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High connectivity in a long-lived High-Arctic seabird, the ivory gull *Pagophila eburnea*

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Abstract

Species may cope with rapid habitat changes by distribution shifts or adaptation to new conditions. A common feature of these responses is that they depend on how the process of dispersal connects populations, both demographically and genetically. We analyzed the genetic structure of a near threatened High Arctic seabird, the ivory gull (*Pagophila eburnea*) in order to infer the connectivity among gull colonies. We analyzed 343 individuals sampled from 16 localities across the circumpolar breeding range of ivory gulls, from northern Russia to the Canadian Arctic. To explore the roles of natal and breeding dispersal we developed a population genetic model to relate dispersal behavior to the observed genetic structure of worldwide ivory gull populations. Our key finding is the striking genetic homogeneity of ivory gulls across their entire distribution range. The lack of population genetic structure found among colonies, in tandem with independent evidence of movement among colonies, suggests that on-going effective dispersal is occurring across the Arctic Region. Our results contradict the dispersal patterns generally observed in seabirds where species movement capabilities are often not indicative of dispersal patterns. Model predictions show how natal and breeding dispersal may combine to shape the genetic homogeneity among ivory gull colonies separated by up to 2800 km. Although field data will be key to determine the role of dispersal for the demography of local colonies and refine the respective impacts of natal versus breeding dispersal, conservation planning needs to consider ivory gulls as a genetically homogeneous, Arctic-wide metapopulation effectively connected through dispersal.

Introduction

The distribution of natural habitats worldwide is currently changing as a direct consequence of global climate trends, and this is happening particularly fast in the Arctic, where climate warming is maximal (ACIA 2004; IPCC 2007). Species that live in the Arctic or in other rapidly changing environments might cope with this rapid change by shifting their distributions, by adjusting through phenotypic plasticity or by evolving adaptations to the new local climatic conditions (reviewed by Chen et al. 2011; Gienapp et al. 2008; Gilg et al. 2012; Hoffmann and Sgro 2011; Parmesan 2006). These responses partly depends on the process of dispersal; that is, the movement of individuals between birth and reproduction (natal dispersal), and possibly between successive reproduction events (breeding dispersal). Besides its role in the spatial structure and demographic dynamics of populations, dispersal is important in the context of habitat change because it is one key driver of the potential rate of spread of a population and, as the process by which genes are moved among populations, it influences the rate of adaptation to changing conditions and the potential for evolutionary rescue (Bell and Gonzalez 2011; Travis et al. 2013). Thus, understanding, predicting and managing biodiversity responses to rapid climate change demands a full consideration of a species' dispersal characteristics and their demographic and genetic consequences.

We focus here on the ivory gull *Pagophila eburnea*, a bird that completes its life-cycle entirely in the Arctic. Over its entire breeding range (Canadian Arctic, Greenland, Svalbard and Russian Arctic islands) it breeds either on inland cliffs and 'nunataks', *i.e.* rocky outcrops emerging from icecaps, or on high-Arctic barren islands or flatlands (Gilg et al. 2009; Mallory et al. 2008). In Canada, where the status of the species has been designed 'Endangered' (COSEWIC 2006), studies indicated that 80% of the breeding population was lost during the past 20 years (Gilchrist and Mallory 2005). The species is listed as Near Threatened by the IUCN (BirdLife International 2012) and an international circumpolar

90 ‘Conservation Strategy and Action Plan’ has been presented by leading seabird experts from Arctic countries to gain more insight into how this bird responds to increasing threats from
92 disappearance of sea ice habitat, natural resource exploration and increased contaminant loads (Gilchrist et al. 2008).

94 Ivory gulls are capable of travelling thousands of kilometers either on single foraging trips or to reach wintering grounds in the north Pacific (Bering Sea and Sea of Okhotsk) and
96 in the northwest Atlantic (Davis Strait and Labrador Sea) where most of the world population is thought to spend the winter (Gilg et al. 2010; Mallory et al. 2008). However, most seabirds
98 have an extraordinary ability to travel long distances and yet show evidence of restricted gene flow and exhibit high levels of philopatry, sometimes returning to breed within a few meters
100 of their natal nest (Friesen et al. 2007). A species' movement capabilities thus do not automatically inform us about demographic and genetic connectivity among colonies. This is
102 the “seabird paradox”, *i.e.*, the apparent paradox between high vagility and low effective dispersal (Milot et al. 2008).

104 Dispersal may take place at different stages of an individual's life. For ivory gulls, natal dispersal may happen during the two first years of life before the individual becomes sexually
106 mature and joins a breeding colony. However, the behavior of ivory gulls during that time is almost completely unknown. In addition, adult ivory gulls may disperse among colonies from
108 one breeding season to the next. Such breeding dispersal could effectively contribute to demographic and genetic exchanges among colonies, but our knowledge of these aspects for
110 ivory gulls currently relies only on incidental observations (O. Gilg, A. Aebischer and M.L. Mallory, unpubl. data).

112 Here we take a genetic approach to investigating dispersal in order to complement ongoing mark-recapture and satellite tracking efforts (Gilg et al. 2010; Spencer et al. 2014).
114 Genetic data can complement other approaches to measure dispersal either by providing direct

information on individual movements (e.g., through parentage or population assignment) or indirect signatures of dispersal patterns (e.g., through analyses of genetic structure). Disentangling the effects of natal dispersal and breeding dispersal on realized gene flow is, however, challenging, and has rarely been addressed in the molecular ecology literature (Broquet and Petit 2009), although Rousset (2001) and Laporte and Charlesworth (2002) present general class-structured models that lay the foundations to such an endeavor.

The aim of this study was to explore population structure and spatial dispersal pattern in the ivory gull and to infer natal versus breeding dispersal among colonies. For that purpose, we analyzed a genetic data set representative of the entire species range and developed a population genetic model to infer lower bounds on natal and breeding dispersal consistent with the observed genetic structure of ivory gull populations worldwide.

MATERIAL AND METHODS

Study species

The ivory gull is a long-lived High Arctic seabird (annual survival estimated to 0.86; Stenhouse et al. 2004; and maximum record 28 years; Mallory et al. 2012), which is associated with sea ice all year round (Gilg et al. 2010; Spencer et al. 2014). Breeding colonies are scattered in Arctic Canada, Greenland, Svalbard, and the northern islands of Russia in the Barents and Kara seas (Table 1). The current total global population of the ivory gull was estimated to be approximately 19,000-27,000 breeding pairs (BirdLife International 2012). The Russian population is estimated to number in the range of 14,500-22,000 individuals (Gavrilo 2011). The population in Canada has declined since the 1980s (Mallory et al. 2008). In Norway (Svalbard) the population probably declined in the first part of last century, but after 1970 the trend is uncertain (Mallory et al. 2008). Population trends in Greenland are unclear due to sparse historical information (Gilg et al. 2009). Ivory gulls are

thought to first breed after their second year, based on the fact that they acquire adult plumage in their second winter, and that individuals in less than full adult plumage are rarely seen at breeding colonies (Mallory et al. 2008). Unlike most gulls, which regularly lay 3 eggs, the ivory gull usually lays 1–2 eggs, more rarely 3 eggs. Most of the world population is thought to spend the winter in two main wintering grounds (Mallory et al. 2008): the north Pacific (Bering Sea and Sea of Okhotsk) and the northwest Atlantic (Davis Strait and Labrador Sea, Figure 1).

