperse rather widely after the breeding season. Murres banded at the breeding colonies at Heligoland have been recovered from the Bay of Biscay to central Norway, western Sweden, and Great Britain; and the pattern of dispersal for the British murres is very similar (Stechow, 1938). Many murres banded at colonies near Cape Whittle, Canadian Labrador, have been taken in winter off eastern Newfoundland (Johnson, 1940).

The returns in the United States Fish and Wildlife Service files show that common murres banded in Oregon tend to winter off Washington and British Columbia. Of 54 returns, 25 were retaken in Oregon (24 within two months of the time of banding), 12 in Washington, 14 in British Columbia, and 3 in California.

There is considerable evidence, on the other hand, that nearly all the first-winter murres taken off California between November and April belong to the Alaska populations. Forty-three such birds have wing lengths ranging from 189 to 217 mm., with a mean of 208.3±0.9. Thirty-three adult breeding murres from California are of similar size (193–218, 208.0±0.8), as are 18 first-winter birds from Alaska (200–217, 207.9±1.1). Table 7 shows that the wings of the first-year murres average seven to ten millimeters shorter than those of adults. Hence, most of the young murres wintering off California probably represent the race *inornata.*

Furthermore, on February 13, 1949, I watched a northward migration of murres past Point Reyes. For about an hour, flocks of as many as 125 murres (more than 90 per cent in winter plumage) were constantly passing the point. Altogether nearly a thousand birds must have passed. At this time the breeding colony at the point was at its full breeding strength (about 5,000 birds), and all but a few of these birds were in breeding plumage.

Much less is known about the movements of guillemots. As with the murres, guillemots tend to return to a nesting place year after year. The files of the United States Fish and Wildlife Service have records of 23 black guillemots banded as adults on the nesting grounds in Quebec and New Brunswick returning to the same place for up to four years. At least three of these birds were captured at the same nest on consecutive years. Two guillemots banded as juveniles returned to the nesting grounds: one, two years later, and the other, four years later.

Guillemots, especially the young, tend to disperse after the breeding season. Austin (1932:138) records five guillemots banded as nestlings in southern Labrador and taken in Newfoundland. Two others, also banded as nestlings in Labrador, were recaptured at Godbout, Quebec. Black guillemots, which nest only as far south as Maine, are regularly found south to Massachusetts in winter.

In the region of Bering Strait (Bailey, 1948:257) and elsewhere in the north, Mandt's guillemots move south with the advancing edge of the pack ice. The Baltic population also moves south with the advancing ice. Pigeon guillemots are scarce throughout much of the breeding range in winter. This applies to the population of the Bering Strait region (Bailey, 1948:258) and the coast of California, but apparently not to the Washington and British Columbia birds. There may be a connection between this apparent migratory habit and the longer wings of the former birds and the shorter wings of the more sedentary populations of Washington and British Columbia.

Ordinarily the thick-billed murre, *U. l. lomvia,* does not move far south of its breeding range, but in some years great flights of these murres appear over eastern North America. Fleming thought (1907) that the birds were forced from their regular wintering grounds on Hudson Bay by unfavorable ice conditions. This is apparently not the whole story, however, because more than 90 per cent of the specimens taken during these flights are first-year birds. There is probably some connection between this phenomenon and the general propensity for young common murres and guillemots to wander more widely than older birds, and it is also possible that selection is actively at work here. Few of the birds going south survive, whereas birds which might go north or east to open water are probably much better off in the aggregate.

Although there is enough dispersal of common murres in winter to bring three subspecies together off western Sweden and two subspecies together off other parts of Europe and off California, it is apparent that the urge to return to the native range is sufficiently strong in enough individuals to prevent extensive mixing of the subspecies. The same probably holds true for the guillemots, which, however, seem to be considerably more sedentary.

GEOGRAPHIC VARIATION

Cepphus

The guillemots form a group of three closely related species with nearly complementary ranges. The black guillemot, *Cepphus grylle,* has a wide range in the Atlantic and Arctic oceans, nesting from Maine and northern Europe (Denmark and the British Isles) north as far as there is open water during the breeding season. The species occurs along the north coasts of Asia and Alaska. South of Bering Strait it is replaced by the pigeon guillemot, *Cepphus columba,* which nests south along the Pacific coasts of North America and Asia to southern California and the Kurile Islands, respectively. The third species is the spectacled guillemot, *Cepphus carbo,* which differs from the other two species in having the plumage entirely black except for white areas around the eyes and the base of the bill. The range of *C. carbo* is roughly the borders of the Sea of Okhotsk and the Sea of Japan south to eastern Korea.

In order to determine the amount of geographic variation, I have broken up the whole range of the guillemots into populations small enough to be relatively homogeneous and yet represented by enough individuals (ten or more) to provide statistically significant samples. Adjacent populations which closely resembled each other were often combined. In determining the limits of these populations, natural barriers to dispersal were used where possible. In some instances small samples differing from adjacent groups were kept separate. The following is a list of the populations into which the guillemots have been divided for purposes of analysis.

Bay of Fundy and south. Nova Scotia from Halifax, south and west, the Bay of Fundy and the coast of Maine.

Newfoundland and Nova Scotia. The north and east coasts of Nova Scotia, north and east of Halifax, and the north, east, and south coasts of Newfoundland; that is, all coasts not bordering the Gulf of St. Lawrence.

Gulf of St. Lawrence. The shores bordering the Gulf of St. Lawrence on the east, south, and west; Prince Edward and the Magdalen islands.

North shore St. Lawrence. The upper reaches of the St. Lawrence River, northeast to St. André de Kamouraska on the south shore and along the north shore of the river and of the Gulf of St. Lawrence through the Straits of Belle Isle.

Southern Labrador. Newfoundland Labrador south of the region about Hamilton Inlet.

Northern Labrador. Newfoundland Labrador from Hopedale north to Nain.

James Bay. The east shore and islands of James Bay south of Cape Jones.

East shore Hudson Bay. The east shore and adjacent islands of Hudson Bay from Cape Wolstenholme to Cape Jones.

Northwestern Hudson Bay. The northwest shore of Hudson Bay and Southampton Island.

Southern Baffinland. Baffin Island from Frobisher Bay to the Foxe Peninsula, including Resolution Island.

Cumberland Sound. The region around Cumberland Sound on southeastern Baffin Island.

Northern Baffinland, Devon, Cobourg, and Somerset islands. Baffin Island north of latitude 72° north, Somerset, Devon, and Cobourg islands.

Ellesmereland. The east coast of Ellesmere Island.

Etah area. The northwest coast of Greenland north of Cape Atholl.

Upernavik area. Upernavik, Agpamuit, and Devil's Thumb, western Greenland.

Disco Bay. Western Greenland from Disco Bay to Svartenhuk.

Sukkertoppen area. Western Greenland from Godthaab north to Holsteinborg.

British Isles

Norway and western Sweden. The coasts of Norway and Sweden north of Falsterbo.

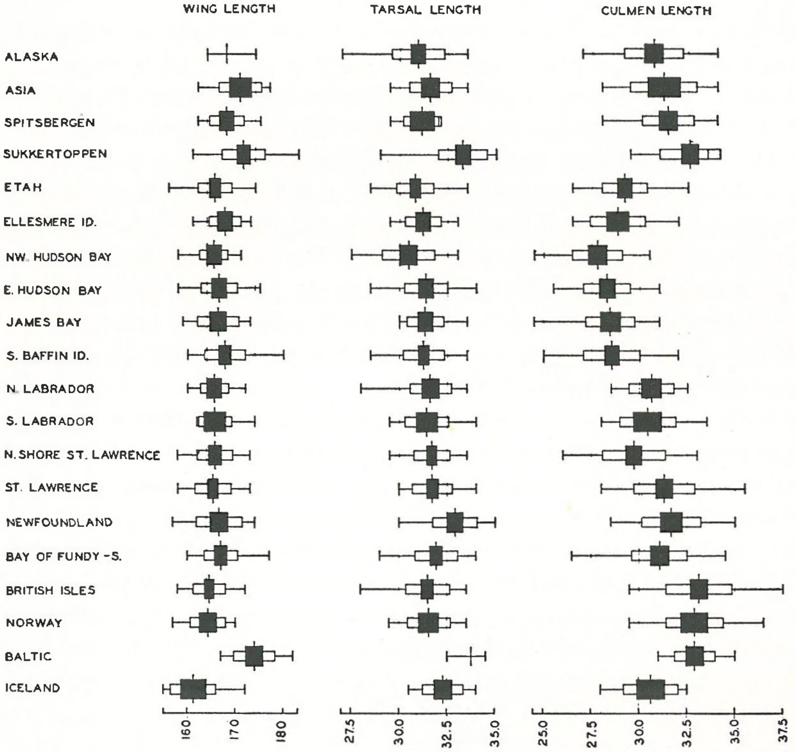


Fig. 10. Geographic variation in wing, tarsal, and culmen lengths in *Cepphus grylle* expressed as Dice squares showing the range and mean ± $2\sigma_m$ and ± σ for each population.

Baltic. The shores of the Baltic Sea, including Sweden, southern Finland, northern Germany, and Danzig.

Northeast Greenland. The east coast of Greenland. Specimens from between 70° and 75° north latitude examined.

Spitsbergen

Alaska. All localities from which specimens of *grylle* were examined.

Asia. The Arctic coast of Siberia east of Cape Bolshaja Baranov, and Wrangel and Herald islands in the Arctic Ocean.

Iceland

Faeroes. Between Iceland and Scotland.

California

Oregon

Washington

British Columbia

Alaska coast.—Coastal Alaska south of Bering Strait, including the Aleutian Islands west to and including Unalaska.

Islands of Bering Sea.—The Pribilof, St. Matthew, St. Lawrence, King, and the Diomede islands.

Siberia.—Eastern Siberia from Kamchatka north to Cape Serdze.

Outer Aleutian and Commander islands.—The Commander Islands and the Aleutian Islands from Atka west.

Kurile Islands.—Between Kamchatka and Japan.

CEPPHUS GRYLLE

Wing length.—On the western side of the Atlantic there is little variation in wing length (see table 17 and fig. 10). The guillemots of the Gulf of St. Lawrence seem to have somewhat shorter wings than the rest, a possible correlation with the more protected waters in which they live. A short mean wing length is found in the populations of birds from Hudson and James bays.

Along the west coast of Greenland there is a cline of increasing wing length from north to south, the birds from southwestern Greenland (Sukkertoppen) being significantly longer-winged than any western Atlantic population; only the Baltic birds are larger. At the northern end of the Greenland cline (Etah) the guillemots average two millimeters shorter in wing length than the population of central Ellesmereland less than fifty miles away across Smith Sound. This difference, although slight, may reflect the sedentary habits of the birds and their coming back to breed at the same areas where they were raised.

On the east side of the Atlantic the population inhabiting the Baltic Sea, *C. g. grylle,* has the longest wings, averaging ten millimeters longer than the populations of western Sweden, Norway, and Great Britain. The isolated populations of Iceland and the Faeroes are both short of wing, that of the latter group seemingly the shortest of the genus. Unfortunately very few specimens of this form are available.

The high-arctic race, *mandtii,* has rather long wings, the population of eastern Siberia apparently being slightly longer-winged than those of Spitsbergen and the Arctic coast of Alaska.

Tarsal length.—There is a general decrease in tarsal length in the guillemot populations from Maine to Ellesmereland (see table 18 and fig. 10). Along the west coast of Greenland the southward cline for increasing wing length is paralleled by an even more marked cline for increasing tarsal length.

The birds from the British Isles, Norway, and western Sweden average somewhat shorter in tarsal length than the Maine and Bay of Fundy birds, and the Baltic population (on the basis of four specimens) seems significantly larger than the other forms of *grylle.*

The short-winged Iceland guillemots have long tarsi; only the Newfoundland-Nova Scotia, southwest Greenland, and Baltic populations are larger.

The high-arctic populations have tarsi of moderate length.

Culmen length.—As in the tarsal length, there is a cline of decreasing bill length (see table 19 and fig. 10) from Maine to Ellesmereland, but there is a distinct break at Hudson Strait. Again there is a parallel cline along the west coast of Greenland. There are, however, apparent irregularities in the clines, the Maine-

TABLE 17

GEOGRAPHIC VARIATION IN WING LENGTH OF GUILLEMOTS

Locality	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
Bay of Fundy and south	40	177	160	167.1±0.59	3.73	2.23
Newfoundland and Nova Scotia	27	174	157	166.6±0.93	4.85	2.91
Gulf of St. Lawrence	50	173	158	165.3±0.53	3.76	2.27
North shore St. Lawrence	35	173	158	165.8±0.66	3.88	2.35
Southern Labrador	17	174	162	167.2±0.80	3.32	1.99
Northern Labrador	23	172	160	166.1±0.63	3.18	1.82
James Bay	24	173	159	166.3±0.87	4.28	2.57
East shore Hudson Bay	30	175	158	166.5±0.71	3.89	2.34
Northwestern Hudson Bay	16	171	158	165.4±0.76	3.05	1.84
Southern Baffinland	50	180	160	167.8±0.61	4.32	2.57
Cumberland Sound	6	174	159	166.5	....	....
Northern Baffinland, Devon, Cobourg and Somerset is.	13	172	163	167.2±0.82	2.95	1.76
Ellesmereland	20	173	161	167.7±0.75	3.35	2.00
Etah area	43	174	156	165.6±0.55	3.62	2.19
Upernavik area[a]	13	169	156	165.1±1.11	4.00	2.42
Disco Bay	5	171	166	168.4	....	....
Sukkertoppen area	46	183	161	171.5±0.66	4.46	2.60
British Isles	56	172	158	164.6±0.44	3.31	2.01
Norway and western Sweden	16	170	157	164.3±0.94	3.74	2.28
Norway and western Sweden[a]	53	173	155	162.6±0.56	4.04	2.49
Baltic (Sweden)[a]	24	182	167	174.0±0.87	4.26	2.45
Baltic	4	181	169	175.8	....	....
Northeast Greenland[a]	2	161	159	160.0	....	....
Northeast Greenland	3	175	165	169.0	....	....
Spitsbergen[a]	26	175	162	168.0±0.72	3.69	2.20
Alaska (*mandtii*)	8	177	164	168.7	....	....
Asia (*mandtii*)	16	177	162	170.9±1.10	4.41	2.57
Iceland	13	172	155	161.3±1.31	4.74	2.94
Iceland[a]	6	163	155	159.0	....	....
Faeroes[a]	3	158	155	156.3	....	....
California	172	197	176	187.5±0.31	4.01	2.14
Oregon	18	193	178	187.2±0.94	3.99	2.13
Washington	33	190	171	179.8±0.82	4.69	2.61
British Columbia	85	191	173	180.7±0.45	4.16	2.30
Alaska Coast	93	192	173	183.2±0.44	4.22	2.30
Islands of Bering Sea	25	194	178	186.2±0.80	3.99	2.14
Siberia (*columba*)	16	193	178	186.5±1.03	4.10	2.20
Outer Aleutian and Commander is.	19	183	169	177.3±0.87	3.81	2.15
Kurile Is. (*snowi*)[a]	2	192	190	191	....	....
Kurile Is. (*snowi*)	6	189	181	184.0	....	....
C. carbo, all localities	19	215	188	202.6±1.53	6.65	3.28

[a] Calculated from the data (individual measurements) of Salomonsen (1944).

TABLE 18

Geographic Variation in Tarsal Length of Guillemots

Locality	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
Bay of Fundy and south	55	34.0	29.0	31.95±0.15	1.12	3.50
Newfoundland and Nova Scotia	37	35.0	30.0	32.43±0.19	1.18	3.62
Gulf of St. Lawrence	56	34.0	30.0	31.73±0.14	1.04	3.28
North shore St. Lawrence	77	33.5	29.5	31.70±0.11	0.93	2.94
Southern Labrador	25	34.0	29.5	31.50±0.20	1.01	3.20
Northern Labrador	25	33.5	31.0	31.86±0.14	0.69	2.17
James Bay	26	33.5	30.0	31.31±0.19	0.96	3.07
East shore Hudson Bay	37	34.0	28.5	31.35±0.18	1.12	3.58
Northwestern Hudson Bay	40	33.0	27.5	30.97±0.22	1.39	4.49
Southern Baffinland	65	33.5	28.5	31.25±0.13	1.06	3.39
Cumberland Sound	16	34.0	29.0	31.06±0.31	1.22	3.93
Northern Baffinland, Devon, Cobourg, and Somerset is.	18	32.5	28.5	30.83±0.27	1.15	3.73
Ellesmereland	23	33.0	29.5	31.22±0.19	0.92	2.95
Etah area	58	33.5	28.5	30.78±0.13	0.97	3.15
Upernavik area	2	32.0	29.0	30.50	....	....
Disco Bay	7	35.0	31.0	33.14	....	....
Sukkertoppen area	50	35.0	29.0	33.13±0.21	1.49	4.49
British Isles	55	33.5	28.0	31.50±0.16	1.16	3.68
Norway and western Sweden	19	33.5	29.5	31.53±0.26	1.12	3.56
Baltic	4	34.5	32.5	33.75	....	....
Northeast Greenland	5	34.0	31.0	32.25	....	....
Spitsbergen	10	32.0	29.5	31.15±0.31	0.97	3.12
Alaska (*mandtii*)	59	33.5	27.0	31.16±0.16	1.25	4.00
Asia (*mandtii*)	21	33.5	29.5	31.57±0.24	1.09	3.44
Iceland	19	34.0	30.5	32.29±0.24	1.03	3.18
California	157	39.0	32.5	36.13±0.10	1.27	3.52
Oregon	18	37.5	32.5	35.39±0.29	1.25	3.53
Washington	33	37.0	32.5	34.61±0.17	1.00	2.89
British Columbia	85	37.5	31.5	34.55±0.12	1.12	3.25
Alaska Coast	105	38.0	31.0	34.64±0.13	1.28	3.69
Islands of Bering Sea	25	36.5	31.5	34.60±0.25	1.24	3.58
Siberia	16	37.5	33.5	35.00±0.26	1.04	2.97
Outer Aleutian and Commander is.	27	35.5	31.0	33.72±0.23	1.19	3.53
Kurile Is. (*snowi*)	6	36.5	32.5	34.05	....	....
C. carbo, all localities	20	39.5	35.0	37.23±0.31	1.38	3.71

Note: Salomonsen gives no figures for tarsal length.

TABLE 19

Geographic Variation in Culmen Length of Guillemots

Locality	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
Bay of Fundy and south	51	34.5	26.5	31.07±0.24	1.70	5.47
Newfoundland and Nova Scotia	31	35.0	28.5	31.68±0.28	1.54	4.86
Gulf of St. Lawrence	50	35.5	28.0	31.29±0.22	1.58	5.05
North shore St. Lawrence	72	33.0	26.0	29.73±0.19	1.63	5.48
Southern Labrador	18	34.5	28.0	30.69±0.38	1.61	5.25
Northern Labrador	23	32.5	28.5	30.78±0.26	1.23	4.00
James Bay	26	31.0	24.5	28.48±0.25	1.28	4.49
East shore Hudson Bay	37	31.0	25.5	28.27±0.20	1.23	4.33
Northwestern Hudson Bay	32	30.5	24.5	27.77±0.23	1.29	4.65
Southern Baffinland	57	32.0	25.0	28.57±0.19	1.47	5.15
Cumberland Sound	14	30.0	25.5	27.75±0.39	1.45	5.22
Northern Baffinland, Devon, Cobourg, and Somerset is.	17	31.5	27.0	29.00±0.32	1.31	4.52
Ellesmereland	22	32.0	26.5	28.82±0.30	1.43	4.96
Etah area	52	32.5	26.5	29.20±0.17	1.19	4.08
Upernavik area[a]	14	30.0	26.5	28.50±0.53	2.00	7.02
Disco Bay	7	36.5	31.0	33.00	....	....
Sukkertoppen area	45	33.5	29.5	32.60±0.23	1.57	4.81
British Isles	62	37.5	29.5	33.27±0.22	1.71	5.14
Norway and western Sweden	18	36.5	29.5	32.89±0.35	1.49	4.53
Norway and western Sweden[a]	56	35.0	29.0	31.36±0.18	1.36	4.34
Baltic (Sweden)[a]	24	35.0	31.0	32.92±0.22	1.06	3.22
Baltic	6	35.0	29.5	33.00	....	....
Northeast Greenland	5	33.5	31.5	32.40	....	....
Spitsbergen[a]	31	34.0	28.0	31.39±0.24	1.34	4.27
Alaska (*mandtii*)	53	34.0	27.0	30.78±0.22	1.59	5.16
Asia (*mandtii*)	18	34.0	28.0	31.22±0.41	1.73	5.54
Iceland	17	32.5	28.0	30.62±0.35	1.43	4.67
Iceland[a]	6	32.0	29.0	30.5	....	....
Faeroes[a]	3	33.0	31.0	32.0	....	....
California	161	39.5	33.5	36.53±0.11	1.35	3.70
Oregon	18	36.5	33.0	35.19±0.25	1.06	3.01
Washington	38	38.0	31.0	33.82±0.25	1.55	4.59
British Columbia	91	38.5	32.0	34.51±0.14	1.35	3.91
Alaska Coast	102	36.5	30.5	33.97±0.13	1.32	3.89
Islands of Bering Sea	21	34.5	29.0	32.38±0.29	1.34	4.14
Siberia	16	35.0	30.5	32.31±0.31	1.22	3.78
Outer Aleutian and Commander is.	25	33.0	29.0	31.20±0.26	1.32	4.23
Kurile Is. (*snowi*)[a]	2	34.0	30.0	32.0	....	....
Kurile Is. (*snowi*)	6	35.5	29.5	33.28	....	....
C. carbo, all localities	18	45.5	38.5	42.42±0.48	2.04	4.81

[a] Calculated from the data (individual measurements) of Salomonsen (1944).

Bay of Fundy birds averaging shorter-billed than the birds immediately to the north, the birds from Cumberland Sound being somewhat smaller-billed than those from Ellesmereland, and the small Disco Bay sample averaging smaller than the population from Sukkertoppen to the south. Perhaps larger samples from these areas would show that these irregularities are not real.

The European populations from the Baltic, British Isles, and Norway and western Sweden are all similarly long-billed; and there seems to be an east-west cline in bill length in the southernmost populations of *C. g. arcticus*. These populations in order of increasing bill length are: Maine-Bay of Fundy, Nova Scotia-Newfoundland, Sukkertoppen, and British Isles-Scandinavia. Wing and tarsus lengths do not vary clinally in this direction.

The Iceland guillemots are short-billed, as they are short-winged, but judging from Salomonsen's three birds from the Faeroes, the form inhabiting these islands (*faeroeensis*) averages longer-billed than *islandicus* from Iceland.

C. g. mandtii is longer-billed than the other high-arctic guillemots (*ultimus*) but less so than Salomonsen (1944) thought.

White in the outermost primary.—The per cent of white in the outermost primary (fig. 2) is a character not well adapted to statistical analysis, as it has been shown (p. 127) to be one in which there is a significant amount of both sexual and age variation. Thus the population samples are of necessity small, including only adult males in one group and adult females in the second. Furthermore, inaccuracies probably result from the inability to distinguish birds of the southern populations in their first breeding plumage from birds in their second and subsequent breeding plumage (p. 126). This separation, however, is possible and has been made in the more northern populations. But, as the first-year birds tend to have more white on the primaries than the adults, the clines of increasing amount of white from south to north which occur on both sides of the Atlantic are actually more pronounced than they appear since some first-year birds are undoubtedly included in the figures for the southern populations.

As in the cline for bill length, there is a break (see table 20) between northern Labrador and southern Baffinland in the western Atlantic coast cline for white in the outermost primary. The western Greenland cline appears to be more smooth.

Birds from Iceland are predominantly dark-primaried, and there seems to be a cline of increasing amount of white in the primaries thence to the British Isles, Scandinavia, and into the Baltic Sea.

Like the other northern guillemots, individuals of the populations of Spitsbergen, Asia, and northern Alaska have much white in the outer primaries, but the samples available are too small to indicate differences among these populations.

White on the secondary coverts.—Regional differences in this character are summarized in table 21. The categories A, O, B, C, D, and E have been illustrated earlier (fig. 3). In this character there are well-marked northward clines of increasing amount of white on both the west coast of Greenland and the east coast of North America; a sharp break in the latter cline is evident at Hudson Strait. On the eastern side of the Atlantic the southern populations have notably more dark than the northern ones.

TABLE 20

GEOGRAPHIC VARIATION IN THE PER CENT OF WHITE IN THE OUTER PRIMARY IN ADULT BLACK GUILLEMOTS

Population	Sex	None or trace	1–3	4–6	7–9	10–12	13–15	16–18	19–21	22–24	25–27	28–30	31–33	34–36
Bay of Fundy and south	♂♂	4	..	..	3	2	3	2	1	..	..	..	..	..
	♀♀	1	..	..	..	1	5	..	..	..	1	..	..	..
Nova Scotia and Newfoundland	♂♂	6	..	..	1	1	2	4	2	1	1	..	..	..
	♀♀	2	..	..	..	..	1	..	1	2	..	..	..	..
Gulf of St. Lawrence	♂♂	1	..	..	..	..	2	2	2	3	2	..	1	..
	♀♀	7	..	..	..	1	5	1	4	5	1	..	1	..
North shore St. Lawrence	♂♂	2	..	..	..	1	2	1	1	..	1	1	..	..
	♀♀	..	..	..	..	..	..	1	4	1	3	..	..	..
Southern Labrador	♂♂	1	..	..	..	1	..	..	1	..	..	1	..	..
	♀♀	..	..	..	1	..	..	1	1	..	2	1	..	1
Northern Labrador	♂♂	1	..	..	..	..	..	2	2	1	2	..	..	..
	♀♀	..	..	..	1	..	..	3	1	1	1	2	..	..
Sukkertoppen	♂♂	3	..	..	1	1	1	4	1	3	5	1	1	..
	♀♀	..	..	..	..	2	1	2	2	2	1	1	3	..
Iceland	♂♂	7	1	..	..	1	..	1	..	..	..	..	1	..
	♀♀	5	..	1	1	..	1	1	1	..	1	1	1	..
British Isles	♂♂	21	..	..	3	2	2	1	2	1	..	..	..	..
	♀♀	15	..	..	..	..	2	2	1	..	1	..	..	..
Norway and western Sweden	♂♂	8	2	3	5	5	1	4	..	1	..	..	1	..
	♀♀	8	..	2	2	2	2	2	3	3	..	..	..	..
Baltic	♂♂	7	..	..	2	2	1	2	1	1	..	..	..	..
	♀♀	..	..	..	..	..	..	1	2	2	..	..	..	..

