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MORPHOLOGIC AND GENETIC VARIATION AMONG BREEDING COLONIES OF THE ATLANTIC PUFFIN (*FRATERCULA ARCTICA*)

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ABSTRACT.—Atlantic Puffins (*Fratercula arctica*) exhibit clinal variation in body size. Taxonomists have used this variation to differentiate three subspecies (*F. a. grabae, F. a. arctica, F. a. numanni*). I collected morphological data and blood samples from five Atlantic Puffin colonies to assess differences in body size and allozyme patterns over large geographical distances. I analyzed differences within and among colonies and between *F. a. grabae* and *F. a. arctica*. Body size among all but the two most southerly colonies differed significantly. Isoelectric focusing of serum proteins revealed that 5 of 32 loci studied were polymorphic. An average measure of heterozygosity within a colony relative to the total population studied (F_{ST} = 0.0031) indicated genetic differentiation among colonies was low and similar. Nei's (0.0005) and Rogers' (0.0096) average genetic distances also indicated the colonies were similar genetically. Body sizes of puffins generally increased with latitude but not on a cline predicted by ocean temperature alone. I speculate that variation in body sizes among colonies of the Atlantic Puffin is due to the combined environmental effects of ocean temperature and food quality. *Received 23 July 1990, accepted 18 April 1991.*

ALTHOUGH Atlantic Puffin (*Fratercula arctica*) colonies show no geographic differences in plumage, there is an increase in average body size from southeast (Great Britain) to northwest (Greenland) (Harris 1984). Near the turn of the century, three subspecies (*F. a. grabae, F. a. arctica, F. a. numanni*) were differentiated based solely on body size (Harris 1984). Subspecies of the Atlantic Puffin are still recognized but controversial because of gradual rather than distinct geographic differences among colonies. The gradient, or cline, in body size is presumably maintained by colder ocean temperatures and variable food distribution. These environmental characteristics may act as sources of selection or merely influence the expression of particular morphologies.

The interaction between habitat quality and variation in allelic frequencies at protein-coding loci on the expression of morphological traits is unknown but generally assumed to be selectively neutral (Endler 1986, Evans 1987). Bacon (1979) and Evans (1980) demonstrated a correlation between variation at the EST-1 locus and clutch size and laying date; however, such correlations do not necessarily imply causation. My intent was to evaluate morphological and genetic variation among five colonies of the Atlantic Puffin through wing and bill measurements and allozyme patterns. Allozyme variation detected in this study may reflect the extent of neutral differentiation between the puffin colonies but probably has no affect on body size. I discuss the subspecific status of *F. a. grabae* and *F. a. arctica* (Howard and Moore 1980) based on my findings.

METHODS

Fieldwork.—Between May and July, 1988, I collected morphological data and blood samples from >40 puf-

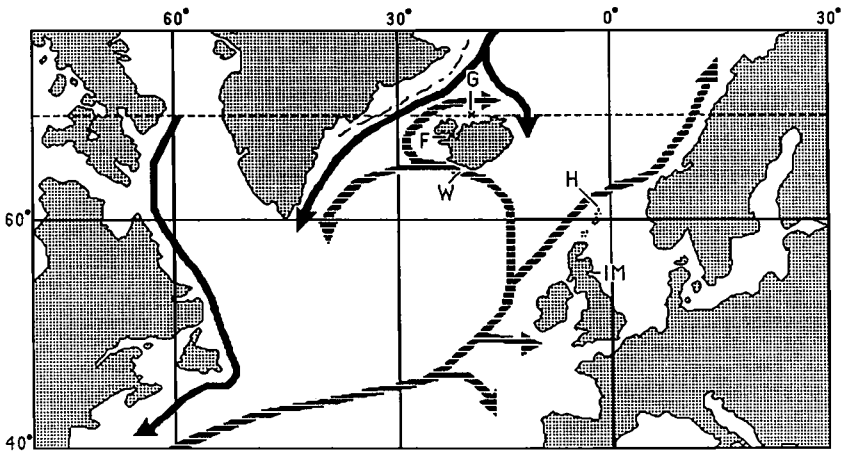

Fig. 1. Map of the northern Atlantic Ocean showing surface currents in August and the Atlantic Puffin colonies involved in this study. Colonies are designated as follows: Isle of May [IM], Hermaness [H], Westman Islands [W], Flatey Island [F], Grimsey Island [G] (Adapted from maps 206–207 *in* World Ocean Atlas 1979).

