

# The seabird paradox: dispersal, genetic structure and population dynamics in a highly mobile, but philopatric albatross species

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## Abstract

The philopatric behaviour of albatrosses has intrigued biologists due to the high mobility of these seabirds. It is unknown how albatrosses maintain a system of fragmented populations without frequent dispersal movements, in spite of the long-term temporal heterogeneity in resource distribution at sea. We used both genetic (amplified fragment length polymorphism) and capture–mark–recapture (CMR) data to identify explicitly which among several models of population dynamics best applies to the wandering albatross (*Diomedea exulans*) and to test for migration–drift equilibrium. We previously documented an extremely low genetic diversity in this species. Here, we show that populations exhibit little genetic differentiation across the species' range ( $\Theta^B < 0.05$ , where  $\Theta^B$  is an  $F_{ST}$  analogue). Furthermore, there was no evidence of hierarchical structure or isolation-by-distance. Wright's  $F_{ST}$  between pairs of colonies were low in general and the pattern was consistent with a nonequilibrium genetic model. In contrast, CMR data collected over the last decades indicated that about one bird per cohort has dispersed among islands. Overall,  $F_{ST}$  values were not indicative of contemporary dispersal as inferred from CMR data. Moreover, all genotypes grouped together in a cluster analysis, indicating that current colonies may have derived from one ancestral source that had a low genetic diversity. A metapopulation dynamics model including a recent (postglacial) colonization of several islands seems consistent with both the very low levels of genetic diversity and structure within the wandering albatross. Yet, our data suggest that several other factors including ongoing gene flow, recurrent long-distance dispersal and source-sink dynamics have contributed to different extent in shaping the genetic signature observed in this species. Our results show that an absence of genetic structuring may in itself reveal little about the true population dynamics in seabirds, but can provide insights into important processes when a comparison with other information, such as demographic data, is possible.

**Keywords:** AFLP, dispersal, genetic structure, metapopulation, migration–drift equilibrium, wandering albatross

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## Introduction

Movement capabilities may not be indicative of dispersal patterns within animal species. An outstanding example are albatrosses, which can forage over thousands of kilometres in a single week (Weimerskirch *et al.* 1994, 1997b; Brothers

*et al.* 1998; Fernandez *et al.* 2001; Pinaud & Weimerskirch 2005), and yet they exhibit very strong fidelity to their natal colony for breeding (Harris 1973; Prince *et al.* 1994; Weimerskirch *et al.* 1997a; Sagar *et al.* 1998). This example underlines the fact that dispersal evolves under the influence of diverse and often opposed forces, such as kin competition and selection, inbreeding avoidance, spatial and temporal heterogeneity in resources, competition for partners and resources, and fitness costs incurred by

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dispersal itself (Clobert *et al.* 2001). These are predicted to interact in various ways and to be modified by the feedback effect of dispersal rates evolving in response to them (e.g. Gandon & Michalakis 2001).

In pelagic seabirds, the apparent paradox between vagility and reluctance to disperse has raised a number of questions pertaining to dispersal and its evolution in the marine realm, such as the benefits of philopatry and coloniality (e.g. Coulson 2002), the barriers to dispersal (Friesen *et al.* 2007) and the dynamics of colony formation and extinction (Matthiopoulos *et al.* 2005). These issues are fundamental to our understanding of the persistence of populations in the marine environment where foraging areas are often far away from breeding sites. This is well exemplified by the case of the wandering albatross, *Diomedea exulans*, a long-lived bird with an extended range in the Southern Ocean. On the one hand, the virtually unlimited mobility of this species, which is facilitated by a low flight cost (Weimerskirch *et al.* 2000) along with a long immature period, does not appear to limit the geographical distance a bird could travel before settling in a habitat to reproduce. On the other hand, constraints associated with resource distribution and environmental conditions at sea may limit natal and breeding dispersal. In particular, to achieve a low flight cost, the birds must use flight techniques which heavily depend on wind velocity. Therefore, dominant winds and patchily distributed prey have a tremendous effect on the flight path followed by foraging albatrosses (Weimerskirch *et al.* 1997c, 2000). Consequently, specific oceanic areas are used predominantly by these birds (e.g. Prince *et al.* 1998; Weimerskirch 1998; Pinaud & Weimerskirch 2007). This, in turn, may reduce their chances to encounter islands with colonies and contribute to restrict species range. Moreover, wandering albatrosses are solitary foragers (although they can aggregate at prey patches), a behavioural trait that may further limit their opportunities to learn from conspecifics about other existing breeding colonies. Alternatively, natal philopatry could have been an important condition to the emergence of a life-history strategy which relies on food resources that are likely more predictable over an animal's entire lifetime, rather than over shorter time periods. Hence, philopatry is perhaps the obligate strategy for a majority of individuals undertaking their first breeding attempt, although the question remains open.