TABLE 20—*Continued*

Geographic Variation in the Per Cent of White in the Outer Primary in Adult Black Guillemots

Population	Sex	None or trace	16–18	19–21	22–24	25–27	28–30	31–33	34–36	37–39	40–42	43–45	46–48	49–51	52–54	55–57
James Bay	♂♂	..	1	..	1	3	1	6	1	1	3	..	1	..	..	..
	♀♀	..	..	..	..	..	1	..	1	2	..	..	..	..	..	..
East shore Hudson Bay	♂♂	..	..	1	..	..	2	4	2	3	3	1	1	..	..	..
	♀♀	..	..	..	..	..	..	1	2	2	2	1	..	1	1	..
Northwestern Hudson Bay	♂♂	..	..	..	..	..	..	1	3	1	..	..	..	..	..	..
	♀♀	..	..	..	..	..	..	1	1	..	1	..	..	..	..	..
Southern Baffinland	♂♂	..	..	..	1	2	3	5	1	3	1	..	1	..	..	..
	♀♀	..	..	..	..	1	..	1	3	2	1	..	2	..	..	1
Northern Baffinland, Devon, Cobourg, and Somerset is.	♂♂	..	..	..	..	..	..	1	2	3	1	1	1	..	..	..
	♀♀	..	..	..	..	..	..	1	..	1	..	1	1	..	..	..
Ellesmereland	♂♂	..	..	..	..	2	..	..	3	1	2	1	2	..	..	..
	♀♀	..	..	..	..	..	..	2	1	..	2	..	1	1	1	..
Etah area	♂♂	..	..	..	..	2	2	1	1	8	4	4	1	..	..	..
	♀♀	..	..	..	..	..	1	2	1	1	1	3	2	3	2	..
Upernavik	♂♂	..	..	..	..	..	..	..	2	2	1	..	..	..	..	..
	♀♀	..	..	..	..	..	2	2	3	1	..	..	..	..	..	..
Spitsbergen	♂♂	..	..	..	..	..	..	3	4	..	1	..	..	..	..	..
	♀♀	..	..	..	..	1	1	1	1	2	2	1	..	..	..	..
Asia	♂♂	..	..	..	1	1	..	1	..	2	2	..	..	..	..	..
	♀♀	..	..	..	..	1	..	1	4	1	..	1	..	..	..	..
Alaska	♂♂	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	♀♀	..	..	..	1	..	1	1	..	..	..	1	..	..	..	..

CEPPHUS COLUMBA AND CEPPHUS CARBO

Wing length.—The gap in mean wing length of nearly 20 millimeters between the northern populations of *C. grylle* and the larger *C. columba* which occurs in the region of geographic contact is an absolute one, that is, there is no overlap. Within the populations of *C. columba* there is a steady cline of decreasing wing length from eastern Siberia through the islands of Bering Sea to the coast of Alaska and down the coast to Washington (table 17 and fig. 11). The populations of Oregon and California are similar and abruptly and significantly larger than that of the coast of Washington. It is of interest to note that the few specimens available from the west coast of Washington are small, like those from Puget Sound.

TABLE 21

Geographic Variation in Amount of White in Secondary Coverts in *C. grylle*

Population	A	A–O	O	O–B	B	B–C	C	C–D	D	D–E	E
Bay of Fundy and south	..	..	..	..	..	1	3	5	8	10	12
Newfoundland and Nova Scotia	..	..	..	..	..	..	5	1	15	5	7
Gulf of St. Lawrence	..	..	..	..	..	..	6	5	11	10	6
North shore St. Lawrence	1	..	1	..	3	3	5	5	7	2	..
Southern Labrador	..	..	..	..	1	1	8	2	6	1	..
Northern Labrador	..	..	1	..	..	1	6	10	4	2	..
James Bay	11	2	6	3	4	..	..	..	..	..	..
East shore Hudson Bay	20	4	5	1	3	..	..	..	..	..	..
Northwestern Hudson Bay	11	2	6	..	8	..	1	..	..	..	..
Southern Baffinland	3	1	2	5	..	..	..	..	..	..	..
Cumberland Sound	7	..	..	..	1	..	..	..	..	..	..
Ellesmereland	11	..	1	..	10	..	..	..	..	..	..
Etah area	23	..	10	..	1	..	1	..	..	..	..
Disco Bay	..	..	..	..	3	..	2	..	..	..	..
Sukkertoppen	..	..	..	..	8	..	16	3	17	3	5
British Isles	..	..	..	..	..	..	4	5	36	8	10
Norway and western Sweden	..	..	..	..	..	..	3	..	4	..	5
Iceland	..	..	..	..	..	..	1	..	1	5	2
Spitsbergen	5	..	1	..	1	..	..	..	1	..	..
Alaska-Asia	1	3	8	..	9	..	2	..	..	..	..

The guillemots of the outer Aleutian (Atka and Kiska) and Commander islands are small and have been separated as the race *kaiurka*. Presumably, there is a cline of decreasing wing length going out the Aleutian chain, but this remains to be demonstrated. The birds from Unalaska and Akutan are indistinguishable from those of coastal Alaska, and I have seen no material from the central part of the Aleutian chain.

On the Asiatic side the race *snowi* of the Kurile Islands appears, from the few specimens examined, to be approximately the same size as the Siberian population. However, there is a sharp break between *snowi* and *C. carbo* of the Sea of Okhotsk; the latter is the largest form of the genus.

Tarsal length.—Geographic variation in the length of the tarsus (table 18, fig. 11) closely follows that in wing length but is less marked. The single exception is the Oregon population, which, instead of resembling closely the California birds, is intermediate between the latter and those from Washington and British Columbia.

Culmen length.—There is a cline of decreasing bill length from California to Siberia (table 19, fig. 11), the only irregularity being the Washington population, which is smaller-billed than either the British Columbian or the coastal Alaska birds.

As in the other mensural characters discussed, *C. c. kaiurka* has the smallest and *C. carbo* the largest bill of the Pacific forms of *Cepphus.*

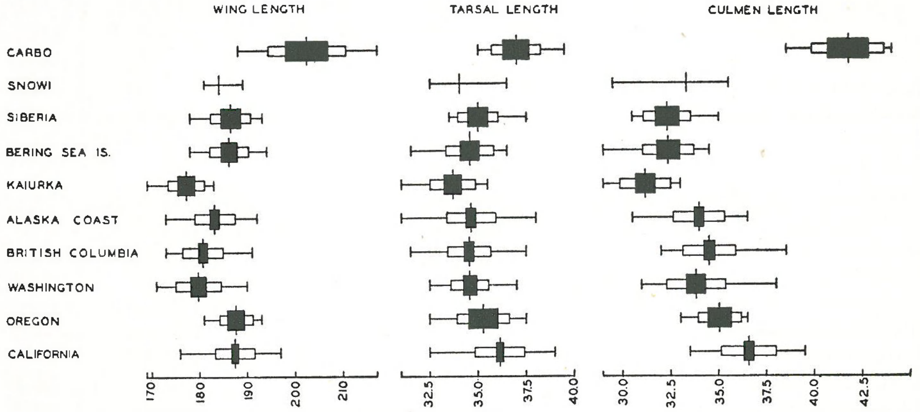


Fig. 11. Geographic variation in wing, tarsal, and culmen lengths in *Cepphus columba* and *Cepphus carbo* expressed as Dice squares.

White on outermost primary.—In the pigeon guillemots, the white spot on the outer primary may be present and well defined, diffuse, or absent. Because separate genetic factors are probably responsible for the presence or absence of the spots and for their extent, these have been analyzed separately. Table 22 shows the geographic variation in the expression of this character. No clines are evident from this table, except one of increasing per cent of dark-primaried birds from the islands in Bering Sea to the Kuriles.

The size of the spot in the various populations is shown in tables 23 and 24. In the former, the relative size of the spot is expressed in the same manner as for the populations of *C. grylle,* and represents the groups of birds with clear-cut spots. On the other hand, table 24 represents the birds with diffuse spots. These birds were compared with a set of standards set up by Austin (1929:3). These categories are represented by the letters "a" to "e," "a" being that of the largest white spot and "e" the smallest. Both these tables show an increase in the size of the white area from south to north.

White in the under wing coverts.—Although the fact is not generally recognized, many specimens of *C. columba* have white areas in the region of the under wing coverts. In examining specimens I set up a series of standards (fig. 4) with which specimens were compared. Table 25 shows the geographic variation in

TABLE 22

GEOGRAPHIC VARIATION IN TYPE OF MARKING ON OUTER PRIMARY IN CEPHUS COLUMBA AND C. CARBO

Population	Mark clear-cut		Mark diffuse		Mark absent		Total
	Number	Per cent	Number	Per cent	Number	Per cent	
C. carbo	..	....	..	....	13	100	13
C. c. snowi	..	....	..	....	4	100	4
C. c. kaiurka	2	10.5	12	63.2	5	26.3	19
Siberia	1	6.7	6	40.0	8	53.3	15
Islands of Bering Sea	6	22.3	20	74.0	1	3.7	27
Alaska Coast	17	21.0	29	35.8	35	43.2	81
British Columbia	8	9.7	19	23.2	55	67.1	82
Washington	6	23.1	8	30.8	12	46.1	26
Oregon	4	36.4	1	9.1	6	54.5	11
California	45	25.0	52	28.9	83	46.1	180

TABLE 23

GEOGRAPHIC VARIATION IN AMOUNT OF WHITE IN OUTERMOST PRIMARY IN THE FORM OF CLEAR-CUT SPOTS IN CEPPHUS COLUMBA EXPRESSED AS PER CENT OF EXPOSED FEATHER

Population	Number	Range	Mean
Islands of Bering Sea	6	20–49	35.3
Alaska Coast	13	20–48	29.0
British Columbia	5	15–25	19.6
California	42	12–33	22.5

TABLE 24

GEOGRAPHIC VARIATION IN AMOUNT OF WHITE IN OUTERMOST PRIMARY IN THE FORM OF WHITE IN DIFFUSE SPOTS IN CEPPHUS COLUMBA

Population	b	c	c-d	d	d-e	e	Total
Siberia	..	3	..	1	..	..	4
Islands of Bering Sea	1	4	3	7	..	2	17
C. c. kaiurka	..	4	1	3	..	4	12
Alaska Coast	..	1	3	8	1	10	23
British Columbia	..	..	..	5	2	10	17
Washington	..	..	..	1	..	6	7
Oregon	..	..	..	..	..	1	1
California	..	..	..	11	2	39	52

this character; and, like the tables showing variation in the white on the outermost primary, it is based on only the adults in the series. The birds from the islands of the Bering Sea and Siberia tend to have more white in the under wing coverts than either the birds from the Kuriles (*C. c. snowi*) or the birds from the west coast of North America. The Commander Island guillemots resemble the birds from the islands of Bering Sea in having on the average a considerable

TABLE 25

Geographic Variation in Amount of White in Under Wing Coverts in Cepphus columba and Cepphus carbo

Population	Much	Moderate to much	Moderate	Little to moderate	Little	Very little to little	Very little	None to very little	None	Total
C. carbo	..	..	..	..	..	..	..	..	13	13
C. c. snowi	..	..	..	..	1	..	..	1	2	4
Siberia	5	..	..	..	3	..	1	..	..	9
Islands of Bering Sea	5	..	5	7	2	1	5	..	..	25
C. c. kaiurka	1	6	4	..	3	..	2	..	1	17
Alaska Coast	2	1	24	2	21	..	23	6	6	85
British Columbia	..	..	5	2	18	..	19	8	14	66
Washington	2	..	2	2	11	..	5	..	5	27
Oregon	..	..	2	1	3	1	2	1	..	10
California	..	..	19	4	49	2	68	6	29	177

amount of white under the wing. Specimens of *C. carbo* all have uniformly dark wings.

Number of rectrices.—All previous discussions of variation in guillemots have emphasized the number of rectrices. It was thought formerly that the individuals of *C. grylle* all had twelve rectrices and all those of *C. columba* and *C. carbo,* fourteen. I have not counted the rectrices of the birds which I have examined both because of lack of time and because accurate counts can be made only on freshly killed birds or on alcoholic specimens. However, Salomonsen's findings (1944) are noteworthy in showing that the gap between *grylle* and *columba* in this character is not absolute.

Correlations between characters.—In both groups of guillemots variations in wing length and tarsal length parallel each other, although the magnitude of variation in the latter is considerably less than in the former. These variations show clinal tendencies, but these tendencies do not appear to be directly correlated with any single external factor. On the other hand, the length of the bill and the amount of white in the wing (both outer primary and wing coverts) both vary clinally in a north-south direction and may, as Salomonsen (1944:73) suggested, be directed at least in part by water temperature.

A discussion of the gaps between *C. carbo, C. columba,* and *C. grylle* and of their specific status is reserved for a later section (p. 194).

URIA

The genus *Uria* is composed of two species, the common murre (*U. aalge*) and the thick-billed murre (*U. lomvia*). Both species occur in the North Atlantic and the North Pacific; and in each area, although there is considerable overlap, *lomvia* has the more northern breeding range. Individuals of both species may be found breeding side by side in colonies on the Pribilof Islands, Kamchatka, eastern North America, Iceland, Bear Island, Novaya Zemlya, and elsewhere. To date, no hybrid between these two species has been found.

The interrupted breeding ranges of the murres as compared with the relatively continuous ones of the guillemots, as well as over-all differences in range and representation in collections, have made it necessary to make a somewhat different geographic breakdown of the birds examined than that employed for the guillemots.

URIA AALGE

The specimens examined were grouped into the following populations. As in the guillemots, intermediate groups too small to treat statistically will be discussed under the subspecies (pp. 207–215).

Eastern North America. The Gulf of St. Lawrence and Canadian and Newfoundland Labradors.

Iceland and western Sweden. Iceland and the adjacent islands and the west coast of Sweden north of Falsterbo.

Iceland. Iceland and the adjacent islands.

Baltic. The islands of Gotland and Stora Karlsø in the Baltic Sea.

Britain. The breeding birds of Heligoland, Ireland, England, and parts of southern Scotland.

Faeroes. Between Iceland and Scotland.

Tromsø. Salomonsen's (1944) series from Tromsø, northern Norway.

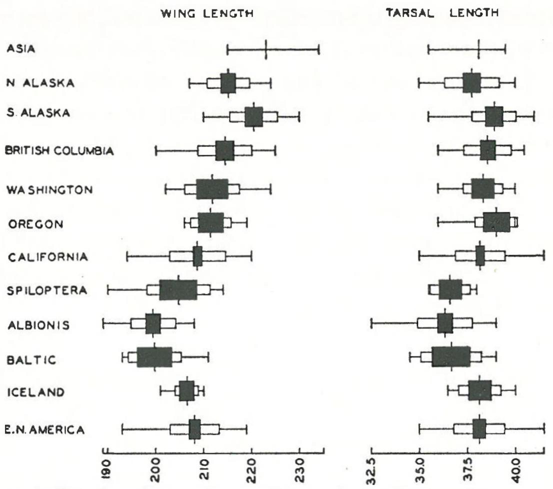


Fig. 12. Geographic variation in wing and tarsal lengths in *Uria aalge* expressed as Dice squares.

TABLE 26

Geographic Variation in Wing Length in Uria aalge

Population	Number	Maximum	Minimum	Mean qnd standard error	Standard deviation	Coefficient of variation
Eastern North America	79	219	193	208.1±0.59	5.20	2.50
Iceland and western Sweden	10	210	201	206.7±0.75	2.37	1.15
Iceland and western Sweden[a]	27	208	192	202.1±0.85	4.42	2.19
Baltic	10	211	193	199.8±1.75	5.54	2.77
Baltic[a]	34	211	192	201.7±0.74	4.32	2.14
Britain	40	208	189	199.4±0.74	4.70	2.36
Faeroes	12	214	190	204.8±1.88	6.55	3.20
Tromsø[a]	4	218	205	211.1	....	....
California	152	220	194	208.8±0.40	4.87	2.33
Oregon	11	219	206	211.5±1.26	4.16	1.97
Washington	13	224	202	211.8±1.57	5.66	2.67
British Columbia	35	225	200	214.5±0.93	5.50	2.56
Southern Alaska	30	230	210	220.5±0.90	4.91	2.34
Northern Alaska	40	224	207	215.1±0.69	4.37	2.03
Asia	5	234	215	223.0	....	....

[a] Data (individual measurements) from Salomonsen (1944).

California

Oregon

Washington

British Columbia

Southern Alaska. Alaska south of the Alaska Peninsula.

Northern Alaska. Alaska north of the Alaska Peninsula plus the islands of Bering Sea (St. Lawrence, St. Matthew, King, and the Diomedes and the Pribilofs).

Asia. The east coast of Asia from East Cape, Siberia, south to Japan.

Wing length.—Geographic variation in wing length is shown in table 26 and figure 12. Of the Atlantic populations, the pale race, *albionis,* from the British

Isles south to Portugal, has on the average the shortest wing. *U. a intermedia* of the Baltic is intermediate between *albionis* and the longer-winged population of *aalge* in western Sweden. From the limited number of specimens available, there appears to be a cline of increasing wing length from the Baltic to western Sweden and southern Norway (*aalge*) and thence to northern Norway, Bear Island, and Novaya Zemlya (*hyperborea*). The southern populations also appear to vary clinally from the small *albionis* to the somewhat longer-winged population of Iceland (*aalge*) and the apparently still longer-winged population (also *aalge*) of eastern North America. The dark Faeroe birds are intermediate in wing length between *albionis* to the south and *hyperborea* to the north.

TABLE 27
GEOGRAPHIC VARIATION IN TARSAL LENGTH IN URIA AALGE

Population	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
Eastern North America..	82	41.5	35.0	38.14±0.15	1.32	3.46
Iceland and western Sweden..............	15	40.0	36.5	38.17±0.29	1.11	2.92
Baltic..................	10	39.0	34.5	36.65±0.49	1.54	4.21
Britain.................	59	39.0	32.5	36.36±0.18	1.42	3.89
Faeroes.................	13	38.0	35.5	36.61±0.28	1.01	2.78
California..............	180	41.5	35.0	38.18±0.10	1.27	3.34
Oregon..................	11	40.0	36.0	39.05±0.34	1.12	2.86
Washington..............	13	40.0	36.0	38.35±0.29	1.04	2.71
British Columbia........	43	40.5	36.0	38.59±0.18	1.21	3.14
Southern Alaska.........	34	41.0	35.5	38.90±0.20	1.14	2.93
Northern Alaska.........	43	40.0	35.0	37.77±0.22	1.42	3.76
Asia....................	6	39.5	35.5	38.12	....	....

NOTE: Salomonsen gives no tarsal measurements.

Among the Pacific populations there is a cline of increasing wing length from California to southern Alaska. The birds from northern Alaska and the islands of Bering Sea are significantly smaller than those from southern Alaska. The five adult common murres available from Asia also seem to represent a shorter-winged population.

Tarsal length.—As was true in the guillemots, the tarsal lengths follow generally the trends of variation in wing length, but the differences are less pronounced (see table 27 and fig. 12). Of the Atlantic populations, *albionis* has the shortest tarsi and *aalge* the longest. (Tarsal measurements of *hyperborea* are not available.)

The cline of increasing wing length from California to southern Alaska is paralleled by a similar cline in tarsal length, the small sample of Oregon birds being the only one which is out of line. The birds from northern Alaska and the islands of Bering Sea have shorter tarsi than those from southern Alaska, and the limited material from Asia shows an increase in size over the northern Alaska birds.

Length of culmen.—Owing to the necessity of segregating the sexes in the analyses of bill-measurement data, the samples of the various populations are rather small and statistical treatment is possible in only a few instances. Of the

Atlantic populations, that from eastern North America has the shortest bills (table 28 and fig. 13), and the Faeroe race, *spiloptera,* and the Baltic race, *intermedia,* the longest. *U. a. hyperborea,* a long-winged form, has a short, stout bill; and the British murres, which are short-winged, have relatively long bills. Thus it would seem that the clines for wing length and culmen length run in opposite directions in a north-south axis on the coast of Europe and also in an east-west axis from eastern North America to southern Scandinavia.

TABLE 28

GEOGRAPHIC VARIATION IN CULMEN LENGTH IN URIA AALGE

Population	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
			Males			
Eastern North America	36	48.0	41.5	44.58±0.29	1.74	3.90
Iceland	5	49.5	45.0	47.20 } 46.70	....	....
Iceland[a]	5	49.0	44.0	46.20	....	....
Baltic	4	48.0	46.0	46.88	....	....
Baltic[a]	19	51.0	45.0	48.77±0.33	1.44	2.95
Britain	22	51.0	42.5	47.43±0.48	2.25	4.72
Faeroes	5	52.5	44.0	47.20	....	....
Tromsø[a]	3	48.0	46.0	47.00	....	....
California	117	53.5	43.0	49.23±0.19	2.05	4.16
Oregon	7	52.5	45.5	48.89	....	....
Washington	7	53.0	46.5	50.57	....	....
British Columbia	15	51.5	45.5	49.00±0.48	1.87	3.82
Southern Alaska	15	53.0	45.5	48.80±0.56	2.15	4.41
Northern Alaska	24	49.0	43.5	46.52±0.33	1.60	3.44
Asia	1	45.0	45.0	45.00	....	....
			Females			
Eastern North America	39	51.5	39.0	43.21±0.38	2.40	5.55
Iceland	4	46.0	43.0	44.13	....	....
Iceland[a]	2	45.0	44.0	44.50	....	....
Baltic	5	53.0	45.0	48.90	....	....
Baltic[a]	10	48.0	43.0	45.60±0.54	1.72	3.77
Britain	9	50.0	43.0	46.88	....	....
Faeroes	5	50.0	47.0	48.00	....	....
Tromsø[a]	3	47.0	42.0	44.00	....	....
California	62	52.0	41.5	47.13±0.29	2.25	4.77
Oregon	9	49.5	44.0	47.33	....	....
Washington	5	49.0	47.0	48.70	....	....
British Columbia	24	51.5	43.5	47.02±0.42	2.04	4.36
Southern Alaska	7	52.0	44.5	47.26	....	....
Northern Alaska	15	48.0	42.0	44.97±0.34	1.33	2.95
Asia	2	47.0	43.5	45.25	....	....

[a] Data (individual measurements) from Salomonsen (1944).

If the inconclusive data from Washington and Oregon are eliminated, there is a cline of decreasing bill length from California to northern Alaska. There is, however, very little difference between the birds from California and southern Alaska, the most pronounced change coming between the two Alaska populations.

Bill depth.—Table 29 shows that Salomonsen's measurements of bill depth are considerably larger than mine, owing no doubt to a different method of measuring. Accordingly, considerable leeway must be made in their use. The Atlantic populations of the subspecies *aalge* and *intermedia* are remarkably uniform and of intermediate depth. Birds of the forms *spiloptera* and *albionis* have the shallowest bills, and individuals of the race *hyperborea* have very deep ones. Of the Pacific populations, the birds from northern Alaska and California have less deep bills than those of birds from southern Alaska and British Columbia.

Color.—The color of the back and wings and the head and neck is subject to considerable geographic variation, but unfortunately an appallingly large number of variables enters into an analysis of these color differences. In the first place, adult birds of the southern populations may acquire their breeding plumage in November or December, whereas this is not achieved by second-year birds until early spring and by first-year birds until late spring. Thus in a given population there are three groups of birds which are not clearly separable, the individuals of which may differ in the breeding season (May to August) as much as six months in the age of their nuptial plumage on the head and neck. This is an important consideration, because as the season progresses there is considerable fading. The effects of weathering are probably hastened by the chemical action of guano with which the birds on the breeding colonies are frequently splashed. Added to this is the fact that the birds in the north acquire breeding plumage later than those in the south.

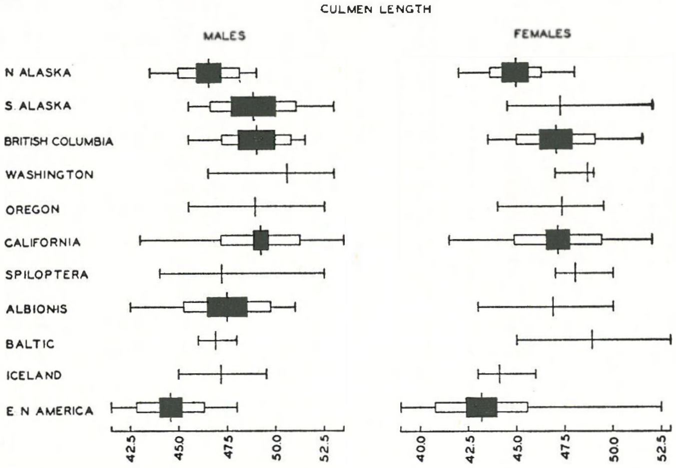


Fig. 13. Geographic variation in culmen length in *Uria aalge* expressed as Dice squares.