Sample collection

Field works took place in summers 2006 to 2012, during the breeding season (late June to August). Sample locations were distributed across the entire breeding range of the species, including the Canadian Arctic Archipelago, north-eastern Greenland, Svalbard Archipelago, Franz Josef Land Archipelago, Severnaya Zemlya Archipelago and Kara Sea islands (16 sampling locations overall, listed in Table 1 and Figure 1). We collected samples either in breeding colonies or opportunistically near two military stations where ivory gulls are attracted by food remains (namely Alert, Canada and Station Nord, Greenland). Three nondestructive DNA sampling methods (mouth swabs, plucked feathers and blood) and a noninvasive sampling method (shed feathers) were used. Pieces of tissue were also opportunistically collected on dead birds.

Juveniles (chicks of the year) were sampled in two sites from Greenland in 2009: Amdrup Land and Station Nord (Table 1 and Figure 1) in order to perform parentage analyses. In these cases, buccal swabs and tissue samples were used as DNA sources. All other samples were taken from adult birds, where we considered two classes of individuals according to their breeding status. Field observations suggest that non-breeding adults visit or stay in colonies during the breeding season. Moreover, satellite transmitters indicated that breeding birds

visited colonies as far as 200 km from their own breeding colony (O. Gilg & A. Aebischer, unpublished data). Hence in any one site adult birds were classified as "breeding" only if they were seen hatching eggs or raising chicks, and "unknown status" otherwise. Thus, “unknown” birds included: i) the non-breeding component of the population (the so-called ”floaters”; Penteriani et al. 2011), but also ii) birds found in colonies but that were not reproducing locally and that may reproduce elsewhere in an unknown colony; and ii) birds that they were identified from shed feathers collected on the ground. This distinction is relevant for analyzing the genetic structure of colonies since non-breeding birds or individuals lacking information on their breeding location (all called here "unknown") could be transient visitors. Due to field constraints we generally have information on only one of these two classes of adults within each sampling site (reported in Table 1), either because samples were taken only from breeding individuals or because the breeding status was ignored altogether (*e.g.*, shed feathers or transient birds). However in one repeatedly visited site from Greenland (called Station Nord), we could collect precise mark-resight data on both breeding and unknown (see above) individuals, and obtain sizable samples from these two classes of birds (referred to as "breeding" and "unknown" in Table 1).

All samples from Greenland, Norway and Russia (Table 1) were obtained using non-destructive (collection of mouth swabs and plucked feathers) and non-invasive DNA sampling methods (collection of shed feathers) as described in Yannic *et al.* (2011). In addition, birds from Alert (Canada) were caught with rocket nets near a military base. Immediately following capture, a blood sample (about 0.3 ml) was collected from the brachial vein in heparinized micro-hematocrit capillary tubes, before release. Blood samples were centrifuged on site at 13,200 g for 15 min. Red blood cells and plasma were separated and stored frozen at -20°C until laboratory analyses).

190 **DNA extraction and genotyping**

Genomic DNA from all individuals was extracted from shed and plucked feathers, tissue,
192 blood or buccal swab following protocols described in Yannic *et al.* (2011) (see also Supplementary material 1). Previously optimized microsatellite markers were used in four
194 polymerase chain reaction (PCR) multiplexes, totaling 22 markers (Yannic et al. 2011). For samples obtained from shed feathers we performed three independent PCR replicates of each
196 locus to obtain reliable genotypes (see Yannic et al. 2011). The microsatellite amplicons were loaded on an ABI PRISM 3100 (Applied Biosystems Foster City, CA, USA) automated DNA
198 sequencer. Microsatellite alleles were detected, scored, and manually verified using GENEMAPPER 3.7 (Applied Biosystems).

200

Genetic structure

202 All loci were found to be independent of one another (linkage disequilibrium test performed in FSTAT 2.9.4 (Goudet 2005), using 10 000 permutations and *p-values* adjusted for multiple
204 comparisons using the Benjamini and Yekutieli false discovery rate procedure with initial α = 0.05). We used two sets of loci depending on downstream analyses. All 22 loci were used for
206 the parentage analyses because: i) all genetic data from the juveniles came from good quality samples (tissue and buccal swab); and ii) genotyping errors or null alleles can be identified
208 and taken into account (see below). For the analysis of spatial genetic structure some data come from "low quality" samples (shed feathers, Table 1). Hence for these analyses we used a
210 subset of 13 loci (listed in Table 2) chosen for their polymorphism and reliability as reported in Yannic et al. (2011).

212 We investigated the differentiation among ivory gulls sampling sites by estimating F_{ST} (Weir and Cockerham 1984). We ran some of the analyses using only the samples with >10 adults.
214 Global F_{ST} was computed with FSTAT for different combinations of samples: overall adults (*n*

= 15 localities), over sites with >10 adults (n = 9 localities), and among breeders only (n = 6
216 localities). The significance of the differentiation was tested using two approaches. First we used the log-likelihood G statistic calculated for observed data and compared to that of 10 000
218 randomized datasets obtained through permutation of individuals among samples (as implemented in Fstat; Goudet 2005; Goudet et al. 1996). Second, for a strict comparison with
220 results from our evaluation of power (see below), we also used Fishers' Exact Test as implemented in GENEPOP. In that case the distribution of alleles within individuals is ignored
222 and thus genic rather than genetic differentiation among samples is tested. Furthermore, the null distribution is obtained using a Markov Chain algorithm rather than permutations,
224 performed here with defaults GENEPOP parameters. Pairwise F_{ST} among all samples were also calculated with FSTAT.

226 The statistical power to detect a significant genetic heterogeneity at various true levels of differentiation for the present set of samples, number of loci and allele frequencies was
228 evaluated using POWSIM 4.1 (Ryman and Palm 2006). POWSIM simulates samples of genes from a specified number of populations that have drifted to an expected predefined level of
230 differentiation (measured as F_{ST}). These samples are then used for testing genetic homogeneity using Fisher's Exact Test. With this procedure we estimated the power that we
232 had when looking for genetic differentiation using all adults and breeders only (see Table 1). Estimates of power were given by the proportion of significant outcomes when repeating the
234 simulations 1000 times for each level of simulated F_{ST}. The use of post hoc power analyses should however be used with caution as stressed by Hoenig and Heisey (2001). But, here our
236 goal is not to modify a hypothesis test a posteriori (the problematic situation identified by Hoenig and Heisey (2001)) but rather to give an idea of the degree to which our data are
238 informative.

240 **Reproductive success and effective number of breeders**

To interpret our observations of genetic structure across colonies we needed an estimate of
242 effective colony sizes. This can be approximated using the effective number of breeders (N_b)
(N_b; Waples and Teel, 1990), a parameter that depends on the census number of adults in a
244 colony (here noted N_c) and the distribution of reproductive success among individuals within colonies following (Kimura and Crow 1963): $N_b = (N_c k - 1)/[k - 1 + (V_k/k)]$, where k is the
246 mean and V_k the variance in reproductive success among individuals. As a first approximation we estimated these figures from field observations of the number of juveniles per nest in
248 colonies Amdrup Land and Station Nord, considering that there are two and only two adults associated with a given nest.

