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GEOGRAPHIC VARIATION IN THE WINGTIP PATTERNS OF BLACK-LEGGED KITTIWAKES

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Abstract. This paper reports geographic variation in wingtip patterns of Black-legged Kittiwakes (*Rissa tridactyla*) from the circumpolar Arctic. The amount of black in the wingtip increased and the amount of white decreased from Arctic Canada–west Greenland, counterclockwise to the Pacific. Differences were greatest between Pacific and Atlantic, but were also apparent within the Atlantic sample. Patterns of variation were not clinal. Known levels of philopatry in kittiwakes would tend to maintain both phenotypic and genotypic differences between regions, but the similarity of birds from Newfoundland, British Isles, and Barents Sea suggests some degree of dispersal over this wide area. Wingtip pattern data support continued separation of Pacific and Atlantic kittiwakes into two subspecies under the biological species concept. Under the phylogenetic species concept, Pacific and Atlantic Black-legged Kittiwakes may represent two species.

Key words: geographic variation, kittiwakes, *Rissa tridactyla*, taxonomy, wingtip patterns.

Variación Geográfica en los Patrones de Coloración de la Punta del Ala de *Rissa tridactyla*

Resumen. Este trabajo presenta la variación geográfica existente en los patrones de coloración de la

punta del ala de *Rissa tridactyla* en el área circumpolar ártica. La cantidad de negro en la punta del ala incrementó y la cantidad de blanco disminuyó desde el ártico canadiense y el oeste de Groenlandia en sentido contrario a las agujas del reloj hacia el Pacífico. Las mayores diferencias se registraron entre el Pacífico y el Atlántico, pero también fueron evidentes en la muestra del Atlántico. Los patrones de variación no fueron graduales. Los niveles conocidos de filopatría en *R. tridactyla* tenderían a mantener las diferencias tanto fenotípicas como genotípicas entre regiones, pero la similitud de las aves de Newfoundland, las Islas Británicas y el Mar de Barents sugiere algún grado de dispersión a través de esta extensa área. Considerando el concepto biológico de especie, los datos sobre los patrones de la punta del ala apoyan la separación de las aves del Pacífico y del Atlántico en dos subespecies. Considerando el concepto filogenético de especie, los individuos de *R. tridactyla* del Pacífico y del Atlántico pueden pertenecer a dos especies diferentes.

The Black-legged Kittiwake (*Rissa tridactyla*) is a small gull distributed throughout coastal and marine

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areas of the circumpolar north (Baird 1994). Two subspecies have been recognized: the more widely distributed *R. t. tridactyla* inhabiting the north Atlantic and adjacent waters northeast to the eastern Canadian Arctic, and northwest to Wrangel Island; and the more restricted *R. t. pollicaris* from the Bering and Chukchi Seas, Sea of Okhotsk, Gulf of Alaska, and the North Pacific. Differences between the subspecies in body size, foot morphology, and plumage have been reported (Dwight 1925, Witherby et al. 1944, Dement'ev et al. 1951, Sluys 1982, Portenko 1989). Specifically, *R. t. pollicaris* has, on average, a longer wing and culmen, more frequently shows a well-developed hind toe with claw, shows more extensive black in the wingtips, and more often shows black on primary five.

Sluys (1982) reappraised geographic variation in Black-legged Kittiwakes. His results confirmed subspecific differences in wing and culmen length, extent of black in the wingtips, and differences in foot morphology reported previously. However, because of the overlap he observed between *R. t. pollicaris* and *R. t. tridactyla* in some measurements, and apparent clinal pattern of morphometric variation, he concluded that the two subspecies were not distinct and should not be recognized. Earlier, Vaurie (1965) had come to the same conclusion. Despite this work, the two subspecies continue to be recognized in the most recent species accounts (Baird 1994, Burger and Gochfeld 1996).

During field trips to Black-legged Kittiwake colonies in the eastern Canadian Arctic (Prince Leopold Island, Coburg Island, Nunavut, Canada) in the late 1980s, I noticed that local, breeding kittiwakes more frequently showed apical white spots on the black-tipped primaries than those with which I was more familiar from Britain and Newfoundland. This was clearly visible in flying birds and gave the impression of a small *Larus* gull. Differences warranted an investigation of geographic variation in the character. I also studied geographic variation in the amount of black in the outer primaries because differences between the two subspecies had been reported previously (Sluys 1982). This paper reports geographic variation in the frequency and amount of black and white in the wingtips ("wingtip pattern") of Black-legged Kittiwakes from various regions around the Arctic. The results shed light on kittiwake dispersal patterns and the taxonomy of the species.