However, in spite of these difficulties, several differences are conspicuous. Individuals of the British race, *albionis,* are the palest on the head and back whereas the Faeroe and northern birds (*spiloptera* and *hyperborea*) are the darkest, and individuals of typical *aalge* are nearly as dark. The Baltic birds are intermediate between *aalge* and *albionis* in color, as are the Pacific birds. The latter show a clinal tendency in color, the northern birds being the palest and the California

TABLE 29
Geographic Variation in Bill Depth in Uria aalge

Population	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
Males						
Eastern North America	35	15.2	12.6	13.78±0.10	0.61	4.43
Iceland and western Sweden[a]	21	16.0	13.5	14.87±0.14	0.65	4.37
Iceland	4	14.9	12.9	13.70	....	....
Baltic	5	14.7	12.9	13.70	....	....
Baltic[a]	21	16.0	14.0	15.12±0.15	0.67	4.43
Britain	16	14.2	11.8	13.08±0.14	0.54	4.03
Faeroes	4	13.3	12.4	13.03	....	....
Tromsø[a]	3	18.0	17.5	17.83	....	....
California	65	15.6	12.5	13.96±0.08	0.64	4.58
Oregon	3	15.2	13.5	14.23	....	....
Washington	7	15.1	12.8	13.94	....	....
British Columbia	10	15.5	13.9	14.81±0.16	0.52	3.51
Southern Alaska	17	16.2	13.5	14.92±0.18	0.76	5.09
Northern Alaska	19	14.9	12.6	13.93±0.15	0.67	4.81
Asia	..	....	....	....	....	....
Females						
Eastern North America	38	14.5	12.6	13.33±0.08	0.51	3.84
Iceland and western Sweden[a]	7	15.0	14.0	14.36	....	....
Iceland	2	14.0	12.5	13.25	....	....
Baltic	4	14.8	13.8	14.45	....	....
Baltic[a]	15	16.3	14.0	15.27±0.14	0.56	3.67
Britain	10	13.7	12.1	12.97±0.15	0.46	3.55
Faeroes	2	13.1	12.6	12.85	....	....
Tromsø[a]	5	16.0	15.0	15.80	....	....
California	56	15.2	12.5	13.79±0.08	0.57	4.13
Oregon	8	14.8	12.4	13.80	....	....
Washington	4	14.2	13.7	13.93	....	....
British Columbia	20	15.9	12.6	14.19±0.20	0.88	6.20
Southern Alaska	7	14.4	13.3	13.79	....	....
Northern Alaska	12	15.0	12.4	13.48±0.22	0.77	5.71
Asia	4	14.2	12.8	13.45	....	....

[a] Data (individual measurements) from Salomonsen (1944).

birds the darkest. These color differences include not only the color of the back and wings but also that of the head and neck.

Spotting on under wing coverts.—Table 30 shows the geographic variation in the amount of spotting on the under wing coverts. Salomonsen (1932) gives the heavy spotting of the middle and lesser coverts as a character of the races *spiloptera* and *hyperborea,* and the predominence of spotting in these forms is well shown in the table. The birds of the other populations have predominently white under wing coverts, although the Irish and southern Norwegian birds show intergradation between the two principal types.

Heavy spotting does not occur in birds of the Pacific populations, but in the southern groups (British Columbia to California) an occasional bird has entirely black or sooty gray under wing coverts. This is associated with a general melanism in one specimen (CAS 18072) and a partial melanism in at least two others (MVZ 82123 and CAS 16078) in which many of the flank feathers are entirely dark.

Correlations between characters.—As was true in the guillemots, tarsal length in the common murres varies with wing length, but shows less variation from one population to the next. In both the Atlantic and Pacific series of populations wing and tarsal length tend to increase from south to north as bill length tends to decrease. Bill depth and color differences show no consistent geographic trends. As discussed elsewhere (p. 184), the percentage of "ringed" murres in the Atlantic populations increases from south to north.

TABLE 30

GEOGRAPHIC VARIATION IN SPOTTING OF UNDER WING COVERTS IN URIA AALGE

Population	White	A few small spots or shaft streaks	A few large or medium-size spots	Heavily spotted	All dark
Britain (albionis)	31	7	2	..	..
Britain (albionis)[a]	20	..	2	..	..
Ireland	11	4	6	3	..
Northern Scotland	2	3	1	..	..
Faeroes	..	2	1	9	....
Faeroes[a]	1	1	8	29	..
aalge (England and Europe)	8	5	..	..	..
Southern Norway[a]	16	..	4	4	..
Iceland[a]	14	..	4	..	..
Eastern North America	59	28	4	..	..
intermedia	3	7	..	..	..
intermedia[a]	5	..	1	..	..
hyperborea	..	..	2	1	..
hyperborea[a]	1	..	1	8	..
Asia	6	..	..	..	..
Northern Alaska	44	..	1	..	..
Southern Alaska	35	1	..	..	..
British Columbia	19	5	5	..	1
Oregon	3	4	..	..	1
California	75	..	62	..	2

[a] Data from Salomonsen (1932).

URIA LOMVIA

The following is a list of populations into which the specimens of thick-billed murres examined were grouped:

St. Lawrence. The Gulf of St. Lawrence from the Straits of Belle Isle south.

Baffin Bay. The west coast of Greenland; the east coasts of Ellesmere, Baffin, and Devon islands; Hudson Strait; and Hudson and Ungava bays.

Iceland. Iceland and the adjacent islands.

Greenland Sea. Spitsbergen, Bear Island, and the east coast of Greenland.

Wrangel Island. Wrangel and Herald islands and the adjacent parts of the Arctic Ocean.

Bering Strait. The Chuckchee Peninsula east of Kolyuchin Bay; the Alaska coast from 60° N lat. to Barrow; and St. Lawrence, St. Matthew, King, and the Diomede islands.

Kamchatka. The Kamchatka Peninsula and the Commander and outer Aleutian (Attu and Agattu) islands.

Pribilof Islands. The Pribilofs and Bogoslof Island in the inner Aleutians.

Wing length.—The St. Lawrence population (see table 31 and fig. 14) is the longest-winged in the Atlantic, whereas the Baffin Bay population is the shortest-winged group. On the west side of the Atlantic the birds become smaller northward, whereas the opposite appears to be true from Iceland to Spitsbergen. In the Pacific the Pribilof population is significantly smaller than the Bering Sea population, and the birds from Wrangel Island are smaller yet. Portenko (1944:226) proposes the subspecific name *heckeri* for the birds of Wrangel Island, and gives the following wing measurements for his series: 27 males, 213–234 (mean 222); 19 females, 204–240 (221). These means are close to that of the birds which I examined.

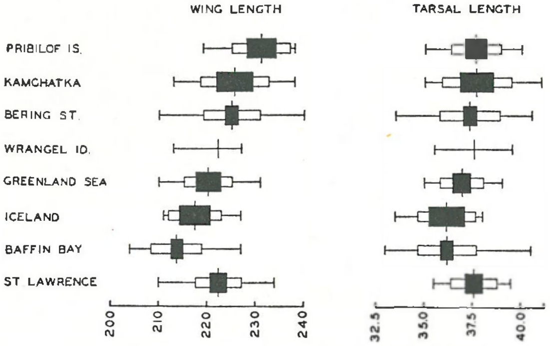


Fig. 14. Geographic variation in wing and tarsal lengths in *Uria lomvia* expressed as Dice squares.

TABLE 31

GEOGRAPHIC VARIATION IN WING LENGTH IN URIA LOMVIA

Population	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
St. Lawrence	29	234	210	222.4±0.9	4.85	2.18
Baffin Bay	81	227	204	213.8±0.6	5.25	2.46
Iceland	11	227	211	217.5±1.6	5.47	2.51
Greenland Sea	16	231	210	220.2±1.3	5.00	2.27
Wrangel Island	6	227	213	222.3	....	....
Bering Strait	71	240	210	225.5±0.7	5.90	2.62
Kamchatka	15	238	213	225.6±1.9	7.18	3.18
Pribilof Islands	16	238	219	231.1±1.5	6.07	2.63

Tarsal length.—Geographic variation in tarsal length (see table 32 and fig. 14) of the Atlantic groups generally follows that for wing length but is of smaller magnitude. No significant differences in tarsal length for the Pacific populations are evident from my data.

Culmen length.—The males of the Baffin Bay and St. Lawrence populations (table 33 and fig. 15) differ significantly in culmen length, the latter having the longer bill. The difference in the bills of the females, however, may not be significant. The Greenland Sea and Iceland birds are closer to the St. Lawrence population than to the Baffin Bay one. In the Pacific populations bill length decreases from south to north, and this change is evident in the samples of both the males and the females.

TABLE 32

GEOGRAPHIC VARIATION IN TARSAL LENGTH IN URIA LOMVIA

Population	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
St. Lawrence	31	39.5	35.5	37.61±0.22	1.20	3.19
Baffin Bay	82	40.5	33.0	36.20±0.17	1.50	4.13
Iceland	11	38.0	33.5	36.14±0.45	1.49	4.12
Greenland Sea	21	39.0	35.0	36.93±0.24	1.11	3.01
Wrangel Island	6	39.5	35.5	37.53	....	....
Bering Strait	88	40.5	33.5	37.29±0.17	1.56	4.18
Kamchatka	18	41.0	35.0	37.64±0.42	1.79	4.75
Pribilof Islands	21	40.0	35.0	37.62±0.28	1.26	3.35

TABLE 33

GEOGRAPHIC VARIATION IN CULMEN LENGTH IN URIA LOMVIA

Population	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
Males						
St. Lawrence	10	40.0	36.5	38.50±0.38	1.22	3.16
Baffin Bay	41	41.0	30.5	35.67±0.31	1.97	5.52
Iceland	7	40.5	36.5	38.53	....	....
Greenland Sea	5	41.0	37.0	38.56	....	....
Wrangel Island	1	....	....	37.10	....	....
Bering Strait	34	46.0	35.0	40.06±0.42	2.46	6.13
Kamchatka	6	46.5	41.5	43.02	....	....
Pribilof Islands	8	47.0	43.5	45.26	....	....
Females						
St. Lawrence	17	41.5	33.0	36.59±0.48	2.00	5.45
Baffin Bay	31	39.0	33.0	35.32±0.49	2.74	7.75
Iceland	4	36.5	36.0	36.35	....	....
Greenland Sea	11	39.0	33.5	36.68±0.55	1.83	4.98
Wrangel Island	4	39.5	37.0	38.48	....	....
Bering Strait	39	44.5	35.0	38.68±0.37	2.32	6.00
Kamchatka	7	48.0	39.5	42.24	....	....
Pribilof Islands	8	44.5	38.0	41.33	....	....

Bill depth.—The St. Lawrence birds (table 34 and fig. 15) have, on the average, the deepest bills of the Atlantic populations. The bills of the Iceland birds average slightly less deep than those of the more northern birds, but the samples are small and the overlap is large. In the Pacific populations bill depth varies too little for trends to be ascertained.

Color.—As explained in connection with *U. aalge,* color differences are difficult to evaluate in the murres; furthermore, since the birds examined were never brought together in one place, few comparisons could be made. It seems, however, that the Pacific birds are somewhat lighter on the head and throat, and the color of the latter is a warmer brown than that of the Atlantic birds. Portenko (1937:226 and 1944:226) has described three races from the Arctic coast and islands of Siberia. Two of these, from Wrangel and the New Siberian islands are said to be pale; and the other, from Franz Josef Land, is said to be dark. I have not seen enough material to verify these color differences.

TABLE 34
Geographic Variation in Bill Depth in Uria lombia

Population	Number	Maximum	Minimum	Mean and standard error	Standard deviation	Coefficient of variation
			Males			
St. Lawrence	9	15.4	13.8	14.88	....	....
Baffin Bay	40	15.6	12.7	13.82±0.11	0.67	4.85
Iceland	6	14.3	13.0	13.77	....	....
Greenland Sea	4	14.8	13.1	14.45	....	....
Wrangel Island	1	....	....	14.0	....	....
Bering Strait	31	15.8	13.6	14.68±0.10	0.57	3.88
Kamchatka	5	16.1	13.8	15.06	....	....
Pribilof Islands	8	15.7	13.9	14.70	....	....
			Females			
St. Lawrence	18	15.8	12.7	14.13±0.18	0.75	5.31
Baffin Bay	30	15.6	12.0	13.48±0.15	0.83	6.14
Iceland	3	13.8	12.5	13.33	....	....
Greenland Sea	6	14.5	12.3	13.67	....	....
Wrangel Island	4	15.4	13.7	14.48	....	....
Bering Strait	36	15.6	12.9	14.27±0.12	0.70	4.91
Kamchatka	5	14.9	13.1	14.10	....	....
Pribilof Islands	10	15.3	13.7	14.18±0.19	0.59	4.16

Portenko also claims (1944:225–226) that the Atlantic thick-billed murres have a greater amount of white on the tips of the secondaries than the Pacific forms. Examination of thirty adults in the Museum of Vertebrate Zoölogy indicates that the opposite is true. In this series, measurements of the width of the tip of the second or third most proximal white-tipped secondary are as follows: twenty-four *Uria lomvia arra,* 3.4 to 12.5 mm. (mean, 8.3); six *U. l. lomvia,* 2.5 to 7.6 (5.9). Evidently this is not a valid character for differentiating these two races.

Correlations between characters.—Length of wing and tarsus decreases from south to north in the Pacific and in the western Atlantic populations. The opposite is true for the eastern Atlantic groups. Bill length and depth appear to follow these trends in both the Atlantic and Pacific populations. The evidence for this, however, is not strong, since sexual dimorphism in these characters prevents combining in the calculations the measurements for the two sexes. This of necessity reduces the size of the samples.

Portenko's measurements (1944:227) indicate a cline of increasing wing length across the Arctic Ocean from Spitsbergen to Bering Strait. His data on bill measurements and color differences show no geographic trends.

VARIANTS

Sporadic or polymorphic variants occur more commonly in the alcids than in most other groups of birds; such variants have been termed "mutants" by Salomonsen (1944). This term may imply single gene differences which in these sea birds would be extremely difficult to prove. Nevertheless, most of these rather striking variants may easily have their origins in such simple genetic differences.

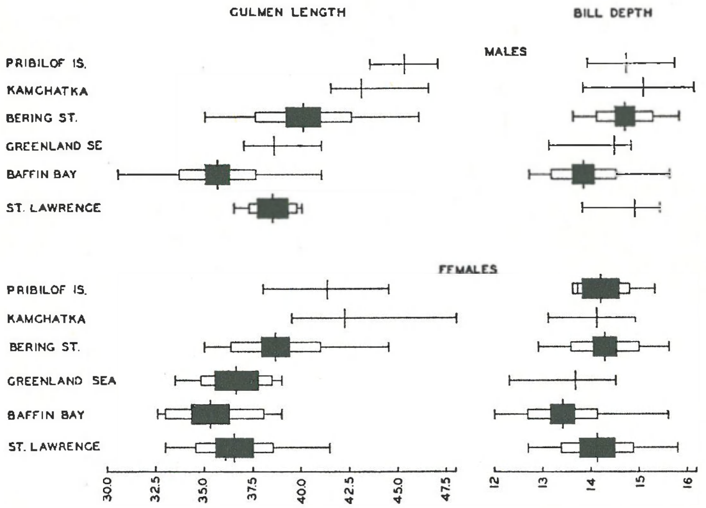


Fig. 15. Geographic variation in culmen length and bill depth in *Uria lomvia* expressed as Dice squares.

Number of rectrices.—There is some variation in the number of rectrices in the guillemots. Individuals of *C. columba* regularly have 14, whereas those of *C. grylle* normally have 12. Salomonsen (1944) has found that some specimens of *C. grylle* have 13 or 14 rectrices.

Melanism.—In a variety of *C. grylle* known as *C. motzfeldi* the entire wing is black. There is considerable variation, however, some birds having the speculum and under wing coverts somewhat paler than the other feathers. There is further variation in the winter plumage, some having the normal black and white body plumage, some being entirely black, and some having particolored feathers below. This rather wide variation indicates that more than one genetic factor is involved. Salomonsen, who has reviewed this form fully (1941), records 17 specimens from Greenland between Julianehaab and Upernavik and one from Kristiansund, Norway. There are doubtful records from Iceland and Baffinland.

Salomonsen (*ibid.*) figures a juvenal bird from the Faeroes which is intermediate between the *"motzfeldi"* and the normal color types.

Among the pigeon guillemots the subspecies *snowi* of the Kurile Islands shows a progressive decrease in the amount of white in the speculum from north to south, the cline ending in birds of the *"motzfeldi"* type. *Cepphus carbo* is likewise dark-winged.

The short-winged population of pigeon guillemots inhabiting the coasts of Washington and British Columbia is remarkable in the amount of variation in color in the juvenile specimens. Most are as light in color as those from other parts of the range of the species, but two (MVZ 101529 and Wash. State Mus. 17314) appear dark all over. In the former specimen, a male taken on August 6, 1928, at Comox, British Columbia, the speculum feathers and those of the under parts are light only at their bases. The latter, a male taken on August 29, 1933, at Everett, Snohomish County, Washington, is similar except that a small amount of white shows in the speculum. Since all young guillemots have more or less dark tipping on the feathers of the speculum and under parts, there is no basis for considering these birds comparable to the *"motzfeldi"* variant.

Melanism also occurs in the common murre. There is an all-black California murre (number 18072) in the collection of the California Academy of Sciences. It was taken on May 30, 1911, on the Farallones and has been figured by Loomis (1918:116, pl. 16). Clarke (1913:345) records a sight record of an all-black murre in Yorkshire, England, July 9, 1912.

Occasional specimens of the California murre (such as MVZ 82123 from Comox, British Columbia) show partial melanism, involving the under wing coverts and flanks. *U. a. spiloptera* of the Faeroes and *U. a. hyperborea* of northern Norway represent populations in which a partial melanism of this type has become characteristic.

Although I know of no melanistic thick-billed murres, there is considerable variation in the amount of dark tipping on the throats of the first-year birds of this species.

Albinism.—Deane (1876:23) records an albino black guillemot and an albino common murre, and I have examined a completely albino common murre in the collection of John R. Arnold. This bird was taken August 29, 1949, at Dillon Beach, Marin County, California, and is a bird of the year (Arnold, 1950:141).

Partial albinism is known to occur in both species of murres. The American Museum of Natural History possesses a partial albino common murre (number 748006) in which the crown is white and melanin is absent from two small areas on the maxilla. Newton (1877:2) records a specimen of the same species with white claws and a yellow bill and feet. This yellow pigment is usually masked by melanin, but earlier in the evolutionary history of the group it may have been the normal bill color.

In the American Museum there are also two partial albino thick-billed murres (numbers 748007 and 747966). The back of the first is approximately 85 per cent white, resembling that of a molting guillemot, but the wings are normal except for a few small white feathers near the leading edge. In the second specimen, the lower back has approximately 5 per cent; and the head, neck, and upper back, 35 to 40 per cent white feathers. There are also three white rectrices, and the bill and feet are without melanin.

I have examined five albinistic thick-billed murres (UMMZ 68403; AMNH 747971, 797970, 747964, and 3946). In this type of albinism (see pl. 1) the normal pattern is retained, but the dark color of the upper parts is replaced by pale, buffy tan, light gray, or a darker grayish brown. A similar type of albinism is shown by a dovekie, *Plautus alle,* (number 55758) in the University of Michgan collection (see pl. 1).

It may be significant that albinism is of more frequent occurrence in the more boreal species of murre (*U. lomvia*) than in *U. aalge.* At least in heat conservation, albinos would have a selective advantage in the far north (see p. 188). The apparent lack of melanistic specimens of *U. lomvia* may also be significant in this connection.

The "ringed" or "bridled" murres.—The most celebrated of the variants or mutants is the so-called "ringed" or "bridled" murre, a form of the common murre in which there is a narrow white line extending around the eye and for a short distance backward and downward from the eye. This mutant has been found in all the Atlantic races of the common murre but not in the Pacific populations. Southern (1939) and Southern and Reeve (1942) have worked out the geographic variation in this character and have found that there is a cline of increasing occurrence of this mutant from south to north (0.1 per cent in Brittany to 70 per cent in southern Iceland and 50 per cent in northern Norway and Bear Island). It is thought that this is a single factor character. Whether it is spreading through the populations or whether the cline of its abundance results from a balance between a slight selective advantage and some climatic factor has yet to be determined. This merits further study.

THE FOSSIL MURRES AND GUILLEMOTS

Birds in general are not well represented in the fossil record, and murres and guillemots are no exception. Three fossil species of murres have been described, one each of Miocene, Pliocene, and Pleistocene age.

Marsh (1870:213–214) described *Catarractes* (=*Uria*) *antiquus* from the Tertiary deposits of Edgecombe County, North Carolina. Shufeldt (1915:63) figures the type, a nearly complete humerus, and refers it to the Miocene without stating any reason for so doing. Wetmore (*in litt.*) states that if Marsh's supposition of Tertiary origin for the bone is correct, it is reasonable to assume that the specimen came from the St. Mary's beds (Miocene) which are said to underlie all Edgecombe County. The type and only known specimen measures 96.2 mm. in length, and is thus somewhat larger than the modern species (39 humeri of *Uria aalge* from California measure 84.0 to 91.5 mm. [87.53±0.29], and 9 humeri of *U. l. arra* from Alaska, 87.0 to 94.0 [89.4]). Marsh and Shufeldt both compare *U. antiqua* with *U. lomvia,* but no mention is made of *U. aalge* in either paper or in later discussions of *Uria affinis.*

Catarractes (=*Uria*) *affinis* was described by Marsh (1872:259–260) from the Pleistocene near Bangor, Maine. The type, a complete humerus, is, like *U. antiqua,* somewhat larger (95.0 mm. in length) than the living murres. Both specimens must be carefully compared with a large series of both modern species before they can be used in working out the past history of the genus.

Lambrecht (1933:563) lists two Pliocene occurrences of the genus *Uria* in Italy: *Uria ausonia* Portis, described from the distal fragment of a humerus, and *Uria* sp. Regalia, a fragmentary coracoid. The former is said to resemble the common murre.

Two Pleistocene occurrences of the common murre are recorded for California, the first from Playa Del Rey, Los Angeles County (Howard, 1936:212), and the second from Mussel Rock, San Mateo County (Miller and Peabody, 1941:78).

Although there are no known fossil members of the genus *Cepphus,* a related form, *Miocepphus mcclungi,* has been described from the Calvert Miocene of Maryland by Wetmore (1940:35). *Miocepphus* was nearly the size of the modern guillemots and, according to the describer, shows affinities with both *Cepphus* and *Brachyramphus.*

WATER TEMPERATURE AND DISTRIBUTION

There is a good correlation between the surface temperature of the ocean and the breeding distribution of the murres and guillemots. Figure 16, compiled from Sverdrup *et al.* (1942:chart 3) and Mohn (1887:pl. 27), shows isotherms for the surface of the ocean during August. Comparisons of this with the breeding distribution of the various races of these birds shows that the two well-marked high-arctic races of guillemots, *C. g. ultimus* and *C. g. mandtii,* occur in regions where the surface temperature of the water in August is below approximately 2° C. whereas the other guillemots are found in regions of water temperature ranging from 3 (mostly 5) to 16° C. The common murres seem to have a similar range of tolerance of from 5 to 15° C., although one race, *albionis,* has a range of from 13 to 19°. The main breeding range of the thick-billed murre lies in regions where the water temperature is below 10° C., although a few individuals nest south to the 15° isotherm in the Gulf of St. Lawrence and the 12° isotherm at Kodiak Island, Alaska.

In general the breaks in characters between the races of murres and guillemots are few and not sharp. This is probably a reflection of the fact that nowhere in the Northern Hemisphere is there a sudden change in the character of the ocean comparable to the one that occurs at the Antarctic Convergence (Murphy, 1936: 68–69). The sharpest break between contiguous subspecies is probably that between *C. g. arcticus* and *C. g. ultimus* in northern Labrador, and this does not seem correlated with any sharp gradient in climatic factors. Insular forms such as *C. g. islandicus* and otherwise isolated forms such as *C. g. grylle* and *U. a. intermedia* of the Baltic Sea should not enter into this general picture.

Although it is evident that the ranges of the species and subspecies are closely correlated with water temperature, paradoxically this correlation does not appear directly connected with the types of changes seen in most of the characters studied. Table 35 shows clinal changes in these characters. It will be noted that only one character—bill length—varies in the same direction in all groups; and two other characters, both expressions of the amount of white in the wings of guillemots, vary consistently from south to north. These characters and probably some inherent psychological and physiological responses of the birds seem directly connected

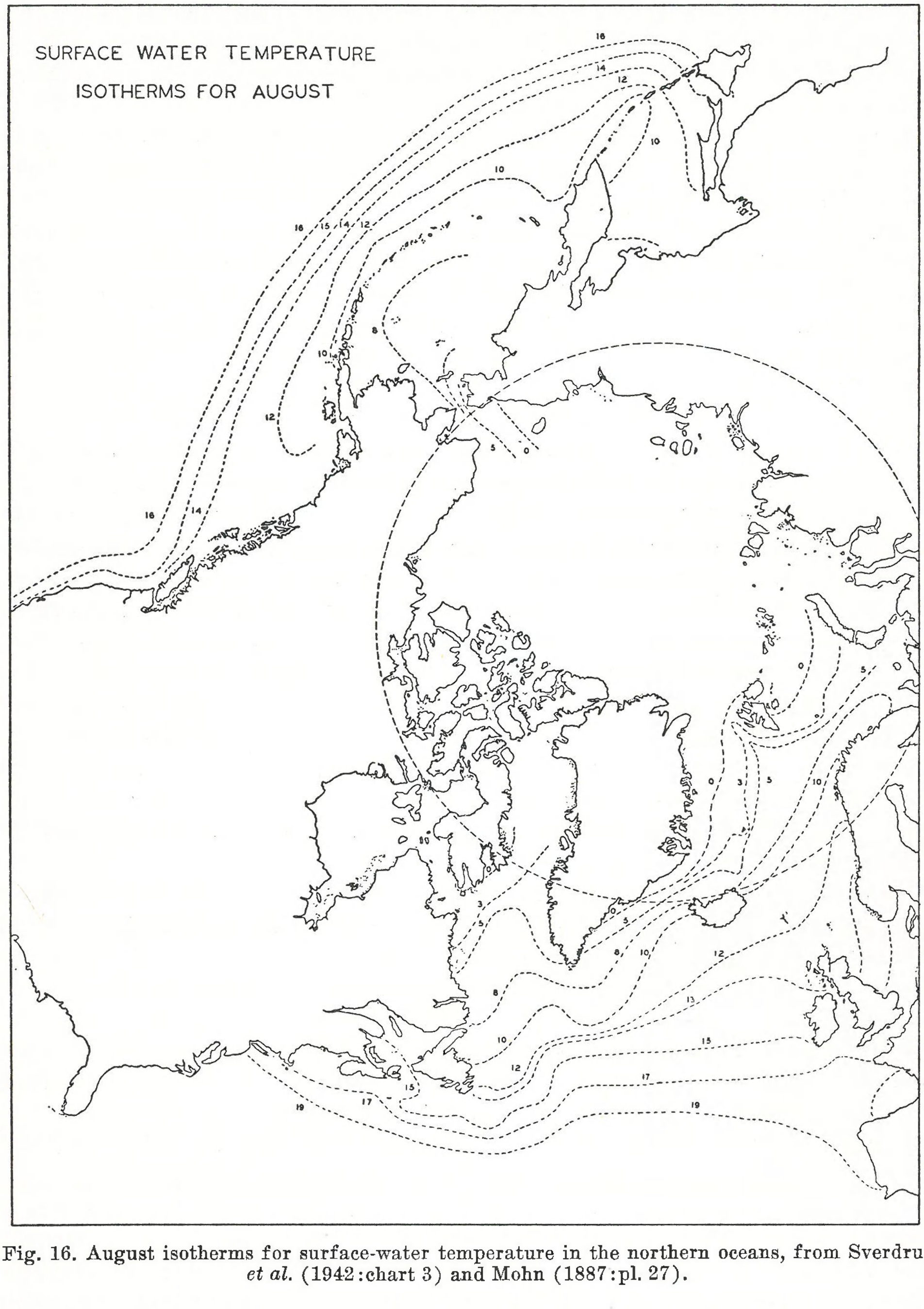


Fig. 16. August isotherms for surface-water temperature in the northern oceans, from Sverdrup *et al.* (1942:chart 3) and Mohn (1887:pl. 27).

with water temperature. Such relationship as may exist between water temperature and the remaining characters must be indirect and complex.