250 This approach assumes that juveniles within a nest descend from the adult pair providing parental care to these offspring. This is a weak assumption since extra-pair paternity is
252 frequent in socially monogamous birds (Westneat and Stewart 2003), meaning that some males may not have sired the juveniles they are taking care of, whilst other males may have
254 parented offspring with more than one female. Hence males may have a slightly higher variance in reproductive success than those calculated from field observations. To check
256 whether social monogamy reflects the actual breeding system we performed genetic parentage assignments in colony Station Nord, where we had DNA samples from a number of juveniles
258 (n=20) and presumed parents (n=24), that is, adults seen hatching eggs or raising chicks. Details of the parentage analysis, performed with the method implemented in COLONY 2.0.4.5
260 (Jones and Wang 2009; Wang 2012) are described fully in Electronic Supplementary Material (Supplementary material 1). We repeated these analyses in the colony of Amdrup Land,
262 where 65 juveniles (but no parents) were sampled.

264 **Model of genetic structure: overlapping generations, natal and breeding dispersal**

Interpreting genetic differentiation in terms of connectivity and dispersal behavior is not trivial given that it requires some knowledge of the effective number of breeders within colonies (*Nb*, which we investigated in this study) and the effect of life-history traits such as longevity and the potential movement behavior of juveniles (natal dispersal) and adults between breeding seasons (breeding dispersal). We therefore used a 2-sample coalescent approach to describe an island model, with overlapping generations and both natal and breeding dispersal. The model is used to explore the dispersal scenarios that are consistent with the observed level of population differentiation (global F_{ST}) among arctic-wide populations of ivory gulls.

The model builds upon Yearsley et al. (2013) to introduce overlapping generations following the general approach laid out by Laporte and Charlesworth (2002). Each deme contains N diploid non-selfing individuals, of which $N_a = \nu N$ are adults who have survived at least one breeding cycle and $N_j = (1- \nu) N$ are first-year juveniles (ν is the adult survival probability per breeding cycle). One breeding-cycle going forward in time represents a unit time step and is composed of: reproduction, mutation, dispersal, adult mortality, juveniles either mature into adults or die, population regulation (*i.e.*, the population size remains constant at every breeding cycle). The model simplifies certain aspects of the ivory gull's life-history. Maturation for ivory gulls is known to be longer than one year whereas our model, to enable an analytical solution, assumes that a maximum juvenile period of one year. From numerical simulations (results not shown) the effect of a prolonged juvenile stage on F_{ST} is small when adult mortality is low (as for the ivory gull). All adults in the model are assumed to have equal reproductive success. Individual variation in reproductive success and non-breeding adults must be accounted for by the effective population size, N. The model also does not describe sex-linked differences in life-history, such as dispersal or survival. At present we do

not have sufficient sex-specific data for the ivory gull to know whether such differences exist for this species.

The model estimate expected coalescence times, genetic diversities, and *F*-statistics for a DNA sequence under the infinite-sites model (Kimura 1969) with a mutation rate μ / generation/sequence. For our model parameterizations the force of mutation upon genetic diversities is weak compared to the forces of genetic drift and gene flow. Our model considers the coalescent for a sample of two DNA sequences that are randomly sampled just prior to population regulation. We define three states for a pair of sampled sequences: two sequences in the same diploid individual, two sequences in different individuals in the same deme, and two sequences in different individuals in different demes (states 1, 2 and 3 respectively). The ancestral history of a pair of sequences can be defined by a transition matrix, $\boldsymbol{G}$, where an element, $G_{i,j}$, gives the probability that a pair of sequences in state *i* had ancestors from the previous generation in state *j* (the rate of coalescence per generation for a pair of sequences in state *i* is then given by $G_{i0} = 1 - \sum_j G_{i,j}$). Using first-step analysis (Wakeley 2009) the expected times to coalescence of two lineages in state *i*, T_i, can be calculated by solving

$$T_i = 1 + \sum_{j=1}^{3} G_{i,j} T_j \qquad (1)$$

This equation is analogous to equation 8 in Laporte and Charlesworth (2002), and details of the approach used to derive equation 1 are given in Yearsley et al. (2013). Using Slatkin's approximation (Slatkin 1991), these coalescence times can be used to approximate *F*-statistics in the small mutation limit as

$$F_{IS} = \frac{T_2 - T_1}{T_2}$$

$$F_{ST} = \frac{T_3 - T_2}{T_3} \qquad (2)$$

Alternatively, mutations can be included in the matrix $\boldsymbol{G}$ and F-statistics calculated from recurrence relationships for identity by descent.

We specified the transition matrix, $\boldsymbol{G}$, by identifying three types of sequence pair: sequences from two juveniles (*i.e.* newly born in the current breeding cycle), sequences from two adults (*i.e.* individuals surviving from the previous breeding cycle), and sequences from one juvenile and one adult (these types are labelled -, +, ± respectively). The transition matrix can be written as $G = G^{-} + G^{\pm} + G^{+}$ where

$$G^{-} = (1-\nu)^2 \begin{pmatrix} 0 & 1/(1-\nu) & 0 \\ \alpha^{-}/2N & \alpha^{-}(N-1)/N & 1-\alpha^{-} \\ \beta^{-}/2N & \beta^{-}(N-1)/N & 1-\beta^{-} \end{pmatrix} \qquad (3a)$$

is the transition matrix when the both sequences in the pair are from juveniles (possibly the same juvenile),

$$G^{\pm} = 2\nu(1-\nu) \begin{pmatrix} 0 & 0 & 0 \\ \alpha^{\pm}/2N & \alpha^{\pm}(N-1)/N & 1-\alpha^{\pm} \\ \beta^{\pm}/2N & \beta^{\pm}(N-1)/N & 1-\beta^{\pm} \end{pmatrix} \qquad (3b)$$

is the transition matrix when one sequence is from a juvenile and one from an adult and

$$G^{+} = \nu^2 \begin{pmatrix} 1/\nu & 0 & 0 \\ 0 & \alpha^{+} & 1-\alpha^{+} \\ 0 & \beta^{+} & 1-\beta^{+} \end{pmatrix} \qquad (3c)$$

is the transition matrix when the both sequences in the pair are from adults (possibly the same adult). The other parameters in the many-deme limit are $\alpha^{-} = (1\text{-}m_j)^2$, $\alpha^{\pm} = (1\text{-}m_j)(1\text{-}m_a)$, $\alpha^{+} = (1\text{-}m_a)^2$, with m_j and m_a the juvenile and adult migration rates, respectively (*i.e.*, m_j and m_a represent natal and breeding dispersal). The parameters β^X make a negligible contribution to F_{ST} in the many-deme limits because they are inversely proportional to the number of demes.

Substituting equation 3a-c into equation 1 and solving, and taking the many-deme limit gives

$$T_1 = T_2 = 2 N_a D / (1-v^2) \quad (4a)$$

$$T_3 = T_2 + D (1 - m_j) (1 + p) M / [(1- M^2) (1+v)] \quad (4b)$$

where $M = (1 - \nu) (1-m_j) + \nu (1-m_a)$, $p = \nu(1- m_a)/M$ and time units are in breeding cycles. To express these coalescence times in numbers of generations they should be divided by generation time (equal to $1/(1 - \nu)$).

