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Philopatry, morphological divergence, and kin groups: structuring in thick-billed murres *Uria lomvia* within a colony in Arctic Canada

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Many seabirds exhibit high natal philopatry despite their extreme dispersal ability and delayed reproduction, and some exhibit phenotypic clustering in colonies and fostering or adoption of neighbouring chicks. Previous investigations of kinship in a small thick-billed murre colony *Uria lomvia* (Alcidae) in Norway revealed high relatedness among breeders on cliff ledges. To investigate the presence of kin groups and within-colony genetic sub-structuring elsewhere, we investigated kinship within a larger murre colony on Coats Island, Nunavut, Canada. Morphological (five characters) and genetic data (five microsatellite loci and a fragment of the mitochondrial cytochrome *b* gene) were analysed. Strong morphological differentiation was found among ledges. Genetic structuring was overall weak but significant at the coarse scale for males among ledges and on the east vs. the west side of the colony. Global spatial autocorrelation analyses did not detect consistent, widespread spatial patterns, although local 2D analyses provided some evidence of a tendency for larger neighbourhood sizes for females and a broad range of small to large neighbourhoods for males. Average within-ledge relatedness was low overall, but ranged widely from slightly unrelated to greater than the level of cousins in both sexes. Kin-level relationships occurred on ledges more frequently for same-sex groups than expected by chance, suggesting that recruiting breeders (especially females) avoid or are unable to settle directly adjacent to relatives particularly of the opposite sex. Behavioural studies of natal dispersal of murres at Coats I. indicating that both sexes are highly philopatric, but that up to one-fifth of females may disperse, are concordant with this study. Overall, structuring was weaker than in Norway, and may be explained in part by genetic marker and sampling artifacts, and by the lack of genetic equilibrium suspected in the much larger Canadian Arctic colony. Natal philopatry may be an important factor driving the diversification of seabirds and kin groups in other colonies and species and may be more widespread than is currently acknowledged.

Natal site fidelity (natal philopatry) can strongly impact the genetic structure of populations. Philopatry over many generations can promote genetic structure both among- and within-populations, and the formation of kin groups. Within small groups evolution can proceed at a faster rate due to non-random mating (Kingston and Rossiter 2004, McKinnon et al. 2004), genetic drift (Luchetti et al. 2005, Sigg 2006, Knopp and Cano 2007), cultural evolution and learning (Cavalli-Sforza and Feldman 1981, Borgerhoff Mulder 1991, Singer et al. 1993, Whitehead 1998, Lachlan and Servedio 2004), and the evolution of cooperation (Hamilton 1964a, Hamilton 1964b, Trivers 1971).

Seabirds are an excellent system to investigate the effects of philopatry on population genetic structure. Despite their high dispersal ability and extended pre-breeding stage often lasting years, many species exhibit strong philopatry to their natal colony, burrow, or site (Gaston 1991, Ovenden et al. 1991, Halley et al. 1995, Bretagnolle and Genevois 1997, Rabouam et al. 1998, Spear et al. 1998, Young 1998, Schjørring 2001, Steiner and Gaston 2005). As many seabirds are colonial and encounter the same neighbours over several breeding seasons, the opportunity arises for helping behaviour to evolve (Trivers 1971), providing a possible mechanism for the reinforcement of philopatry, especially if kin groups are present (with or without kin recognition; Hamilton 1964a, b). Molecular approaches coupled with behavioural and morphometric data enable investigation of the effects of philopatry on diversification.

Progress is being made on exploring the effects of philopatry on differentiation and speciation in waterbirds (Avise et al. 2000, Patirana et al. 2002, Abbott and Double 2003, Burg et al. 2003, Dearborn et al. 2003, Friesen et al. 2007a, b), but few investigations at the within-population level have been undertaken (Ovenden et al. 1991, Austin et al. 1994, Friesen et al. 1996a, Cohen and Dearborn 2004, McKinnon et al. 2006, Sonsthagen et al. 2010). Within seabird colonies, indirect evidence of genetic sub-structuring stems from observations of phenotypic clustering and of helping behaviour. In murres, non-random aggregates of egg morphs and chick plumage types (in thick-billed murres *Uria lomvia* Alcidae, Gaston and Nettleship 1981) and bridling phenotype (a white eye

ring morph in common murre *U. aalge*, Southern et al. 1965, Birkhead et al. 1980) have been observed. Aside from communal defense from predators and intruders, behaviours which are often observed in colonial species, adoption and alloparenting (feeding, defending and brooding) of fostered young (i.e. not the genetic offspring of the parents caring for them) are also observed in some seabirds (Carter and Spear 1986, Pierotti and Murphy 1987, Saino et al. 1994, Brown et al. 1995, Jouventin et al. 1995, Wienecke 1995, Brown 1998), including murres (*U. aalge*, Birkhead and Nettleship 1984, and *U. lomvia*, Gaston et al. 1993b, 1995, Gaston et al. 2005). Although reproductive error (misguided parental care) may explain some instances of adoption and alloparenting, these behaviours may occur even when parent-chick recognition exists. Kin groups have been confirmed in at least two seabird species where adoption and alloparenting were observed, suggesting that kin selection may explain at least some cases of alloparenting and phenotypic clustering (Friesen et al. 1996a, Bukaciński et al. 2000, but see Brown 1998). Within-population sub-structuring in philopatric seabirds may thus occur in several other species that have not been investigated yet and may be more widespread than is presently recognised.

Thick-billed murres are philopatric (Gaston et al. 1994, Steiner and Gaston 2005), cliff-nesting, sexually monomorphic seabirds which share biparental care of the single chick that hatches during the short Arctic breeding season. Despite the possible high cost of parental care in this species (e.g. chicks are fed fish captured far from the colony), adoption and alloparenting occur on Coats Island in the Canadian Arctic (Gaston et al. 1995, Gaston et al. 2005), notwithstanding parent-chick recognition (Lefevre et al. 1998, Ibarguchi 1998). In a small thick-billed murre colony on Hornøya, Norway (~450 breeding pairs), Friesen et al. (1996a) found genetic evidence of extended family groups on breeding ledges based on analyses of allozymes and a fragment of the mitochondrial cytochrome *b* gene; within ledges, murres were related on average to the level of first cousins. In the present study we explore whether kin groups and within-colony genetic structuring may be more widespread, and expand on the Norway study by investigating phenotypic clustering, genetic structuring and relatedness in the larger thick-billed murre colony on Coats I.

Methods

Study site and sampling

Three hundred and three thick-billed murre breeders (i.e. adults incubating or brooding a chick, $n_{males} = 162$, $n_{females} = 135$, $n_{unsexed} = 6$) were caught off cliff ledges within the west subcolony on the northeastern coast of Coats I., Nunavut, Canada (62° 56.79′N, 82° 02.04′W) between June and August 1996 (during incubation and chick-rearing) as part of on-going breeding studies continuing yearly including the recent August 2010 season. The west subcolony consists of ~18 000 breeding pairs and the study ledges are distributed throughout the colony cliff face (Fig. 1A). The west subcolony has been monitored since 1981 for long-term demographic and behavioural studies (Gaston 1991, Gaston et al. 1993a), and many of these long-lived breeders were banded and observed before 1996, during this study in 1996, and in subsequent years.

Attempts were made to trap both breeding partners at each site by sampling during the day, when males tend to be present on ledges, and from midnight to dawn, when females attend the sites at this colony (Gaston and Nettleship 1981, Verspoor et al. 1986, Elliott et al. 2010). Subsets of trapped adults were included for genetic and/or morphometric analyses depending on the data available for the same individuals (from 27 to 39 birds per ledge, representing a third to most of the established breeders at high-quality and more stable sites on the study ledges). Genetic data were obtained from 288 to 290 of the 303 individuals depending on the genetic marker used ($n_{males} = 157$, $n_{females} = 133$); morphometric data were available from 295 of the total birds ($n_{males} = 156$, $n_{females} = 133$, $n_{unsexed} = 6$). Murres do not build a nest; to minimise disturbance to breeding pairs, the ledges sampled were in well-established (occupied for at least 10 years previously) although more peripheral areas of the colony along the top of occupied areas (Fig. 1A). On these selected ledges individual breeding sites were mapped and the birds were identified by colour and metal bands. Mass, wing length, bill length, bill depth and distance from the bill tip to the nares were measured, and blood samples were obtained.

A total of ten ledges in six subareas were photographed, mapped, and sampled (Fig. 1A); these subareas are within study plots under long-term observation and were chosen to obtain representative sampling spaced at approximately every quarter of the colony where plots were accessible. In four of these subareas (Z, FG, S, JB), pairs of ledges on average 4.5 m apart (midpoint to midpoint of ledges) were sampled; the two remaining subareas (X and Q) contained single ledges each separated by a deep gully (Fox Gully, Fig. 1A). Photo enlargements of colony face views were used for estimating distances. Individual ledge photographs with breeders were used to estimate distances between breeding sites (with an average approximate and relative breeding site width of 15 cm), and assigning breeders' approximate X–Y coordinates.