I think that the birds of a given population or race are hereditarily adapted to and limited to a range of water temperature in the breeding season. The mechanism by which this works is not known and might involve the birds' physiology or psychology or both. Salomonsen (1944:69) claims that the spring molt and the breeding season are delayed by low water temperature. This, of course, remains to be proved; but if it is so, birds which normally breed where the water temperature is 15° C. might not come into breeding condition where the water temperature did not rise above 5° C. Thus the limiting of populations to regions with certain ranges of water temperatures may act along with geographic isolation in permitting nonadaptive characters to become established. Some of the characters which do not vary directly with temperature are discussed below.

TABLE 35

CLINAL CHANGES IN CHARACTERS FROM SOUTH TO NORTH

Character	Form	East side Atlantic	West side Atlantic	East side Pacific
Wing length	*Cepphus grylle, C. columba*	Irregular	Irregular	Increase[a]
	Uria aalge	Increase	....	Increase
	U. lomvia	Increase	Decrease	Decrease
Culmen length	*C. grylle, C. columba*	Decrease	Decrease?	Decrease
	U. aalge	Decrease	....	Decrease[a]
	U. lomvia	?	Decrease	Decrease
Bill depth	*U. aalge*	Increase?	....	Irregular
	U. lomvia	Increase?	Decrease	Inconclusive
White in outer primary	*C. grylle, C. columba*	Increase	Increase	Increase
White in secondary coverts	*C. grylle*	Increase	Increase	
White in under wing coverts	*C. columba*	....	....	Increase
Spots on under wing coverts	*U. aalge*	Increase	....	Decrease
Black color	*U. aalge*	Darker	....	Paler

[a] From Washington north only.

The living members of the auk family fall into four major size groups: the large razor-bill and the murres; the medium-sized guillemots and puffins; the small dovekie, murrelets, and most auklets; and the very small whiskered and least auklets. All pursue their prey in a similar manner, and the primary size categories seem to be based on adaptations to preying on organisms of different sizes. Further specializations for obtaining different types of prey such as benthic versus nektonic forms are secondary and are probably not so closely related to body size. In the murres and guillemots wing and tarsal lengths both vary in the same direction from one population to the next, and are hence both indicators of body size. There is no indication of correlation between body size and water temperature, nor do the data on food habits show any constant regional differences. Most individuals of the pigeon guillemot (*C. columba*) inhabit a windward coast, almost continually pounded by heavy seas. The greater strength indicated by the greater size of members of this species may be advantageous in combating the force of the waves breaking around the nesting areas. This may also be reflected in the more pelagic habits of the pigeon guillemots of the California coast and by the fact that the populations inhabiting the quieter waters of Puget Sound and the Gulf of Georgia are smaller in size. The significance of the large size of the spectacled guillemot is not apparent, but less is known concerning the habits and ecology of this guillemot than any other murre or guillemot.

The common murres follow Bergmann's rule in that individuals of the northern populations are larger than those of the southern ones. They do not, however, have proportionally longer wings, although the first-year murres of the Alaska populations appear to migrate farther than the birds of the Atlantic and the more southern parts of the Pacific range of the species.

Within the limits of the other species, *Uria lomvia* and *Cepphus grylle,* variations in size are so irregular that the adaptive significance of size differences is obscured. The large size of the Baltic guillemot (*C. g. grylle*) has been attributed by Salomonsen (1944:69) to the low temperature of the Baltic Sea in spring. There is not, however, a general correlation between size and water temperature elsewhere within the range of the species.

The length of the bill in both murres and guillemots conforms in general to Allen's rule, since clines in decreasing bill length from south to north are apparent in all the species for which sufficient material is available. Bill depth, on the other hand, varies irregularly, both in itself and in proportion to bill length.

In the populations of guillemots there is an increase northward in the amount of white in the primaries and in the secondary coverts (the speculum feathers), and in the pigeon guillemot in the amount of white in the under wing coverts. The two high-arctic races, *C. g. mandtii* and *C. g. ultimus,* also have more white on the upper parts of the winter plumage. Salomonsen (1944:72) points out the value of white plumage in conserving heat. According to him, the pigment of the black feathers is replaced by air in the white ones, making the latter better insulators, and black feathers radiate heat more rapidly than white ones. He might have added that black feathers absorb heat more rapidly from the body than white ones. All these factors give white feathers a selective value over black ones in the far north, and are probably the factors responsible for the increased amount of white in the northern forms. It is possible that the white may also have some camouflage value; but since the birds spend much time on the water, this is doubtful.

The other high-arctic alcids, the thick-billed murre, *Uria lomvia,* and the dovekie, *Plautus alle,* have a partial prenuptial molt involving only the head and neck; but it seems significant that the under parts, through which the most heat is potentially lost by contact with water, are white. In fact, the reduction of heat loss may be the most important factor favoring the selection of white under parts which are frequently found in boreal water birds.

The color of the murres does not vary consistently with changes of temperature, and it is difficult to see any adaptational significance in it.

POPULATION SIZE

The maximum population size attainable by an alcid species is determined primarily by the environment either through limitation of the food supply or nesting sites, and these are both determined by the inherent behavior patterns of the species. Throughout most of their ranges the guillemots feed in shallow water near shore and nest in scattered groups along rocky coasts, the size of their breeding populations being determined by the number of nesting sites available. Thus, the factor limiting the distribution of guillemots is essentially linear. Murres, on the other hand, nest in enormous numbers on open rocks and ledges. Their numbers are not limited by the availability of nesting sites, for where suitable nesting places occur at all they are usually abundant. The food supply is probably the limiting factor for the size of murre populations; and since these birds feed over the relatively broad continental shelf, this factor is two-dimensional. From this it might be expected that along a coast equally suited to the ecological requirements of both murres and guillemots, the numbers of the former would be roughly proportional to the square of those of the latter. Some few data available seem to bear this out. Off the coast of central California the guillemots number a few hundred, and the murres, tens of thousands. The largest nesting group of guillemots reported in the literature (Gross, 1937:34) is 2,000 (Austin, *in litt.*, reports 10,000 *Cepphus carbo* in one colony on Teure-jima), whereas the largest murre colony (Krasovski, 1937:88) numbers more than 1,600,000.

The size and distribution of effective breeding populations have an important bearing on the rate and type of evolution. In large, panmictic populations the fixation of genes through the effects of chance does not occur, and an extremely variable, relatively slow-changing population results. On the other hand, in small, isolated populations chance fluctuations in gene frequency, aided by inbreeding, may cause the fixation of genes. Such genetic variability as exists within the population becomes fixed relatively rapidly, but the over-all evolution is limited by mutation rate. This produces populations which are relatively homogeneous genetically and in which evolution tends to be nonadaptive. Thus, among completely isolated, panmictic populations, those of medium size present the optimum conditions for rapid evolution. Simpson (1944:68) estimates this optimum as between 250 and 25,000 individuals. According to Wright (1945:416), an even more favorable condition for rapid evolution is to be found in "a population which may be large but which is subdivided into many small local populations almost but not quite completely isolated from each other." Wright has also shown (1943) that populations which are linear in their distribution resemble insular populations in their dynamics.

The over-all breeding distribution of murres and guillemots is essentially linear, but the local populations of murres are large, insular ones and those of guillemots are smaller, more strictly linear ones. The available evidence tends to show that murres are less sedentary than guillemots, but that this greater dispersal of murres effects more of an interchange of birds among the breeding colonies has yet to be proved. There are no data to indicate that there is a significant difference in Wright's "migration factor" in the two genera. Hence, the difference in size of the local breeding populations of murres and guillemots seems to be the most important factor influencing the contrasting rates of differentiation within the two genera. Guillemot populations appear to conform more closely to Simpson's optimum figure than do those of murres; and, assuming that the length of time involved has been the same in both genera, the guillemots have probably differentiated the more rapidly for this reason. This greater amount of differentiation is shown by the larger number of taxonomically distinct forms of guillemots, three species and twelve subspecies, as opposed to two species and nine subspecies of murres. The smaller size of the guillemot populations is partly offset by their greater continuity, whereas the larger size of murre colonies is partly balanced by their greater isolation and by the greater fluctuations in numbers to which large breeding colonies are subject.

THE EVOLUTIONARY HISTORY OF THE MURRES AND GUILLEMOTS

The fossil evidence shows that murres existed in the Pacific area in the Pleistocene and in the Atlantic at least as far back as the Pliocene and possibly to the Miocene. This suggests that the murres originated in the Atlantic, as also does the fact that the murres' nearest relatives, the razor-bill and the great auk, were confined to the Atlantic. The dovekie (*Plautus*) is the only other alcid with a similar plumage pattern and likewise is exclusively an Atlantic form; it may be closer to the auks and murres than is currently thought.

The origin of the guillemots is more problematical. The finding of the related *Miocepphus* in Maryland suggests an Atlantic origin. The family Alcidae as a whole, however, probably arose in the Pacific area, since of the 14 genera and 23 species currently recognized, 3 genera and 5 species are of exclusively Atlantic distribution, 8 genera and 16 species are of exclusively Pacific distribution, and 3 genera and 2 species are common to both oceans.

The climate of the late Tertiary was characterized by a slow cooling in the north. At some early time (perhaps early Pliocene) when the water temperature of the Arctic Ocean along the north coast of Siberia ranged from 10° C. to 15° C., the ancestral guillemots, which were probably similar to *C. columba* or the southern forms of *C. grylle,* extended their range from the Pacific to the Atlantic or vice versa. At this time the guillemots, which are restricted to coastal areas, could not range farther north into the Arctic Ocean. With the increasing cold in the north, the guillemot populations in both oceans moved southward with the belt of water temperature to which they were adapted. This left the colder northern coasts unoccupied. However, cold oceanic water produces more plankton than warm, not only through the increased oxygen content due to low temperature and low salinity, but also because the deeper water layers, which are rich in phosphorus, nitrogen, and other essential elements, are brought to the surface in the north. Furthermore, as Loeb's data (1908:411–426) on invertebrates show, a drop in temperature increases longevity at a much greater rate than it slows development. This results in both a larger number of generations and individuals of marine organisms in the arctic (or the antarctic) than in equatorial or temperate seas.

Thus the arctic offered an excellent food source, and the black guillemot evolved high-arctic forms (*mandtii* and *ultimus*) to fill the unoccupied habitat. In the meantime the isolated populations in the south differentiated; and because Bering Strait was closed at this time (late Pliocene or early Pleistocene), the pigeon guillemots became isolated from the high-arctic black guillemots and became specifically distinct or nearly so. The closure of the strait also resulted in a greater temperature differential between Bering Sea and the Arctic Ocean, because at that time the warm Japanese Current, which now flows in part through the strait, must have been deflected to the west (Taber, 1943:1531). Thus *C. columba* did not have the opportunity to develop high-arctic forms, and has been able to colonize only a very small area to the north of the strait since the latter became open. What differentiation has taken place in the guillemots from north to south on the Pacific coast of North America is slight compared with that on the Atlantic coast, where the temperature gradient is much steeper. It is of interest to note that the length of bill and the amount of white in the wing vary in the same directions along the two coasts, an indication that both characters are influenced by temperature.

A reconstruction of the history of the evolution of *Cepphus carbo* is more difficult. It seems to have been derived from *columba*-like stock in the Sea of Okhotsk. The lowering of the sea in late Pliocene or early Pleistocene times was probably sufficient to make an almost complete land bridge from Kamchatka to Hokkaido, leaving only three or four small connections between the Sea of Okhotsk and the Pacific. This would provide nearly complete isolation of the guillemot population of the Sea of Okhotsk from that of the Pacific, a condition necessary to permit the differentiation of *carbo*. On the other hand, the connections between the two bodies of water permitted a small amount of gene flow between the populations, which might account for the tendency of the race now inhabiting the Kurile Islands (*C. columba snowi*) to have dark wings like *carbo*.

Differentiation in the guillemots seems to have occurred most rapidly in areas between which there has been a steep climatic gradient. A steepening of temperature and salinity gradients between the Sea of Okhotsk and the Pacific undoubtedly occurred when contact between the two was reduced to a few narrow straits, and this in turn probably accelerated the differentiation of *carbo*.

The origins of the characters of *C. carbo* present some interesting problems. The larger size of *carbo* is paralleled by *C. g. grylle* of the Baltic Sea. Salomonsen (1944:69) attributes the large size of the Baltic races of the guillemot and the eider (*Somateria mollissima*) to the cold temperatures of that body of water. It may be significant that the high-arctic forms of the black guillemot are not significantly larger than those which inhabit warmer waters. It is likely that the Sea of Okhotsk was even less saline at the time when *C. carbo* was evolving than it is now, and that decreased salinity, possibly acting through decreased density, is a selective factor favoring increased size of diving birds.

The dark wing of *C. carbo* is similar to that of the *"motzfeldti"* mutant of *C. grylle* and probably is the result of a similar genetic change which has become stabilized in the population.

The white around the eye of *C. carbo* is foreshadowed in the pigeon guillemot, as is seen in the differential fading of mounted birds. In a habitat group in the California Academy of Sciences the pigeon guillemots have faded more in the region around the eyes than elsewhere, thus strongly suggesting the facial pattern of *C. carbo.*

The pattern of evolution in the murres is somewhat different. Murres are in general more specialized than guillemots in their morphology (Storer, 1945) and in their behavior. Also as a result of their much larger populations, they tend to change more slowly. Thus it can be seen that the evolution of the forms of the common murre followed the same general pattern as that of the guillemots, that is, first a spread from the Atlantic to the Pacific (probably not the opposite in this case) at a time when the Arctic Ocean was warmer than it is now. This was followed by a recession from the Arctic with the cooling in the Pliocene. As has already been shown, populations of murres are larger than those of guillemots, and for this reason the formation of subspecies of murres in both oceans took place at a slower rate than in the guillemots. This is readily seen in the fewer subspecies of murres and in the lesser degree of geographic variation of which this is a reflection.

Uria lomvia arose in the arctic, probably north of Siberia. Perhaps a small or fluctuating population of murres was able, through preadapation or a rapid evolution, to remain in the north after most of the ancestral species moved south. Continued rapid evolution in the north, where feeding conditions were extremely favorable but other conditions less favorable, led to the development of *U. lomvia.* This species spread southward and met *U. aalge,* which was spreading northward as its more northern populations became adapted to colder conditions. Finally, by the time the two species came together they had developed reproductive isolation.

The extensive overlap in the ranges of two such similar species is not a common one and merits considerable study. It would be particularly interesting to determine the mechanism which prevents their interbreeding and to what extent they differ in their ecological preferences in the regions where they occur together.

The evolution of these alcids has not involved the newer forms in the north pushing the older forms southward. Rather, the older forms followed the climatic belts to which they were adapted, and they left unoccupied an area suitable to the evolution of new forms which could become adapted to the colder climate. This is borne out by the greater degree of apparently random variation to be found among the southern populations which have evolved into several well-marked races as well as several more incipient ones.

SUMMARY AND CONCLUSIONS

The genera *Uria* and *Cepphus* (the murres and guillemots) have nearly congruent ranges in the Northern Hemisphere. The birds of these genera are closely related but differ in behavioristic and minor anatomical features.

The guillemots are closer to the ancestral stock of the family than are the murres. They nest in natural crevices in rocks and feed on benthic organisms near shore. Murres nest in large colonies on open rocks or ledges and feed on nektonic organisms. The murres' habit of nesting in densely packed groups on open places is directly or indirectly responsible for many of the differences between the two genera. The courtship patterns in murres have been compressed, and those requiring much space have been lost.

The size of a guillemot population is limited by the number of available nest sites. The size of a murre population is not so restricted, since there are usually many suitable sites unoccupied. The limits of population size are set by the food supply, but the feeding by murres on nektonic organisms has made possible the further increase in size of their populations. Thus, in an area suitable to the existence of murres and guillemots, the limiting factor for the guillemots, nesting sites, is a linear one; and that for the murres, food supply, is two-dimensional. Consequently, the size of a population of murres in such an area is roughly the square of that of the guillemots.

The difference in population size seems to have been an important factor in the evolution of the species and subspecies of these genera. The greater amount of variation in the guillemots is reflected in the greater number of taxonomically distinct forms of that group, there being three species and twelve subspecies of guillemots and two species and nine subspecies of murres.

The geographic distribution of the forms of these birds is primarily correlated with surface water temperature. The restriction of populations of murres and guillemots to given ranges of temperature is probably through the psychology and/or physiology of the individuals. Two characters—the amount of white in the plumage of guillemots and the length of the bill in both genera—vary consistently with water temperature. Variation in most other characters appears to be random and nonadaptive.

In the evolutionary history of the genera, the older forms were those inhabiting relatively warm water. With the cooling during the Pliocene, these moved south with the belt of water temperature to which they were adapted. The newer, more boreal forms evolved in the more northern areas after the retreat of the older forms.

TAXONOMIC APPENDIX

Since the analysis of data on geographic variation has shed new light on the ranges and characters of the subspecies of murres and guillemots, a synopsis of these forms has been appended. Salomonsen (1944) has already published extensive synonomies of the Atlantic forms, so only the original references and changes made subsequent to his treatment are given for these forms. Fuller synonomies are given for the Pacific forms.

The known ranges of variation are given for each subspecies. Means and standard deviations for the various populations within the subspecies are tabulated in the section on geographic variation.

Genus **Cepphus** Pallas

Cepphus Pallas, Spicil. Zool., 1, fasc. 5, 1769:33. Type by monotypy, *Cepphus lacteolus* Pallas = *Alca grylle* Linnaeus.

Remarks.—I recognize three species in this genus, *Cepphus grylle* of the Atlantic and Arctic oceans, *C. columba* of the Pacific Ocean, and *C. carbo* of the Sea of Okhotsk and the Sea of Japan.

The relationships between *Cepphus columba* and *C. grylle* on the one hand and *C. carbo* on the other where their breeding ranges meet have not yet been worked out satisfactorily. That the breeding ranges do meet seems probable. In the collections of the Museum of Comparative Zoölogy there are two specimens of *C. g. mandtii:* a pair in adult breeding plumage taken by John Koran on July 23, 1910, at Cape Serdze, Siberia, and one typical specimen of *C. columba,* an adult male in breeding plumage taken on the same date at the same place by the same collector. There is also, in the collection of the Academy of Natural Sciences of Philadelphia, a specimen of *C. columba:* an adult female taken at Cape Serdze by Dr. Sharp on July 12, 1895. Yamashina (1931) states that *C. carbo* has been collected on the island of Yetorofu in the Kuriles. In the collection of the University of Michigan there is an all-black specimen of *C. columba snowi* from "Etrof" (= Yetorofu) Island. In spite of this overlapping of ranges, I have seen no specimen which was not distinctly either *carbo, columba,* or *grylle.* This does not mean, however, that *columba* does not interbreed with the other two species. Indeed, the decreased amount of white in the speculum in *snowi* from north to south may be explained as an infiltration of genes from *C. carbo* before the latter became specifically distinct. I think, however, that the increased amount of white in the under wing coverts and outer primary of *C. columba* is a case of parallel evolution rather than intergradation with *C. g. mandtii.*

The current trend in taxonomy is to treat allopatric forms as subspecies unless proved species by lack of interbreeding, but the indications that the breeding range of *C. columba* overlaps those of both *C. grylle* and *C. carbo* and that hybrids between these forms are unknown put the burden of proof on whoever wishes to unite all three forms in a single species. In this instance, retaining *grylle, columba,* and *carbo* as species has a definite practical advantage in contrasting the sharp breaks in characters which occur between *columba* and each of the other species with the gradual changes occurring from one population of *grylle* (or *columba*) to another. The important thing in any event is not the names applied to the forms but the relationships between them.

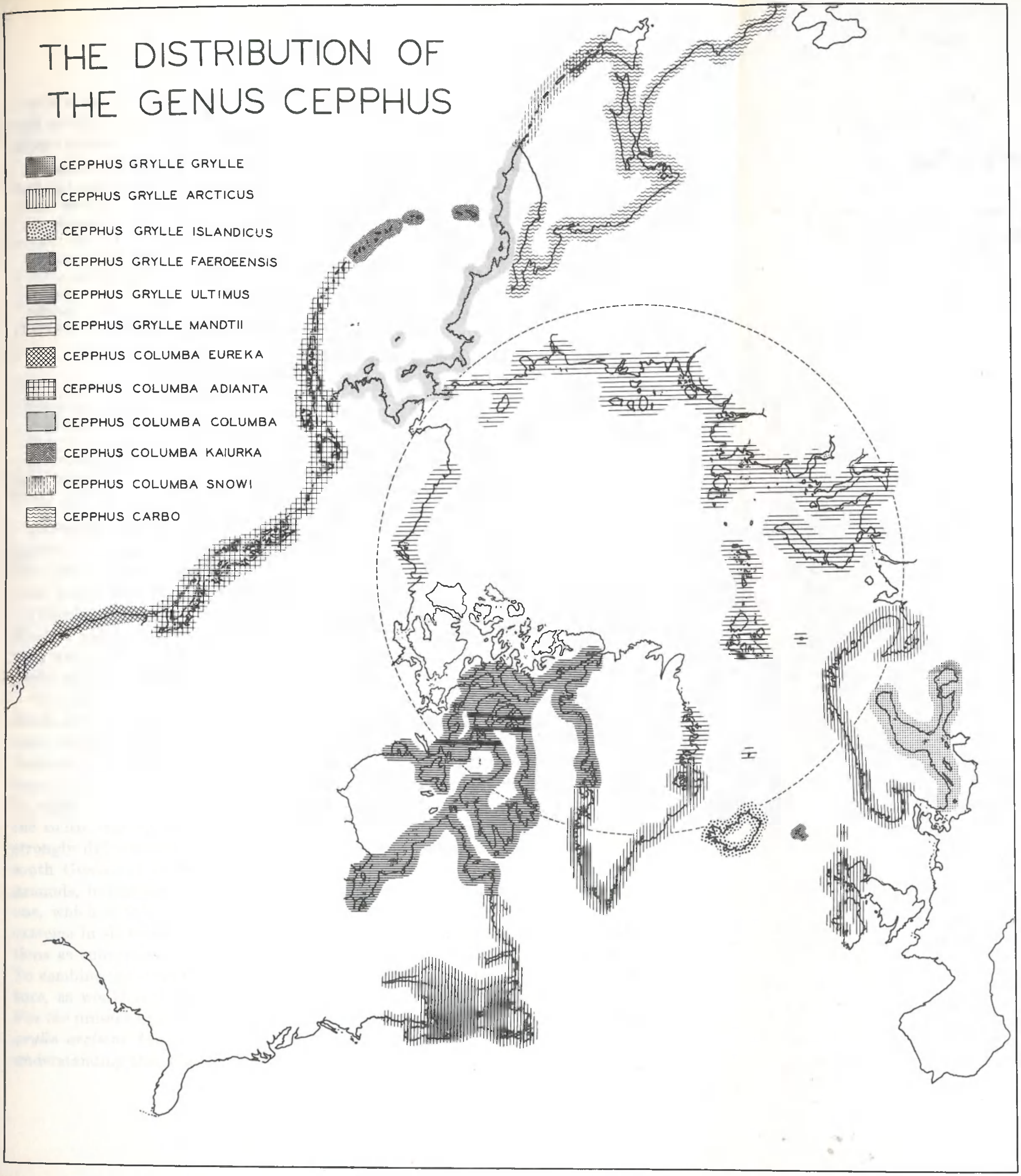
Cepphus grylle grylle (Linnaeus)

Alca Grylle Linnaeus, Syst. Nat. ed. 10, pt. 1, 1758:130.

Type locality.—Restricted by Salomonsen (1944:60) to the Island of Gotland in the Baltic Sea.

Description.—Wing length, 167 to 182 mm. (mean, 174); tarsal length, 32.5 to 34.5 mm. (33.75); culmen length, 29.5 to 35.0 mm. (33.0); per cent white in outer primary $\left\{\frac{100c}{b+c}\right\}$ 0 to 24; white in secondary coverts, c to e (most, d). This race resembles the populations of *C. g. arcticus* of Norway and the British Isles but is significantly larger.

Remarks.—This race is an offshoot of *C. g. arcticus* and probably evolved in the Baltic Sea after the lake formed by the melting of the Scandinavian ice cap became connected with the ocean. According to Daly (1934:59–61), this lake was connected with the ocean (and thus was salt or brackish) from approximately 8300 to 7800 B.C., after which the connection with the ocean was lost and the water became fresh again. About 5000 B.C. new connections with the ocean became opened and the present Baltic Sea was formed. Thus if *C. g. grylle* arose in the



To accompany R. W. Storer, "A Comparison of Variation, Behavior, and Evolution in the Sea Bird Genera Uria and Cepphus," Univ. Calif. Publ. Zoöl., Vol. 52, No. 2

Fig. 17. The distribution of the species and subspecies of the genus *Cepphus*.