Substituting equations 4 into equations 2 gives the *F*-statistics, $F_{IS} = 0$ and an expression for F_{ST} in the small mutation limit of

$$\frac{1-F_{ST}}{F_{ST}} = 2N_a \frac{1-M^2}{M^2} \frac{1}{1-p^2} \quad (5)$$

For non-overlapping generations ($v = 0$) and small migration rates equation 5 gives the classic result $(1-F_{ST}) / F_{ST} = 4N_a m_j$ (Wright 1931). The model also correctly predicts the inbreeding effective population size $N_e = N_a / (1+v)$ for a single isolated population with overlapping generations (Felsenstein 1971; Hill 1972), equivalent to the case when $m_j=m_a=0$.

Equation 5 shows how the genetic differentiation among ivory gull colonies depends upon adult survival (v), effective colony size (N_a), natal dispersal (m_j) and breeding dispersal (m_a). Adult annual survival rate was estimated to $v = 0.86 \pm 0.04$ (95% CI: 0.75;0.91) (Stenhouse et al. 2004). We used our model with the mean annual survival rate, $v = 0.86$ and the upper limit of the confidence interval $v = 0.91$. Using a higher survival value will tend to underestimate migration rates, making our interpretation more conservative. Effective colony size N_a cannot be precisely parameterized because contrary to our model's assumptions the number of breeding adults is variable across colonies. Known colony sizes (reviewed in Table 3) show a skewed distribution, with a few large colonies (in the order of 100 – 2000 breeding pairs) and many smaller ones (below 100 pairs). Furthermore we did not know the prevalence and year-to-year behavior of adults that are apparently non-breeding at some observation time point.

Such individuals can inflate N_a if they have or will enter reproduction at some other breeding season. Based upon i) field observations of colony sizes (Table 3), ii) the fact that low variance in reproductive success should inflate local effective numbers of breeders (see results for N_b/N_c in colonies Amdrup Land and Station Nord), and iii) remaining uncertainties about the resulting parameter N_a, we explored the model behavior for N_a ranging 50-1000. Using equation 5 we then worked out the conditions of juvenile and adult migration that would result in a F_{ST} value equal to the observed global $F_{ST} = 0.001$. This allows us to estimate and discuss the lower bound on migration rates for ivory gulls.

RESULTS

Genetic structure

Number of alleles, observed and expected heterozygosity in each sample and for each of the 13-microsatellite loci are shown in Table 1 and in Electronic Supplementary Material (Table S1 in Supplementary material 1), respectively. With 13 loci examined in 15 samples, nine locus/site combinations showed a significant deficit in heterozygotes. There was no consistent pattern across samples or loci, and only one locus in one sample (B125, Schmidt Island, Russia) remains significant if one corrects for multiple testing. Yet it is plausible that a small number of allelic dropouts remained undetected in genotypes obtained from shed feathers despite marker selection and genotyping repetitions. The number of genotyping repetitions that we used is based upon average error rates reported in Yannic et al. (2011) but individual shed feathers may happen to be unusually poor sometimes (Yannic et al. 2011). For this reason, we reported differentiation statistics with and without data from shed feathers. The mean observed heterozygosity (0.63–0.85) and mean expected heterozygosity (0.73–0.82) across loci are shown in Table 1.

No genetic differentiation was observed among breeding samples (n = 6, F_{ST} = 0.000, 95%CI: -0.006;0.005; G statistic permutation test p = 0.61, Fisher's Exact Test p = 0.40; Table 2) or among samples containing more than 10 individuals (n = 9, F_{ST} = 0.000, 95%CI: -0.002;0.003; G statistic permutation test p = 0.15, Fisher's Exact Test p = 0.14; Table S2 in Supplementary material 1), while very low and non-significant differentiation was found overall adult samples (n = 15, F_{ST} = 0.001, 95%CI: -0.002;0.005; G statistic permutation test p = 0.09, Fisher's Exact Test p = 0.09; Table 2). This figure was unaffected when removing all shed feather samples (n = 8, F_{ST} = 0.000). Pairwise F_{ST} values were also very low, ranging from -0.032 to 0.043 and none of these pairwise values was significant after correction for multiple testing (Benjamimi–Yekutieli correction; Table S3 in Supplementary material 1). There was no significant difference in relatedness among breeders *vs* among unknown birds sampled the same year in the same colony (*i.e.*, Station Nord in 2009: "Effect of transient individuals on genetic structure" section in Supplementary material 1), suggesting that breeders and unknown birds belong to a homogeneous pool. These results were further confirmed by model-based clustering that suggests that our ivory gulls most likely form one worldwide population ("Model-based clustering" section in Supplementary material 1) and by the absence of isolation-by-distance over long distance ("Isolation by distance**"** section in Supplementary material 1).

Simulations demonstrated that our sample sizes and genetic markers provided sufficient power to detect weak population structure. Population structure was found significant for all simulated populations (*i.e.* power = 100%) with an F_{ST} of 0.006 when using all adult sampling sites (n = 17; Figure 2). Even when F_{ST} was reduced to 0.0035, structure was correctly detected in 90% of the simulations. For F_{ST} values as low as, or lower than the observed value (*i.e.,* global F_{ST} among all adults = 0.001), power drops to 25%. When using only breeders sampling sites (n = 6 sites), the sample sizes and the genetic markers contain

406 sufficient power to detect population structure with 90% accuracy for simulated populations with F_{ST} values ≥ 0.007 (Figure 2).

408

Reproductive success and effective number of breeders

410 In the colony Amdrup Land, we counted 98 adults (49 nests) with one offspring, 82 adults (41 nests) with two offspring, and 12 adults (6 nests) with an unknown number of offspring

412 (Yannic et al. 2014a). Assuming that the latter show the same distribution of reproductive success than all other adults, this gives $k \approx 1.46$, $V_k \approx 0.25$, and $N_b \approx 445$. In Station Nord we

414 observed 24 adults with one offspring and 48 adults with two, which gives $k \approx 1.67$, $V_k \approx 0.23$, and $N_b \approx 148$.

416 Genetic parentage assignment at Station Nord identified the two parents (from our sample of adults) for 6 juveniles out of 20. Twelve additional juveniles had one of their parents

418 identified from the candidate adults. The "second parents" of these juveniles and the two parents of the remaining juveniles ($n = 2$) were not identified from the adult samples but their

420 genotype was reconstructed by the software COLONY, meaning that these adults could still be used to check for extra-pair paternity (*e.g.*, if one unsampled male had sired three of our

422 offspring with different unsampled females, this would be visible in the data). As it turned out, the parent-offspring relationships observed in the field were all confirmed by the genetic

424 assignment (that is, for all the individuals with a DNA sample available), with one exception: one adult that was observed caring for a juvenile did not appear to be its genetic parent.

426 Moreover, this true parent was identified from our sample of adults and it was found to have a second offspring with a different mating partner (field observation, independently confirmed

428 by the genetic data). This suggests one plausible event of extra-pair paternity.

We repeated these analyses in the colony of Amdrup Land, where 65 juveniles (but no

430 parents) were sampled. But with such small clutch size (one or two offspring in general) and

without any actual parent genotyped, we did not succeed to recover reliable sibship information in this colony (data not shown).

In summary, observable parental behavior seems a reliable indicator of parentage, and field observations suggest that the effective breeding size N_b is approximately twice the census colony size N_c. This figure results from the near-zero variance in breeding success among birds seen in colonies. This variance could be slightly inflated by extra-pair paternity, but with very little consequences for the N_b/N_c ratio (*e.g.*, N_b decreases from 148 to 142 in colony Station Nord if one considers one event of extra-pair paternity where one bird has no success and another one has fathered three offspring).