Statistical analyses of morphological data

Mass, wing length, and bill traits were compared (ANOVA) between the sexes and among birds from different ledges. Significance of pairwise comparisons between all ledges (having unequal sample sizes) within groups (all birds, males only, and females only) was tested using Tukey-Kramer procedures ($\alpha = 0.05$), which consider the experiment-wise error rate (i.e. Type I errors; Sokal and Rohlf 1995) and are thus conservative. Because birds of a given size could in theory congregate at a ledge based on factors such as competitive ability, ledge size, age, or environmental factors, the effect of variation among groups due to body size was removed using the procedure derived by Burnaby (1966) and the program '*Burnaby*' (reviewed by Rohlf and Bookstein 1987) within the *MacLeod* package (MacLeod 1990). Briefly, the procedure removes the effect of body size through the transformation of morphometric variables. Differences among ledges in the transformed measurements

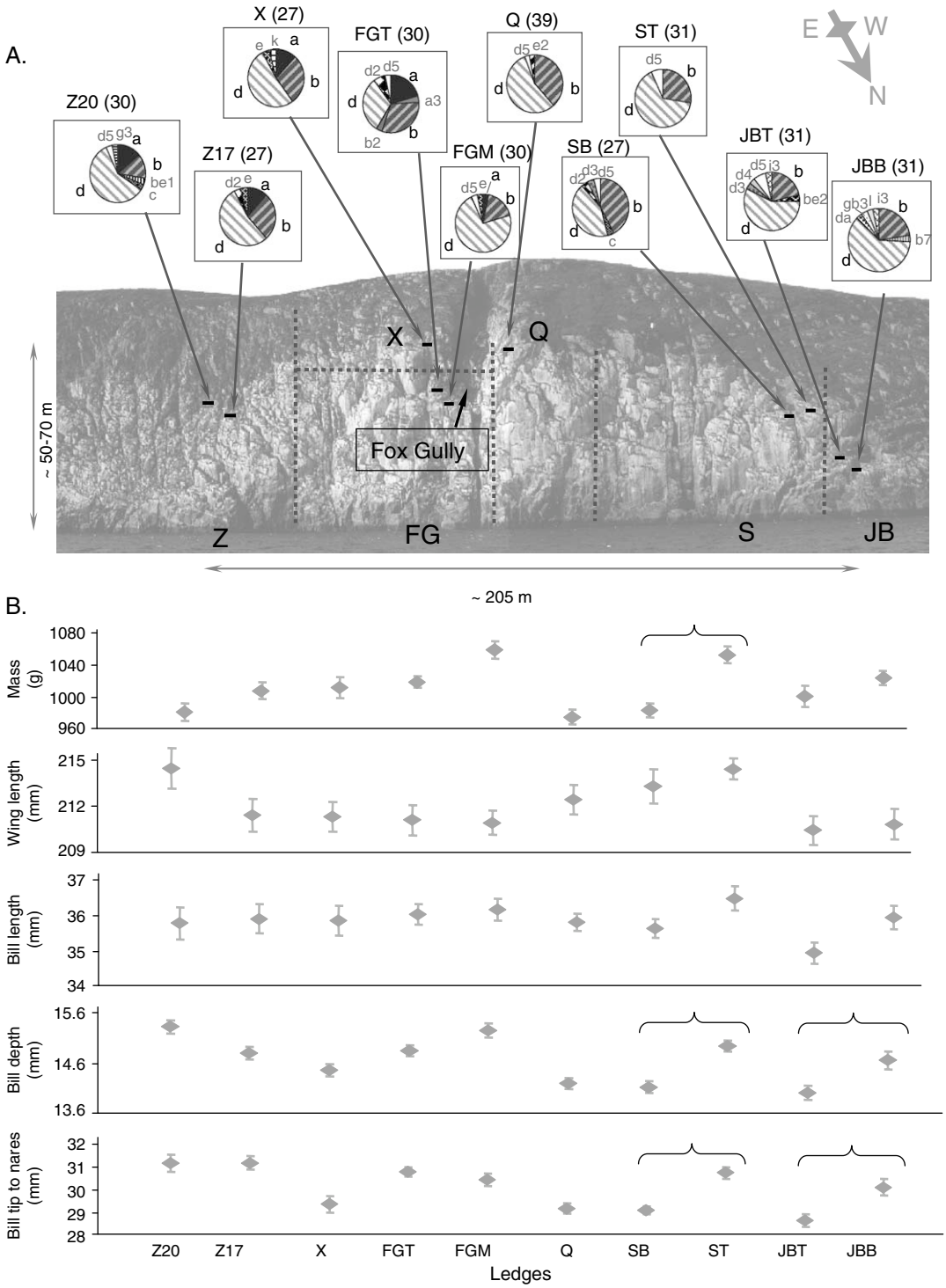

Figure 1. The west subcolony of thick-billed murres on Coats Island, Nunavut. A. Cliff face view and diagram of the ten breeding ledges sampled in six subareas. The numbers of sampled breeders are shown for each ledge (black numbers in brackets after the ledge name). The frequencies of cytochrome *b* haplotypes on ledges are indicated, each representing ~30 breeders of both sexes (lower case letters in bold are the three most common haplotypes). B. Averages of morphological traits (mass, wing length, bill length, and bill tip-to-nares distance, [±SE]) of murres on ledges. Brackets indicate pairs of ledges within the same subarea that are significantly different from each other.

were compared also (ANOVA and Tukey-Kramer tests). Analyses were conducted with both sexes pooled and separate, as settlement patterns could differ between the sexes, or if a greater degree of variation in morphology or stronger natural selection occurred in one sex. Morphological characters and size-corrected characters were treated independently as traits did not appear to vary systematically in the same way on most ledges (see below and Fig. 1). As few analyses involved multiple tests of the same hypothesis, correction for Type I errors was not necessary; however, as a

conservative approach to account for four multiple contrasts (males versus females, and each group among ledges), the Benjamini and Yakutieli (B-Y) method was applied also (based on controlling the proportion of falsely rejected hypotheses, the false discovery rate; Benjamini and Hochberg 1995, Benjamini and Yekutieli 2001). The method is preferred over Bonferroni corrections as power is increased (thus decreasing type II errors in addition to type I errors), and can be used when dependence exists among hypothesis tests (Benjamini and Yekutieli 2001, Narum 2006). The adjusted critical value is 0.024 for four contrasts (see Narum 2006).

Genetic analyses

Genetic sub-structuring was investigated at two scales: a coarse level (among subareas and among ledges across the colony) and a fine scale (within ledges). DNA was extracted by protease K digestion and phenol/chloroform methods, followed by isopropanol and sodium acetate precipitation (Kocher et al. 1989, Ibarguchi et al. 2004). As murres cannot be reliably sexed from external measurements, sex was corroborated genetically (through sex-specific length variation in the intron within the CHD locus of the avian sex chromosomes, Griffiths et al. 1998). A 306 bp fragment of the maternally inherited mitochondrial cytochrome *b* gene was screened (primers L14841 and H15149, Kocher et al. 1989) using analyses of single-strand conformational polymorphisms followed by direct sequencing of representatives of the most common haplotypes (Friesen et al. 1996b, Ibarguchi et al. 2004). In addition, five bi-parentally inherited murre microsatellite nuclear loci were screened (*ulo12a12*, *ulo12a22*, and *ulo14b29* from thick-billed murres, and *uaa1-23* and *uaa5-8* from common murres; Ibarguchi et al. 2000). The combined probability of exclusion for these loci, the probability that two individuals share a genotype by chance (Hanotte et al. 1991, Bruford et al. 1992) was 1.47×10^{-7} (Ibarguchi et al. 2004) and provided enough power for the size of this colony. Including both types of mitochondrial and nuclear markers was advantageous as improved temporal and spatial resolution could be gained: hypervariable microsatellites evolve more quickly than cytochrome *b*, providing different temporal scales, while mitochondrial DNA undergoes little (Rokas et al. 2003) or no recombination, is haploid, and is more sensitive for detecting population subdivision, thus improving spatial resolution and facilitating tracing the evolutionary history of populations.

Statistical analyses of molecular data

Population-wide analyses of deviations from Hardy-Weinberg equilibrium were conducted in POPGENE (Yeh et al. 1999) for microsatellite data to detect possible null alleles at high frequencies, and loci were tested for linkage.

At the coarse scale, measures of genetic subdivision among ledges and among areas were obtained by estimating Φ-statistics and analogues (Excoffier et al. 1992, Peakall et al. 1995) from haplotypic data and *F*-statistics (based on the approach by Weir and Cockerham 1984) from microsatellites using Arlequin v. 2 (Schneider et al. 2000) and GenAlEx v. 6 (Peakall and Smouse 2006.

Spatial autocorrelation

As breeding sites are continuous across the cliff face, the assignment of ledges as the sampling unit is rather artificial; genetic clusters could hypothetically span more than one ledge, or each ledge could contain multiple (similar or dissimilar) discrete clusters of breeders. To partially circumvent the problem of artificial sampling units, multivariate spatial autocorrelation analyses were conducted at the global and local (two-dimensional or 2D Local Spatial Autocorrelation) scales based on the approaches by Smouse and Peakall (1999), Peakall et al. (2003) and Double et al. (2005), as implemented in GenAlEx v. 6 (Peakall and Smouse 2006). Global analyses can be used to investigate genetic processes (which influence structuring) operating consistently and at a large scale across a study area, while local analyses permit investigation of processes at the level of the individual within a neighbourhood of a given size (Peakall et al. 2003, Double et al. 2005, Sonsthagen et al. 2010). Briefly, the autocorrelation coefficient R (ranging from -1 to 1, with zero meaning lack of autocorrelation, and here using uppercase R rather than the usual lowercase r to distinguish from the coefficient of relatedness, below; Smouse and Peakall 1999), based on the strength of the association between genetic similarity of individuals and their spatial proximity, is obtained between individuals at a given spatial distance. R coefficients, together with their statistical significance, provide indicators of the cluster size within which individuals share genetic similarity for distance intervals contained within the chosen distance classes (Peakall and Smouse 2006). Typical spatial autocorrelation plots show the response of R along an axis of linear distance or distance classes (Suppl. material Appendix 1). The significance of R coefficients, those falling above or below a 95% confidence interval for a given distance or distance class, was tested by permutation within GenAlEx 6 (999 permutations were conducted per R).