fins from each of five colonies. Two colonies of *F. a. grabae* were located in Scotland at the Isle of May (56°12'N, 2°30'W) and Hermaness Nature Reserve on Unst Island (60°50'N, 0°53'W). Three colonies of *F. a. arctica* were located in Iceland at the Westman Island of Heimaey (63°50'N, 20°15'W), Flatey Island and surrounding islands (65°23'N, 22°55'W), and Grimsey Island (66°36'N, 18°00'W) (Fig. 1). All birds were taken from their burrows, except some on Flatey Island were caught in flight with a net on a pole (fleyged). I measured bill length, bill depth, bill-curve length (Corkhill 1972), and wing-chord length as indicators of body size. I counted bill grooves to eliminate measurements of subadult birds from the morphological analysis; individuals with fewer than 2 grooves were considered subadults (Petersen 1976). I collected a 1.0-cc blood sample from the brachial vein into a heparinized syringe. After sampling, the birds were returned to their burrows. I stored uncentrifuged blood samples in 0.5 ml cryogenic straws frozen in liquid nitrogen or on dry ice. Samples were frozen within 3 h of collection.

Sample preparation and isoelectric focusing.—In the laboratory, blood samples were thawed, then centrifuged at 2,500 rpm, 4°C for 30 min to separate lysed cell fluids from cellular debris and DNA (Barrowclough and Corbin 1978). I refroze lysed cell fluids in liquid nitrogen until electrophoretic analyses began. Following the methods of Corbin et al. (1988), samples of plasma supernatant were run on thin-layer gels using the LKB Multiphor System for isoelectric focusing (IEF). Isoelectric focusing was monitored by observing the migration of hemoglobin and was terminated when distinct hemoglobin bands formed. This resulted in running times of about 1 h and 1.5 h for gels of pH 4–6.5 and pH 3–10, respectively.

I assayed gels for allozymes with staining recipes based on Shaw and Prasad (1970), Barrowclough and Corbin (1978), Dykes et al. (1982), and Evans (1987). Of the 18 enzyme systems analyzed, 6 were inactive or unscorable; 12 produced a total of 32 scorable loci (Table 1). To promote accuracy, I scored each gel three times independently, labeling alleles in anodal to cathodal order. I ran poorly focused samples a second time or excluded them from the analysis. I scored a minimum of 180 individuals for each allozyme.

Data analysis.—I performed *t*-tests, pairwise multivariate analysis of variances (MANOVA), and a principal component analysis (SAS Institute 1985) on wing and bill measurements to assess morphological differences among colonies. I also tested morphological difference between *F. a. grabae* and *F. a. arctica* with MANOVA. I did this by lumping recognized subspecies and then by comparing the two northernmost colonies to the three more southerly colonies. I analyzed genetic variation with program GENESYS (Corbin and Wilkie 1988) that calculates allelic frequencies, Hardy-Weinberg equilibria, Chi-square values for the deviation of observed genotypic distributions from those expected, and Wright's *F*-statistics (Wright 1951, 1965, 1978). The program also calculates Nei's identity and distance corrected for sampling error (Nei 1972, 1978), Rogers' genetic distance (Rogers 1972), and Cavalli-Sforza and Edwards' (1967) chord and arc distances.

RESULTS

Morphological differentiation.—Analyses were done without regard to sex because, within a colony, character variables were distributed normally, and puffins cannot be accurately assigned to gender without dissection. The sexes

TABLE 1. Enzyme systems and presumptive gene loci analyzed. Abbreviations and current Enzyme Commission numbers (Webb 1988) are in parentheses. The number of resolved loci for the twelve active systems is indicated.