Model of genetic structure: natal versus breeding dispersal

We explored the conditions of natal dispersal (dispersal of juveniles) and breeding dispersal (movement of adults among colonies across breeding seasons) that would be consistent with the low level of observed genetic structure.

A general result obtained with the model is that breeding dispersal is very effective at homogenizing the distribution of the genetic variation across populations in long-lived species with overlapping generations. For instance with the ivory gulls, with $\nu = 0.91$ (Figure 3B) and N_a=1000 and no natal dispersal (that is, perfect philopatry) then a breeding dispersal of only 4.6% is required to yield an F_{ST} as low as 0.001. By contrast, above 30% natal dispersal would be required in the absence of breeding dispersal.

The above scenario is conservative, providing lower bounds on dispersal rates because we used our highest observation of global F_{ST} (F_{ST} = 0.001; see Table 2), large colony size, and high survival. A slightly less conservative scenario (F_{ST} = 0.001, N_a = 500, ν = 0.86, visible in Figure 3A) gives: 14% breeding dispersal or 48% natal dispersal (or any combination along the F_{ST} = 0.001 contour line in Figure 3A). Any smaller (*i.e.*, less conservative) value for N_a

456 or F_{ST} will increase the minimum level of dispersal. As expected, predictions of genetic structure were highly sensitive to effective colony size (as shown by the different contour
458 lines within Figures 2A and 2B) and survival (compare Figure 3A against 3B).

460 **Discussion**

The key finding from this research is the striking genetic homogeneity of the ivory gull across
462 its entire distribution range. Even with conservative assumptions for local effective breeding numbers and survival rate this suggests that gene flow regularly occurs among distant regions
464 in order for populations to become, and remain, genetically homogenous. We develop below the interpretation of these results indicating genetic homogeneity among populations
466 separated by up to 2800 km.

468 **A single Arctic-wide population**

Information retrieved from microsatellites suggests that the ivory gull represents a single,
470 Arctic-wide metapopulation. We found no significant genetic differentiation among breeding colonies of ivory gull (F_{ST} = 0.000, $CI_{95\%}$: -0.006; 0.005) or among overall adult samples (F_{ST}
472 = 0.001, $CI_{95\%}$: -0.002; 0.005). We did not observe significant isolation-by-distance among breeding colonies and among overall adult samples across the range of the species ("Isolation
474 by distance" section in Supplementary material 1). These results agree with the weak differentiation found using mitochondrial data (Royston and Carr 2014 and this study;
476 Supplementary material 1).

This absence of genetic structure is *a priori* not surprising for a species capable of travelling
478 thousands of kilometers either on single foraging trips or to reach its wintering grounds (Gilg et al. 2010). Genetic homogeneity is, however, not the rule in seabird species with similar
480 flying capability. Out of forty-seven seabird species reviewed by (Friesen et al. 2007), only

few were reported to have as little genetic structure as the ivory gull. The grey-faced petrel
482 *Pterodroma macroptera gouldi* (Lawrence et al. 2014), the little auk *Alle alle* (Wojczulanis-Jakubas et al. 2014) and the wandering albatross *Diomedea exulans* (Milot et al. 2008) are
484 examples of seabird that present weak genetic structure throughout their distribution. But the vast majority of seabird species rather seem to show a stronger level of genetic divergence,
486 even among geographically proximate colonies (*e.g.*, the Hawaiian petrel *Pterodroma sandwichensis* (Welch et al. 2012) or Cory's shearwater *Calonectris diomedea* (Genovart et
488 al. 2013). Genetic divergence among seabird populations inhabiting the Polar Regions seems then to be generally lower in comparison with those breeding at lower latitudes.
490 Patterns of genetic structuring in species capable of long-distance dispersal may be driven by multiple mechanisms, including restricted gene flow as a result of high natal philopatry,
492 cryptic barriers to dispersal, or behavioral mechanisms (Friesen et al. 2007). In addition, local adaptation to differing ecological conditions and strong selective pressures may promote
494 geographic patterns of differentiation. Our results show that such gene flow limiting processes are not at work in the ivory gull population and high intercolony dispersal genetically
496 homogenizes the populations. It is however worth noting that our results are based on neutral genetic loci (*i.e.,* microsatellite loci) and adaptive differences could exist among colonies.
498

Our interpretation of the data assumes that the F_{ST} is at migration-drift equilibrium. With
500 small deme size and large migration rates, F_{ST} reaches equilibrium very rapidly [*i.e.* in the order of a few dozen of generations, Rousset (2004)], contrary to gene diversity which may
502 take a much longer time to reach equilibrium (Crow and Aoki 1984). The hypothesis that we believe to be most parsimonious in the case of ivory gulls is that F_{ST} has long been
504 equilibrated and there is large-scale genetic exchange between colonies, most likely due to a combination of natal and breeding dispersal. An alternative hypothesis may be that the

worldwide population is sub-structured into poorly connected demes and the genetic homogeneity observed in ivory gull today is a consequence of the evolutionary history of the species, *i.e.*, a northward expansion of population from a single homogeneous refugia after the deglaciation of the Arctic region (e.g., Wojczulanis-Jakubas et al. 2014). However, while it is temperate species were restricted to refugial area during glacial stages, taxa found in more northern latitudes today are known to have had greater distributions during the glacial phases (e.g., Lorenzen et al. 2011; Yannic et al. 2014b). This suggests that colder adapted species were in more restricted areas during interglacial and not during glacial stages (Stewart and Dalen 2008; Stewart and Lister 2001). From this perspective, ivory gulls could be said to be in "refugia" today and not necessarily in the Late Pleistocene.

Natal versus breeding dispersal

To disentangle the respective role of natal dispersal, *i.e.* the movement from the natal site to the site of first reproduction (Greenwood and Harvey 1982), and breeding dispersal, *i.e.* movement between successive breeding attempts in the ivory gull, we developed an infinite island model with overlapping generations that we used to calculate the expected global F_{ST} at equilibrium for a range of adult and juvenile migration rate scenarios. Our results show that breeding dispersal is very effective at reducing genetic differentiation across populations in long-lived seabird with overlapping generations. We used this model here in an attempt to better understand the demo-genetics of a featured high-artic seabird species, but the modeling framework that we presented here is very general. Our model could be used further to look at the effect of overlapping generations and variations in natal vs breeding dispersal, two aspects that have largely been ignored from empirical molecular ecology research so far.

Long-term field data are lacking for the ivory gull (see next section below), but breeding dispersal is thought to be less than natal dispersal for seabirds in general (e.g., Gauthier et al. 2010). In many long-lived seabird species with low reproductive rate, breeding philopatry is believed to be very high, although actual dispersal rates have been rigorously quantified for a few species only: roseate tern *Sterna dougallii* (ma=0.00-0.09 yr-1; Lebreton et al. 2003), common tern *Sterna hirundo* (ma=0.04-0.08 yr-1; Nisbet and Cam 2002), wandering albatross (ma=0.00-0.30 yr-1; Gauthier et al. 2010) or Adélie penguin *Pygoscelis adeliae* (ma< 0.01 yr-1; Dugger et al. 2010). In these species, breeding dispersal rates appear to be very low and strongly limited by the distance among colonies, although dispersal could vary with ice conditions (e.g., Dugger et al. 2010). These observations suggest that there are behavioral constraints on adult movement amongst breeding colonies (Friesen et al. 2007). Many seabirds have an extraordinary ability to travel long distances and yet show evidence of restricted gene flow and exhibit high levels of philopatry, sometimes returning to breed within a few meters of their natal nest (Friesen et al. 2007). The ultimate causes for such philopatric behavior are not known, although familiarity with natal and/or previous breeding habitats (Friesen et al. 2007) and fitness costs incurred by dispersal itself (Clobert et al. 2001) seem likely to be involved.