METHODS

I observed primaries of live birds attending nest sites at breeding colonies using a 15× or 25× spotting scope, or 7× binoculars (depending on distance from birds) at Prince Leopold Island, Nunavut, Canada, in August 1988; Cape St. Mary's, Newfoundland, in June 1991; and Witless Bay, Newfoundland, from 1994–1999. Additionally, I examined study skins of kittiwakes collected at the colony during the breeding season either directly at the Royal Ontario Museum, British Museum, Memorial University of Newfoundland Department of Biology, and Newfoundland Museum, or from photocopies of the dorsal sides of wings made at the National Museum of Canada, University of Amsterdam Zoological Museum, National Museum of Natural History (Smithsonian Institute, Washington,

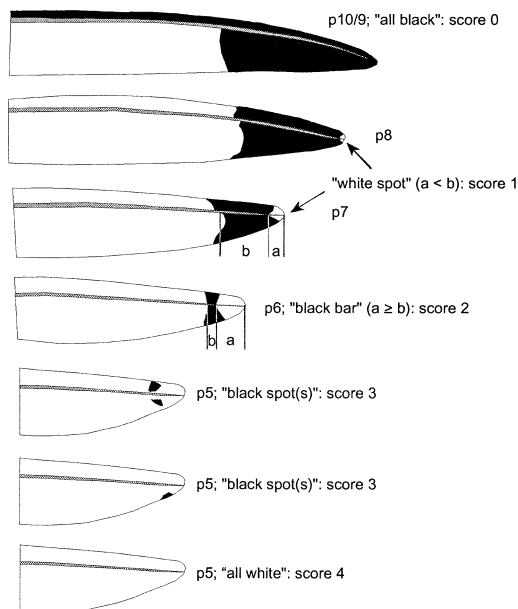


FIGURE 1. Black-legged Kittiwake primary-tip categories and scores (0–4). Primaries (numbered from inside outwards from p5–p10) typical of each category are illustrated.

DC), and Zoological Museum, Copenhagen, Denmark. All photocopies included a ruler for scale. Skins were randomly selected from cabinet drawers, or complete samples of skins in collections were taken when possible. I obtained further samples of wingtip patterns from 35-mm color slides of breeding kittiwakes taken by myself and others at colonies in northern England, Scotland, Newfoundland, and Arctic Canada between 1978 and 1999. Slides were backlit and examined with a 10× Zeiss binocular microscope. I only included slides that were clearly photographed at an angle that allowed unambiguous classification of primaries. Finally, colleagues provided wings of depredated birds or birds collected at various colonies in Newfoundland and north Norway. I recorded the sex of each bird if known. Throughout, I refer to samples of kittiwakes by the region or ocean area from which they were sampled, rather than by subspecies.

I assessed kittiwake wingtip patterns using a primary-feather classification system developed for this study. I designed the system so that under a variety of conditions, including field situations using binoculars or a spotting scope, each of the outermost six primaries (those that usually show a pattern of black and white) could be classified according to the pattern of black and white at the primary tip. Throughout I use the convention of numbering the primaries from the innermost, outwards (excluding the alula). Thus, I classified primary 5 (p5) through p10. I classified primaries from one wing per individual (the right unless it was worn, not visible, or not available) into five categories according to the presence and amount of white and black in the primary tip (Fig. 1). In order from