Correlograms (plots of R and distance, with intervals of a chosen distance class size, Suppl. material Appendix 1) were obtained for global analyses spanning the length of the study area ($\sim$200 m), and spanning the maximum length of individual ledges (less than 6 m). For colony-wide analyses, distance classes tested were 1 m, 3 m (approx. average ledge size), 5 m, 10 m, 20 m, 50 m and 100 m. For ledge-wide analyses, distance classes tested were chosen at 15 cm (for analyses involving all birds to include breeding partners at a site), 30 cm, 45 cm, 60 cm, 90 cm, 150 cm and 180 cm. For microsatellites, colony-wide analyses of all birds (sexes pooled) could not be performed because of software limitations, thus only the separate sexes were included for this category.

For local 2D autocorrelation analyses, local R coefficients can be calculated for neighbourhoods involving focal individuals and their neighbours, so that 'distance classes' are the increasing neighbourhood size (as the number of neighbours), rather than distance per se (Double et al. 2005). For 2D local analyses, the number of neighbours tested in the present study was arbitrarily increased by 2

from 2 to 38 birds, subsequently increased by 4 birds up to 50, and then increased by 10 neighbours up to 120.

Mantel's tests

Mantel's tests were used to test for correlations between geographic and genetic distance between individuals (Mantel 1967) and were conducted in *GenAlEx* v. 6, based on geographic distance as above and genetic distance using Φ_{PT} (analogous to Φ_{ST}, with the advantage that haploid and codominant data can be compared; Peakall et al. 1995, Peakall and Smouse 2006).

Kinship

To further investigate fine-scale genetic structure, coefficients of relatedness r (Queller and Goodnight 1989, not the same coefficient as the spatial correlation coefficient R above) based on variation in cytochrome *b* (divided by two to estimate overall relatedness from mitochondrial data; Friesen et al. 1996a) and microsatellites were calculated using *Kinship* v. 1.3.1 (Goodnight et al. 1999). Pairwise relatedness was calculated within each ledge for all birds, and separately for males and females, and a global average was obtained from the ten ledge means for each group (where 0.125 if the expected average among first cousins). Pairwise coefficients were also obtained for breeding partners to test for non-random mating, and to compare the resolution power of the markers based on birds of known relationship, coefficients were also obtained for known legitimate parent-chick pairs from a previous study (Ibarguchi et al. 2004), which included some of the breeders here. Because clusters of distinct families (in turn unrelated) could potentially co-exist on a ledge, obtaining an average coefficient of relatedness for a ledge could underestimate the degree of structure. To partially circumvent this, pairwise relatedness coefficients among same-ledge individuals were classified into each of three bins: highly unrelated ($r < -0.1$), background or low relatedness ($-0.1 \leq r \leq 0.1$), or kin ($r > 0.1$, where 0.125 is the expected average among cousins and 0.5 is the average for parent-offspring pairs and for full siblings). Subsequent to their classification, proportions within ledges in each relatedness bin were calculated to compare five groups: all birds (sexes pooled), males only, females only, breeding partners, and randomly generated birds. The latter group was constructed by randomly assigning artificial birds a genotype from real allele and haplotype frequencies in the population and a random ledge using a simple Visual Basic algorithm within Microsoft Excel. Within-ledge proportions in each bin were compared among bird groups using non-parametric Kruskal-Wallis tests in JMP v. 6.0.2 Statistical Discovery (SAS Institute, Inc., Cary).

Analyses of barriers: incorporating genetics and morphology

Monmonier's maximum difference algorithm (Monmonier 1973) is a geometric-geographic approach that detects the most abrupt rate of change in one or more variables among population pairs (as distance measures; Manni et al. 2004). To examine the concordance in patterns of structure, and treating ledges as subpopulations, distance matrices were obtained from cytochrome *b* data (Φ_{ST}), microsatellites (F_{ST}, both obtained as above, from Arlequin v. 2), and the five morphological traits combined (based on Canberra distance in Clustering Calculator; Brzustowski 2002). Using the ledge midpoints as X-Y coordinates for these subpopulations, these distance matrices, along with the above matrices, were used in Barrier v 2.2 (Guérard and Manni 2002) to examine structuring within the colony (i.e. 'barriers').

Analyses of behaviour

Data on philopatry (movement between the hatching and breeding sites) was available for 57 females and 42 males banded as chicks (part of a larger study, Steiner and Gaston 2005; raw data including two birds also in the present study are from U. Steiner and A. Gaston, unpubl.). Dispersal distances were binned into 5 m, 10 m, 20 m and greater than 20 m (up to $\sim$60 m). Dispersal distances were compared between sexes using a Fisher's exact test and χ^2 tests. For χ^2 tests, to account for small values in some cells and to test for statistical significance, Monte Carlo permutations ($n = 1\,000$) of the data were conducted to generate the null distribution of expected χ^2 values (Roff and Bentzen 1989) using the program RandoChi (Delport 2007).

Results

Analyses of morphology

Highly significant differences were found between the sexes for bill length, bill depth, and the bill-tip to nares distance (Table 1), with males being the larger sex. Removing the effect of body size resulted in females being significantly heavier than males, while males showed greater bill depth than females. Means of characters differed significantly among ledges for all birds (sexes pooled) except for bill length. After removing the effect of size, all characters differed significantly among ledges for all birds (Fig. 1B and Table 1). Males and females among ledges analysed separately displayed this same pattern, except that wing length was not significantly different for females before removing the effect of size. Tukey-Kramer test results within contrasts were of interest simply to determine if any consistent patterns existed for specific ledges or subareas of the colony, and if these were consistent among groups (pooled birds versus each sex). For most characters, gradual changes in morphology were observed from east (ledges at Z) to west of the cliff to Fox Gully (Fig. 1B); however, abrupt changes were observed in some characters from west of Fox Gully (ledge Q) to the far west cliff face (JB). Significant differences were observed between pairs of ledges within subareas S and JB (i.e. ledges only a few metres apart within subareas) for mass (S subarea only), bill depth, and bill-tip to nares distance (S and JB, Fig. 1B).

Table 1. Analyses of variance of morphological characters among groups (F ratios and their significance [1]), means by sex and standard errors (in bold), and numbers of significant pair-wise ledge comparisons (Tukey-Kramer tests within contrast, out of 45 comparisons); results after removing the effect of size are shown in italics (size corr; see text).

Character	ANOVA				T-K Tests significant pair-wise ledge comparisons (in 45) per contrast (All, Males, Females)
	Between sexes	Among ledges			
	M vs F n = 289	All Birds n = 295	Males n = 156	Females n = 133	
Mass (g)			**1013.6 ± 4.9** [2]	**1005.3 ± 5.3** [2]	
F-ratios	1.31 (NS) [1]	7.87 ****	3.96 ***	8.31 ****	10, 4, 13
size corr	*7.40* ** [2]	*5.26* ****	*3.32* ***	*4.89* ****	*6, 2, 6*
Wing length (mm) [3]			**212.35 ± 0.4**	**211.52 ± 0.5**	
F-ratios	1.80 (NS)	2.39 *	2.95 **	1.27 (NS)	none, 4, none
size corr	*1.50 (NS)*	*3.55* ***	*2.77* **	*2.50* *	*3, 2, 1*
Bill length (mm)			**36.31 ± 0.1**	**35.1 ± 0.1**	
F-ratios	37.63****	1.33 (NS)	0.90 (NS)	1.07 (NS)	none, none, none
Size corr	*1.15 (NS)*	*7.80* ****	*4.47* ****	*4.69* ****	*14, 5, 7*
Bill depth (mm)			**14.82 ± 0.1**	**14.35 ± 0.1**	
F-ratios	28.23 ****	12.27 ****	7.78 ****	6.69 ****	20, 12, 16
size corr	*6.06* *	*6.08* ****	*4.08* ****	*2.53* *	*9, 7, none*
Bill tip to nares (mm)			**30.39 ± 0.1**	**29.45 ± 0.1**	
F-ratios	23.48 ****	9.91 ****	6.59 ****	6.47 ****	18, 15, 13
Size corr	*0.27 (NS)*	*5.58* ****	*2.51* *	*4.58* ****	*12, 1, 5*

[1] P values prior to applying corrections are denoted by asterisks (* = $P < 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$); NS, non-significant (including all corrections). No changes occurred after applying Benjamini & Yekutieli corrections for the four contrasts for each trait are indicated (adjusted critical values of 0.024).
[2] After accounting for size (size correction), the mean of females was larger than that of males.
[3] Wing length before applying size correction did not fit a normal distribution for all birds and for males only (Shapiro-Wilk tests: all birds. $W = 0.975$, $P = 0.035$; males, $W = 0.970$, $p = 0.043$). Non-parametric tests to compare wing length means gave the same results (Wilcoxon/Kruskal-Wallis tests, Chi-square approximation, between the sexes, $\chi^2 = 1.009$, $p = 0.315$; among all birds, $\chi^2 = 23.703$, $p = 0.005$; and among males on ledges, $\chi^2 = 20.958$, $p = 0.013$). After applying the size correction, wing length approximated a normal distribution.