Our results contradict in some ways the general pattern found in the literature (Friesen et al. 2007). According to our models (and recalling that we are considering lower bounds on migration rates), it seems unlikely that the low breeding dispersal rates reported above for seabirds are compatible with the genetic pattern observed here for the ivory gull, even if natal dispersal is strong. To be compatible with our observations, a level of breeding dispersal below 0.1 would have to be associated with extremely frequent natal dispersal (that is, a complete mixture of young adults, see Figure 3 with m_a in 0-0.1). Demographic data from the

554 field will be very important to test this suggestion. Information on the movement behavior of juvenile birds and additional estimates of adult survival would be particularly valuable.

556

Movement of adult ivory gulls inferred from ecological data

558 Ring recoveries are in line with large-scale movement in ivory gulls and suggest long distance travel events (> 3400 km; Gaston et al. 2008; Lyngs 2003). However, it is often not known 560 whether recovered birds were actually breeding in the areas where they were found, making inferences about the frequency of effective dispersal at large spatial scales difficult. Recent 562 advances in movement ecology using satellite transmitters indicated similar post-breeding flyways over long distance for ivory gulls breeding in the north east Atlantic, *i.e.,* for birds 564 breeeding in north Greenland, Svalbard and Franz Josef Land, Russia (Gilg et al. 2010). Wintering grounds were reached in December, in southeast Greenland and along the Labrador 566 Sea ice-edge, where Canadian birds also overwinter or in the Bering Strait region (Gilg et al. 2010; Mallory et al. 2008). Data also indicate that birds from different colonies, however, 568 migrate eastwards towards wintering area in the Bering Strait region, hence demonstrating a bi-directional migration pattern (Figure 1).

570 Similar flyways and wintering area for birds from different colonies over the entire species range may result in the recruitment of birds to distant colonies after the overwinter period 572 (*i.e.*, birds never return to the natal colony). Such movement events may be accidental (*i.e.*, birds are unable to return to the natal area) or may reflect behavioral variation in philopatry 574 among individuals (Weatherhead and Forbes 1994). The tendency for birds to disperse may also be linked to the conditions in the natal colony the year they were born and to the local 576 dynamics of the colonies that they recruit to. Such long-distance dispersal events or reshuffling of individuals on the pre-breeding flyways may be sufficient to eliminate the 578 traces of regional structure among populations. The fidelity of ivory gulls to the breeding site

is unknown but at least some marked individuals return to the same breeding colony from one year to the next (MacDonald 1976), and an example of extreme breeding site fidelity has been reported (Mallory et al. 2012). Populations that breed on flat land of Russia, where the highest census population size are observed (Table 3), are often prone to move from site to site (de Korte and Volkov 1993).

Dispersal and connectivity under climate change

Climate change is geographically shifting the climatic envelope of many species and this is predicted to occur rapidly in the Arctic (up to ~ 0.40 km/yr; Loarie et al. 2009). The capacity of populations to respond to climate change will depend of evolutionary and demographic processes (*i.e.*, plasticity, adaptation or migration) (Bourne et al. 2014). Specifically, level of additive genetic variance within population can directly influence evolutionary outcomes in response to environmental change by providing the necessary genetic variation upon which selection can act (Bourne et al. 2014; Lande and Shannon 1996). Now, our genetic results suggest high connectivity and gene flow among populations that furthermore still maintain high level of genetic diversity and higher evolutionary potential within each population, despite recent declines in population census size in some regions (*e.g.*, Canada).

Following these results, two important points call however for further investigations. First, the very high level of genetic connectivity revealed by this study remains difficult to translate into an estimate of demographic connectivity. We have made some efforts to disentangle the effects of dispersal from local population size, but there remains too much uncertainty in our estimates to determine whether the extent of dispersal that ensures genetic homogeneity is enough to have an effect on local demography (a relevant issue in high gene flow species; Waples 1998; Waples and Gaggiotti 2006). Information on the behavior of first- and second-year ivory gulls and adult survival estimates will be key to reduce the space of dispersal

parameters that are compatible with our genetic findings. We need to know more about the movement of birds between their natal site and first breeding attempt. Second, while our findings show that the genetic diversity within colonies is currently high, further studies will have to determine whether this state is stable or show signs of disequilibrium (*e.g*. in line with findings from demographic surveys that show a strong decline in colony numbers and size). The effects of overlapping generations and metapopulation functioning will have to be taken into account when looking for genetic signatures of demographic stability or decline (Broquet et al. 2010; Chikhi et al. 2010; Leblois et al. 2006).

Conservation implications

Resources for conservation management of endangered species are always limited, and therefore an understanding of population differentiation and connectivity can help identify conservation priorities and inform management decisions. Here our results indicate that the ivory gull should be considered a wide-range, genetically homogeneous metapopulation. The lack of population genetic structure found among colonies, in tandem with independent evidence of movement among colonies, suggests ongoing effective dispersal is occurring across ocean basins. This intercolony movement over large spatial scales can potentially enhance the persistence of highly fragmented seabird colonies. The generally large nonbreeding component of populations may also play an important role on the structure, dynamics and persistence of populations in buffering the effects of mortality with compensatory recruitment (although it may also hide a recent population decline, Penteriani et al. 2011; Votier et al. 2008). Our study suggests immigrant recruitment from distant populations could have similar effects. Understanding patterns of connectivity among disjunct populations of highly vagile colonial seabirds is vital to appropriately manage their populations and help predict the effect of future environmental change.

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840 **Table 1**. Estimates of genetic variability for sampled sites of ivory gull (*Pagophila eburnea*). *N* gives the number of samples genotyped at 13 microsatellite markers. Statistics include number of alleles (*nA*), allelic richness (*Ar*; estimated for $n \geq 10$ individuals and based on min. sample 842 size of 8 diploid individuals successfully genotyped at 13 loci), observed heterozygosity (H_O) and expected heterozygosity (H_E). Sampled areas are identified by their abbreviation (Abbr.) throughout the study