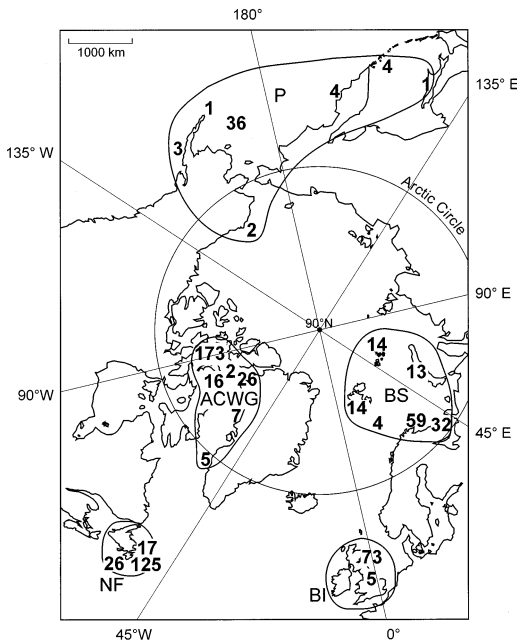


FIGURE 2. Map of circumpolar Arctic showing sampling locations, sample sizes, and regions over which samples were pooled. ACWG = Arctic Canada-west Greenland, NF = Newfoundland, BI = British Isles, BS = Barents Sea, P = Pacific.

less to more white, these categories were “all black,” “white spot” (apical white spot whose extent along the feather shaft was less than extent of black), “black bar” (apical white spot whose extent along feather shaft was equal to or greater than extent of black), “black spot(s)” (one or two subterminal black spots within white primary tip; if there were two spots, they occurred on separate vanes and did not touch at the feather shaft), and “all white.”

I calculated an index of the amount of black in the wingtip (Black Length) by measuring p8, p9, and p10 from the tip of the primary to the intersection of the proximal margin of black on the inner vane and the feather shaft, and then summing the lengths for the three primaries. I used the same method as Sluys (1982) for comparison. I calculated an index of the amount of white in the wingtip (White Score) by assigning scores of 0, 1, 2, 3, or 4 respectively to all black, white spot, black bar, black spot(s), and all white primary categories (Fig. 1), and summing across p5, p6, and p7. These primaries were chosen so as to eliminate the possibility of covariance of White Score and Black Length, which was possible if both measures were taken from the same primary.

I classified a total of 662 kittiwake wings for this study (Fig. 2). Due to small sample sizes at some locations, I pooled samples of birds from nearby locations, a priori, into five geographically separate regions as follows: Arctic Canada-west Greenland ($n = 229$), Newfoundland ($n = 168$), British Isles ($n = 78$), Barents Sea ($n = 136$), and Pacific ($n = 51$). Sample sizes

were sometimes smaller because some primaries were hidden by outer primaries in live birds observed in the field, or could not be scored due to wear at the tip.

STATISTICAL ANALYSES

I set the tolerance for making a type I error at 0.05 for individual or groups of simultaneous tests (using Bonferroni correction). Throughout I use the term “significant” to indicate $P < 0.05$ in a statistical test; no implication of biological significance is intended.

I tested differences in proportions using χ^2 (corrected for continuity when $df = 1$), and in means using ANOVA. In all models, I inspected probability plots of raw data and residuals, which did not deviate appreciably from normality. I performed stepwise discriminant analysis (DA) using SPSS v10 (SPSS 1999) with jackknife (leave-one-out) validation. Variables remained in the analysis if they caused a significant reduction in Wilks' lambda. I checked for, and found, equality of group covariance matrices (a requirement of DA) using Box's M -tests.

All DAs involved classifying birds into one of two groups only. SPSS does this by calculating a posterior probability (PP) of membership in one group or the other according to the value of the discriminant score (D) using Bayes' Rule. A case is classified into a particular group if PP for membership in that group is >0.5 . The relationship between PP and D is given by the logistic equation

$$PP = \frac{1}{1 + e^{kD - c}},$$

where k and c are constants. I estimated these constants by fitting a logistic curve to saved values of PP and D provided in the DA (Phillips and Furness 1997). In order to find the critical discriminant score associated with $PP = 0.5$, I rearranged equation 1 and solved for D after substituting values for k and c previously estimated. For $PP = 0.5$, the equation simplifies to $D_{crit} = c/k$. Note that $PP = 0.5$ does not necessarily correspond to $D_{crit} = 0$ (follows that $c = 0$) as has been erroneously assumed in several papers published in the avian literature in the past (see Phillips and Furness 1997).