Genetic analyses at the coarse scale

High genetic diversity and polymorphism were detected in both mitochondrial and nuclear DNA. Gene diversity (Nei 1987) obtained from cytochrome *b* was 0.62 and 21 haplotypes were found, although three predominated in frequency (Fig. 1A; haplotypes *a, b*, and *d*; GenBank accession numbers GU017323, GU017322 and GU017321, respectively). Haplotype *a*, found exclusively east of Fox Gully, was the third most common, and reached 20.7% within ledges (e.g. ledge FGT, Fig. 1A). Haplotypes b, d, and a correspond to Birt-Friesen et al.'s (1992) common haplotypes (1, 3, and 2, respectively); *a* was found in most Atlantic and Canadian Arctic colonies in their study and likely predates the origin of the Coats I. colony (i.e. not unique to this population; see below). For microsatellites, the combined observed heterozygosity was 0.805, and 93 alleles were observed (Ibarguchi et al. 2000; for the sample size in this study, heterozygosities for *ulo12a22* and *uaa5-8* were 0.766 and 0.659, respectively).

At the coarse scale, genetic structuring was slight but significant based on both markers among males on ledges east versus west of Fox Gully, and among ledges based on microsatellites (Table 2). Structuring was overall higher for males than females, and borderline significant for all birds (sexes pooled) among ledges, and between ledges east versus west of Fox Gully based on cytochrome *b*. Measures of structuring based on microsatellites (*F*-statistics) were overall lower than for cytochrome *b* (except for females; Table 2). Based on results from *Barrier* analyses (above), and separating ledges into East, Central, and Far West groupings (Table 2), significant structuring was detected for males based on both mitochondrial and nuclear markers. Applying Benjamini & Yekutieli corrections resulted in no significant genetic structure based on cytochrome *b* for any group, and the subareas detected from *Barrier* analyses were no longer significant based on microsatellites for males; however, significant genetic structure remained for males among ledges and east vs. west of Fox Gully, based on microsatellites (Table 2).

Spatial autocorrelation

Briefly, global colony-wide (200 m) and ledge-wide (< 6 m) spatial autocorrelation analyses revealed a weak pattern of oscillating R coefficients (mostly non-significant) along the distance axis based on mitochondrial data for both males and females (examples and further detail in Appendix 1). The pattern from microsatellites consisted of low R coefficients oscillating close to zero in correlograms (i.e. approximating a random pattern resulting from no structure).

Ledge-wide analyses showed similar patterns to colony-wide analyses, although patterns varied by ledge, sex, and distance class size chosen. However, significant R

Table 2. Measures of genetic structure [1] (Φ_{PT} for cytochrome *b* and F_{ST} for microsatellites, from analyses in *GenAlEx*) and their significance [2] at the coarse scale among ledges, among six subareas (as in Fig. 1A), areas East versus West of Fox Gully, and on East, Central, and West areas based on results from Barrier analyses (see text).

Scale	Genetic structure for each group		
	All birds	Males	Females
Cytochrome *b* (Φ_{PT})			
Among ledges	0.016	0.096	0.000
Among subareas [3]	0.000	0.000	−0.017
East vs West of Fox Gully [4]	0.012	**0.029** * / NS-BY	−0.009
Areas based on Barrier [5]	0.014	**0.026** * / NS-BY	−0.006
Microsatellites (F_{ST})			
Among ledges	0.000	**0.006** *	0.004
Among subareas [3]	−0.001	0.004	0.005
East vs West of Fox Gully [4]	−0.001	**0.005** *	0.000
Areas based on Barrier [5]	0.000	**0.004** * / NS-BY	0.000

[1] Φ_{PT} is an Φ_{ST} analogue (Peakall et al. 1995); both measures of genetic structure were equivalent.
[2] Significance was tested by 999 permutations in GenAlEx and is indicated by an asterisk (* = $p < 0.05$; bold); trends are also indicated in italics ($0.05 < P < 0.09$). Tests that were not significant after applying Benjamini and Yekutieli corrections (NS-BY) for three groups (all birds, males, and females) at different geographic scales per genetic marker are indicated (adjusted critical value: 0.0272).
[3] Subareas Z, X, FG, Q, S, JB.
[4] East includes subareas Z, X and FG; West includes subareas Q, S, JB.
[5] Ledges were lumped by areas based on Barrier analyses which incorporated genetic and morphological data (Fig. 5; East = Z20, Z17, X, FGT; Central = FGM, Q, SB; Far West = ST, JBT, JBB).

coefficients occurred on several ledges especially at a distance of 180 cm (mainly at smaller distance classes) particularly for males, and at 300 cm on a few ledges, especially for females (for brevity, summarised in Appendix 1). These trends were subtle, but perhaps indicate slight sex biases in settlement patterns of philopatric individuals (see below).

Results from finer-scale 2D local spatial autocorrelation analyses differed between females versus males, and for the mitochondrial versus nuclear data (Fig. 2). For both sexes, the proportions of clusters with significant R were overall low (less than 14% for any neighbourhood size). Based on cytochrome *b*, females showed a narrow range of large neighbourhood sizes (i.e. especially between 10 to 22 neighbours), while males showed a much broader range of small to large neighbourhood sizes (2 to 20 neighbours), and some weak secondary structuring at a much larger scale (42 to 90 neighbours or approximately half the colony sample; Fig. 2). When all birds were considered (i.e. birds of opposite sex could be compared), based on cytochrome *b*, the pattern resembled that obtained for microsatellites (Fig. 2). The proportion of significant R clusters based on microsatellites increased from neighbourhood sizes of 2 up to 42 neighbours, subsequently decreasing for females while continuing to increase for males.

Mantel's tests

The only significant correlation between genetic and geographic distance detected in large-scale, colony-wide Mantel's tests occurred among females based on microsatellites but was weak and became non-significant when Benjamini and Yekutieli (2001) corrections were applied (Table 3). Within ledges, few associations occurred, but some significant negative relationships were observed for all birds (both microsatellites and cytochrome *b* and for females (cytochrome *b* only; Table 3). These slight trends were noted simply to provide insight into possible subtle differences in settlement patterns among bird groups and by sex (see below).

Genetic analyses at the fine scale

Kinship

Global averages of the ten within-ledge relatedness means obtained for males and females were similar, and higher based on cytochrome *b* than microsatellites (Table 4). Within-ledge averages were low, but varied widely by ledge, ranging from −0.059 (unrelated and of slightly different genetic composition) to 0.201 and 0.147 (highly related) for females and males, respectively, for cytochrome *b*. High mean relatedness based on mtDNA did not necessarily correspond with high averages based on microsatellites, nor was high average relatedness for males necessarily correlated with that among females on the same ledges (see below; detail in Appendix 2).

The most variable average within-ledge and within-pair relatedness was composed of breeding partners, for which the highest average relatedness coefficients were obtained (excepting parent-chick pairs) and for which the most unrelated birds were also found (Table 4, Appendix 2). In fact, some breeding partners appeared to be inbreeding or mating assortatively, some were mating randomly, and some were avoiding relatives (given the extremely large and negative r coefficients on some ledges).

Average relatedness coefficients for ledges were perhaps not an ideal way of detecting kin clusters as smaller family groups unrelated to other families may have been present (thus reducing the global average r for that ledge). When pairwise relationships within ledges were classified into highly unrelated, background or low relatedness, and kin bins (Fig. 3), proportions of relatedness varied widely among groups (females, males, all birds, partners and randomly-generated birds) and among ledges within groups (individual ledges represented by single points on graphs in Fig. 3; detail in Appendix 2). Based on cytochrome *b*, groups differed significantly within the background and