Enzyme system	No. of loci
Inactive or unscorable enzyme systems	
Isocitrate dehydrogenase (IDH, 1.1.1.42)	
Xanthine dehydrogenase (XDH, 1.2.1.37)	
Glucose-6-phosphate dehydrogenase (G-6-PDH, 1.1.1.49)	
Adenylate kinase (AK, 2.7.4.3)	
Fructose-1-6-diphosphatase (F-1-6-DP, 3.1.3.11)	
Superoxide dismutases (SOD, 1.15.1.1)	
Active enzyme systems	
Non-specific plasma protein	11
Hemoglobin	4
Esterase (EST, 3.1.1.-)	6
Lactate dehydrogenase (LDH, 1.1.1.27)	2
Valyl-leucine dipeptidase (PEP-A, 3.4.11.11)	1
Leucyl-glycyl-glycine dipeptidase (PEP-B, 3.4.11.4)	1
Leucyl-alanine dipeptidase (PEP-C, 3.4.11)	1
Phenyl-alanyl-proline dipeptidase (PEP-D, 3.4.11)	1
Glucose phosphate isomerase (GPI, 5.3.1.9)	1
6-phosphogluconate dehydrogenase (6-PGDH, 1.1.1.44)	1
Malate dehydrogenase (MDH, -1.1.1.37)	2
Glutamate oxalate transaminase (GOT, 2.6.1.1)	1
Total Loci	32
Polymorphic loci	5
Rare polymorphic loci	2
Monomorphic loci	25

of two breeding pairs of puffins from the colony on Hermaness could not be determined by bill measurements as suggested by Corkhill (1972) and Harris (1984). I assumed that males and females were sampled in similar proportions among the colonies throughout the analyses.

The average wing length of Atlantic Puffins increased from southeast to northwest (Table 2) with one nonsignificant exception: the birds that breed around Flatey Island exhibited a mean wing length that was longer ($t = 0.448$, $P = 0.657$, df = 40) than the average on Grimsey Island, approximately 290 km to the northeast. Average bill measurements generally increased with latitude. Exceptions occurred on Grimsey Island, where bill measurements were shorter than on Flatey Island, and on Hermaness, where average bill and curve lengths were shorter than on the Isle of May (Table 2).

Pairwise MANOVA tests indicated that the puffin colonies, except those on the Isle of May and Hermaness ($P = 0.019$, $F = 3.132$, df = 4, 80), were significantly different from each other at a confidence level of $P = 0.005$. A confidence level of $P = 0.005$ complies with Bonferroni's rules for multiple pairwise comparisons. The intermediate colony on the Westman Islands appeared to be most similar to the colonies on

TABLE 2. Mean (±SD) of mensural characters from five colonies of Atlantic Puffin. Measurements are expressed in mm, and colonies are presented in order of increasing latitude.

		Bill			
Colony	*n*	Curve	Depth	Length	Wing length
Isle of May	44	44.78 ± 1.95	35.28 ± 1.44	29.72 ± 1.23	161.73 ± 3.93
Hermaness	41	43.94 ± 1.38	35.48 ± 1.62	29.36 ± 0.92	163.58 ± 3.60
Westman	40	46.04 ± 1.83	38.14 ± 1.83	30.54 ± 1.24	168.73 ± 4.04
Flatey	39	49.62 ± 1.61	41.25 ± 1.58	31.76 ± 1.05	175.20 ± 4.38
Grimsey	40	47.90 ± 2.04	40.23 ± 1.68	31.01 ± 1.48	174.02 ± 4.07