Baltic area, the differentiation cannot have taken longer than ten thousand years and probably less than seven thousand if the colonization of the Baltic occurred after the second set of connections with the ocean became opened.

Range.—Confined to the Baltic Sea, nesting on the east coast of Sweden from the Gulf of Bothnia to southern Blekinge, Lake Ladoga, and the coast of Finland south to Estonia. In winter, ranges south to southern Denmark and northern Germany.

Specimens examined.—8, of which 5 are in adult nuptial plumage, 2 are molting adults, and 1 is a first-winter bird.

DANZIG. 1 (AMNH).

FINLAND. Sibbo, Estluotan, 1 (MVZ); Sjundea, Pickalavik, 1 (MVZ).

GERMANY. East Prussia, Pillau, 1 (AMNH).

SWEDEN. Fran Angskar, 1 (AMNH); Stockholm, 1 (USNM); Stockholms Skargard, 1 (USNM); unspecified, 1 (AMNH).

Cepphus grylle arcticus (Brehm)

Uria arctica Brehm, Lehrbuch d. Naturgesch. europ. Vögel, 2, 1824: 923 (original description).
Cepphus grylle atlantis Salomonsen, Göteborgs Kungl. Vetenskaps-Och Vitterhets-Sämhalles Handlingar Sjätte Följden Ser. B, Band 3, N:o 5, 1944:77.

Type locality.—Restricted by Salomonsen (1944:97) to southeastern Greenland.

Description.—The most variable subspecies. Wing length, 155 to 183 (means 164.3 to 171.5); tarsal length, 28.0 to 35.0 (means 31.44 to 33.13); culmen length, 26.0 to 37.5 (means 29.73 to 33.11); per cent white in outer primary, 0 to 36; white in secondary coverts, b to e (1,a; 1,o).

Remarks.—No two populations from Maine to at least central Newfoundland Labrador are in any way sufficiently different to warrant subspecific separation. The principal break in the north-south clines for culmen length and white in the outer primary and secondary coverts occurs between Nain and Cape Chidley. The northern populations from extreme northern Ellesmere Island to and including Hudson Strait, James and Hudson bays, and from extreme northwestern Greenland south to Disco Bay are quite similar, and all should be referred to *Cepphus grylle ultimus* Salomonsen.

The three southernmost populations in the Atlantic all differ from each other. Birds of the south Greenland population have the longest wings and tarsi and have culmens of intermediate length; the birds of the British Isles and western Scandinavia have short wings and tarsi and long culmens; and the North American birds have wings and tarsi of intermediate length and short culmens. It might be expected that since these three populations are probably older than that in the Baltic, during their longer period of isolation they would have become more strongly differentiated. This, however, is not true. Subspecific separation of the south Greenland birds from the European ones can be justified on statistical grounds, but neither of these populations can be separated from the American one, which is intermediate in wing and tarsal lengths only and represents the extreme in shortness of culmen. If it were possible to separate all three populations as subspecies, the situation would be adequately expressed taxonomically. To combine the American birds with the Greenland birds would confuse the picture, as would combining them with the geographically remote European ones. For the present I prefer to combine all three under one name; and because *Cepphus grylle arcticus* (Brehm) is the oldest, it must be used. This is done with the understanding that the three populations are incipient subspecies. Thus *Cepphus* *grylle atlantis* Salomonsen becomes a synonym of *Cepphus grylle arcticus* (Brehm). Should it be thought desirable to separate the European birds subspecifically, *atlantis* would be applicable, as the type locality is Göteborgs Skärgärd, Bohuslän, Sweden.

Range.—Breeds along the coasts of North America from Maine to northern Newfoundland Labrador (Nain), western Greenland north to Disco Bay, the British Isles, western Sweden, Norway, and north and east to and including the Murman Coast. Largely sedentary, but some individuals, mostly young birds, move south in winter.

Specimens examined.—528, of which 298 are in adult nuptial plumage or nearly so.*

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* Because of his forthcoming work on the birds of the Ungava Peninsula, Mr. W. E. C. Todd has requested me not to publish the exact localities of birds in the Carnegie Museum from that region.

NEWFOUNDLAND LABRADOR. Battle Harbor, 2 (PMZ), 5 (UMMZ), 6 (MMP); Chateau Bay, 3 (Bowdoin); Davis Inlet, 1 (USNM), 1 (MCZ); Dominoe Point, 1 (MCZ); Gannet Island, 2 (CNHM); Gready, 2 (MCZ); Groswater Bay (=Lake Melville), 1 (AMNH), 3 (USNM); Hamilton Inlet, 1 (MCZ); Hopedale, 1 (UMMZ), 2 (CNHM), 4 (Bowdoin); Indian Harbor, 2 (CNHM); Jack Lane's Bay, 3 (CNHM); Lance au Loup (=Loup Bay), 1 (MCZ); Merrifield Bay, 1 (AMNH), 4 (CNHM); Nachvak, 2 (MCZ), 1 (USNM); Nain, 1 (MCZ); Port Manvers, 1 (CNHM); Red Bay, 32 (UMMZ); Webeck Harbor, 4 (Bowdoin); Windy Tickle, 2 (UMMZ). Carnegie Museum, 7.

"LABRADOR." Ice Tickle Islands, 1 (AMNH); south coast, 1 (MCZ); unspecified, 1 (CNHM). Carnegie Museum 3.

NEWFOUNDLAND. Bay Bulls, Avalon Peninsula, 1 (USNM); Bay de Nord, 2 (USNM); Bay of Isles: Blow-me-downs, 3 (MCZ); unspecified, 1 (MCZ). Big Cove Head, near Trout River, 1 (USNM); Cape St. Marys, 1 (USNM); Codroy, 1 (CNHM), 1 (MCZ); Custlett, 15 (MCZ); Denier Islands, 2 (ROMZ); Exploits Bay, 1 (MCZ); Great Cormorandier Islands, 1 (USNM); Green Island, off Random Island, 2 (USNM); White Bear Bay, 1 (USNM); White Island, off Quirpon, 1 (USNM); unspecified, 3 (ROMZ).

QUEBEC. Bonaventure Island, 6 (CNM); Canadian Labrador: Blanc Sablon, 6 (UMMZ), Bonne Esperance, 9 (CNM), Cape Whittle, 1 (AMNH), 2 (ROMZ), 3 (MCZ), Eskimo Point, 2 (MCZ), Harrington Harbor, 2 (CNM), Seal Net Point (=Point au Maurier), 1 (MCZ), Trout River, Moisie Bay, 1 (CNM), 1 (MCZ), Carnegie Museum, 9; Gaspé Basin, 1 (CNM); Gulf of St. Lawrence, 2 (CAS); Magdalen Islands: Bird Rock, 1 (CNHM), Entry Island, 3 (MCZ), Grosse Isle, 13 (AMNH), Grosse Isle, Fauriel, 10 (CM), unspecified, 8 (CNHM), 1 (MCZ), 3 (AMNH); Old Bluff Island, 1 (CM); Percé, 2 (LACM), 1 (USNM), 7 (CNM), 2 (MCZ), 1 (SD); Percé Harbor, 2 (USNM); St. André de Kamouraska: Grosse Isle de Kamouraska, 1 (CNHM), Long Pilgrim Island, 1 (ROMZ), Pilgrim Island, 1 (ROMZ), unspecified, 1 (MVZ), 1 (UMMZ), 1 (USNM), 2 (CNHM); St. Lawrence River, 1 (ROMZ); Tadousac, 19 (AMNH); unspecified, 1 (MVZ).

NOVA SCOTIA. Bay of Fundy, 1 (USNM); Cape Breton: Bird Islands, 2 (MVZ), Margaree Harbour, 1 (ROMZ); Halifax, 5 (ROMZ); Hawk Point, 1 (MCZ); Isle a Haute, 6 (CNM); Mud Island, 2 (CNM), 1 (MCZ); Yarmouth, 1 (MCZ).

PRINCE EDWARD ISLAND. Charlottetown, 1 (ROMZ); Malpeque, 1 (MCZ); New London, 2 (AMNH).

NEW BRUNSWICK. Bay of Fundy, 1 (MCZ); Grand Manan: North Head, 1 (Bowdoin), unspecified, 3 (MVZ), 6 (CNHM), 2 (MCZ), 2 (AMNH); Miscou Island: Wilson's Point, 4 (CNM), 1 (CNHM), 1 (PMZ), 1 (SD), unspecified, 1 (CNM); Point Lepreaux, 2 (MCZ); St. Andrews, 4 (MCZ); White Horse, 1 (MCZ).

MAINE. *Hancock County:* Bar Harbor, 1 (AMNH), 1 (MCZ); Bucksport, Penobscot Bay, 1 (AMNH); Cranberry Island, 1 (CAS); Ilsford, 1 (MCZ); Little Duck Island, 2 (MCZ). *Knox County:* Isle au Haut, 1 (CAS); Seal Island, 1 (MCZ). *Lincoln County:* Fishermans Island, 1 (MCZ). *Washington County:* Cowyard Ledge, 1 (MCZ); Eastport, 1 (USNM), 1 (CNHM); Roque Island, 2 (MCZ). *County unspecified:* Penobscot Bay, 1 (MCZ), 1 (Bowdoin).

MASSACHUSETTS. *Barnstable County:* Provincetown, 2 (MCZ), 1 (AMNH). *Essex County:* Nahant, 1 (USNM); Rockport, 1 (MCZ). *Plymouth County:* Cohasset, 4 (MCZ); Plymouth, 1 (MCZ). *County unspecified:* Boston Harbor, 3 (MCZ).

NEW YORK. *County unspecified:* Long Island, 1 (AMNH).

GREENLAND. Aofit, 2 (AMNH); Cape Tattershall, 2 (CNHM); Disco Harbor, 2 (AMNH); Godhavn, 2 (UMMZ), 1 (MCZ); Godthaab, 2 (USNM), 1 (CNHM), 3 (UMMZ), 2 (AMNH); Holsteinborg, 1 (CNHM), 36 (AMNH); Scoresby Sound, 1 (ANSP); Sukkertoppen, 2 (CNHM), 5 (MCZ), 3 (AMNH), 1 (Bowdoin); Waigattet (=the Vaigat), 1 (ANSP); Whale's Head, 1 (MCZ).

U.S.S.R. Kola Bay, 1 (MCZ); Murman Coast, 1 (MCZ); Solvetsk Island, Archangelsk District, 1 (AMNH).

NORWAY. Bergen, 2 (USNM); Christiania, 4 (ROMZ); Christiansund, 3 (AMNH); Stavangaer, 1 (USNM); Vesteraalen, Melbo, 3 (AMNH).

SWEDEN. Bohuslän, 2 (ROMZ), 1 (MCZ), 2 (AMNH); Kallskåren, 1 (AMNH). "Suecia Occid. 58°," 1 (USNM).

DENMARK. Helsingoer, 2 (AMNH).

ENGLAND. *Lancashire:* Fleetwood, 1 (MVZ); Southport, 1 (CNHM). *Somerset:* Bath, 1 (AMNH); Weston-Super-Mare, 1 (AMNH). *Yorkshire:* Spurn Head, 1 (AMNH).

IRELAND. *County Dublin:* Lambay Island, 3 (MCZ). *County Kerry:* Blasket Islands, 1 (MCZ). *County Mayo:* Erris, 2 (MCZ); Mayo, 5 (MCZ); North Mayo, 1 (MCZ); Pulathomas, 1 (Dickey); unspecified, 16 (MCZ).

SCOTLAND. *Inverness:* Skye, Sconser, 5 (AMNH); Harris, Tarbert, 1 (ROMZ). *Orkney:* South Ronaldshay, 1 (CAS); Stromness, 1 (ROMZ), 1 (AMNH), 7 (CNHM), unspecified, 1 (USNM), 12 (AMNH), 1 (CAS), 2 (MCZ). *Ross and Cromarty:* Lewis, Broad Bay, 1 (AMNH). *Shetland:* Scalloway, 4 (ROMZ), unspecified 3 (ROMZ), 6 (AMNH). *County unspecified:* west Scotland, 1 (MVZ).

Cepphus grylle islandicus Hørring

Cepphus grylle islandicus Hørring, Rep. 5th. Thule Exped., 2, no. 6, 1937:87 (original description).

Type locality.—Iceland.

Description.—Wing length, 155 to 173 (161.3); tarsal length, 30.5 to 34.0 (32.29); culmen length, 28.0 to 32.5 (30.62); white in outer primary 0 to 33; white in secondary coverts, c to e. This race differs from all others in the extension of black in a narrow line along the outer edge of the white feathers in the speculum. This is well illustrated by Salomonsen (1944:86).

Range.—The coasts of Iceland. According to Hantzsch (1905:112), adult guillemots are rarely seen near land in the fall and winter months.

Specimens examined.—19, of which 11 are adults in nuptial plumage or nearly so, 4 are adults in winter plumage, and 5 are birds of the year.

ICELAND. Arctic Ocean north of Iceland, 1 (ROMZ); Havet (=the sea), north Iceland, 1 (ROMZ); Höfn, 2 (CNHM); Husavik, 1 (MVZ); Isafiord, 2 (MCZ), 1 (ANSP); North coast of Iceland, 5 (AMNH), 2 (ROMZ); unspecified, 3 (AMNH), 1 (USNM).

Cepphus grylle faeroeensis Brehm

Cephus faeroeensis Brehm, Handb. Naturgesch. Vögel Deutschlands, 1831:990 (original description).

Type locality. "An den felsigen Küsten Färöes."

Description.—This subspecies is known from relatively few specimens, hence its range of variability has not been adequately determined. Ranges and means of four adult specimens (three listed by Salomonsen, 1944:85, and AMNH 748094) are wing length, 155 to 160 (157); culmen length, 31.0 to 33.0 (32); white in outer primary, 0 to 13. The tarsus of AMNH 748094 measures 31.5 mm.

Remarks.—The validity of this form has yet to be proved by an examination of an adequate series of specimens. None of the four specimens examined by Salomonsen had white on the outer primary as does AMNH 748094, and lack of this white is one of the characters used by Salomonsen in resurrecting the subspecies. The small size and large amount of dark in the speculum feathers will probably prove sufficient to validate the form.

Range.—Restricted to the Faeroes between Scotland and Iceland. Salomonsen (1935:116) states that "in winter (Aug.–Jan.) not infrequently observed at some distance from land, although many stay close to the coast."

Specimens examined.—One adult in nuptial plumage. A young bird in first winter plumage from the Brehm collection (AMNH 748119, November 28, 1822, Helsingoeer) is labeled *"Cephus faeroeensis* Brm". This bird, although small and dark, is within the range of variation of first-year birds of *C. g. arcticus* from the British Isles and western Scandinavia. If the locality on the label means that the bird was taken at Helsingoeer (= Elsinore) and not received from a museum there, it should be listed as *C. g. arcticus;* it probably is the specimen on which Brehm based his statement (1831:991) to the effect that *C. g. faeroeensis* reached northern Germany in winter.

FAEROES. 1 (AMNH).

Cepphus grylle ultimus Salomonsen

Cepphus grylle ultimus Salomonsen, Göteborgs Kungl. Vetenskaps-Och Vitterhets-Samhälles Handlingar Sjätte Följden, Ser. B. Band 3, N:o 5, 1944:93 (original description).

Type locality.—Frozen Strait, Melville Peninsula, High-arctic Canada.

Description.—Wing length, 156 to 180 (mean, 165.4 to 167.8); tarsal length, 27.5 to 34.0 (means 30.78 to 31.35); culmen length, 24.5 to 32.5 (means 27.56 to 29.20); white in outer primary, 16 to 57; white in secondary coverts, a to b (1, c).

Remarks.—This form differs from *C. g. arcticus* in the greater amount of white in the outer primary and the secondary coverts, and from both *arcticus* and *mandtii* in having a shorter bill. The latter character reaches its extreme in the region around Hudson Bay and Baffin Island.

C. g. ultimus is separated from *C. g. mandtii* to the west by the archipelago to the west of Baffin, Devon, and Ellesmere islands which appears to constitute a barrier to the dispersal of alcids, since the waters of this area are open for only a brief period each summer. This period is, at least in most years, shorter than the time needed for a pair of guillemots to breed successfully. It is possible, but unlikely, that the ranges of *ultimus* and *mandtii* meet in extreme northern Greenland. Certainly *ultimus* approaches *mandtii* in culmen length most closely in northwestern Greenland and Ellesmere Island.

C. g. ultimus intergrades with *C. g. arcticus* along the west coast of Greenland in the region of Disco Bay and along the north coast of Newfoundland Labrador between Cape Chidley and Nain.

Range.—Breeds in arctic America from James Bay, Ungava Bay, and extreme northern Newfoundland Labrador to northern Ellesmere Island, and along the west coast of Greenland north of Disco Bay. Largely sedentary.

Specimens examined.—350, of which 233 are in adult nuptial plumage or nearly so.*

NORTHWEST TERRITORIES, FRANKLIN. *Baffin Island:* Amadjvak Bay, 3 (CNM); Bowdoin Harbor, 2 (CNM), 8 (MCZ); Cape Dorset, 1 (MVZ), 32 (CNM); Cape Havn, 3 (USNM); Crooks Inlet, 1 (ROMZ); 25 miles west of Crooks Inlet, 1 (ROMZ). *Cumberland Sound:* 1 (USNM); Annanucta Harbor, 1 (USNM); Arctic Island, 1 (ROMZ); Blacklead Island, 1 (CNM); Harrison Island, 1 (USNM); Niantilik, 8 (USNM); Davis Strait, 1 (AMNH); Duck Islands, 1 (CNM); Enowoling Point, 1 (CNM); Frobisher Bay, 1 (AMNH); Gordon Bay (= Andrew

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* Because of his forthcoming work on the birds of the Ungava Peninsula, Mr. W. E. C. Todd has requested me not to publish the exact localities of birds in the Carnegie Museum from that region.

Gordon Bay), 1 (CNM); Hudson Strait, 2 (AMNH); Lake Harbor, 3 (ROMZ); Lower Savage Islands, 3 (CNM), 4 (Bowdoin); Pangnirtung Fjord, 1 (MVZ), 8 (CNM); Pond Inlet, 1 (ROMZ); Resolution Island, 5 (CNM); Saddleback Islands, 1 (ROMZ); White Strait, 1 (AMNH); William Fox Islands, 4 (CNM). *Devon Island:* Beechey Island, 1 (CNM); Dundas Harbor, 3 (USNM), 5 (CNM). *Ellesmere Island:* Bache Island, 10 (USNM); Bedford Pim Island, 1 (USNM); Buchanan Bay, 1 (CNM), 1 (MCZ); Cape Durville, 1 (PMZ); Cape Nares, 6 miles ± off, 2 (AMNH); Cape Sabine, 3 (USNM); 2 (MCZ), Cobourg Island, 2 (AMNH); Fram Harbor, 1 (CNM); Hayes Sound, 2 (USNM); Payer Harbor, 2 (USNM); Smith Sound, 1 (USNM); Wrangle Bay, 2 (AMNH); Resolution Island, 5 (CNM). *Somerset Island:* Port Leopold, 5 (ROMZ); unspecified, 1 (ROMZ).

NORTHWEST TERRITORIES, KEEWATIN. *Hudson Bay:* Belcher Islands, 1 (CNM); Cape Fullerton, 7 (CNM); Chesterfield, 3 (CNM); Chesterfield Inlet, mouth, 1 (USNM); Depot Islands, 2 (ROMZ); Sleeper Islands, Didgit Point, 7 (ROMZ); Carnegie Museum, 18. *James Bay:* Round Island, 2 (CNM); Carnegie Museum, 7. *Southampton Island:* Bear Island, South Bay, 8 (CM); Coral Inlet, 4 (CM); Kikkuktouyak Island, 1 (CM); Munnimunnek Point, 1 (CM); Native Point, 16 (CM); Prairie Point, 1 (CM); Seahorse Point, 1 (CM); Tern Islands, 3 (CM).

QUEBEC. *Hudson Bay:* East Coast, 1 (ROMZ); Great Whale River, 15 miles north, 1 (CNM); Port Harrison, 1 (CNM). Carnegie Museum, 15. *James Bay:* East Main, 1 (MCZ); Fort George, 1 (MVZ), 1 (MCZ), 1 (USNM); Carnegie Museum, 15. *Ungava Bay:* Fort Chimo, 1 (CNM), 1 (AMNH), 2 (USNM); island 3 miles north of Gyrfalcon Island, 2 (CNM); Port Burwell, 1 (Bowdoin); Carnegie Museum, 2.

NEWFOUNDLAND LABRADOR. Carnegie Museum, 2.

ONTARIO. *James Bay:* Moose Factory, 1 (USNM).

GREENLAND. Booth Sound, 2 (UMMZ); Cape Cleveland, 4 (ANSP); Carey Islands, 76°45′ × 73°30′, 1 (ROMZ), 1 (USNM); Dalrymple Rock, 3 (PMZ); Devil's Thumb, 1 (ANSP); Esterslogten, 1 (AMNH); Etah, 2 (LACM), 2 (UMMZ), 11 (CNM), 3 (ANSP), 12 (AMNH), 2 (CAS), 2 (SD); Hakluyt Island, 2 (Bowdoin); Littleton Island, 2 (UMMZ); McCormick Bay, 1 (CM), 3 (ANSP); Northumberland Island, 1 (MCZ); Thule, 7 (USNM); Umanak, 1 (MCZ); Upernivik, 1 (AMNH).

Cepphus grylle mandtii (Mandt)

Uria Mandtii Mandt, Obs. Hist. Itin. Groenl., 1822:30 (original description).

Cepphus grylle tajani Portenko, Comptes Rendus (Doklady) de l'Academie des Sciences de l'URSS, 43, 1944:227.

Type locality.—Spitsbergen.

Description.—Wing length, 159 to 177 (means 168.0 to 170.9); tarsal length, 27.0 to 34.0 (means 30.94 to 32.29); culmen length, 27.0 to 34.0 (means 30.70 to 31.39); white on outer primary, 22 to 45; white in secondary coverts, a to c.

Remarks.—*C. g. mandtii* intergrades with *C. g. arcticus* along the east coast of Greenland. Two birds from Cape Tattershall seem nearer *arcticus;* and two adults taken in July at sea (73°39′ N, 15°26′ W and 73°30′ N, 16°50′ W) seem nearer *mandtii.* The population of *mandtii* from eastern Siberia shows somewhat larger dimensions than those of Spitzbergen and Alaska. Portenko's (1944:227) recently described *C. g. tajani* from Wrangel Island is based on the greater amount of green gloss on the black feathers and, in part, on a somewhat larger size (wing, 166–181 mm., mean 172, 41 specimens) than those of neighboring populations. Five guillemots in the collection of the Chicago Natural History Museum taken at Cape Hawaii, Wrangel Island, on August 14, 1927, are large (wing, 167–175, mean, 171.4) but do not differ significantly in size from other Siberian birds. The Cape Hawaii birds have considerable green gloss but are matched by a bird from Kolyuchin Island, Siberia; and a one-year-old bird from Barrow, Alaska (where the species is not known to nest), is even greener. Thus it would appear that if *tajani* is a valid race, it is not an insular form but should include the populations nesting from eastern Siberia to northern Alaska. However, because the gloss on the feathers is subject to considerable variation owing to wear and age, I prefer to consider *tajani* a synonym of *mandtii* at least until I can examine more material from Spitsbergen and northern Asia.

Range.—Breeds from the northeast coast of Greenland east to Jan Mayen, Spitsbergen, Franz Josef Land, Novaya Zemlya, and the Arctic coasts of Siberia and Alaska. In winter there is some southward movement of young birds, at least through Bering Strait and as far south as St. Lawrence Island and St. Michaels, Alaska.

Specimens examined.—125, of which 30 are in adult nuptial plumage or nearly so. Approximately half these birds are from the region of Point Barrow, where the species is not known to nest and where adult birds have been taken only infrequently.

GREENLAND. Lat. 73°30′ N, long. 16°50′ W, 1 (AMNH); Lat. 73°39′ N, 15°26′ W, 1 (AMNH); Stor Fsen, 74° N, 1 (AMNH).

BEAR ISLAND. "Lummenfelsen," 1 (CNHM).

SPITSBERGEN. 80° N, 4 (AMNH); Anser Islands, Ice Fjord, 1 (AMNH); Green Harbor, 1 (USNM); Kings Bay, 1 (USNM); Lady Franklin Bay, 2 (KU); Yfjanden (sp?), 1 (USNM); unspecified, 1 (USNM).

FRANZ JOSEF LAND. Hooker Island, 2 (MCZ).

NOVAYA ZEMLYA. Off Gooseland, 1 (AMNH); Kostin Schar, 1 (AMNH).

SIBERIA. 63°54′ N, 173°20′ W, 1 (MCZ); Cape Bolshaja Baranov, 1 (USNM); Cape Kyber, 5 (MCZ); Cape Irkaipij, 1 (MCZ); Cape Serdze, 2 (MCZ); Herald Island, Arctic Ocean near, 4 (MCZ), 1 (USNM); Kolyuchin Island, Kolyuchin Bay, 1 (CNHM); New Siberian Islands: Bennett Island, a new island NE of (75°43′ N, 152°36′ E), 1 (MCZ), Kotelny Island, 1 (MCZ); Wrangel Island, 80 miles off, 1 (MCZ), Cape Hawaii, 5 (CNHM).

ALASKA. Barrow, 2 (Dickey), 2 (MVZ), 10 (CNHM), 7 (MMP), 10 (ChAc), 15 (SD); Cape Lisburne, 2 (SD); Cape Prince of Wales, 1 (MVZ); Cape Vancouver, 1 (MCZ); Point Barrow, 3 (CM), 6 (USNM), 1 (CNM), 11 (AMNH), 2 (SD); St. Lawrence Island, Gambell, 1 (USNM); St. Michaels, 1 (USNM), St. Michaels, Steward Island, 1 (USNM); Sledge Island, 1 (CNHM); Teller, Grantley Harbor, 1 (CNM); Wainright, 1 (MVZ); Wales, 1 (ChAc); "Yukon," 2 (CAS).