RESULTS

GEOGRAPHICAL VARIATION IN PRIMARY CLASSIFICATION

All p10s through p7s were either all black or white spot (Fig. 3). Where testable ($>20\%$ of cells with expected value >5), proportions differed significantly among regions (all $\chi^2_4 > 58$, all $P < 0.001$). Inter-regional trends in classification for each primary were similar although the absolute proportions differed among primaries. Overall, there was a strong tendency for the all-black proportion to increase and the corresponding white-spot proportion to decrease from Arctic Canada-west Greenland counterclockwise around the Arctic to the Pacific. Proportions from intervening regions of Newfoundland, British Isles, and Barents Sea were numerically similar and, where testable, did not differ significantly from each other (p8, $\chi^2_4 = 5.2$, $P = 0.08$). There was a tendency for birds from more northerly regions (Arctic Canada-west Greenland and

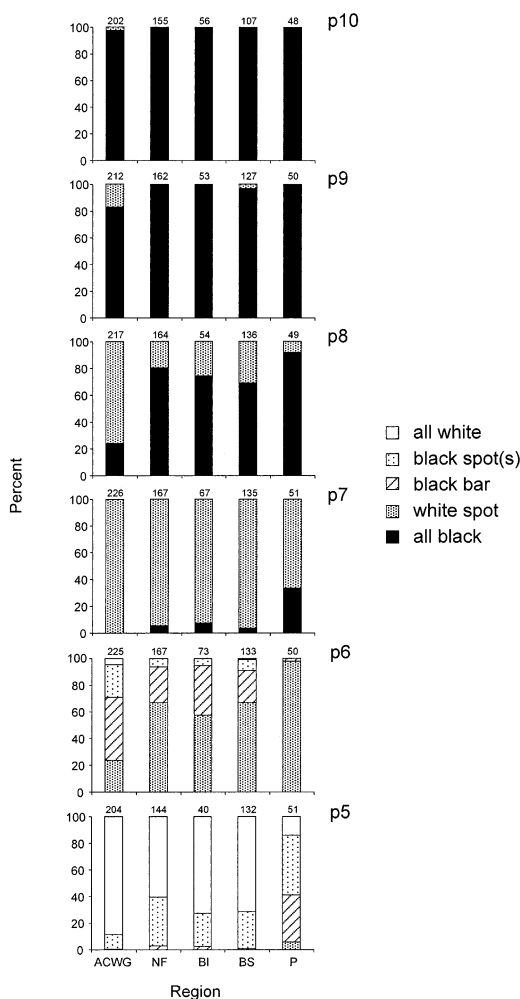


FIGURE 3. The proportions of each primary 10 through 5 classified as all black, white spot, black bar, black spot(s), and all white (see Fig. 1) according to region. ACWG = Arctic Canada–west Greenland, NF = Newfoundland, BI = British Isles, BS = Barents Sea, P = Pacific. Numbers above bars indicate sample sizes.

Barents Sea) to show higher proportions of white spot than more southerly regions, but the difference was most marked in eastern North America (compare Arctic Canada–west Greenland vs. Newfoundland, Fig. 3).

For p5 and p6, proportions of each primary category differed significantly among regions (Fig. 3; $\chi^2_8 = 145.5$, $P < 0.001$, all-white primaries were excluded due to sparse cells; p5, $\chi^2_8 = 199.2$, $P < 0.001$, white-spot primaries were excluded due to sparse cells). The proportion of p6s classified as white spot increased from Arctic Canada–west Greenland to the Pacific. Proportions from the intervening regions of Newfoundland–British Isles–Barents Sea did not differ significantly from each other ($\chi^2_4 = 4.5$, $P = 0.34$). The

corresponding proportion of birds showing more white on p6 in the form of black bar, black spot(s) and all white categories decreased from Arctic Canada–west Greenland to the Pacific.

The proportion of p5s showing any black (white spot, black bar or black spot(s) categories) increased from Arctic Canada–west Greenland to the Pacific. Proportions from intervening regions did not differ significantly from each other ($\chi^2_2 = 4.4$, $P = 0.11$). There was no clear indication of a north-south trend in proportions in these primaries. Results for p6 and p5 were concordant with those for p10 through p7 in that they indicated a general reduction in the amount of white and an increasing amount of black in the wingtip from Arctic Canada–west Greenland counterclockwise to the Pacific.