ID	Country	Estimated regional population	Region	Site	Abbr.	Latitude	Longitude	Status	DNA source	N	*nA*	*Ar*	H_O	H_E
#1	Greenland	> 2000 pairs[a]	National Park	Station Nord	StNo	81.60	-16.66	adult unknown	swab	81	9.9	6.01	0.76	0.78
#2					StBr	81.61	-16.49	adult breeding	swab	25	8.3	6.08	0.77	0.78
#3					StJv	81.61	-16.49	juvenile	swab/tissue	19/1	7.6	5.95	0.82	0.79
#4				Amdrup Land	AmLa	80.85	-14.63	juvenile	swab/tissue	33/12	9.2	6.04	0.79	0.79
#5	Norway	350-500 pairs[b]	Svalbard	Svenskoya	Sven	78.72	26.63	adult breeding	blood	9	6.8	-	0.84	0.82
#6				Auga	Auga	78.50	21.74	adult breeding	swab/blood	1/17	7.5	6.05	0.76	0.78
#7				Hübnerbreen	Hübn	78.41	21.69	adult breeding	swab	7	5.7	-	0.85	0.76
#8				Freemanbreen	Free	78.38	21.43	adult breeding	swab/plucked feathers	34/2	9.7	6.50	0.76	0.80
#9	Russia	14,500 – 22,000 pairs[c]	Franz Josef Land	Nagurskoje	Nagu	80.72	48.22	adult unknown	shed feathers	5	3.9	-	0.63	0.73
#10				Rudolf Island	Rudo	81.75	58.39	adult unknown	shed feathers	17	7.4	6.12	0.67	0.79
#11				Eva-Liv Island	EvLi	81.64	63.22	adult unknown	shed feathers	5	4.8	-	0.70	0.80
#12			Severnaya Zemlya	Schmidt Island	SchI	81.04	90.76	adult unknown	shed feathers	12	6.6	5.94	0.73	0.76
#13				Domashny Island	Doma	79.51	94.84	adult unknown	shed feathers/swab	17/6	8.5	6.19	0.80	0.77
#14				Komsomalets Island	Koms	80.77	91.05	adult unknown	shed feathers	6	5.7	-	0.83	0.80
#15				Sukhaya River	Sukh	80.77	96.75	juvenile	shed feathers	7	5.8	-	0.76	0.80
#16			Kara Sea Islands	Heiberg Islands	HeiI	77.61	101.51	adult unknown	shed feathers	4	4.2	-	0.73	0.77
#17	Canada	900 pairs[d]	Nunavut	Seymour Island	SeyI	76.80	-101.27	adult breeding	Swab/plucked feathers	11	6.5	5.84	0.75	0.78
#18				Ellesmere Island (Alert)	AlEI	82.50	-62.33	adult unknown	blood	12	6.7	5.87	0.80	0.77
		19,000 – 27,000 pairs								343				

844 [a] Gilg *et al.* (2009); [b] Gilchrist *et al.*(2008); [c] Gavrilo (2011); [d] Environment Canada (2013)

Table 2. F_{ST} and exact *G*-test probability values obtained for each autosomal microsatellite and over all loci for two different datasets of ivory gull (*Pagophila eburnea*)

	All adults sites (n = 15)		Breeding colonies (n = 6)	
Loci	F_{ST}	*P-value*	F_{ST}	*P-value*
A111	-0.005	0.78	-0.014	0.94
B125	0.002	0.32	0.004	0.61
C7	0.009	0.83	0.003	0.45
D126	0.004	0.27	0.002	0.62
D5	0.004	0.17	0.013	0.16
D9	-0.008	0.76	0.001	0.23
A112	-0.003	0.65	-0.012	0.99
A132	0.010	0.37	-0.011	0.85
B114	-0.009	0.76	-0.010	0.92
D103	0.006	0.11	-0.004	0.62
C6	0.002	0.20	0.018	0.54
B103	0.008	0.62	-0.006	0.08
D1	0.007	0.04	0.013	0.04
Over all loci	**0.001**	**0.09**	**-0.000**	**0.61**
Jackknifing over loci	0.001		0.003	
Bootstrapping 95% CI	-0.002;0.005		-0.006;0.005	

Table 3. Census colony size across the breeding distribution of ivory gull (*Pagophila eburnea*)

Country	Number of ivory gulls	Number of colonies
Greenland [a]	Records between 1854 and 2009	
	<5	13
	5-24	6
	25-99	11
	100-300	5
Norway [b]	Maximum records	
	<5	7
	4-10	5
	11-30	19
	31-60	7
	61-100	3
	101-135	1
Russia [c]	Historically maximum records	
	2 – 20	>10
	22 – 100	19
	200 – 700	13
	800 – 1600	7
	2000 +	5
	1990s - 2000s	
	2 – 20	0
	22 – 100	17
	200 – 700	11
	800 – 1600	6
	2000 +	3
Canada [4]	Historically records Between 1976 and 1992	
	<5	0
	5 – 24	3
	25 – 50	6
	50 – 99	6
	100 – 340	2
	Recent time records between 2001 and 2003	
	<5	10
	5 – 24	9
	25 – 50	2
	50 – 99	1
	100 – 300	0

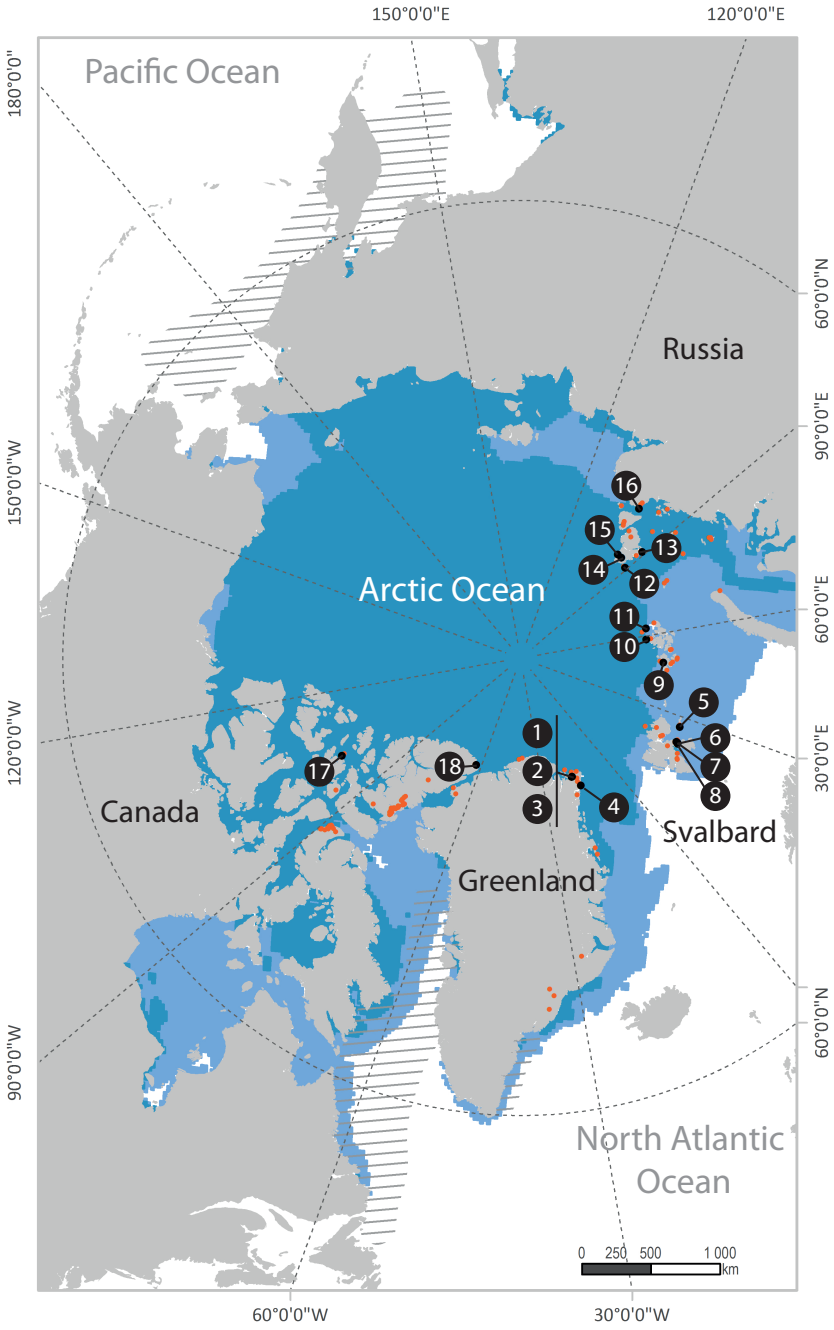
[1] Gilg et al. (2009); [2] Norwegian Polar Institute; [3] Maria Gavrilo, unpublished data; [4] Gilchrist and Mallory (2005)