Cepphus columba eureka Storer

Uria grylle, Heermann, Cat. Oöl. Coll. Acad. Nat. Sci. Phila., 1853:32.

Uria columba, Cassin, Pac. R. R. Rept. 9, 1858:912.

Cepphus columba, Baird, Brewer, and Ridgway, Water Birds N. Amer., 2, 1884:494.

Pseuduria columba, Sharpe, Handl. Birds, 1, 1899:131.

Cepphus columbæ, Emerson, Condor, 6, 1904:66.

Uria columba columba, Hartert, Vögel Palaärkt. Fauna, 3, 1921:1777.

Cepphus columba columba, Alexander, Birds of the Ocean, 1928:248.

Cepphus grylle columba, Salomonsen, Göteborgs Kungl. Vetenskaps-Och Vitterhets-Samhälles Handlingar Sjätte Följden, Ser. B, Band 3, N:o 5, 1944:108.

Cepphus columba eureka Storer, Condor, 52, 1950:28 (original description).

Type locality.—The Farallon Islands.

Description.—Wing length, 176 to 197 (187.5); tarsal length 32.5 to 39.0 (36.13); culmen length 33.5 to 39.5 (36.57); white on outer primary when present, d to e; white on under wing coverts when present, very little. This long-winged, long-billed form is distinguished from *adianta* by a combination of wing and bill measurements, and from *columba* by its much shorter bill and, on the average, lesser amount of white in the wing.

Molt.—The prenuptial molt probably occurs between December and March, but very few specimens have been taken during these months. An adult taken on December 1 has only a few dark feathers on the under parts. Another taken on February 18 is approximately 80 per cent black below. By late March, when the birds return to the breeding grounds, the adults are in complete nuptial plumage or nearly so. Birds of the year molt later than the adults, apparently in

March, April, and May. First-year birds taken on April 3 and May 6 are approximately 35 and 50 per cent through the molt.

The fall molt may begin in July, and some birds may still be molting in late November; accordingly, the times of the two molts may overlap. One bird taken on July 30 has already molted the remiges and is approximately 50 per cent white below. On the other hand, two birds taken on August 26 have not begun the molt, and three others taken on August 17 and 21 and on September 6 have just begun the molt. A bird taken on November 27 is in winter plumage except for a few dark feathers below and the old rectrices.

Remarks.—The specimens examined from Oregon are intermediate between this race and the next in bill and tarsal measurements but are much nearer *eureka* in wing length. For this reason they are referred to the present subspecies.

Range.—Breeds from the mouth of the Columbia River south to the Santa Barbara Islands off southern California. Most of these birds leave the breeding grounds after the young are fledged. Whether they move north like the young of the Oregon murres or whether they winter at sea off the coast of California has yet to be determined.

Specimens examined.—298, of which 210 are adults in nuptial plumage or nearly so.

OREGON. *Tillamook County:* Netarts, 2 (AMNH), 3 (SD), 5 (SGJ); Pacific City, 1 (MMP). *Lincoln County:* Depoe Bay, 2 (SD), 1 (ENH), 1 (UOr); Newport, 1 (UOr). *Lane County:* Heceta Head Lighthouse, 1 (MMP). *County unspecified:* 1 (USNM), 1 (UOr).

CALIFORNIA. *Humboldt County:* Eureka, 1 (MCZ); Trinidad Harbor, 1 (MVZ), 1 (AMNH). *Mendocino County:* Little River, 1 (PUC). *Marin County:* Bear Valley, 2 (AMNH); Point Reyes, 4 (MCZ), 1 (CM), 1 (CNHM), 1 (CAS). *San Francisco County:* Farallon Islands, 4 (CAS), 5 (MVZ, including type), 3 (AMNH), 4 (USNM), 1 (MCZ), 1 (ENH); San Francisco, 1 (MCZ), 1 (CNHM). *San Mateo County:* Año Nuevo Island, 25 (CAS), 2 (CNHM), 2 (MVZ). *Santa Cruz County:* Davenport, 1 (MVZ); Santa Cruz, 3 (CAS), 6 (MVZ). *Monterey County:* Carmel Bay, 1 (CNHM), 3 (RE); Carmel Point, 8 (MVZ); Monterey, 8 (MCZ), 10 (AMNH), 1 (MMP); Monterey Bay, 1 (MMP), 109 (CAS), 17 (MVZ), 3 (AMNH); Pacific Grove, 17 (CAS), 1 (MCZ); Point Lobos, 1 (CAS), 2 (AMNH); vicinity of Point Pinos, 1 (MVZ). *San Luis Obispo County:* Morro Bay, 1 (MVZ); unspecified, 1 (LACM). *Santa Barbara County:* San Miguel Island, 1 (USNM), 1 (CNHM), 2 (ANSP), 1 (LACM); Prince Island, San Miguel Island, 8 (SD); Santa Cruz Island, 1 (AMNH). *Ventura County:* San Nicolas Island, 1 (USNM). *Los Angeles County:* Santa Barbara Island, 2 (Dickey), 2 (LACM), 3 (CAS).

Cepphus columba adianta Storer

[Uria grylle]β, Latham, Index Ornith. 2, 1790:797.

Uria columba, Cassin, Pac. R. R. Rept., 9, 1858:912.

Cepphus columba, Baird, Brewer, and Ridgway, Water Birds N. Amer., 2, 1884:494.

Pseuduria columba, Sharpe, Handl. Birds, 1, 1899:131.

Uria columba columba, Hartert, Vögel Palaärkt. Fauna, 3, 1921:1777.

Cepphus columba columba, Alexander, Birds of the Ocean, 1928:248.

Cepphus grylle columba, Salomonsen, Göteborgs Kungl. Vetenskaps-Och Vitterhets-Samhälles Handlingar Sjätte Följden, Ser. B, Band 3, N:o 5, 1944:108.

Cepphus columba adianta, Storer, Condor, 52, 1950: 28 (original description).

Type locality.—Nanaimo, Vancouver Island, British Columbia.

Description.—Wing length, 171 to 191 (180.2); tarsal length, 31.5 to 37.5 (34.57); culmen length, 31.0 to 38.5 (34.61); white on outer primary, when present, d to e; white on under wing coverts, none to moderate (2, much). This short-winged, moderately long-billed form is best distinguished from both *columba* and *eureka* by a combination of bill and wing lengths.

In some young birds of this race (for example, MVZ 101529 and MCZ 225892) the dark tipping on the white feathers of the speculum and the under parts reaches its extreme, and these birds may appear dark all over. Other juveniles resemble those of the other races.

Molt.—The prenuptial molt of the majority of individuals of this race takes place in January, February, and March. Three birds taken on March 10 are in full breeding plumage. Birds in all stages of the molt from nearly complete winter plumage to 90 or more per cent nuptial plumage have been taken in all these months. Molting birds, apparently adult, have been collected as late as June. Young molting into their first breeding plumage have been taken in May and June. Thus, as in the murres, the young molt later than the adults.

The annual molt takes place from August to October. One specimen taken on August 9 at Glacier Bay has already molted the remiges but not the rectrices, and the body plumage is about 50 per cent winter. Another bird taken on September 15 at Pavlof Bay is in approximately the same stage of molt of the wing and tail, but the body plumage is approximately 10 per cent winter. A bird taken on September 4 is still in complete nuptial plumage.

Remarks.—The pigeon guillemots of southern Alaska are intermediate between this form and *C. c. columba* but are somewhat closer to the present form in bill length and white in the wing. The line between *columba* and *adianta* is arbitrarily drawn just north of the Alaska Peninsula.

Range.—The coasts and islands of Washington, British Columbia, and Alaska north to and including the Alaska Peninsula and the inner Aleutians. These birds are apparently resident throughout their range.

Specimens examined.—269, of which 190 are adults in breeding plumage or nearly so.

ALASKA. Admiralty Island, Windfall Harbor, 2 (MVZ); Aleutian Islands: Akutan Island, Akutan Harbor; 1 (MVZ), Akutan Island; 1 (CAS), Unalaska Island, Captain's Harbor, 1 (CNM), 3 (AMNH), Unalaska Island, Unalaska Bay, 4 (MVZ), Unalaska Island, 1 (MVZ), 1 (USNM), 1 (CNHM), Unimak Island, 1 (CNHM); Canoe Bay, Alaska Peninsula, 1 (CHNM); Chicagof Island, Hooniah, 2 (MVZ), 2 (USNM); Dall Island, 1 (MCZ); Fitzgerald Island, Yakutat Bay, 3 (ROMZ); Forrester Island, 2 (LACM); Glacier Bay, 1 (MVZ), 4 (USNM); Holkham Bay, 1 (MVZ); Howkan, 1 (SD); Juneau, 1 (UMMZ); Keku Straits, 1 (USNM); Kodiak, 2 (USNM), 1 (UMMZ); Kodiak Island, 10 (MVZ), 4 (MMP), 4 (MCZ); Kukak Bay, 1 (USNM); Montague Island, Stockdale Harbor, 1 (MVZ); Pavlof Bay, 5 (CAS), 1 (ANSP), 1 (CM), 1 (CNHM); St. Lazaria Island, Sitka Bay, 2 (CAS); Seldovia, 3 (AMNH); Seldovia, Bird Island, 5 (AMNH); Seward, 3 (CM); Shumagin Islands; Eagle Harbor, 1 (USNM), Range Island, 1 (USNM), Ungald, 2 (SD), unspecified, 5 (ANSP); Sitka, 2 (MVZ), 1 (LACM), 8 (MCZ), 1 (AMNH); Wolf Rock, 3 (CM); Wrangell, 1 (USNM).

BRITISH COLUMBIA. Bear Island, 1 (AMNH), 1 (CNHM); Bella Bella, 2 (ROMZ); Burrard Inlet, 1 (ROMZ), 4 (AMNH), 3 (MCZ); Calvert Island, 7 (TTMcC); Georgian Gulf, 3 (MCZ); Gulf of Georgia, 1 (CNM); off Lund, 1 (TTMcC); off Pender Island, 1 (MCZ); Queen Charlotte Islands: Cox Island, Parry Passage, 2 (ANSP), Graham Island, 1 (UMMZ), Graham Island, Massett, 1 (MVZ), 3 (MMP), 1 (ANSP), Langara Island, 4 (MMP), 12 (ANSP), north end Langara Island, 5 (ANSP), Lucy Island, 1 (CNM), 2 (CNHM); Saturnia Island, 1 (MCZ); near Sointula, 1 (TTMcC); Swanson Bay, 1 (TTMcC). *Vancouver Island:* Barclay Sound, 1 (AMNH); Cape Scott, 2 (CNM); Clayoquot, 5 (CNM); Comox, 9 (MVZ), 1 (UMMZ), 1 (ROMZ), 5 (CNM), 5 (AMNH), 2 (MCZ), 5 (CM), 2 (CNHM); Departure Bay, 4 (CNM); English Bay, 1 (ROMZ); Esquimalt, 1 (MCZ); Nanaimo, 1 (MVZ, TYPE); Shushertie, 2 (CNM); Sidney, 1 (MCZ); Sidney Island, 1 (CNHM); Snake Island, Departure Bay, 5 (CNM); Victoria, 1 (AMNH); Yellow Point, Strait of Georgia, 1 (MVZ); unspecified, 1 (MVZ).

WASHINGTON. *Whatcom County:* Bellingham, 2 (UMMZ). *San Juan County:* Richardson, 1 (Dickey); Skipjack Island, 1 (MCZ). *Skagit County:* Guemas Island, 1 (WSM). *Snohomish County:* Everett, 6 (WSM); Marysville, 1 (WSM). *King County:* Puget Sound near Seattle, 1 (WSM). *Pierce County:* Tacoma, 3 (Dickey), 1 (CM). *Kitsap County:* Eagle Harbor, 3 (Dickey). *Clallam County:* 10 miles off Cape Flattery, 3 (USNM); Clallam Bay, 1 (Dickey); Lapush, 1 (USNM); Neah Bay, 1 (USNM); Port Angeles, 1 (UMMZ). *Jefferson County:* at sea off, 1 (Dickey); Port Townsend, 3 (USNM), 7 (CNHM). *Grays Harbor County:* Granville, 3 (USNM); Taholah, 1 (USNM). *County unspecified:* Puget Sound, 1 (MCZ), 1 (USNM), 1 (SD); Gatos (=Patos?) Island, 1 (MCZ); Portis Island, 1 (MCZ).

Cepphus columba columba Pallas

[*Uria grylle*]E, Latham, Index Ornith., 2, 1790:798.
Cepphus columba, Pallas., Zoogr. Rosso-Asiat., 2, 1811:348 (original description).
Uria columba, Keyserling and Blasius, Wirb. Europ., 1840:xcii.
Pseuduria columba, Sharpe, Handl. Birds, 1, 1899:131.
Uria columba columba, Hartert, Vögel Paläarkt. Fauna, 3, 1921:1777.
Cepphus columba columba, Alexander, Birds of the Ocean, 1928:248.
Cepphus grylle columba, Salomonsen, Göteborgs Kungl. Vetenskaps-Och Vitterhets-Samhälles Handlingar Sjätte Följden, Ser. B, Band 3, N:o 5, 1944:108.

Type locality.—Kamchatka and Bering Strait.

Description.—Wing length, 178 to 194 (186); tarsal length, 31.5 to 37.5 (35); culmen length, 29 to 35 (32); white on outer primary, when present, b to e; white on under wing coverts, very little to much. The combination of the short bill and the long wing distinguishes this race from the other pigeon guillemots.

Molt.—The spring molt is apparently not always complete in adults. Four July-taken birds with the speculum feathers lacking the dark tips of the first-winter plumage have from a few to nearly 50 per cent of the feathers of the under parts white. Two of these birds (MVZ 60583 and 60586) had enlarged gonads and were presumably breeding. Adults in complete breeding dress have been taken as early as May 16 and as late as August 29.

An adult taken September 1 has molted the remiges and is well along in the annual molt.

Remarks.—Intergrades with *adianta* along the coast of Alaska and presumably with *snowi* in southern Kamchatka or the northern Kuriles. The population of the inner Aleutians, which is intermediate between *columba* and *adianta,* probably intergrades with *kaiurka* in the central Aleutians, but this situation needs clarification.

Range.—Breeds along the coasts and islands of Bering Sea south to Kamchatka, the region about Nushagak, Alaska, and Nunivak and St. Matthews islands, also the Arctic coast of Siberia west to Cape Serdze. There is no definite breeding record for the Pribilof Islands, and although Palmer (1899:389) found them common near Walrus Island on June 13, 1890, later observers have not found them nesting on islands of that group.

At least the northern populations of this race move southward after the breeding season, reaching the Kuriles and possibly Hokkaido (Hachisuka *et al,* 1942:169). According to Preble and McAtee (1923:25), this species is common in winter on the Pribilofs. They give December 2 and May 26 as the dates of extreme occurrence.

Specimens examined.—58, of which 47 are adults in nuptial plumage or nearly so.

SIBERIA. Anadyr, 1 (AMNH); west side Bering Sea, 1 (MCZ); Cape Serdze, 1 (MCZ), 1 (ANSP); Chuk Ches Peninsula 2 (CM); East Cape, 2 (MCZ); Emma Harbor, 6 (USNM); Indian Point, 1 (AMNH); Plover Bay, 1 (Dickey); Straits of Seniavine, 2 (USNM).

ALASKA. Diomedes Islands, 1 (MCZ), 2 (USNM), 1 (CNHM); Kings Island, 1 (AMNH); Little Diomede Island, 2 (CNHM); Nome, 1 (MVZ); Nunivak Island, 1 (CAS); Nushagak, 2 (USNM); Pribilof Islands: St. Paul Island, 1 (USNM) unspecified, 1 (AMNH); St. Lawrence Island: Camp Collier, 2 (MVZ), Gambell, 6 (USNM), Punuk Island, 4 (MVZ), Sevoonga, 1 (MVZ), 10 miles east of Sevoonga, 2 (MVZ), unspecified, 3 (MVZ), 1 (CNHM); St. Matthew Island, 2 (MVZ), 2 (USNM); Sledge Island, 3 (MCZ), 1 (CM).

Cepphus columba kaiurka Portenko

Uria columba, Taczanowski, Bull. Soc. Zool. France, vii, 1882:398.
Cepphus columba, Stejneger, Proc. U. S. Nat. Mus., vii, 1884:222.
Pseuduria columba, Sharpe, Handl. Birds, 1, 1899:131.
Uria columba columba, Hartert, Nov. Zool., 27:130, 1920.
Cepphus columba columba, Alexander, Birds of the Ocean, 1928:248.

Cepphus columba kaiurka Portenko, Mitt. Zool. Mus. Berlin, 22, 1937:228 (original description).

Cepphus grylle kaiurka, Salomonsen, Göteborgs Kungl. Vetenskaps-Och Vitterhets-Samhälles Handlingar Sjätte Följden. Ser. B, Band 3, N:o 5, 1944:108.

Type locality.—Copper Island, Commander Islands.

Description.—Wing length, 169 to 183 (177); tarsal length, 31.0 to 35.5 (33.7); culmen length, 29.0 to 33.0 (31.2); white on outer primary, when present, c to e; white on under wing coverts, very little to much (1, none). The combination of the short wing and the small bill distinguishes this population from those of the other pigeon guillemots.

The spring molt is apparently prolonged in this form as in other guillemots, and the older birds usually acquire breeding plumage before the first-year birds. The first-winter white speculum feathers, with their large dark apical spots, are retained through the first breeding season. A young female (AMNH 748141) taken on May 11, 1912, at Bering Island has the under parts approximately 20 per cent dark. An adult female (AMNH 748147) taken on April 8, 1912, at Copper Island is 15 per cent dark below, whereas another adult female (AMNH 748142) taken on April 15, 1912, at Bering Island is in complete nuptial plumage. A first-year male and an adult male (MCZ 250775 and 250776), both taken on June 15, 1911, at Atka Island, still retain some white feathers on the under parts.

A pair of adults (AMNH 748137 and 748138) taken on October 14, 1910, at Bering Island have molted the rectrices, and the new remiges have not as yet attained their full length. The body plumage is 90 per cent winter.

Remarks.—The status of the pigeon guillemots of the central Aleutian Islands is not known, but presumably they are intermediate between *kaiurka* and the *adianta-columba* intergrades of the inner Aleutians.

Range.—Breeds on the Commander and western Aleutian islands (Kiska and Atka). According to Stejneger (1885:20), these birds make their appearance at the Commander Islands in mid-March. I have seen specimens from the breeding range taken from April 8 until October 25. The wintering grounds of this race are unknown.

Specimens examined.—28, of which 19 are adults in nuptial plumage or nearly so.

SIBERIA. Commander Islands: Bering Island, 12 (AMNH), 2 (USNM); Cooper Island, 1 (MCZ), 5 (AMNH).

ALASKA. Aleutian Islands: Atka Island, 1 (USNM), 2 (MCZ); Kiska Island; 3 (MCZ), Kiska Harbor, Kiska Island, 2 (USNM).

Cepphus columba snowi Stejneger

Cepphus grylle (?), Whitely, Ibis, 1867:210. [The wing measurement listed by Whitely (7.5 in. = 190 mm.) precludes the possibility of this bird's being *C. grylle.* Ogilvie-Grant (Cat. Birds Brit. Mus. Vol. 26:588, 1898) refers this bird to *snowi;* and Blakiston and Pryer (Ibis, 1878:211) refer it to *carbo.* It is probably either *snowi* or typical *columba;* but unless the specimen can be found, this must remain in doubt.]

Uria columba, Blakiston and Pryer, Trans. As. Soc. Japan, x, 1882:91.

Alca columba, Seebohm, Birds Japan, 1890:275.

Cepphus snowi Stejneger, Auk, 14, 1897:201 (original description).

Pseuduria snowi, Sharpe, Handl. Birds, 1, 1899:131.

Uria columba snowi, Hartert, Vögel Palaärkt. Fauna, 3, 1921:1778.

Cepphus carbo, Laing, Vict. Mem. Mus. Bull. 40, Biol. Ser. 9, 1925:8. (The two "black guillemots" seen at Broughton Bay, Shimishir Island, on July 13 almost certainly were of this form. Laing (*in litt.*) states: "The birds appeared *black.*... I doubt any white check-patches.")

C[epphus] c[olumba] snowi, Alexander, Birds of the Ocean, 1928:248.

Cepphus grylle snowi, Salomonsen, Göteborgs Kungl. Vetenskaps-Och Vitterhets-Samhälles Handlingar Sjätte Följden, Ser. B, Band 3, N:o 5, 1944:108.

Type locality.—Raikoke Island, Kurile Islands.

Description.—Wing length, 181 to 189 (184); tarsal length, 32.5 to 36.5 (34.1); culmen length, 29.5 to 35.5 (33.3); white in outer primary, none; white in under wing coverts, none to little.

In summer plumage *snowi* resembles typical *columba* except for the reduction or loss of white in the speculum. In some specimens the white may be reduced to five narrow bands, and in others to as few as two bands (fig. 18). According to Stejneger (1898:272), more than half the birds he saw in the Kuriles completely lacked white on the wings. Yamashina (1931:533) states that most specimens from the northern Kuriles show two thin white wing bars whereas most of those from the middle Kuriles lack white in the wing. This suggests a north-south gradient which would bear investigation.

One specimen in first-winter plumage is, except for the reduction of white in the speculum, similar to the corresponding plumage of the other races of *C. columba.* The dark crown, eye patch, and line running posteriorly from the eye suggest the corresponding plumage of *Uria aalge,* and the dark eye patch is just the opposite of the pattern in *C. carbo.*

The only molting specimen seen (UMMZ 96557) was taken on August 8, 1932, at Etroff Island, and is in worn nuptial plumage with a scattering of white feathers on the breast.

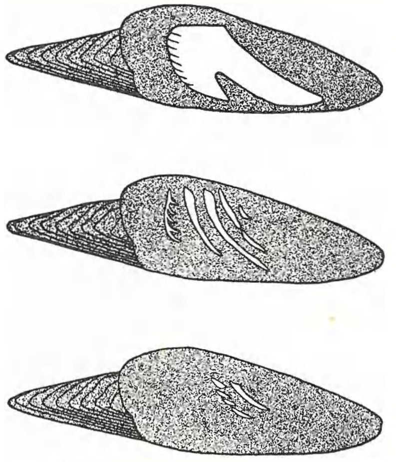


Fig. 18. Variation in the white in the speculum of *Cepphus columba.* Upper, *C. c. adianta,* UMMZ 99637, Juneau, Alaska; middle, *C. c. snowi,* USNM 159349, Mushir Rocks, Kurile Islands; lower, *C. c. snowi* (type), USNM 159351, Raikoke Island.

Remarks.—Presumably this form intergrades with *C. c. columba* in the northern Kuriles or southern Kamchatka. The relationship between *snowi* and *carbo* in the southern Kuriles remains to be determined. The limited evidence available suggests that they act like full species.

Range.—Breeds on the Kurile Islands from Paramushiru to Etorofu. Recorded from Paramushiru (Yamashina, 1929:96), Ekarma (Bergman, 1935:254), Mushir Rocks and Raikoke (Stejneger, 1897:201), North and South Ushishir (Stejneger, 1898:273), Ketoi (Seebohm, 1890: 276), Shimushiru (Clark, 1910:30), Uruppu (Stejneger, 1899:273), and Etorofu. Clark's statement (*loc. cit.*) that this form is common about Cape Lopatka, Kamchatka, has yet to be proved by collecting.

Winters south to southern Hokkaido (Muroran, January 25, 1949). The latter specimen is a bird of the year, and it is likely that the birds wintering south of the breeding range are largely first-year birds.

Specimens examined.—I have been able to locate only six specimens of *snowi* in this country. All these birds except the one from Muroran are adult birds in breeding plumage.

The two specimens listed by Salomonsen (1944:109) bear the same date (August 17, 1929) as those listed by Bergman (1935:254) from Ekarma and are almost certainly the same birds.

JAPAN. *Kurile Islands:* Mushir Rocks, 3 (USNM); Raikoke Island, 1 (USNM, type); Etroff (=Etorofu) Island, 1 (UMMZ). *Hokkaido:* Muroran, 1 (MCZ).

Cepphus carbo Pallas

Cepphus carbo Pallas, Zoogr. Rosso-Asiat., 2, 1811:350 (original description).
Uria carbo, Brandt, Bull. Acad. Sci. St. Petersb., 2, 1837:346.
Alca carbo, Schlegel, Mus. Pays Bas, 6, 1867:17, (not seen).
Pseuduria carbo, Sharpe, Handl. Birds, 1, 1899:131.

Type locality.—Kurile Islands.

Description.—Wing length, 188 to 217 (202); tarsal length, 35.0 to 39.5 (37.0); culmen length, 38.5 to 44.0 (41.6); white on outer primary, none; white on under wing coverts, none; a white area present around the eye and the base of the bill in both adult plumages.

The first-winter plumage resembles the adult winter plumage except that the white feathers of the under parts are tipped with varying amounts of dark and that the white markings around the eye and the base of the bill are lacking (Giglioli and Salvadori, 1887:593). In winter plumage (see pl. 2) the back is solid black, the feathers never being tipped with white as are those of the other species of guillemots.

The prenuptial molt of the adults appears to take place in January and February, at least in northern Japan. A bird from Tsugaru Straits taken on February 3, 1949, is in the early stages of the molt; whereas a bird from south of Hachinohe taken on February 17, 1949, has only two white feathers below, and a bird from Obuchi taken on the same date is in complete nuptial plumage. Three birds of the year taken in April and May are molting.

Remarks.—The black pigment fades from a sooty gray on the under parts and a shiny black on the upper parts in freshly taken specimens to a dull brownish sooty in specimens fifty or more years old. Similar fading is shown by specimens of the other guillemots but is perhaps less marked.

The present species overlaps *C. c. columba* in wing and tarsal length but not in bill length. The white markings on the head are unique in the genus, but a similar white eye patch is found in the puffins.