GEOGRAPHICAL VARIATION IN WHITE SCORE AND BLACK LENGTH

White Scores differed significantly among regions (Fig. 4a; ANOVA; $F_{4,556} = 74.5$, $P < 0.001$) and generally decreased from Arctic Canada–west Greenland to the Pacific. The trend was not indicative of a cline as there were major discontinuities between Arctic Canada–west Greenland and Newfoundland, and between Barents Sea and Pacific regions. Post-hoc multiple comparisons showed that means for Newfoundland, British Isles, and Barents Sea did not differ significantly (all $P \geq 0.53$). Both Arctic Canada–west Greenland and the Pacific differed significantly from all other regions (all $P < 0.001$). No consistent north-south trend was apparent. Expressed in relation to the mean White Score for the Pacific, mean White Scores for Barents Sea, British Isles, Newfoundland, and Arctic Canada–west Greenland regions were 39%, 40%, 33% and 58% higher, respectively.

A similar regional trend was apparent within each sex (Fig. 4a lower panel; Newfoundland and British Isles excluded due to small sample sizes). ANOVA revealed significant main effects of region ($F_{2,183} = 72.9$, $P < 0.001$) and sex ($F_{1,183} = 7.4$, $P < 0.01$) on White Score, with a significant interaction term ($F_{2,183} = 4.1$, $P < 0.05$). With the exception of the Barents Sea sample, males on average had lower White Scores than females.

Overall, Black Length differed significantly among regions (Fig. 4b; ANOVA; $F_{4,280} = 188.3$, $P < 0.001$) and increased from Arctic Canada–west Greenland counterclockwise to the Pacific, but again, there was no evidence that the trend was clinal. The largest discontinuity in Black Length occurred between Barents Sea and Pacific regions. Post-hoc multiple comparison tests showed that means for Newfoundland, British Isles, and Barents Sea were numerically similar and did not differ significantly (all $P \geq 0.83$). Both Arctic Canada–west Greenland and the Pacific differed significantly from all other regions (all $P < 0.001$). No consistent north-south trend was apparent. Expressed in relation to the mean Black Length for the Arctic Canada–west Greenland sample, mean Black Lengths for Newfoundland, British Isles, Barents Sea, and Pacific were 7%, 10%, 10%, and 39% longer respectively.

A similar regional trend in Black Length was apparent within each sex (Fig. 4b lower panel; New-