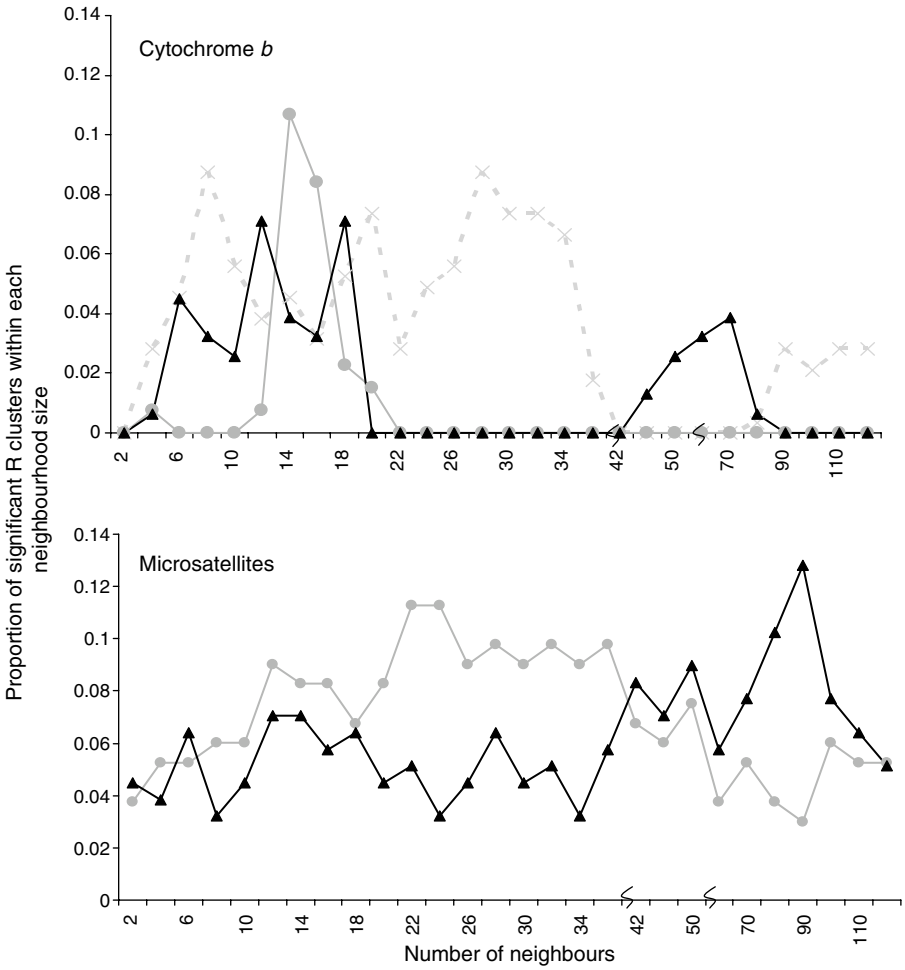

Figure 2. Local two-dimensional spatial autocorrelation analyses, based on mitochondrial and nuclear data, represented as a proportion of significant genetic correlation coefficient (R) clusters within increasing neighbourhood sizes (number of neighbours). Females are represented by gray lines and circles, males by black lines and triangles, and all birds (for cytochrome *b*, for clarity) by dashed light gray lines and 'x' symbols. Note the truncated x-axis and changing scales of increasing neighbourhood size by 2 birds (up to 38), 4 birds (up to 50), and 10 birds (up to 120).

highly unrelated bins, but not within kin bins (Fig. 3; Kruskal-Wallis tests, background, $\chi^2_{(4)} = 12.6$, $p = 0.013$; highly unrelated, $\chi^2_{(4)} = 10.4$, $p = 0.034$; kin, $\chi^2_{(4)} = 0.80$, $p = 0.94$). The most distinct group was females, whose proportions relative to all other groups were much higher in highly unrelated bins, much lower in background bins, and similar to others in kin bins. However, kinship patterns within groups based on microsatellites did not resemble those based on mitochondrial data, and females had the highest mean proportions of kin based on these biparentally-inherited nuclear markers (Fig. 3). For microsatellites, group differences were highly significant within kin and highly unrelated bins, but not background (kin, $\chi^2_{(4)} = 20.4$, $p < 0.001$; highly unrelated, $\chi^2_{(4)} = 18.6$, $p < 0.001$; background, $\chi^2_{(4)} = 3.75$, $p = 0.44$). The all-birds group (sexes pooled) was distinct in that significantly more within-ledge relationships were in highly unrelated bins than other groups, and significantly lower proportions were kin (see below). For breeding partners, the highest proportions of pairwise relationships fell within the background bins for both markers, close to the global averages for kin, and interestingly, lowest in the highly unrelated bins (which may have been expected to be highest if active inbreeding avoidance occurred) compared to other bird groups. Ledges where breeding partners shared high relatedness sometimes (e.g. ledges FGT, ST, and Q; Appendix 2) but not always corresponded with female or male groups with high relatedness.

Analyses of barriers: incorporating genetics and morphology

Combining mitochondrial, nuclear, and morphometric data to investigate where barriers occurred (i.e. where variables displayed an abrupt rate of change) revealed two main breaks along the colony supported by all three data sets (Fig. 4). The first occurred at Fox Gully and included all ledges east of this barrier (i.e. Z20, Z17, X and FGT) in one group; FGM was placed in a second central group along with Q and SB (Fig. 4 and Fig. 1A). A barrier along the top of Fox Gully (i.e. separating X from Q) was supported by two data sets (genetic data; Fig. 4). A second barrier supported by all three data sets was located on the far west side of the colony, placing ST, JBT and JBB in a third group; the lower segment of this barrier was supported by two of the data sets only (SB from the far west; morphological and mitochondrial data, Fig. 4). The Fox Gully barrier has been mentioned previously as males

Table 3. Summary of trends from global (colony-wide) and local (within ledges, results from 10 ledges) Mantel's tests for all birds (sexes pooled), males and females. Bold coefficients remain significant after applying corrections [1] for comparing ten ledges within group and genetic marker (the number of ledges out of ten with significant and non-significant coefficients are indicated).

	Cytochrome *b*		Microsatellites		
	R^2 Coefficient [1]	Slope [2]		R^2 Coefficient [1]	Slope [2]
Across colony					
All birds	NS	+		NS	+
Males	NS	+		NS	+
Females	NS	−		0.001 */NS-BY	+
Within ledges (summaries from 10 ledges)					
All birds					
Total		4 +, 6 −	Total		4 +, 6 −
Eight ledges	NS		Eight ledges	NS	
Two ledges:	0.008 */NS-BY	+	Two ledges:	**0.035 ****	−
	0.018 *	−		0.020 */NS-BY	−
Males					
Total		6 +, 4 −	Total		6 +, 4 −
Ten ledges	NS		Eight ledges	NS	
			Two ledges:	0.036 */NS-BY	−
				0.052 */NS-BY	−
Females					
Total		2 +, 8 −	Total		5 +, 5 −
Nine ledges	NS		Nine ledges	NS	
One ledge:	**0.023 ***	−	One ledge:	0.067 */NS-BY	−

[1] P-value: NS, not significant (including correction); * = $p < 0.05$; ** = $p < 0.01$. Tests that were not significant after applying Benjamini and Yekutieli corrections (NS-BY) within each group and genetic marker are indicated (an adjusted critical value of 0.0171 for three comparisons per marker were used for colony-wide tests, and 0.01707 for ten within-ledge comparisons per group, respectively); values in bold remained significant after applying correction.
[2] (+) Positive correlation; (−) Negative correlation.

displayed slight but significant structuring based on this landscape feature (e.g. Φ and *F*-statistics; Table 2), and where haplotype *a* was observed on the east side of the colony only. When ledges were grouped based on the results from barrier analyses (i.e. East, Central and Far West; Fig. 4), significant genetic differentiation was observed for males based on both mitochondrial and nuclear markers (Table 2, but not after applying Benjamini & Yekutieli corrections).

Analyses of behaviour

Based on the data available for a subset of sexed birds banded as chicks and under long-term observations (Steiner and Gaston 2005; U. Steiner and A. Gaston, unpublished), both sexes displayed a peak at dispersal distances of 3 m or less, but the sexes displayed slightly different behaviours; the difference was not statistically significant (Fig. 5; Fisher's Exact Test, $p_{\text{sum of extreme tables}} = 0.068$; $\chi^2 = 6.3$, DF = 3, $p = 0.088$). Whereas the sampled males dispersed mostly

Table 4. Average coefficients of relatedness r (Queller and Goodnight, 1989) and ranges within ledges (or within pairs, for breeding partners and parent-chick pairs), for all birds and by sex. Global averages were calculated from 10 means of within-ledge relatedness for 10 ledges.

Group	n	Cytochrome *b*	Microsatellittes
All birds	290	0.046 (−0.040 to 0.148)	−0.001 (−0.031 to 0.017)
Males	157	0.056 (−0.059 to 0.147)	0.007 (−0.017 to 0.054)
Females	133	0.040 (−0.059 to 0.201)	0.009 (−0.012 to 0.060)
Partners	111 pairs	0.079 (−0.262 to 0.228) [1] (−0.365 to 0.5) [2]	0.024 (−0.180 to 0.086) [1] (−0.416 to 0.704) [2]
Parents-chicks [3]			
All	23 parent-chick pairs, 15 families	0.3379 (−0.319 to 0.5) [2,3]	0.497 (0.305 to 0.694) [2,3]

[1] Ranges of average relatedness within ledges.
[2] Ranges of average relatedness within pairs.
[3] Genetic data were available from previous breeding studies (Ibarguchi et al. 2004); these coefficients were obtained based on legitimate parent-chick pairs without mismatches only, excluding possible cases of mutation, null alleles, misassignment, extra-pair paternity, or adoption. Parent-chick pairs included cases where only one parent and its chick were genotyped, while families included cases where both parents and their chick were all genotyped. Based on cytochrome *b*, a maternally-inherited marker, mother-chick pairs all shared 0.5 relatedness (adjusted by dividing by 2 for comparison with other relatedness estimates), and father-chick pairs averaged 0.2 relatedness (range: −0.319 to 0.5).