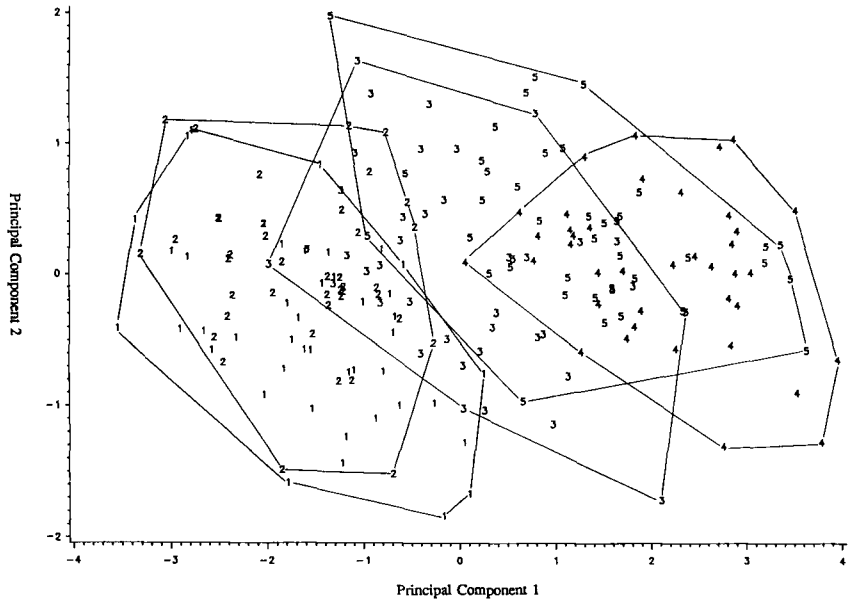

Fig. 2. Scatter plot of the first two principal components designated by colony. The puffins on Flatey Island (4) are generally larger than those on Grimsey Island (5). Colonies on both Grimsey (5) and Westman (3) exhibit wider ranges in size than do the other colonies. All ranges overlap except those of Flatey and the Scottish colonies.

Grimsey ($P < 0.001$, $F = 12.608$, df = 4, 75) and on Hermaness ($P < 0.001$, $F = 17.955$, df = 4, 76). A MANOVA test showed highly significant differences between the recognized subspecies *F. a. arctica* and *F. a. grabae*. Highly significant differences were also demonstrated when I grouped the Westman colony (*F. a. arctica*) with the Scottish colonies (*F. a. grabae*).

The first two principal components represented 90.44% (78.63 and 11.81%, respectively) of the morphological variance. Correlations between variables ranged from 0.58 (wing length–bill length) to 0.84 (bill depth–curve length). The first principal component (PC1) exhibited roughly equal loading on all variables and may be the best index of size (Zink and Remsen 1986, Davies et al. 1988, Freeman and Jackson 1990). The second principal component (PC2) measured the importance of wing length over bill measurements in determining body size but added little information to analysis. Graphing PC2 against PC1 showed a progressive trend in body size from the Isle of May to Flatey Island (Fig. 2). An anomaly to the expected trend from south to north was the PC range of the puffins on Flatey Island. Puffins on Flatey appeared to be morphologically more distinct and larger in size than those in any of the other four colonies. The PC ranges indicated morphological similarities among all colonies except Flatey, which did not share its range with either of the Scottish colonies.

Allozyme differentiation.—Of 32 loci, five (EST-1, EST-6, PEP-B, PEP-D, LDH-2) were polymorphic. Two loci, 6-PGDH and MDH-2, exhibited rare alleles that appeared with a frequency of <0.01 within all the colonies. Secondary modification of MDH-1, in the form of a hazy second band, appeared to be associated with heterozygosity at the MDH-2 locus. Genotypic frequencies at PEP-B, PEP-D, and LDH-2 were in Hardy-Weinberg equilibrium, whereas the observed frequencies of EST-1 and EST-6 genotypes differed significantly from expected frequencies in some colonies. Allelic frequencies calculated from observed genotypic distributions did not demonstrate detectable trends nor did calculations of individual heterozygosity (Table 3). The percentage of polymorphism, P, found in puffins was 0.156 (5 polymorphic loci/32 loci detected). Estimated heterozygosity corrected for sampling bias (Nei 1978), H_e, was 0.053 ± 0.002 [SE] over the five colonies. Observed heterozygosity (H_o) averaged 0.043. The divergence from Hardy-Weinberg equilibrium of EST-1 and EST-6 was primarily responsible

TABLE 3. Allelic frequencies of five polymorphic loci from lysed cell fluids of Atlantic Puffins. Individual heterozygosities (h) corrected for sampling bias are in parentheses.