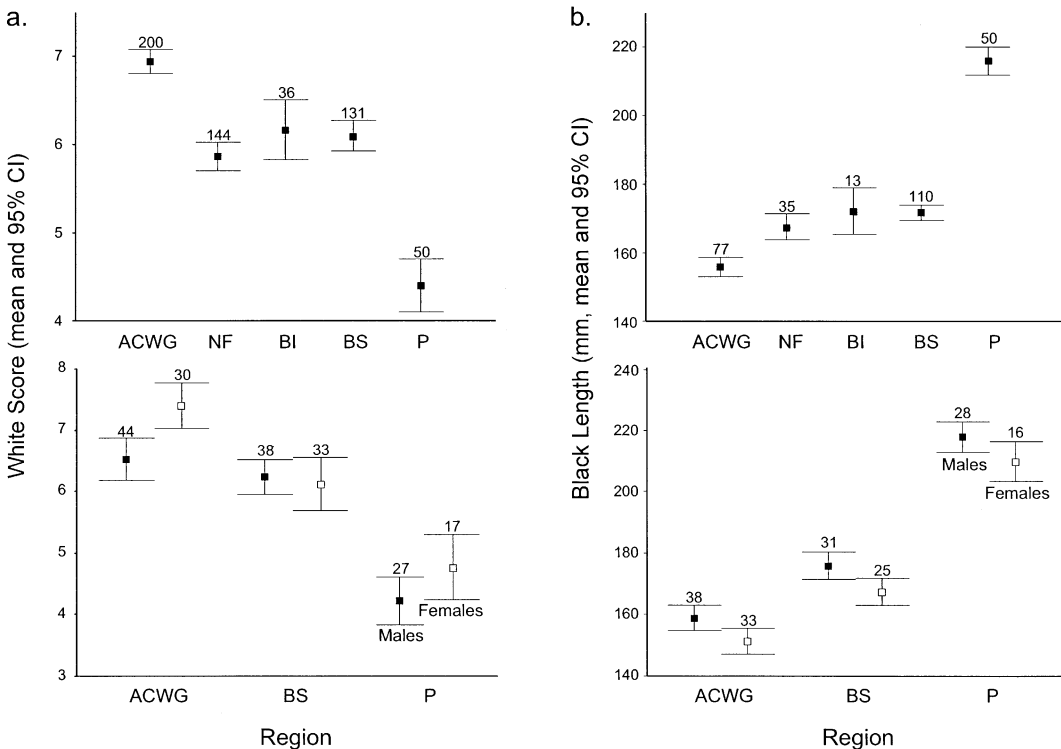


FIGURE 4. Mean White Score (a) and Black Length (b) according to region for all Black-legged Kittiwakes (upper), and for known males and females (lower). ACWG = Arctic Canada–west Greenland, NF = Newfoundland, BI = British Isles, BS = Barents Sea, P = Pacific. Sample sizes (indicated above datapoints) of known-sex birds from NF and BI were small, and so these regions were excluded from the lower panels.

foundland and British Isles excluded due to small sample sizes). ANOVA revealed significant main effects of region ($F_{2, 165} = 318.7$, $P < 0.001$) and sex ($F_{1, 165} = 18.5$, $P < 0.001$) on Black Length, with a nonsignificant interaction term ($F_{2, 165} = 0.04$, $P = 0.96$). In all regions, males on average had longer Black Lengths than females; the overall average difference was 8.1 mm (95% CI: 4.4–11.8 mm), or 5% of the mean Black Length of females.

DISCRIMINANT ANALYSIS

Pacific and Atlantic birds could be distinguished based on Black length (BL) alone with a success rate of 98% ($D = 0.07BL - 12.55$, where D is the discriminant score; Wilks' $\lambda = 0.35$, $F_{1, 283} = 532.8$, $P < 0.001$). Birds with a score larger than 1.17 (D_{crit} ; equivalent to a Black Length of 191 mm) were classified as Pacific and less than 1.17 as Atlantic. The stepwise analysis did not include White Score (WS) in the discriminant function. Classification success rates were similarly high when males (98%) and females (96%) were considered separately.

DISCUSSION

This paper has shown significant variation in wingtip patterns of Black-legged Kittiwakes from Atlantic and Pacific areas, and to a lesser extent between regions

within the Atlantic. There was a general trend toward increasing amount of black (Black Length) and decreasing amount of white (White Score) from Arctic Canada–west Greenland counterclockwise to the Pacific. The trend did not suggest a clinal pattern because of significant discontinuities between Arctic Canada–west Greenland and Newfoundland, and between the Barents Sea and the Pacific, with similar wingtip patterns being seen in birds across a broad geographic area from Newfoundland, British Isles, and the Barents Sea.

Geographical trends in wing length could have caused the trends in Black Length reported here. Geographic variation in Black-legged Kittiwake wing length is reported in Sluys (1982). He did not have a sample from Arctic Canada but did measure birds from west Greenland, as well as British Isles, Barents Sea, and Bering Sea (equivalent to Pacific sample here). Mean wing lengths for his British Isles, Barents Sea, and Bering Sea samples were –1%, 3%, and 5% longer than his west Greenland sample, whereas mean Black Lengths reported here were 10%, 10%, and 39% longer respectively. Thus, longer wing lengths did not explain the longer Black Lengths, particularly in Pacific birds. Male kittiwakes have wings ca. 3% longer than females (Coulson et al. 1983), and Black Lengths

about 5% longer (this study), so Black Length was roughly proportionately longer in males compared to females.

Regional differences in wingtip patterns could be the result of selection driven by adaptation to different local environments (Zink and Remsen 1986). Alternatively, nonselective agents such as genetic drift or founder effects could have been the source of the differences. Although unlikely (see Hailman 1986), kittiwake wingtip patterns could be under complete environmental control. If kittiwake wingtip patterns are genetically based to some degree, then the continued existence of geographic variation, regardless of its origin, suggests that dispersal and gene flow between regions are sufficiently low for the variation to be maintained. So long as strong selection is not maintaining the geographic variation in the face of high levels of gene flow, geographic variation in a phenotypic character such as wingtip patterns may indicate general patterns of dispersal in kittiwakes. Based on geographic differences and degree of variation, data presented here suggest (1) highly restricted dispersal between Atlantic and Pacific, (2) less-restricted dispersal between Arctic Canada–west Greenland and Newfoundland–British Isles–Barents Sea areas, and (3) widespread dispersal within the Newfoundland–British Isles–Barents Sea area.