Two birds from Gichiga, northeastern Siberia, are relatively long-winged (210 and 212 mm.) and short-billed (36.5 and 39.5 mm.); but too little material is available to determine the significance of this apparent geographic variation.

Range.—Breeds on the coasts and islands of the seas of Okhotsk and Japan from the Taiganose Peninsula south to northern Honshu (Bentenjima at the mouth of Mutsu Bay, Hachisuka *et al.*, 1942:169) and northeastern Korea (Ran Island, and possibly the Kuk Islands, Austin, 1948: 136–137). Apparently breeds on the southern Kuriles (Kunashiri and Etorofu, Yamashina, 1931:533).

Nonbreeding birds have been taken in Kamchatka (MCZ 66677) (Cape Shipunski), and south to southern Honshu (Seven Isles of Izu) and Tsushima (Hachisuka, *et al., loc. cit.*). There is a sight record for Bering Island, Commander Islands, April 28, 1883 (Stejneger, 1885:23).

Specimens examined.—20, of which 16 are in nearly or complete adult nuptial plumage.

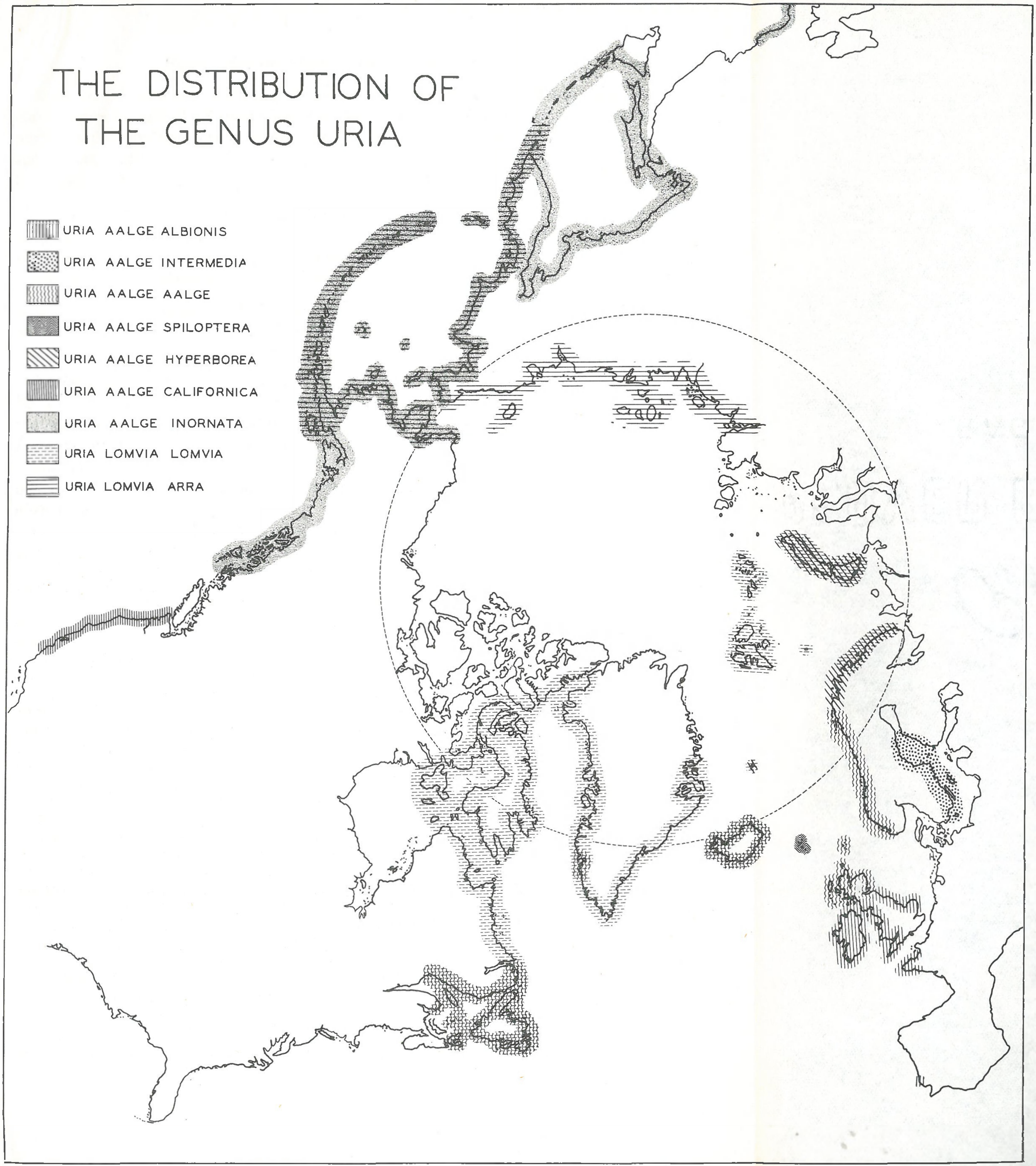
USSR. Siberia: Kamchatka, Cape Shipunski, 1 (MCZ); Gichiga, 2 (AMNH); vicinity of Vladivostok, 1 (MCZ).

JAPAN. *Hokkaido:* Akaiwa Tesio, 1 (AMNH); Teurejima, 3 (MCZ); Yagisiri Tesio; 1 (AMNH), Iburi, 1 (AMNH); Hakodate, 1 (AMNH); unspecified, 3 (AMNH); Tsugaru Straits, 1 (USNM). *Honshu:* south of Hachinohe, 1 (USNM); Iwate Prefecture, Obuchi, 1 (MCZ); Sendai, 1 (ANSP).

KOREA. Gensan, 1 (AMNH); unspecified, 1 (AMNH).

Genus **Uria** Brisson

Uria Brisson, Ornith., 1760, 1:52; 6:70. Type by tautonymy *Uria* Brisson = *Colymbus aalge* Pontoppidan.



To accompany R. W. Storer, "A Comparison of Variation, Behavior, and Evolution in the Sea Bird Genera Uria and Cepphus," Univ. Calif. Publ. Zoöl., Vol. 52, No. 2

Fig. 19. The distribution of the species and subspecies of the genus *Uria*.

Remarks.—There are two living species of murres, *Uria aalge* and *Uria lomvia.* Each occurs in both the Atlantic and Pacific oceans, *Uria lomvia* having the more northern distribution. There is considerable overlap in the ranges of these two species; and although birds of the two species nest side by side in many areas, no hybrids are known.

Uria aalge albionis Witherby

Uria aalge albionis Witherby, Brit. Birds, 26, 1923:324 (original description).
Uria aalge helgolandica Lönnberg, Fauna och Flora, 1923:161.

Type locality.—Flamborough, Yorkshire, England.

Description.—Back palest of all subspecies; wing length, 189 to 208 (199.4); tarsal length, 32.5 to 39.0 (36.4); culmen length, males, 42.5 to 51.0 (47.5), females, 43.0 to 50.0 (46.9); bill depth, males, 11.8 to 14.2 (13.04), females, 12.1 to 13.7 (12.97); under wing coverts, white in 80 per cent of all specimens examined.

Remarks.—Intergrades with *U. a. aalge* in southern Scotland. The series in the Museum of Comparative Zoölogy from County Mayo, Ireland, is not typical, showing some evidence of intergradation with *U. a. spiloptera.* The three specimens from Heligoland in the American Museum are indistinguishable from the English birds. The dark shaft streaks which Lönnberg used to separate the Heligoland birds can be found, as Salomonsen (1944:31) pointed out, in faded birds of *albionis* and other races.

Range.—Breeds along the coasts of the British Isles from the Farne Islands and Ailsa Craig south, Heligoland, and from Brittany south to the Berlengas Islands, Portugal. In winter, individuals of this race, largely first- and second-year birds, commonly move as far west as southwestern Sweden and as far south as the Bay of Biscay. *U. aalge* has been recorded from the Mediterranean Sea (Saunders, 1871:402) and the Canary Islands (Bolle, 1857:248); but these records were made before *U. a. albionis* was described, and are not definitely allocated as to subspecies.

Specimens examined.—75, of which 39 are adults in nuptial plumage.

ENGLAND. *Cornwall:* Scilly Isles, 1 (AMNH). *Devon:* Kingsbridge, 2 (CAS). *Dorset:* Weymouth, 1 (AMNH). *Hampshire:* Bournemouth, 3 (AMNH); Freshwater, Isle of Wight, 1 (AMNH. *Lancashire:* Blackpool, 1 (CNHM); Fleetwood, 1 (Dickey), 2 (CNHM), 2 (ROMZ); Rossal, 2 (CNHM). *Northumberland:* Farne Islands, 1 (CNM); North Sunderland, 1 (AMNH). *Yorkshire:* Bantham Sands, 1 (CM); Flamborough, 2 (ROMZ); Scarborough, 2 (AMNH); Thurlstone Sands, 1 (USNM).

IRELAND. *County Donegal:* Dunfanaghy, 1 (AMNH). *County Dublin:* Dublin Waters, 2 (MCZ). *County Kerry:* Ballyferriter, 3 (MCZ); Blasket Islands, 1 (MCZ). *County Mayo:* Belmullet, 1 (ROMZ), 5 (AMNH); North Mayo, 5 (MCZ); unspecified, 3 (MCZ). *County Wexford:* Saltee Islands, 1 (AMNH). *County unspecified:* 1 (MCZ).

SCOTLAND. *Argyll:* Mull, 1 (AMNH). *Caithness:* unspecified, 1 (MCZ). *East Lothian:* Haddington, 3 (AMNH). *Inverness:* Sconser, Skye, 1 (AMNH). *Moray:* Tugnet, 1 (MCZ). *Ross and Cromarty:* Loch Alsh, 1 (AMNH); Tarbat Ness 1 (MCZ); Wexford, 1 (MCZ). *County unspecified:* Firth of Forth, 2 (ROMZ); 1 (MVZ); 1 (USNM).

WALES. *Anglesey:* Holyhead, 1 (CNHM). *Pembrokeshire:* Tenby, 1 (AMNH); unspecified, 1 (CM). *County unspecified:* The Brides, 1 (ROMZ).

GERMANY. Heligoland, 3 (AMNH).

THE NETHERLANDS. Scheveningen, 1 (MCZ); Ymuiden, 1 (MCZ).

FRANCE. Cherbourg, 1 (MCZ); Le Havre, 1 (AMNH), 3 (USNM).

Uria aalge intermedia Nilsson

Uria intermedia Nilsson, Skandinav. Fauna Fogl., Ed. 2, 2, 1835:506 (original description).

Type locality.—The Baltic Sea.

Description.—Back color and size intermediate between *albionis* and *aalge;* wing length, 193 to 211 (200); tarsal length, 34.5 to 39.0 (36.7); culmen length, males, 45.0 to 51.0 (48.8), females, 43.0 to 48.0 (45.6); bill depth, males, 12.9 to 14.7 (13.7), females, 13.8 to 14.8 (14.4); under wing coverts, pure white or with shaft streaks or few small spots.

Remarks.—The Baltic form is the least differentiated race of *Uria aalge.* It is also the only race of which we can estimate the age; for if *U. a. intermedia* arose in the Baltic, it must have evolved in the last 10,000 years, since the Scandinavian ice cap melted (see discussion of *Cepphus g. grylle,* p. 194).

Because individuals of both *U. a. aalge* and *U. a. albionis* winter off the coasts of Norway and western Sweden, it is likely that colonization of the Baltic was effected by both these forms and that the present intermediate population has resulted from hybridization followed by stabilization of characters.

Range.—Breeds on islands of the Baltic Sea from near Bornholm north to the Gulf of Bothnia. More widely distributed in winter, reaching the Kattegat.

Specimens examined.—10, all in nuptial plumage.

SWEDEN. Gotland, 8 (MCZ); Stora Karlsö, 2 (AMNH).

Uria aalge aalge (Pontoppidan)

Colymbus Aalge Pontoppidan, Danske Atlas, Vol. 1, 1763:321 and pl. 26 (original description).

Type locality.—Iceland.

Description.—A dark-backed form. Wing length, 193 to 219 (mean, 202 to 208); tarsal length, 35.0 to 41.5 (38.1); culmen length, males, 41.5 to 49.5 (44.6 to 47.2), females, 39.0 to 51.5 (43.2 to 44.1); bill depth, males, 12.6 to 16.0 (13.7 to 13.8), females, 12.5 to 14.5 (13.3); under wing coverts, mostly pure white, many with shaft streaks or few spots, a few heavily spotted.

Remarks.—Four somewhat isolated populations have been assigned to this subspecies by Salomonsen and others. These are, from west to east, the birds from eastern North America, those from Iceland, those from Scotland and the Hebrides, and those from southern Norway. These populations, although not differing from each other sufficiently to warrant taxonomic separation, are not identical and seem to be the results of three separate origins. The birds from southwestern Scandinavia are intermediate (except in back color) between *U. a. hyperborea* of northern Norway and *U. a. albionis* of the southern British Isles and Heligoland. Similarly, the murres of northern Scotland are intermediate between *albionis* and *U. a. spiloptera* of the Faeroes. These two populations of *U. a. aalge* may have arisen through secondary intergradation of the adjacent forms, and thus have come to resemble the birds from North America and Iceland.

It is also possible that typical *aalge* is close to the ancestral stock of the species, that *albionis, spiloptera,* and *hyperborea* have arisen from it, and that the variation among the populations may be owing to divergence. At present it is impossible to say which hypothesis is correct.

U. a. aalge intergrades with *U. a. spiloptera* in the Shetlands and with *U. a. hyperborea* along the coast of Norway in the region of the Vesteraalen.

Range.—Breeds along the coast of North America from Nunarsuk Island to Cape St. Marys, southern Newfoundland (Johnson, 1940), in southwestern Greenland (Sukkertoppen District), Iceland, Scotland, and in Norway north at least to the Vesteraalen, where it intergrades with *U. a. hyperborea.* In winter, individuals of the European populations move south to Denmark and France. Records for the Mediterranean Sea and Canary Islands (see *antea*) may apply to this subspecies. In North America few winter south of Canadian waters, although this form has been taken as far south as New Jersey.

Specimens examined.—146, of which 97 are adults in nuptial plumage.

NEWFOUNDLAND LABRADOR. Anse Eclair, 1 (USNM); Battle Harbor, 2 (UMMZ); Davis Inlet, 1 (USNM); Lance au Loup, 1 (MVZ), 1 (CNHM), 2 (ROMZ), 2 (MCZ), 2 (AMNH); Pompey Island, Sandwich Bay, 1 (USNM); Sandwich Bay, 1 (USNM).

"LABRADOR." Roundhill Island, 1 (USNM); unspecified, 1 (ROMZ), 1 (MCZ).

NEWFOUNDLAND. Cabot Island, Bonavista Bay, 1 (USNM); Cape St. Marys, 19 (MCZ); Custlett, 1 (MCZ); Funk Island, 1 (USNM); Green Island, Witless Bay, Avalon Peninsula, 3 (USNM); unspecified, 1 (CNHM).

QUEBEC. *Anticosti Island:* Gull Bay, East Cape, 1 (CNM). Bonaventure Island, Percé, 1 (ROMZ), 5 (CNM); Canadian Labrador: Beacon Isle, Coacoachu Bay, 1 (MCZ), Cape Whittle, 1 (MCZ), St. Marys Is., 1 (ChAc), Wolf Bay, 1 (MVZ), 1 (ChAc), Carnegie Museum, 3*; Gannet Rock, Gulf of St. Lawrence, 2 (MCZ); Magdalen Islands: Bird Rock, 4 (CNHM), 6 (MCZ), 3 (AMNH), 2 (USNM), 3 (CM), Grosse Isle, Fauriel, 1 (CM), unspecified, 1 (CNHM); Percé, 5 (CNM), 1 (SD); Carnegie Museum*, 7.

NEW BRUNSWICK. Grand Manan, North Head, 5 (CNHM), 6 (CNM).

MAINE. *Cumberland County:* Portland, 1 (AMNH). *County unspecified:* 2 (MCZ).

NEW JERSEY. *Monmouth County:* Asbury Park, 1 (AMNH).

GREENLAND. Godthaab, 1 (ROMZ), 1 (USNM).

ICELAND. Alftatunga myrasysla, 1 (MCZ); Brede Bugt, off Bjortonga, 2 (AMNH); Denmark Strait, 1 (MCZ), 2 (ANSP); north of Grimsö, 1 (ROMZ); Havet (= the sea), 1 (CNHM), 1 (AMNH); Helsingoër (= Denmark?), 1 (AMNH); Husavik, 1 (UMMZ), 1 (MMP); unspecified, 2 (AMNH); Arctic Ocean north of Iceland, 1 (ROMZ).

NORWAY. Christiansund, 1 (AMNH); *Vesteraalen:* Längenö, Nyken, 1 (AMNH); Melbo, 1 (AMNH).

ENGLAND. *Devon:* Kingsbridge, 1 (ROMZ). *Dorset:* Weymouth, 1 (AMNH). *Hampshire:* Bournemouth, 1 (AMNH). *Lancastershire:* Fleetwood, 1 (ROMZ). *Norfolk:* King's Lynn, 1 (AMNH). *Northumberland:* Alnmouth, 1 (AMNH). *Sussex:* Brighton, 2 (AMNH). *Yorkshire:* Filey Cliffs, 1 (AMNH).

IRELAND. *County Dublin:* Dublin Bay, 1 (MCZ). *County Kerry:* Ballyferriter, 3 (MCZ).

SCOTLAND. *Orkneys:* near Scapa Bay, 1 (USNM); unspecified, 1 (MCZ).

BRITISH ISLES. Unspecified, 1 (ROMZ).

THE NETHERLANDS. Scheveningen, 1 (MCZ); Ymuiden, 1 (MCZ).

Uria aalge spiloptera Salomonsen

Uria aalge spiloptera Salomonsen, Ibis, 1932:129 (original description).

Type locality.—The Faeroes.

Description.—The darkest-backed race, under wing coverts heavily spotted, flank streaks very heavy. Wing length, 190 to 214 (204.8); tarsal length, 35.5 to 38.0 (36.6); culmen length, males, 44.0 to 53.5 (47.2), females, 47.0 to 50.0 (48.0); bill depth, males, 12.4 to 13.3 (13.0), females, 12.6 to 13.1 (12.9); under wing coverts heavily spotted in approximately 80 per cent of the population.

Range.—Breeds on the Faeroes. The breeding birds of the Shetland Islands approach this form.

Specimens examined.—13, of which all are adults in nuptial plumage.

FAEROES. Troldhoved, 1 (ROMZ); unspecified, 8 (MCZ), 1 (AMNH).

"SCHWEDEN." 3 (MCZ).†

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* Because of his forthcoming work on the birds of the Ungava Peninsula, Mr. W. E. C. Todd has requested me not to publish the exact localities of birds in the Carnegie Museum from that region.

† Mus. Comp. Zoöl. numbers 186241, 186242, and 186243 are labeled "Schweden" but are obviously from the Faeroes. All the birds have darkly streaked flanks, heavily spotted under wing coverts, and are much darker-backed than the Gotland series. Furthermore, all are "ringed" murres, a variant which is very rare in the Baltic. These birds are without the original labels, bearing only those of the dealer. The three skins are the same "make" of skin as Mus. Comp. Zoöl. numbers 186247, 186248, and 186249, which are labeled "Faeroe Islands" and were taken on the same date as number 186247 (June 4, 1894).

Uria aalge hyperborea Salomonsen

Uria aalge hyperborea Salomonsen, Ibis, 1932:130 (original description).

Type locality.—Bear Island.

Description.—Color as in *U. a. spiloptera*, but wing longer and bill much heavier. Wing length, 205 to 218 (211)*; culmen length, males, 46 to 48 (47)*, females, 42 to 47 (44)*; bill depth, males, 17.5 to 18.0 (17.8)*, females, 15 to 16 (15.8)*; under wing coverts, heavily spotted in most specimens.

Remarks.—A high-arctic form paralleling *U. lomvia* in its fairly large size and short, deep bill. Intergrades with *U. a. aalge* in northern Norway.

Range.—Bear Island, Norway north of the Vesteraalen, the Murman Coast, and Novaya Zemlya (Krasovski, 1937). Wintering grounds not definitely known.

Specimens examined.—4, of which 2 are adults in nuptial plumage.

BEAR ISLAND. 1 (AMNH).

U.S.S.R. Archangel, Tokanga, 2 (MCZ); Murman Coast, 1 (MCZ).

Uria aalge californica (Bryant)

Catarractes californicus Bryant, Proc. Boston Soc. Nat. Hist., 8, 1861:142 (original description).

Type locality.—Farallon Islands, California.

Description.—A fairly dark race, color about as in *U. a. aalge* but throat perhaps slightly redder brown; wing length, 194 to 220 (209); tarsal length, 35.0 to 41.5 (38.2); culmen length, males, 43.0 to 53.5 (49.2), females, 41.5 to 52.0 (47.1); bill depth, males, 12.5 to 15.6 (14.0), females, 12.5 to 15.2 (13.8); under wing coverts white or with few large or medium-sized spots, all dark in approximately 2 per cent of the population.

Remarks.—The Pacific forms of *U. aalge* are not, as Salomonsen states (1944: 54), almost as pale as *U. a. intermedia* or *albionis*. They are nearer *U. a. aalge* in coloration.

Murres from Washington and Oregon are intermediate between *californica* and *inornata* but are somewhat nearer the former. Salomonsen's restriction of *californica* to the Farallon Islands is quite incorrect.

Range.—The coasts of Washington, Oregon, and California, south at least to Hurricane Point, Monterey County (formerly to San Miguel Island). Largely sedentary although there seems to be some northward movement on the part of young birds of at least the Oregon population. Rare in winter to San Diego County, California.

Specimens examined.—354, of which 179 are adults in nuptial plumage or nearly so.

WASHINGTON. *Whatcom County:* Bellingham, 3 (UMMZ). *Snohomish County:* Marysville, 3 (MMP). *Pierce County:* Commencement Bay, Tacoma, 1 (MMP). *Clallam County:* Cape Flattery, 1 (USNM); Lapush, 1 (WSM). *Jefferson County:* at sea off, 1 (Dickey). *Grays Harbor County:* Granville, 2 (USNM); Grays Harbor, 1 (Dickey); Westport, 4 (WSM), 1 (Dickey); unspecified, 1 (WSM). *Pacific County:* Ilwaco, 1 (USNM); Long Beach, 1 (SGJ), 2 (USNM); Ocean Park, 1 (USNM).

OREGON. *Tillamook County:* Barview, 1 (SD); Cape Lookout, 3 (MMP), Netarts; 1 (Dickey), 1 (MMP), 1 (CNHM), 5 (SD); Rockaway, 1 (MMP); Three Arch Rocks, 2 (ENH). *Lincoln County:* Delake, 3 (SGJ), 1 (SD); Depoe Bay, 1 (MMP); Newport, 1 (SGJ), 1 (MMP), 1 (CNHM); Otis, Two Arch Rocks, 4 (UOr); Taft, 1 (SD).

CALIFORNIA. *Del Norte County:* Crescent City, 1 (MCZ). *Humboldt County:* Eureka, 1 (MCZ). *Sonoma County:* Bodega, 1 (USNM); Bodega Bay, 1 (PUC); 1 mile N Bodega Head, 1 (PUC). *Marin County:* Angel Island, 1 (MMP); Bolinas Beach, 1 (CAS); Dillon Beach, 1 (JRA); Point Reyes, 1 (ROMZ), 7 (MCZ), 4 (AMNH); Tiburon, 2 (CAS); Tomales Bay, 2 (MCZ);

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* Data from Salomonsen (1944).

unspecified, 1 (CAS). *Alameda County:* Berkeley, 1 mile W yacht harbor, 1 (MVZ); Hayward, bay shore in vicinity of, 1 (CAS). *San Francisco County:* Farallon Islands, 2 (MVZ), 4 (CAS), 4 (MCZ, including cotype), 4 (USNM, including cotype), 1 (UMMZ), 5 (AMNH), 1 (ROMZ); San Francisco, 1 (CAS), 1 (ROMZ), 1 (CNM), 2 (USNM), 1 (MCZ); South Farallon Island, 1 (MVZ). *San Mateo County:* Mussel Rock, 1 (CNHM); San Mateo, 1 (CAS). *Santa Cruz County:* Moore's Beach, 3 miles SW Santa Cruz, 1 (MVZ); Santa Cruz, 5 (MVZ), 2 (MCZ). *Monterey County:* Carmel, 1 (CNHM), Carmel Bay, 2 (R. Ellis), 1 (CNHM); Monterey, 6 (MCZ), 14 (CNHM), 1 (MVZ), 1 (USNM), 7 (AMNH); Monterey Bay, 26 (MVZ), 1 (R. Ellis), 98 (CAS), 4 (MMP); Moss Landing, 5 (CNHM); Pacific Grove, 22 (CAS), 6 (Dickey), 3 (MCZ), 1 (CNHM), 1 (ROMZ), 16 (AMNH); Point Pinos, vicinity of, 6 (MVZ), 3 (CAS). *Santa Barbara County:* San Miguel Island, 3 (LACM), 1 (Dickey). *Los Angeles County:* Ballona, 1 (CAS); Redondo Beach, 1 (LACM); Santa Monica, 1 (CNHM), Venice; 1 (LACM). *Orange County:* Newport Beach, 1 (Dickey). *San Diego County:* Cardiff, 1 (SD). *County unspecified:* San Francisco Bay, 1 (CAS), 1 (MCZ).

Uria aalge inornata Salomonsen

Uria aalge inornata Salomonsen, Ibis, 1932: 128 (original description).

Type locality.—St. Matthew's Island, Bering Sea.

Description.—Similar to *U. a. californica*, but wing longer and back slightly paler; wing length, 200 to 230 (means 214.5 to 220.5); tarsal length, 35 to 41 (37.8 to 38.9); culmen length, males, 43.5 to 53.0 (46.5 to 49.0), females, 42 to 52 (45 to 47); bill depth, males, 12.6 to 16.2 (13.9 to 14.9), females, 12.4 to 15.9 (13.4 to 14.2); under wing coverts, white in almost all individuals.