Locus	Allele	Colony				
		Isle of May	Hermaness	Westman	Flatey	Grimsey
EST-1	A	0.3026	0.3235	0.1795	0.3125	0.2639
	B	0.4737	0.5000	0.6282	0.5000	0.4722
	C	0.2237	0.1765	0.1923	0.1875	0.2639
	(h)	(0.6425)	(0.6234)	(0.5431)	(0.6270)	(0.6467)
EST-6	A	0.9419	0.8974	0.9348	0.9615	0.9487
	B	0.0581	0.1026	0.0652	0.0385	0.0513
	(h)	(0.1107)	(0.1865)	(0.1232)	(0.0750)	(0.0986)
LDH-2	A	1.0000	1.0000	1.0000	0.9861	0.9868
	B				0.0139	0.0132
	(h)	(0.0000)	(0.0000)	(0.0000)	(0.0278)	(0.0264)
PEP-B	A	0.5125	0.4487	0.4048	0.3875	0.3333
	B	0.4875	0.5513	0.5952	0.6125	0.6667
	(h)	(0.5060)	(0.5012)	(0.4877)	(0.4807)	(0.4502)
PEP-D	A	0.6667	0.7162	0.6000	0.5000	0.6842
	B	0.3333	0.2838	0.4000	0.5000	0.3158
	(h)	(0.4502)	(0.4121)	(0.4861)	(0.5065)	(0.4379)

for the disparity between estimated and observed heterozygosity.

Wright's *F*-statistics (Wright 1951, 1965, 1978) imply that genetic variation among individuals is greater than variation among colonies. The inbreeding coefficients of individuals relative to the colonies (F_{is}) indicated that between 18 and 39% of the total genetic variation occurred among individuals within the colonies. Standard errors associated with the F_{is} values ranged between 8 and 19%. Variance in allelic frequencies among colonies relative to a hypothetical set of colonies with the same overall allelic frequencies (F_{st}) indicated that the five colonies were almost inseparable based on the loci analyzed. The average F_{st} value (0.0031) did not deviate significantly from zero ($\chi^2 = 5.97$, df = 20, $P > 0.995$).

Commonly used measures of genetic difference showed negligible amounts of divergence among puffin colonies. Genetic distances between colonies were quite low (Table 4). Cavalli-Sforza and Edwards' (1967) chord and arc distances fell below 0.0121.

DISCUSSION

Deviations from Hardy-Weinberg equilibrium.—Genotypic frequencies for the EST-1 and EST-6 loci differed significantly from expected frequencies in the Isle of May, Flatey Island, and Grimsey Island (EST-1 and EST-6), Hermaness (EST-6), and Westman Island (EST-1). EST-1 and EST-6 may have failed to attain genetic equilibrium since puffins colonized the islands. Alternatively, recent changes in the marine environment and human exploitation may have disturbed the equilibrium (Coombs 1975, Dickson et al. 1975). Ongoing selection (either acting on these loci directly or via linkage relationships), sampling error, or nonrandom mating may also affect genetic equilibrium. Complications in focusing these loci may also account for the deviations observed.

Genetic comparisons to other taxa.—Genetic polymorphism in Atlantic Puffins (P = 0.156) is lower than the average for birds (P = 0.222 ± 0.128) (Corbin 1987). The observed allozyme heterozygosity ($H_o = 0.043$) of the Atlantic Puffin is typical for birds ($H_e = 0.044$ [Evans 1987]) and comparable to other studies using isoelec-

TABLE 4. Nei's (1978) unbiased genetic distance, *D*, below the diagonal; Rogers' (1972) distance above the diagonal.