In Black-legged Kittiwakes, dispersal is mainly natal with almost no adults moving between colonies once they have started to breed (Porter and Coulson 1987, Coulson and Nève de Mévergnies 1992). In the latter paper, the authors showed that almost 80% of kittiwakes in their sample recruited to the natal colony or to a colony within 50 km of the natal site. The geographic scale of regions and the separation between them in the present study is on the order of thousands of km, so relatively little between-region recruitment would be expected (see also Coulson 1966). This would act to maintain phenotypic (and genotypic) differences between regions. However, Coulson and Nève de Mévergnies (1992) made the point that the 20% of birds that do not return to breed within 50 km of their natal site provide the potential for considerable dispersal in kittiwakes. Whether this dispersal is sufficient to homogenize wingtip patterns over as wide an area as Newfoundland–British Isles–Barents Sea is unclear. Although there are no records of eastern-Atlantic kittiwakes breeding in the western Atlantic, it is well known that immature birds from the Barents Sea and British Isles spend time in coastal areas of southwest Greenland and Newfoundland (Coulson 1966, Coulson and Nève de Mévergnies 1992, Nikolaeva et al. 1997). This may facilitate eventual dispersal of some birds to areas in which they have had previous experience as nonbreeders.

Sluys (1982) argued that overlap in size of Atlantic and Pacific kittiwakes, and a clinal pattern of variation in morphometry, were reasons not to recognize birds from the two oceans as distinct taxa (subspecies). I disagree with this conclusion. The overlap Sluys found was based on a simultaneous test procedure outlined by Gabriel and Sokal (1969), and was the result of a failure to reject the null hypothesis of no difference between samples. It is not surprising that Sluys found

overlap, so characterized, considering his small sample sizes (see Table 1 of Sluys 1982), and attendant low power to detect differences if present. Furthermore, although he suggested a cline in body measurements, his sampling locations were too unevenly distributed (no samples west of west Greenland or east of Spitzbergen, all the way to the Bering Sea) to conclude that trends were indeed clinal from west to east.

Rather than indicate that Pacific and Atlantic kittiwakes are indistinct, wingtip pattern data presented here strongly suggest that they represent separate taxa. Published differences in several body measurements and foot morphology (Dwight 1925, Vaurie 1965, Sluys 1982) lend further support to this. At which taxonomic level should Pacific and Atlantic kittiwakes be separated? This depends on which species concept is followed. Under the biological species concept (Mayr 1970), Pacific and Atlantic kittiwakes would likely remain in separate subspecies of the polytypic species *Rissa tridactyla*, for two reasons: interbreeding may occur, particularly along the northeast coast of Russia, and differences between the two taxa may not be sufficient to warrant separate species status. In contrast, under the phylogenetic species concept (Cracraft 1983, McKittrick and Zink 1986) the difference in Black Length between Pacific and Atlantic birds would be considered diagnostic, and thus the two taxa may represent two phylogenetic species.

Work is now clearly needed on genetic differences both between and within Atlantic and Pacific areas using modern techniques. Also, more detailed analysis of Pacific–Atlantic differences in foot morphology is necessary, together with a clearer understanding of the distribution, movement patterns, gene flow, and ecology of the two taxa where they breed side by side in northeast Russia.

I am very grateful to those who have helped me in this project. Kaj Kampp, David Nettleship, and Ray Prach photocopied kittiwake wings in various museums. I am particularly indebted to Rob Barrett, who went out of his way to collect wings from several areas in the Barents Sea, and provided welcome reminders that I had not yet published the results of this study. John Coulson allowed me to work on the warehouse kittiwake colony at North Shields. Jan Neuman scored wingtips at Cape St. Mary's. Bill Montevecchi provided some 35-mm slides of Newfoundland kittiwakes. Tony Gaston, Ronald Sluys, David Irons, Rob Barrett, Vicki Friesen, David Dobkin, and an anonymous reviewer provided comments that improved the paper.

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