Remarks.—This form parallels *U. a. hyperborea* in having a relatively short, deep bill. The geographic variation in the common murres of the Pacific is not as simple as the recognition of two subspecies would indicate. Wing and tarsal lengths increase in a cline from California to southern Alaska, then with bill length they decrease suddenly from southern to northern Alaska. Description of the population of southern Alaska would point up this variation, but is out of the question because the differences between the two Alaska populations are too slight.

Range.—Breeds from Point Hope, Alaska, south to British Columbia and northern Japan and Korea, and on the islands of Bering Sea south to the Aleutian and Commander islands. In winter some individuals, largely first-year birds, move south as far as central California.

Specimens examined.—252, of which 109 are adults in breeding plumage or nearly so.

Although it is possible to determine certain large first-year birds wintering off California as *U. a. inornata*, I hesitate to identify any young murres wintering in British Columbia waters as *U. a. californica*, although evidence from banding indicates that at least part of the Oregon population winters there. The breeding birds of Oregon and British Columbia are both intermediate between *U. a. californica* and *U. a. inornata*, and the amount of overlap in size between these populations is too great to permit subspecific identification of birds of the mixed wintering population. Consequently, all wintering birds taken in British Columbia have been arbitrarily listed under *U. a. inornata*.

ALASKA. Aleutian Islands: Atka, 1 (CNM), Attu, 1 (USNM), Egg Island, 1 (MVZ), Unalaska Island, 2 (USNM), Unimak Island, False Pass, 1 (MCZ); Barrow, 1 (MMP); Bering Sea, 1 (MCZ); Bethel, 2 (CNHM); Bluff City, 1 (CNHM); Cape Thompson, 3 (MVZ); Chamisso Island, 2 (USNM); Cordova, 3 (CNM); Dall Island, small island off, 4 (LACM); Diomedes Islands, 1 (AMNH); Forrester Island, 1 (SD); Glacier Bay, 1 (USNM); Homer, 3 (AMNH); Hooper Bay, 1 (USNM); ?Kamchatka Peninsula, 1 (Dickey); Keku Straits, 1 (USNM); Kings Island, 1 (MVZ); Knight Island, Drier Bay, Prince William Sound, 1 (MVZ); Knik Station, Cook Inlet, 1 (USNM); Kodiak, 3 (USNM); St. Paul (= Kodiak) 1 (USNM); Kodiak Island, 1 (MCZ); Little Diomede Island, 2 (CNHM); Nunivak Island, 1 (CAS); Nushagak, 3 (USNM); Oliver Inlet, 2 (USNM); Pribilof Islands: Bering Sea near, 1 (MVZ), St. George

Island, 4 (USNM), St. Paul Island, 2 (ANSP), 4 (USNM), Walrus Island, 2 (MCZ), 1 (CNM), 1 (CAS), 1 (USNM), unspecified, 1 (USNM); Prince of Wales Island, Craig, 1 (LACM); St. Lawrence Island: Camp Collier, 1 (MVZ), 10 miles E Sevoonga, 2 (MVZ); St. Matthew's Island, 3 (USNM, including type); St. Michael, 2 (MVZ), 1 (USNM); Seldovia, Bird Island, 9 (AMNH); Sitka, 1 (LACM), 1 (AMNH), 2 (MCZ), 2 (MVZ); Sitka Bay, 1 (LACM); Sledge Island, 1 (MCZ); Stephens Passage, 1 (USNM); Tigara, Point Hope, 2 (MVZ); Windfall Harbor, Admiralty Island, 1 (MVZ); Wrangell, 1 (LACM), 9 (USNM); Yakutat, 1 (CNM); "Yukon," 1 (MVZ).

BRITISH COLUMBIA. Georgian Gulf, 1 (MCZ), 4 (CNM); Horseshoe Bay, 1 (ROMZ); Howe Sound, 1 (ROMZ); Pender Island, 1 (MCZ); Port Simpson, 3 (MVZ), 1 (CNM); Prince Rupert, 1 (ROMZ); Queen Charlotte Islands: Cox Island, Parry Passage, 1 (ANSP), Graham Island, off west coast of, 17 (ANSP), Langara Island, 1 (ANSP), Masset, 4 (MMP), west coast, 2 (CNM); Vancouver, 1 (AMNH); Vancouver Island: Bird Islands, Barcley Sound, 1 (CNM), Cape Scott, 5 (CNM), Clayoquot, 14 (CNM), Comox, 5 (MVZ), 2 (MCZ), 3 (AMNH), Departure Bay, 1 (MMP), 12 (CNM), Kildonan, Uchucklesit Harbor Barkley Sound, 3 (CNM), Ladysmith, 1 (MVZ), Nahmint Bay, Alberni Canal, Barkley Sound, 1 (CNM), Sooke, 1 (MVZ), Tofino, 2 (ROMZ).

WASHINGTON. *Whatcom County:* Bellingham, 2 (UMMZ). *Snohomish County:* Marysville, 1 (MMP). *Kitsap County:* Eagle Harbor, 1 (Dickey).

OREGON. *Tillamook County:* Netarts, 1 (UMMZ). *Lincoln County:* Delake, 1 (MMP).

CALIFORNIA. *San Francisco County:* San Francisco, 3 (CAS), 1 (ROMZ). *Monterey County:* Monterey, 1 (AMNH); Monterey Bay, 8 (MVZ), 1 (R. Ellis), 12 (CAS); Pacific Grove, 2 (CAS), 1 (Dickey), 1 (CNHM), 6 (AMNH); Point Pinos, vicinity of, 1 (CAS).

SIBERIA. Petropaulovski, Kamchatka, 1 (CNM); Commander Islands: Bering Island, 3 (USNM), 3 (MCZ), Copper Island, 1 (AMNH).

JAPAN. Hokkaido, 2 (AMNH); Robber Islands (= Seehund Inseln), near Sakhalin, 1 (AMNH).

Uria lomvia lomvia (Linnaeus)

Alca Lomvia Linnaeus, Syst, Nat. ed. 10, pt. 1, 1758:130 (original description).
Uria lomvia arroides Portenko, Mitt. Zool. Mus. Berlin, 22, 1937:226.

Type locality.—Greenland.

Description.—Wing length, 204 to 234 (means 214 to 222); tarsal length, 33.0 to 40.5 (36.1 to 37.6); culmen length, males, 30.5 to 41.0 (37.5 to 38.6), females, 33.0 to 41.5 (35.3 to 36.7); bill depth, males, 12.7 to 15.6 (13.8 to 14.8), females, 12.0 to 15.8 (13.3 to 14.1).

Remarks.—I have seen only one specimen from Franz Josef Land (topotypical of "*U. l. arroides*"). This bird (MCZ 158778, an adult female taken on June 12, 1914) does not differ from specimens of *U. l. lomvia* of comparable age and wear, except that some of the underwing coverts have apical spots and the flank streaks are somewhat heavier. It is not possible on the basis of this specimen to pass judgment on the validity of "*arroides*," but I suspect that it will not prove tenable.

The range of *U. l. lomvia* is separated from that of *U. l. arra* by the same barrier (the archipelago west of Ellesmere, Devon, and Baffin islands) that separates *C. g. ultimus* from *C. g. mandtii.*

Range.—Breeds along the coasts of North America (south to the Gulf of St. Lawrence), Greenland, Iceland, Jan Mayen, Bear Island, Spitsbergen, Franz Josef Land, the Murman Coast, and Novaya Zemlya. Largely sedentary, but in some years irruptive flights occur over northeastern North America, apparently originating from the area of Hudson Bay (Fleming, 1907).

Specimens examined.—417, of which 149 are adults in nuptial plumage or nearly so. Large numbers of young birds in winter plumage in the rest of the sample were taken during "flight" years. This makes the proportion of breeding adults very small in relation to samples of other forms.

Northwest Territories, Franklin. *Baffin Island:* 62° 24′ N., 65° W., 2 (AMNH), 1 (USNM); 64° N., 65° W., 1 (AMNH); Bowdoin Harbor, 4 (MCZ); Cape Dorset, 3 (CNM); Davis Strait, 1 (USNM); Gordon Bay (= Andrew Gordon Bay), 1 (CNM); Lake Harbor, 2 (ROMZ); Resolution Island, 1 (CNHM); 20 miles W Hatton Headland, Resolution Island, 4 (AMNH). *Devon Island:* Dundas Harbor, 1 (CNM). *Ellesmere Island:* Cobourg Island, 75° 40′ N., 78° 58′ W., 1 (MCZ); Craig Harbor, 1 (CNM). *Somerset Island:* Port Leopold, 8 (ROMZ); SE part, 1 (ROMZ).

Northwest Territories, Keewatin. Hudson Bay: Depot Islands, 1 (ROMZ); Southampton Bay, 1 (AMNH).

Quebec. Bonaventure Island, Percé, 2 (CNM). *Canadian Labrador:* Bonne Esperance, 5 (CNM); Stick Point near Bonne Esperance, 1 (CNM); Cape Wolstenholm, 3 (CNM); Ile aux Grues, 2 (CNHM). *Magdalen Islands:* Bird Rock, 4 (CNHM), 13 (MCZ), 3 (AMNH), 1 (USNM), 9 (CM); unspecified, 3 (CNHM). Point Fortune, 1 (SD); Quebec, 1 (AMNH). *Ungava:* Erik Cove, 2 (MVZ); Fort Chimo, 1 (CNHM), 2 (USNM); Leaf Bay, Ungava Bay, 2 (CNM); Carnegie Museum, 6.* Wolstenholme, 1 (CNM).

Newfoundland. Canada Bay, 1 (USNM); Cape Bauld, off, 2 (USNM); Cape St. Marys, 2 (MCZ), 1 (USNM); Codroy, 1 (MCZ); Custlett, 1 (MCZ); St. Johns, 1 (USNM); Newfoundland Labrador: Groswater Bay (= Lake Melville), 1 (USNM), Lance au Loup (= Loup Bay), 2 (MCZ), Outer Gannet Island, 1 (USNM), Red Bay, 10 (UMMZ), 1 (MMP).

Nova Scotia. Dover, 2 (CNHM); Halifax, 2 (CNHM); Sable Island, 2 (AMNH); Truro, 2 (ROMZ); 2 miles E Wolfville, 1 (MMP); Yarmouth, 2 (MCZ).

New Brunswick. Grand Manan, 1 (CNHM), 4 (MCZ); North Head, Grand Manan, 16 (CNM), 1 (MCZ), 1 (CAS); Jamseg River, 1 (MCZ); Keswick River, 1 (SD); Miscou Island, Wilson's Point, 2 (CNHM), 2 (CNM), 1 (SD).

Ontario. Arnprior, Madawaska River, 1 (CNM); Dunnville, 1 (ROMZ); Etobicoke, 1 (ROMZ); Hamilton, 1 (ROMZ); Hamilton Bay, 1 (ROMZ); Henderson, 1 (ROMZ); Kingston, 1 (CNM); Lake Ontario, 2 (ROMZ); London, 1 (ROMZ); Ottawa, 2 (CNM); Ottawa River, near Ottawa, 2 (CNM); Parry Sound, 1 (ROMZ); Point Pelee, 1 (CNM); Port Sidney, Muskoka, 1 (ROMZ); Prescott County, 1 (AMNH); Prince Edwards County, 1 (CNM); on the Rondeau, 1 (CNM); Toronto, 27 (ROMZ), 1 (CAS), 1 (CNM), 1 (MCZ), 2 (USNM); Wakefield, 1 (CNM).

Michigan. *Wayne County:* Gibraltar, 1 (UMMZ); Windmill Point, Grosse Pointe, 1 (UMMZ).

Maine. *Cumberland County:* Seguin Island, 1 (ROMZ). *Hancock County:* Cranberry Island, 1 (CAS). *Knox County:* Indian Island, 1 (USNM); Matinicus Island, 3 (MCZ). *Oxford County:* Lake Umbagog, (MCZ); B. Pond near Lake Umbagog, 1 (MCZ). *Penobscot County:* Bangor, 3 (CNHM), 2 (AMNH). *Washington County:* Eastport, 1 (CNHM), 1 (AMNH). *County unspecified:* 1 (AMNH).

New Hampshire. *Belknap County:* Lake Winnisquam, 2 (MCZ). *Rockingham County:* Boars Head, 1 (USNM); Hampton, 1 (USNM).

Massachusetts. *Barnstable County:* Cape Cod, 1 (MCZ); Monomoy Island, 1 (MCZ); North Eastham, 1 (MCZ); Provincetown, 1 (MCZ), 3 (AMNH); Woods Hole, 1 (MCZ), 2 (USNM); Yarmouth, 1 (MCZ), 1 (SD); Yarmouthport, 1 (Dickey). *Dukes County:* Vineyard Haven, 4 miles south, 1 (UMMZ). *Essex County:* Ipswich, 1 (MCZ), 1 (AMNH); Nahant, 1 (UMMZ); Swampscott, 2 (MCZ), 1 (USNM). *Nantucket County:* Nantucket, 1 (MCZ). *Norfolk County:* Canton, 1 (MCZ); Quincy, 1 (MCZ). *Plymouth County:* Cohasset, 3 (MCZ); Plymouth, 1 (MCZ); Scituate, 1 (MCZ); South Plymouth, 1 (MCZ).

Rhode Island. *Newport County:* Middletown, 1 (MCZ); Newport, 1 (USNM).

Connecticut. *Fairfield County:* Stamford, 2 (CNHM). *New Haven County:* New Haven, 1 (CNHM); Stony Creek, 1 (CNHM); West Haven, 1 (CNHM); unspecified, 1 (CNHM). *New London County:* New London, 1 (AMNH).

New York. *Bronx County:* Throg's Neck, 1 (AMNH), 1 (USNM). *Niagara County:* Wilson, 2 (USNM). *Orange County:* West Point, 1 (USNM). *Queens County:* Rockaway, 2 (AMNH);

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* Because of his forthcoming work on the birds of the Ungava Peninsula, Mr. W. E. C. Todd has requested me not to publish the exact localities of birds in the Carnegie Museum from that region.

Rockaway Beach, 1 (MCZ), 1 (CAS). *Richmond County:* off Great Kills, 1 (AMNH). *Suffolk County:* Amagansett, 2 (AMNH); Amityville, 1 (AMNH); Bay Shore, 1 (AMNH); Bellport, 1 (AMNH); Greenport, 1 (AMNH); Hampton Bays, 1 (AMNH); Mastic, 1 (AMNH); Montauk Point, 3 (AMNH), 1 (MVZ); Oakdale, 1 (AMNH); Sag Harbor, 1 (AMNH); Shinnecock Bay, 1 (AMNH); South Hampton, 1 (MCZ), 1 (AMNH). *Warren County:* Lake George, 2 (MCZ). *Westchester County:* Elmsford, 1 (AMNH); Ossining, 1 (MCZ). *Long Island,* county unspecified: Atlanticville, 1 (AMNH); Jamaica Bay, 1 (AMNH); Smith's Point, 1 (ROMZ), 1 (MCZ), 1 (AMNH); unspecified, 2 (AMNH).

NEW JERSEY. *Mercer County:* Princeton, 1 (PMZ). *Middlesex County:* Cranbury, 1 (PMZ).

MARYLAND. *Montgomery County:* Kenilworth, 1 (USNM).

VIRGINIA. *Fairfax County:* Four-mile Run, 1 (USNM). *Northampton County:* Cape Charles, 1 (ANSP). *County unspecified:* Occoquan Creek, 1 (USNM).

SOUTH CAROLINA. *Anderson County:* Anderson, 1 (MCZ).

GREENLAND. 72° N., 13° 30′ W., 5 (AMNH); 73° 39′ N., 15° 26′ W., 1 (AMNH); north Greenland, 1 (AMNH); southeast Greenland, 1 (MCZ); Agparsiut, 1 (CNHM); Akpam, 1 (UMMZ), 1 (MMP); 20 miles S Cape York, 3 (ANSP); Devil's Thumb, 1 (ANSP); Etah, 3 (UMMZ), 1 (CNM), 2 (AMNH), 1 (ChAc), 1 (ANSP); Godhavn, 1 (UMMZ); Godthaab, 1 (CNM); Hakluyt Island, 2 (MCZ), 2 (AMNH); Ivijak, 1 (USNM); Jacobshavn, 1 (USNM); Julianhaab, 1 (AMNH); Kangamiut, 1 (AMNH); Littleton Island, 1 (AMNH); McCormick Bay, 3 (ANSP); Melville Bay, 2 (ANSP); Murchison Sound, 1 (USNM); Northumberland Island, 2 (USNM); Ovixak, Disco Island, 1 (USNM); Parker Snow Bay, 2 (USNM); Rathbone Island, 2 (CNHM); Robertson Bay, 2 (CNM); Sukkertoppen, 2 (CNHM); Swartenhuck, 2 (ANSP); Umanak, 1 (UMMZ), 1 (ChAc), 1 (MCZ), 2 (LACM); Upernivik, 4 (AMNH); unspecified, 3 (AMNH).

ICELAND. Ocean north of, 1 (AMNH); Brede Bugt, off Bjortonga, 1 (AMNH); Denmark Strait, 2 (ANSP), 1 (MCZ); Grimsey, 1 (MVZ); Havet (= the sea), 2 (AMNH); Husavik, 1 (CNHM), 1 (MMP), 1 (MVZ); North Cape, 1 (MCZ); Tjörnes, 1 (AMNH).

BEAR ISLAND. Gull Island, South Haven, 1 (AMNH); "Lummenfelsen," 2 (CNHM); Walrus Bay, 1 (AMNH).

SPITSBERGEN. Ice Fjord, 1 (USNM); Kings Bay, 1 (USNM); Lady Franklin Bay, 4 (KU); South Gat, 1 (USNM).

FRANZ JOSEF LAND. Unspecified, 1 (MCZ).

U.S.S.R. Archangel, 1 (MCZ); Murman Coast, 1 (MCZ), 1 (AMNH).

NOVAYA ZEMLYA. Unspecified, 1 (MCZ).

SCOTLAND. Orkney, 1 (MCZ); Shetland Islands, 1 (AMNH).

GREAT BRITAIN. Unspecified, 1 (ChAc).

Uria lomvia arra (Pallas)

Cepphus arra Pallas, Zoogr. Rosso-Asiat. 2, 1811:347 (original description).

Uria lomvia eleonorae Portenko, Mitt. Zool. Mus. Berlin, 22, 1937:227.

Uria lomvia heckeri Portenko, Comptes Rendus (Doklady) Acad. Sci. URSS, 43 (5), 1944:226.

Type locality.—Kamchatka.

Description.—Similar to *U. l. lomvia* but larger; wing length, 210 to 240 (means 222 to 231); tarsal length, 33.5 to 41.0 (37.3 to 37.6); culmen length, males, 35.0 to 47.0 (40.1 to 45.3), females, 35.0 to 48.0 (38.5 to 42.2); bill depth, males, 13.6 to 16.1 (14.7 to 15.1), females, 12.9 to 15.6 (14.1 to 14.5).

Remarks.—As with *U. l. arroides,* I have not seen enough specimens to determine the validity of Portenko's races *eleonorae* and *heckeri* from Khatanga Bay and Wrangel Island respectively. Portenko's measurement data are not sufficient to warrant the separation of these forms, and color differences in this genus must be used with great care owing to the seasonal and age differences.

Range.—The north coast of Siberia, from Khatanga Bay eastward, the Arctic coast of Alaska, the coasts and islands of the Bering Sea, and the North Pacific south to Kodiak Island and the

Kuriles. Largely sedentary, but in winter occasional individuals reach Hondo and British Columbia.

Specimens examined.—176, of which 131 are adults in nuptial plumage.

SIBERIA. Bering Sea, west side, 1 (MCZ); East Cape, 5 (MCZ), 1 (Dickey); Herald Island, 1 (USNM); Arctic Ocean near Herald Island, 1 (AMNH); Indian Point, 4 (AMNH); Kamchatka: Petropaulovski, 5 (CNM), 1 (MCZ); unspecified, 1 (MCZ); Kolyuchin Island, Kolyuchin Bay, 5 (CNHM), 1 (MCZ); Plover Bay, 1 (MCZ); Providence Bay, 2 (MCZ); Wrangel Island, Cape Hawaii, 4 (CNHM).

COMMANDER ISLANDS. Bering Island, 1 (AMNH); Copper Island, 1 (MCZ), 5 (AMNH); unspecified, 1 (AMNH).

JAPAN. *Hokkaido:* Hakodate, 2 (USNM); Otaru, 1 (AMNH); off Toyama, 2 (UMMZ).

ALASKA. *Aleutian Islands:* Agattu Island, 1 (USNM), Attu Island, 2 (USNM), Bogoslof Island, 1 (ROMZ), 2 (MCZ), 1 (USNM), 1 (SD), Umnak Island, 1 (LACM); Barrow, 1 (Dickey), 5 (CNHM), 8 (MMP), 1 (ROMZ), 7 (MVZ), 4 (ChAc); Bering Sea, 1 (CAS); Bethel, 1 (CNHM); Bluff City, 1 (CNHM); Cape Lisburne, 8 (AMNH), 1 (ANSP); Cape Thompson, 13 (MVZ); 3 miles west of Cape Thompson, 1 (MVZ); Diomedes Islands, 2 (AMNH), 2 (CNHM); Elson Bay, Point Barrow, 1 (CNM); Fairway Rock, 1 (SD); Hall Island, 1 (USNM); Howkan, 1 (AMNH); Kodiak, 1 (USNM); Kodiak Island, 1 (MVZ); Nome, 1 (MVZ); Point Barrow, 2 (ANSP), 1 (USNM), 1 (SD); Point Hope, 1 (CNM); Pribilof Islands: Bering Sea near, 1 (MVZ), Otter Island, 2 (USNM); St. George Island, 1 (CNHM), 1 (UMMZ), 1 (AMNH), 5 (USNM); St. Paul Island, 2 (ANSP), 4 (USNM); St. Lawrence Island: Gambell, 6 (USNM); Sevoonga, 1 (MVZ), unspecified, 2 (MCZ), 5 (MVZ); St. Matthew Island, 1 (USNM); Sledge Island, 9 (MCZ), 1 (ANSP); Tigara, Point Hope, 4 (MVZ); Wainright, 1 (MMP); Wales, 2 (ROMZ), 3 (ChAc).

BRITISH COLUMBIA.—Vancouver Island, 1 (CNHM).

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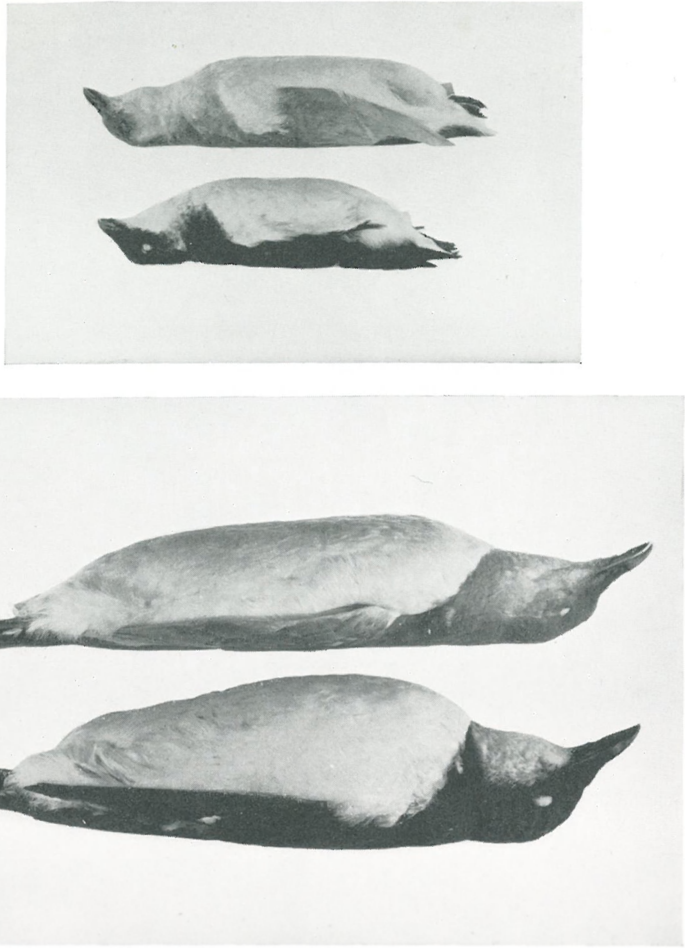

Plate 1. Albinistic and normal dovekies, *Plautus alle,* (above) and thick-billed murres, *Uria lomvia lomvia,* (below); UMMZ 55758, 67746, 68403, and 67757 (from top to bottom).

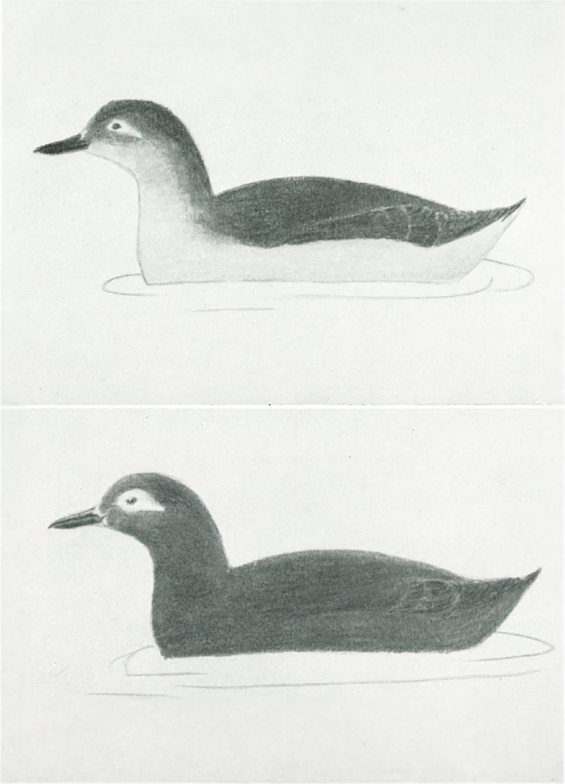

Plate 2. Adult spectacled guillemots in winter (above USNM 406347) and summer (below, USNM 406348) plumages.