	Isle of May	Hermaness	Westman	Flatey	Grimsey
Isle of May	—	0.0062	0.0101	0.0112	0.0080
Hermaness	−0.0004	—	0.0104	0.0115	0.0090
Westman	0.0005	0.0005	—	0.0090	0.0099
Flatey	0.0007	0.0010	0.0002	—	0.0100
Grimsey	0.0004	0.0000	0.0003	0.0006	—

tric focusing techniques (Corbin et al. 1988, Burson 1990). Although the rigor of the analyses would be improved by scoring more enzyme systems, the 32 loci detected adequately represent the level of genetic variation in protein-coding loci (Zink and Remsen 1986). The values calculated for Wright's Fixation Indices (F_{is} and F_{st}) were comparable to those found in other Charadriiformes (Zink and Winkler 1983, Haig and Oring 1988, Burson 1990, V. L. Birt-Friesen pers. comm., V. L. Birt-Friesen unpubl. data). Why some Charadriiformes display unusually low F_{st} values and genetic distances relative to other avian orders is unclear. Low F_{st} values may be due to high dispersal rates or recent speciation.

Biogeographic trends in body size and genetic structure.—The low F_{st} and genetic distance values indicate that allelic differentiation was similar and low among the colonies studied. Such values suggest that either gene flow occurs at high levels (supported by Harris 1984, Kress and Nettleship 1988, but not Ashcroft 1979) or that the colonies were recently isolated (Larson et al. 1984). The simplifying assumption that migration, genetic drift, mutation, and selection have created an equilibrium state in the distribution of genotypic frequencies (Whitlock and McCauley 1990) may be violated by the extinction and recolonization dynamics of Atlantic Puffin colonies. The rate of extinction and recolonization (Harris 1984) possibly allows founding events to influence the genetic composition of puffin colonies more than progress toward equilibrium (Whitlock and McCauley 1990). Founding events involving individuals from several sources within the metapopulation can suppress genetic variation between colonies (McCauley 1991).

The influence of environmental conditions on the expression of genetic codes may account for much of the variation observed in growth, behavior, and morphology of certain populations (Klein 1964, Auckland and Morris 1971, Denton et al. 1973, Breven et al. 1979, James 1983, Heath and Randall 1985). In Red-winged Blackbirds (*Agelaius phoeniceus*), James (1983) detected significant environmental effects on nestling growth. A subsequent study of mitochondrial DNA revealed minimal genetic differences among populations (Ball et al. 1988). Like Red-winged Blackbirds and Thick-billed Murres (*Uria lomvia*) (V. L. Birt-Friesen pers. comm.), Atlantic Puffin colonies exhibited significant differences in body size without significant differences in genetic structure.

Ocean temperatures, rather than the commonly suggested influences of air temperature and humidity (James 1970), may impose the greatest thermoregulatory constraints on puffins because young birds develop in the roughly constant microenvironment of their burrows, fledge at about three quarters of their adult body weight and size, and complete their development on the open ocean (Harris 1984). An attempt to associate a gradient in ocean temperature (Fig. 3) with the average body size of puffins (Fig. 2), does not explain why the mean size of puffins is largest on Flatey Island nor the west to east gradient reported in Scotland (Harris 1984).

Several nongenetic hypotheses may explain significant differences in body size between pelagic populations. The proximity of oceanic currents to breeding areas (Klomp and Wooller 1988) may account for the unexpectedly small size of puffins on Grimsey Island and the puffins' larger size in similar latitudes off the coast of North America by influencing local ocean conditions (Fig. 1). The differences among colonies may be a consequence of proportionately larger thyroid glands in populations at high latitudes (Upenskii 1984). Large thyroid glands, which imply increased metabolic activity, may be stimulated by colder temperatures to produce more thyroxine and thereby account for differences in body size between populations despite genetic similarities.