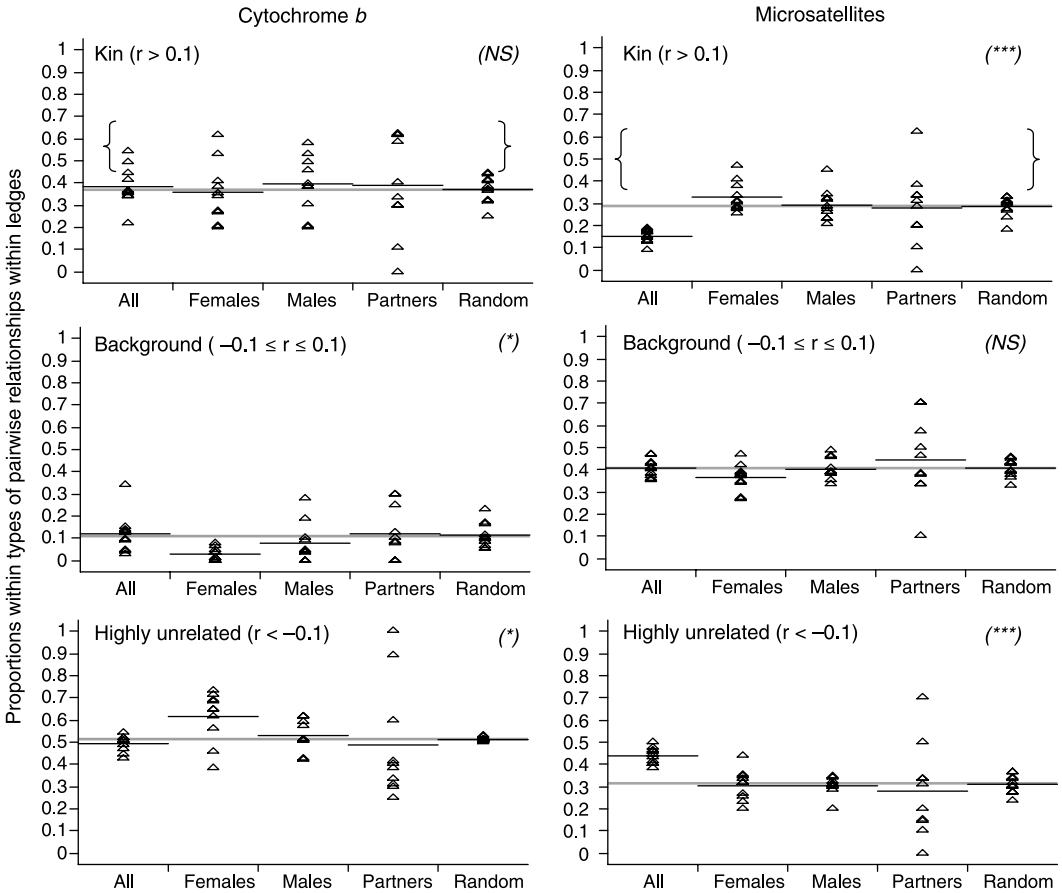

Figure 3. Proportions of within-ledge pairwise relationships in highly unrelated, background, and kin-level relatedness bins. Each point is the proportion for a single ledge. Means of randomly-generated birds are thick gray lines; smaller black lines are the means for each group (all birds with sexes pooled, females only, males only, breeding partners, and randomly-generated birds). Brackets in the top panels emphasize ledges with high proportions of kin-level relationships (above the maximum obtained for the randomly-generated bird groups; see text).

within 5 m, and up to 12 m, with few dispersing more than 20 m, females displayed a bimodal pattern where most settled within 8 m, but up to one-fifth dispersed more than 20 m (Fig. 5). These trends are concordant with results from genetic and spatial analyses (above) and are consistent with females being philopatric but to a lesser extent than males.

Discussion

Philopatry and sex-biases in dispersal

Because murres do not breed until they are between 3 to 7 years of age, measuring dispersal distances between natal and breeding sites for birds banded as chicks requires

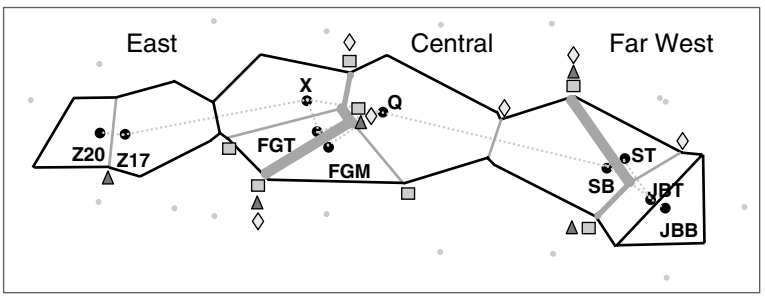

Figure 4. Barriers (gray lines) detected based on morphological (triangles), mitochondrial (squares) and microsatellite data (diamonds) using Monmonier's maximum difference algorithm (Monmonier 1973), as implemented in *Barrier* version 2.2 (Guérard and Manni 2002; see text). Gray line thickness represents concordant barriers based on one (thin), two (intermediate) or all three (thick lines) resampled bootstrap data matrices (three barriers were tested). (Black circles, ledges; small gray circles outside diagram, virtual points drawn by *Barrier*; thin black lines, Voronoï tessellation of ledges; dotted gray lines, Delaunay triangulation; see Manni et al. 2004, Guérard and Manni 2002).

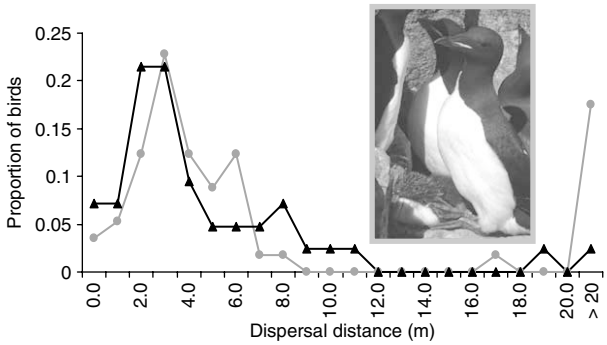

Figure 5. Dispersal distance in murres from hatch site on cliff ledges to breeding site as adults (philopatry). Proportion of males (triangles, black lines; n = 42) and females (circles, gray lines; n = 57) observed within each distance class (data from U. Steiner and A.J. Gaston unpubl. data).

long-term observations. Studies of chicks banded at Coats I. and breeding years later have revealed that on average 56% of birds return to their natal area (ranging from 33% to 78% by area, n = 978, Table 4; Gaston et al. 1994). In more recent studies involving small samples of sexed murres, approximately 60% of banded birds (of known and unknown sex) have been observed to recruit to their natal ledge (returning within less than 4 m; Steiner and Gaston 2005). Established breeders have been observed to return to the same breeding ledge frequently even over a decade later (several adults were still breeding on the same ledge as in 1996 and 1997 during the 2010 breeding season; data unpublished). Although based on the small subset available on natal philopatry for birds banded as chicks (Steiner and Gaston 2005, unpubl. data), both sexes were recorded as highly philopatric to their natal ledge, with males dispersing shorter distances and females displaying a bimodal pattern (Fig. 5). This slight difference between the sexes in settlement patterns may be enough to explain the genetic data: (1) large neighbourhood sizes for females (e.g. Fig. 2), but high relatedness or genetic similarity within some of these patches and within ledges (Table 4), (2) overall stronger structuring for males from fine to coarse scales (as neighbourhoods ranged from small to large, and as slight genetic structuring was detected for colony wide analyses and particularly east vs. west of Fox Gully; Table 2 and Fig. 2), and (3) kin groups detected among same-sex birds in both males and females (Table 4 and Fig. 3) resulting from philopatry. As a single chick is reared during a breeding season, philopatric male and female siblings fledging in different years could result in inbreeding; the slight difference in sex-biased settlement patterns (females settling further away) may decrease the occurrence of inbreeding, although the advantages of increased genetic similarity within a group in this species, or any advantages from breeding near the 'safety' of kin, remain unexplored. More data on dispersal distance and settlement patterns (for example, observing where offspring settle with respect to the sex of each parent still breeding there) would be invaluable in providing insight into the fine-scale processes that may shape within-colony genetic structure.

Evidence of morphological differences among ledges and sexual dimorphism at Coats Island

Slight sexual size dimorphism in murres (with larger males than females) has been documented previously (Gaston and Nettleship 1981, Gaston et al. 1984, Stewart 1993); however, to our knowledge, the present study is the first to compare the sexes through scaling (removing the effect of size), showing significantly heavier females than males for their size, and corroborating observations of greater bill depth in males at this colony as in other studies elsewhere (Birkhead & Nettleship 1984, Gaston et al. 1984, Stewart 1993). The greater mass in females during breeding could be associated with body condition for egg-laying; mass can change throughout the breeding season in both sexes, but decreases for females particularly during chick rearing (Elliott et al. 2010). Slight sexual size dimorphism, possible size-assortative mating, breeding site quality, and their association with reproductive success are being explored elsewhere (G. Ibarguchi, unpublished), but in particular bill depth (with natural size variation without scaling) is perhaps a character under selection as significant differences between the sexes in this trait are consistently present at other murre Arctic colonies and in other alcids, and may be related to snapping power in other waterbirds (Stewart 1993, Koffijberg and van Eerden 1995, Wagner 1999, Berzins et al. 2009). At Coats Island the sexes differ in their preferred prey and their time of foraging (daytime feeding for females catching deep benthic and schooling fish more frequently, and nighttime feeding on invertebrates and shallow benthic fish more frequently for males); the slight bill depth dimorphism has been suggested to be related to their preferred prey as in other waterbirds (Elliott et al. 2010, G. Ibarguchi unpubl. data).