Titles and legends to figures

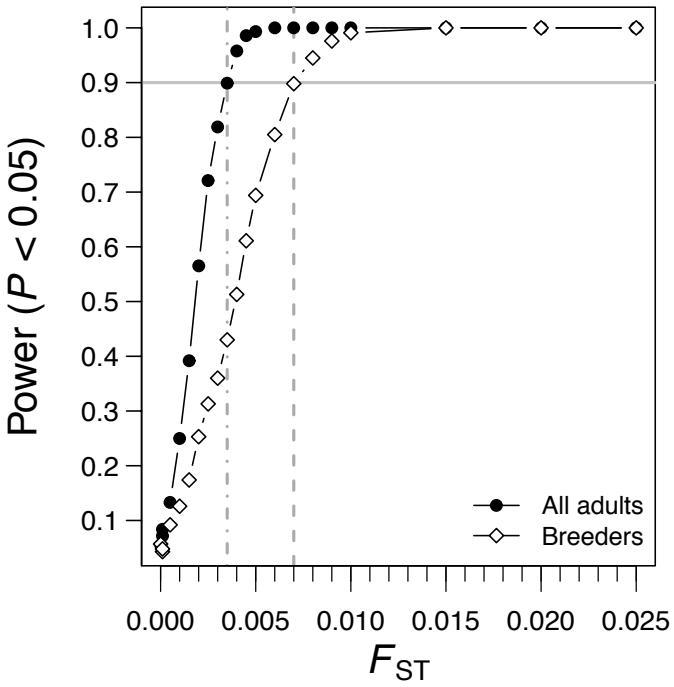
Figure 1. Map of the study area illustrating the Holarctic distribution of ivory gull (*Pagophila eburnea*) breeding colonies. Sampling localities are indicated by the ID corresponding with Table 1; orange dots depict known breeding sites (Gilchrist et al. 2008). Dashed lines: wintering grounds (variable during the winter and among years according to the extension of the sea-ice; modified from Gilg *et al.* (2010)). Background map represent the maximum sea-ice extent in July between 1979-2013 (light blue) and the sea-ice extent in July 2013 (dark blue) (data from the National Snow and Ice Data Centre, Boulder, Colorado; http://nsidc.org/).

Figure 2. Statistical power for obtaining significant outcomes in tests of genetic differentiation involving the specific marker characteristics and sample sizes of ivory gull for i) all adults localities and ii) breeding colonies only. Simulations were performed using POWSIM version 4.1 (Ryman and Palm 2006). The dotted lines indicate the level of genetic differentiation that can be detected with 90% statistical power for the two data sets.

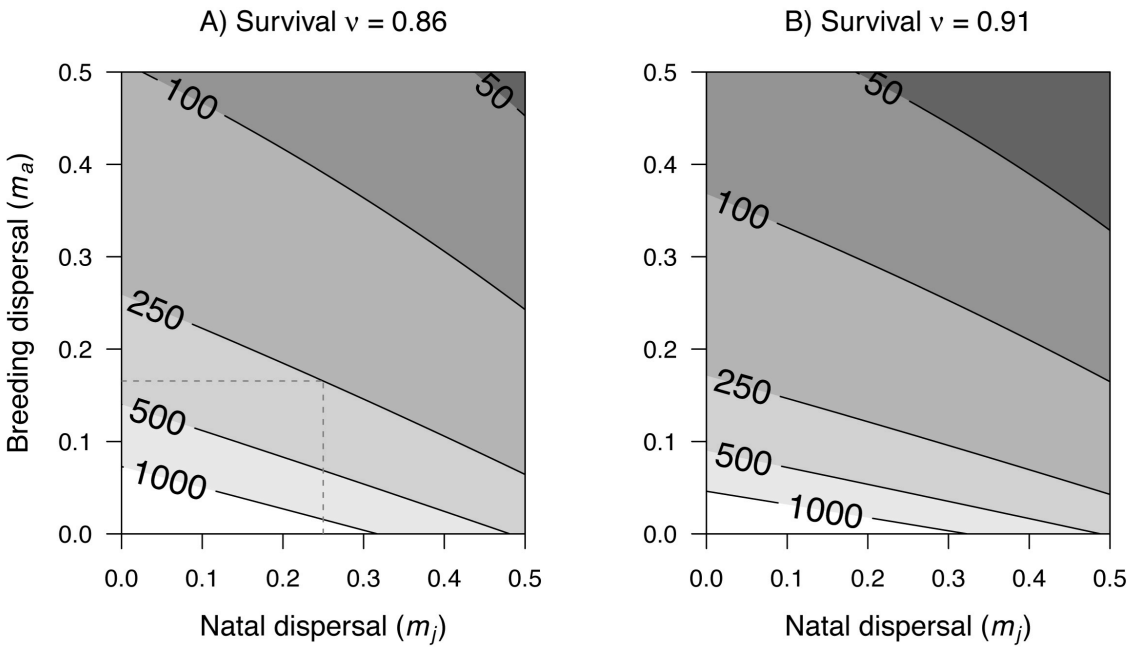
Figure 3. The parameter space (natal dispersal, m_j, breeding dispersal, m_a, effective colony size, N_a (contour lines) and adult survival probability, v) of an overlapping generation model that predicts a global equilibrium F_{ST} (equation 5) equal to the observed value for ivory gull (using all samples $F_{ST} = 0.001$). Given N_a, the plot shows the combinations of natal and breeding dispersal that are required to yield the observed genetic structure in ivory gulls across its distribution range. The dashed lines in panel A show an example: with $v = 0.86$ and $N_a = 250$, a combination of 25% natal dispersal and 16.5% breeding dispersal would predict $F_{ST} = 0.001$ in the simplified conditions of our model


150°0'0"E
120°0'0"E
180°0'0"
Pacific Ocean
Russia
60°0'0"N
90°0'0"E
150°0'0"W
16
15
13
14
12
Arctic Ocean
11
10
60°0'0"E
9
5
6
1
7
120°0'0"W
18
17
2
8
3
4
30°0'0"E
Canada
Svalbard
Greenland
90°0'0"W
60°0'0"N
North Atlantic
Ocean
0 250 500 1 000
km
60°0'0"W
30°0'0"W

880


Power ($P < 0.05$)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
All adults
Breeders
0.000
0.005
0.010
0.015
0.020
0.025
F_{ST}

882


A) Survival ν = 0.86
B) Survival ν = 0.91
Breeding dispersal (m_a)
Natal dispersal (m_j)
50
100
250
500
1000
0.0
0.1
0.2
0.3
0.4
0.5