Because puffins fledge at about three quarters their adult size and weight (Harris 1984), the quality of prefledging diet and the three to five years that juveniles spend developing at sea may greatly influence morphological variation among colonies. The effect of pre-adult nutrition on adult body size has been documented in deer (Klein 1964), chickens (Denton et al. 1973), turkeys (Auckland and Morris 1971), and Jackass Penguins (*Spheniscus demersus*) (Heath and Randall 1985), and implied in other avian studies (Klomp and Wooller 1988, Randi et al. 1989). McNab (1971) concluded that the body sizes of predatory species, like the Atlantic Puffin, reflect the size distribution of available prey and the presence of competitors. Maps of primary production (World Ocean Atlas 1979), used as an indirect measure of fish production, show

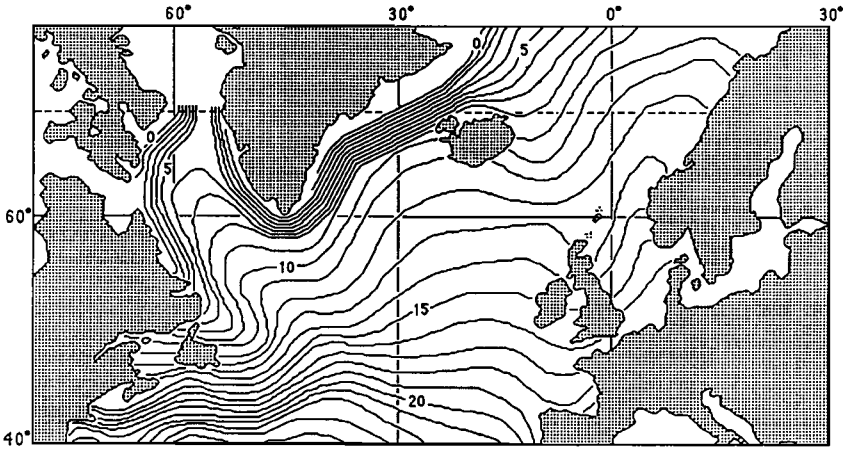

Fig. 3. Map of northern Atlantic Ocean showing mean ocean temperatures at the surface in August. (Adapted from map 135 *in* World Ocean Atlas 1979).

that of the five colonies, the waters around Grimsey, Flatey, and Westman islands are richest in production of organic material (100 mg C/m^2). The Isle of May and Hermaness Nature Reserve lie in areas of moderate production (about 10 mg C/m^2). For several years, the colony on Hermaness Nature Reserve failed to fledge young because of lack of an adequate food supply, presumably a consequence of overfishing by humans (Martin 1989, D. N. Nettleship pers. comm.). If differences in primary production cause differences in nutritional planes, I propose that variation in body size among colonies could reflect a combination of differences in primary production and ocean temperatures. Studies focusing on environmental influences on the body size of the Atlantic Puffin may be possible with the continued success of the reintroduction efforts off the coast of Maine (Kress and Nettleship 1988).

Subspecies.—Atlantic Puffins were assigned to subspecies based on size (Salomonsen 1944, Harris 1984). Although the puffin colony on the Westman Islands has been assigned to the same subspecies as other Icelandic puffins, Harris (1984) noted that, based on wing measurements, this colony was more similar to the smaller puffins from Great Britain. According to my principal component and multivariate analyses, the Westman Island colony is intermediate in bill morphology and wing length relative to the other colonies in Iceland and colonies in Scotland.

Based on the classic 75% Rule regarding morphology (Amadon 1949, Mayr 1969), bill and wing variation measured in this study do not support patterns regarding subspecific designation of Atlantic Puffins. The principal component analysis also leads to some doubt about the morphological basis for recognizing differences between colonies on the Isle of May and Hermaness and the colonies on Westman, Flatey, and Grimsey Islands. Allozyme patterns indicate Atlantic Puffin colonies were similar genetically, having a genetic identity of 0.93 (I = 1.00 would indicate that the colonies are identical). Additional data from the puffin colonies of the Faeros Islands and those of Greenland would make this morphological and genetic assessment of subspecies more rigorous.

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