Among ledges, bill depth was the trait with the most significant pairwise comparisons relative to other traits, and when the size correction was applied, males displayed a stronger difference among ledges than females. Although the significance of the bill tip to nares distance is not explored here, it was the trait with the second-most significant pairwise comparisons relative to the remaining characters, but in this case females displayed the stronger difference among ledges after the size correction (Table 1). The significant differences in morphological traits among ledges over short distances were striking, particularly those between ledges separated by less than a few metres (Fig. 1B). Differences among ledges are unlikely to reflect sampling biases by date or location, since sampling was often conducted over a few days or weeks on multiple ledges, especially when trapping breeding partners. Reproductive success has been estimated for breeders on some of these ledges previously (in 1990–91, DeForest and Gaston 1996). Assuming that trends in morphology were similar in 1990–91, ledges with moderate and high reproductive success (Q in both studies, 'S' in 1990–91 included SB but not ST as in the present study) did not have the largest birds with respect to any trait (this study: Fig. 1B, ledges Q and SB). Within ledges, sites vary in their quality; thus the relationship between reproductive success, site quality, and links with large body size or other traits (and perhaps competitive ability), including genetics, is complex (G. Ibarguchi, unpublished).

The heritability of these traits was not explored here; however, as significant differences among ledges remained even after applying the size corrections (presumably removing at least some environmental effects), the genetic basis of this variation warrants investigation. Furthermore, morphological differences among ledges suggest non-random settlement on ledges (or possible trait-assortative mating; G. Ibarguchi, unpublished). At the population level, morphological differences have been documented among colonies in the Canadian Arctic and differentiation may have occurred within the last 10,000 years or more recently (Gaston et al. 1984); unfortunately the only available published genetic study involving some of these colonies (Birt-Friesen et al. 1992) may lack the temporal resolution (the marker having a slow rate of evolution relative to this short time frame) to investigate the genetic and morphological differentiation among these populations.

Evidence of kin groups and fine-scale genetic patterns within ledges

Despite the low global averages of within-ledge relatedness (Table 4), proportions of kin-level relationships varied within ledges (individual points in Fig. 3; details in Appendix 2) and reached 62.5% for partners, 58.1% for males, and 61.5% for females based on cytochrome *b*, and 62.5% for partners, 45.1% for males, and 46.7% for females based on microsatellites on some ledges. Several ledges had higher proportions of *kin*-level relationships than the maximum obtained for the randomly-generated birds (44.7% and 33.1% from mitochondrial and nuclear markers, respectively; Fig. 3, brackets, and detail in Appendix 2). Therefore kin clusters appeared to exist on many ledges, but were not established on others; the lack of widespread or consistent clusters likely resulted in the weak structuring detected at coarser scales (e.g. results form spatial autocorrelation analyses).

A further consideration is that the nuclear markers utilised in this study may have provided slight underestimates of genetic relatedness. The mitochondrial marker (cytochrome *b*) did recover the theoretical expectation of 0.5 (adjusted for comparison with other estimates; see *Methods*) for mother-chick pairs. For microsatellites, the average relatedness obtained for both parents and their legitimate chicks was close but slightly lower than the expected 0.5 (Table 4, footnote). Mutations were suspected to be frequent and male-biased, especially for loci *uaa1-23*, and *ulo12a12* (Ibarguchi et al. 2004). Thus genetic structure and relatedness measures based on microsatellites may represent underestimates, particularly for males. Although there may be a slight tendency to underestimate relatedness based on microsatellites in the larger population in part due to some mutations and null alleles, the parent-offspring coefficients (Table 4) were obtained from families without mismatches (i.e. some suspected mutations did occur in parent-chick pairs in these markers in a previous study, as well as extra-pair paternity, null alleles, misassignment and adoption, but such pairs were not included in the parent-chick pairs in Table 4; see Ibarguchi et al. 2004). The observed slight underestimate in families may thus indicate that as polymorphism increases in hypervariable loci (e.g. as many as 32 alleles in locus *ulo1-23* in this study), some statistics may become biased by the increasing numbers of rare alleles relative to the sampled group sizes (i.e. ledges in this case with n $\sim$30 sampled birds), which may affect the weighing of variables in estimates (e.g. the r coefficient as estimated by Queller and Goodnight 1989).

The all-birds group (sexes pooled) displayed the extreme lowest kin relationship proportions based on microsatellites (lower than randomly-generated birds; Fig. 3) while the opposite was true for males and females (above). However, when only breeding partners were considered (based on microsatellites), the strict avoidance of breeding with kin occurred within some pairs only. If birds are philopatric to natal ledges, but some generally avoid or are excluded (particularly females) from settling directly adjacent to relatives, especially of the opposite sex, the observed pattern may be generated (i.e. some kin clusters detected on ledges), and is both concordant with Mantel's test trends (where some negative slopes were detected within a few ledges for the pooled sexes and for females; see below), and consistent with results from spatial autocorrelation analyses (where global analyses suggested lack of consistent structure, but local 2D analyses identified larger neighbourhoods for females).

The weak patterns of genetic structuring detected in this study may be the result of subtle but real microevolutionary processes, and are concordant with the differences in morphology observed among ledges, and the subtle differences in behaviour between the sexes. In a study of savannah sparrows *Passerculus sandwichensis*, young birds were highly philopatric, but would not settle in their natal territory if their parent of the opposite sex was still breeding there (Wheelwright and Mauck 1998). Rabouam et al. (1998) reported that recruiting male Cory's shearwaters (*Calonectris diomeda*, a highly philopatric species) were less likely to breed in their natal sites if their fathers were still present there or in the colony; thus competition may also exclude same-sex individuals at least in other seabirds. In murres, parent-chick recognition has been demonstrated (Lefevre et al. 1998); father-offspring discrimination in theory may be more strongly developed, as parents spend approximately 15 days with chicks on cliffs prior to fledging, but males then continue to feed chicks at sea for many weeks. Although this remains unexplored, if males recognize offspring but females fail to recognize sons, some inbreeding could potentially occur through (1) mother-son matings, (2) through siblings, which may fail to recognize each other as they would have hatched in different years, or (3) through other relatives. Two reported cases of inbreeding in a colony of Cory's shearwater (Rabouam et al. 1998) occurred between sons and their mothers while their fathers had not been seen for two previous years. As many breeding sites at Coats I. were not monitored closely, some murres initially classified as partners in the field were subsequently reclassified as alloparents (a few of the same sex; Ibarguchi et al. 2004), and may have caused *kin* proportions to be slightly overestimated in a few cases. However, known-sex parents of legitimate offspring (Table 4) also displayed relatedness coefficients in all three bins, including very high relatedness (e.g. 0.355), suggesting that breeders rearing chicks successfully can sometimes be close relatives. In great

frigatebirds *Fregata minor*, mates actively chose to breed with relatives, although the consequences of such pairings remain largely unknown (Cohen and Dearborn 2004); Cory's shearwaters may inbreed infrequently (Rabouam et al. 1998). In black-legged kittiwakes *Rissa tridactyla*, mates were less genetically similar than expected by chance, and hatching success and chick growth were reduced as parent genetic similarity or offspring homozygosity increased (Mulard et al. 2009). The cost of inbreeding may be lower than the cost of delayed or no breeding due to a lack of suitable sites or mates, or a low survival probability (although less so for long-lived species; Keller and Arcese 1998), particularly in species such as murres which rear a single chick per season.

Large-scale patterns within the colony and evidence of structuring

Incorporating morphological (5 traits) and genetic data (two types of markers, six DNA regions), *Barrier* analyses revealed concordant genetic and morphological signatures between the east and west sides of the colony, with a break along Fox Gully, and interestingly, a break at the far west three ledges (Fig. 4). The break at Fox Gully was observed in the analyses presented in Fig. 1 and Table 2 (e.g. haplotype *a* found east of Fox Gully). The more subtle barrier at the far west of the colony is intriguing because birds at JB on average arrive at the colony, lay eggs, and fledge chicks approximately 5 days to one week later than the rest of the study plots in this population (Hipfner and Gaston 2002; A. Gaston, unpublished). The ST ledge has not been monitored as closely but may belong to the same JB group. Reproductive behaviour is strongly influenced by hormones, and both genetics and environmental cues play important roles in their regulation. Despite the weak degree of structuring and the small sizes of kin clusters detected within ledges at Coats I. at least based on the genetic markers employed, strong among-ledge morphological differentiation and differences in the timing of breeding (e.g. JB) indicate that this structuring is probably biologically significant.

Evidence of subtle but significant genetic structuring stems from results of analyses at both small and large spatial scales. Although significant and positive R coefficients occurred at both colony-wide (200 m) and ledge-wide (< 6m) scales in spatial autocorrelation analyses, very few were associated with the first distance intervals regardless of class size. These patterns fall in between those theoretically expected when: (1) individuals are randomly distributed through space at one extreme, and (2) small clusters of unequal size exist within a study area but are not uniformly distributed in space (e.g. see examples from simulations in Fortin and Dale 2005). Increasing the distance class size generally decreased the number of clusters with significant R, suggesting that when clusters of small size were present they were more likely to go undetected when additional individuals were lumped, producing noise (Appendix 1). A similar effect was observed with respect to kinship on ledges: when multiple kin groups occurred on ledges (sharing high relatedness within groups but low relatedness across groups), a low global average relatedness coefficient for a ledge was not always representative of the proportions of high relatedness among kin within it. As global spatial autocorrelation analyses may not be ideal for detecting variable patterns that occur at small scales, and since only a weak patch structure approximating a random distribution was detected, the results from these analyses were simply interpreted to imply that (1) structuring within the colony may be occurring at different scales (large, among ledges or regions, e.g. Table 2, and small, within single ledges, at less than three or even one metre), (2) that genetic structuring was weak, and (3) that when few clusters did occur, they were not consistent in their size or in their geographic spacing. Ledge-wide analyses indicated subtle trends in the settlement patterns of females (clusters of related individuals at $\sim$3 m) versus males (clusters at $\sim$1.8 m). Finer-scale 2D local spatial autocorrelation analyses revealed overall low proportions of clusters with significant R, but provided insight into the neighbourhood sizes of females, which were generally of larger sizes, while males displayed smaller to moderate neighbourhood sizes and slight structuring at a scale approximating half the colony. Summarising the results from global and local spatial scales, only a trend of slight structuring was detected (weaker for females), larger neighbourhood sizes for females at the local scale, and a stronger signal from cytochrome *b*. These results resemble those based especially on Φ-statistics (Table 2), where structure was stronger and significant for males, occurring at a local scale as well as at a broader scale (halfway across the colony at Fox Gully).

Consistent with results from spatial autocorrelation analyses, Mantel tests indicated that (1) at this scale no strong colony-wide association exists between geographic and genetic distance; (2) patterns vary among and within ledges (and are weak and not consistent in some), and between the sexes; (3) within-ledge settlement patterns (e.g. some negative slopes) may be distinct from larger-scale, colony-wide patterns; and (4) some birds of the opposite sex, and possibly females in particular, may actively avoid or are unable to settle directly adjacent to genetically similar individuals (negative slopes), but may settle a short distance away, or disperse much further. Evidence for the latter is also supported by results from analyses of relatedness bins indicating that, based on the maternally-inherited mitochondrial marker, a much greater proportion of highly unrelated associations occurred among females, but based on the bi-parentally inherited microsatellites, the all-birds group (combining individuals of the opposite sex) were the most highly unrelated (Fig. 3). These trends are concordant with behavioural observations also indicating that females are less philopatric than males (e.g. Fig. 5).

As cytochrome *b* represents the matrilineal signal, and if females are less philopatric than males, then lower estimates of structuring would be expected from mitochondrial data, since only those females that have philopatric daughters will be capable of maintaining the signal long-term. Sons will carry their mothers' haplotype, and although fathers' offspring cannot inherit this marker, if sons are also philopatric, the spatial pattern may be maintained indirectly as well. However, comparing patterns from both types of molecular data (mitochondrial and nuclear) alone without considering each sex separately may not yield sufficient information to interpret behaviour patterns due to differences in the rate and mode of evolution of these different types of markers (and

estimates derived from them; see below). For example, if patterns of genetic structure and relatedness had been interpreted without considering the sexes separately (i.e., analysing all birds pooled), the stronger patterns derived from cytochrome *b* data (e.g. Table 2, Table 4, and Fig. 3) may have lead to the interpretation that females were perhaps the more philopatric sex, a pattern uncommon in birds except for groups such as waterfowl (Greenwood 1980, McKinnon et al. 2006, Sonsthagen et al. 2010). In this study, independent analyses of each sex as well as the pooled sample of birds, in addition to the comparison of maternally-inherited mitochondrial DNA data with biparentally-inherited microsatellites, enabled the distinction between subtle differences in dispersal patterns of males versus females, and although a paternally-inherited marker is not available at this time, such a marker would help to further clarify male settlement patterns.

As slight but significant genetic differentiation exists within Coats I., particularly for males among ledges and east vs. west of Fox Gully (Table 2), these patterns suggest that philopatry indeed may be driving within-population subdivision in this colony. Genetic differentiation within the colony is concordant with among-ledge differences in morphology, and with the observed differences in the timing of reproduction of birds at the far west of the colony (JB plots). These patterns suggest that kin groups may be in the process of forming, although factors such as growing population size (see below) and breeding limitations such as lack of sites or experienced partners (Steiner and Gaston 2005) may influence their maintenance.

Patterns of structure at Hornøya, Norway, vs Coats Isl., Canada

The results from this study contrast with those from Friesen et al. (1996a) at the Norway colony in the degree of structuring. The observed differences may be partly explained by effects of sampling, the markers employed, or the age and size of the colonies. Sampling was conducted at Hornøya during the day, when males may have been attending breeding sites, although this pattern may differ among colonies (Gaston and Nettleship 1981, Verspoor et al. 1986, Elliott et al. 2010); male-biased sampling could have led to the stronger structuring detected in Norway. Twice the cliff distance was sampled at the smaller Hornøya colony (~450 m) versus Coats I. (~200 m), and genetic differentiation might increase with distance (especially for males; e.g. this study). Both studies detected stronger structuring based on the same cytochrome *b* fragment (although a larger sample yielded 22 haplotypes here versus 8 in Norway) than nuclear loci. The polymorphism of the markers may have contributed to the differences in the colonies; three allozyme loci (from two to three alleles) were screened by Friesen et al. (1996a), while five microsatellite loci (from six to 32 alleles, and with a higher mutation rate; Ibarguchi et al. 2004) were used here. Measures of kinship and genetic structure obtained from hypervariable loci may be one order of magnitude lower than those obtained from blood groups or isozymes (at least in part due to the greater mutation rate and to the lack of diversifying selection for hypervariable loci; Morton et al. 1993, Hedrick 1999).

The Norway colony appears to have been founded in the early 1900's and has remained small. During sampling in 1989–1990 (Friesen et al. 1996a) the colony consisted of ~450 breeding pairs and was recovering from a population reduction following a crash in capelin stocks in 1985–1986 (1985: ~450 pairs; 1987, post capelin crash: ~300 pairs; 1992: ~500 pairs; Vader et al. 1990, Barrett et al. 1997). In contrast, the west subcolony on Coats I. is approximately 2000 to 2500 years old (Gaston and Donaldson 1995), has ~18 000 pairs, and expanded between 1972 and 1990 (the east subcolony doubled in size during this period; Gaston et al. 1993a), and continuing until the time of this study. During observations in 1996 and 1997 some new breeding sites on turf were established on the 10 ledges studied here, and by 2010 chicks banded after 1997 were now breeding on expanded areas. Ledges at Coats I. were sampled along the upper periphery of the colony to decrease disturbance at the core of the cliff face; these sampled ledges may be younger than those at the colony centre. Furthermore, changing predation patterns may cause further disturbance to settlement, particularly at more accessible sites including these ledges (e.g. from foxes *Vulpes lagopus* and nesting glaucous gulls *Larus hyperboreus*).

The size of colonies, their age, and the rate of population growth have implications for the formation of genetic structuring. Genetic drift may accelerate the rate of differentiation in smaller populations or those founded by a small number of individuals. Population expansion, on the other hand, may slow the rate of differentiation, especially in larger populations, and particularly if philopatric behaviour is disrupted. Strong competition for quality breeding sites exists in murre colonies (Birkhead et al. 1985, and for experienced partners, Steiner and Gaston 2005); in a growing population, established high-quality sites at the colony centre may become saturated and new recruits may be forced to disperse elsewhere (disrupting patterns of structuring). Although both Hornøya and Coats Island colonies may have been undergoing population growth at the time of sampling, the Norway colony has remained overall small and was recovering from a population reduction, while the Canadian colony has remained large, may be growing at a faster rate and may not yet be in genetic equilibrium. Assuming a generation time of 8.8 years (Southern et al. 1965, Friesen et al. 1996a), less than 285 generations have elapsed since founding. The age of establishment of the ledges at these colonies is not well documented, but at least some ledges within Coats Island may have been established too recently to have reached genetic equilibrium (e.g. SB, a ledge with the highest proportion of highly unrelated comparisons based on microsatellites (Appendix 2), was colonised in 1989–1990; A. J. Gaston, unpubl. data). Within a colony, genetic equilibrium may be reached in a shorter time period when the effective population size (the effective number of breeders on ledges) is small for a given migration rate (see Friesen et al. 1996a). A small colony like Hornøya could attain equilibrium faster than a larger population.

During a stage of non-equilibrium and population expansion, structuring may be subtle, which may explain the discrepancy between this colony and Hornøya, and among: (1) the observed patterns of high philopatry of murres at Coats Island, (2) the significant differences in

morphological traits among ledges, (3) the non-random distributions of alleles and haplotypes over the 200 m of cliff space analysed, but (4) the weak clustering detected based on average relatedness estimates and spatial autocorrelation. Over generations, patterns of structure at both coarse and fine scales should strengthen if population growth stabilizes and birds continue to be philopatric. Analyses of older, more established murre colonies (with stable populations) may be needed to determine the generality and extent of kin groups in this species, as family groups could have important benefits for alloparents (i.e. increased inclusive fitness) or may facilitate the acquisition of nearby sites by offspring and relatives breeding for the first time (Steiner and Gaston 2005). If neighbours are kin, reduced aggression among ledge breeders could increase egg and chick survival; studies have not been conducted to test if adults recognise relatives. Aside from thick-billed murres (Friesen et al. 1996a, and this study), and common gulls (*Larus canus* Bukaciński et al. 2000), the presence of kin clusters in other seabirds has not been investigated but may be more widespread than is currently acknowledged. Kin clusters have been detected in other philopatric waterbirds also such as common eiders (*Somateria mollissima* McKinnon et al. 2006, Sonsthagen et al. 2010), although data on the effect of nesting near kin on reproductive success in waterbirds is needed. Behavioural observations remain a key component in the interpretation of patterns of genetic structure within species and their evolution.

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Suppl. material (Appendix JAB 5023 at <www.oikosoffice.lu.se/appendix>. Appendix 1–2.