Yet, in the long term, dispersal may be essential for populations to follow temporal changes in resource availability. Indeed, a central question remains of how a highly philopatric seabird such as the wandering albatross can maintain a system of fragmented populations despite climatic fluctuations (e.g. glacial periods and shifts of the Antarctic Convergence; Hall 2002 and references therein) that must have modified the distribution both of prey and suitable breeding sites, and thus prompted for shifts in the species' range.

Additional complexity arises from the fact that dispersal in seabirds is often restricted to discontinuous ranges of distances. Thus, the current distribution of suitable breeding sites of wandering albatrosses restricts movements either to short distances within archipelago (i.e. mainly under 100 km), or over long distances between archipelagos (i.e. above 1000 km). Since albatrosses forage well beyond the limits of their nesting archipelago, dispersal, especially when it occurs over short distances, might be driven by factors other than foraging range. Dispersal at that scale might be better envisioned within the framework for conspecific attraction or, more generally, the commodity selection hypothesis (Danchin & Wagner 1997). Under this hypothesis, animals select a breeding patch by the presence and characteristics of potential partners which 'are among the various commodities of variable quality that an individual assesses' (Danchin & Wagner 1997). Conspecific attraction has been demonstrated experimentally in at least one albatross species (Laysan albatross, *Phoebastria immutabilis*; Podolsky 1990). In the wandering albatross, mating is a complex process, and competition for partners is likely intense among individuals (Jouventin *et al.* 1999). Also, inbreeding risk may be of concern for that species and prompt for mechanisms favouring its avoidance (Milot *et al.* 2007). Therefore, mate accessibility and choice might have a strong influence on dispersal decisions, especially over short distances.

The above raises the hypothesis that albatross populations may conform to a metapopulation model, with colonization and extinction (or colony desertion) over long time periods (hundreds or thousands generations), and little demographic dependence among islands and archipelagos over the short-term. Inchausti & Weimerskirch (2002) investigated the short-term dynamics (200 years) in the wandering albatross from capture-mark-recapture (CMR) data and their model suggest that migration has an influence on the persistence of individual colonies, although it is unclear from this study what level of local demographic independence could be achieved between islands. In the most complete genetic study of wandering albatrosses to date, Burg & Croxall (2004) found evidence for a historic model of long-range dispersal which is not in disagreement with a metapopulation dynamics model, in a broad sense. More recently, we found an extremely low genetic diversity within the wandering albatross at amplified fragment length polymorphisms (AFLPs), which may result from metapopulation dynamics associated with the particular life history of these birds (Milot *et al.* 2007). Thus, previous studies on wandering albatrosses provide mixed or limited support for specific metapopulation models. Two alternatives to metapopulation models are isolation by distance, where dispersal is limited to short distances (e.g. the stepwise range expansion of the northern fulmar, *Fulmarus glacialis*; Burg *et al.* 2003), and demographic panmixia where random mating prevails over some geographical area. However,

trying to disentangle among these models using CMR data is often logistically impossible and limited to the study of the contemporary population dynamics. Doing so on the sole basis of genetic data often is also difficult because when populations are not at migration–drift equilibrium, the effect of past and current gene flow, as well as historical association of gene pools may be confounded.

In this study, we combined CMR data with the analysis of genetic variation using AFLPs to infer the hierarchical structure of wandering albatross populations, and document dispersal movements among four archipelagos and among islands within two archipelagos. We aimed at (i) assessing whether populations are currently at migration–drift equilibrium (using the analytical framework of Hutchison & Templeton 1999; see Methods); (ii) identifying explicitly, which among several models of long-term population dynamics is in best agreement with the data for wandering albatrosses: demographic panmixia, isolation by distance where populations are in migration–drift equilibrium, or metapopulation (island, source-sink, with or without colony turnover). Arguably, a single model may not apply to all spatial scales.

All these models make assumptions about dispersal and some assume migration–drift equilibrium. Under demographic panmixia, both an absence of genetic structure and a random geographical distribution of breeders with respect to their natal ground (as known from CMR data) are expected. Under a strict isolation-by-distance model, dispersal is restricted to neighbouring demes (i.e. to short distances relative to the species' range). Therefore, pairwise genetic distances between colonies as well as their variance should increase with geographical distances (Hutchison & Templeton 1999). Metapopulation can be of various types and it is difficult to make simple predictions that would help differentiating among them. We consider the likelihood of different models in the discussion.

## Methods

### *DNA sampling and AFLP amplification*

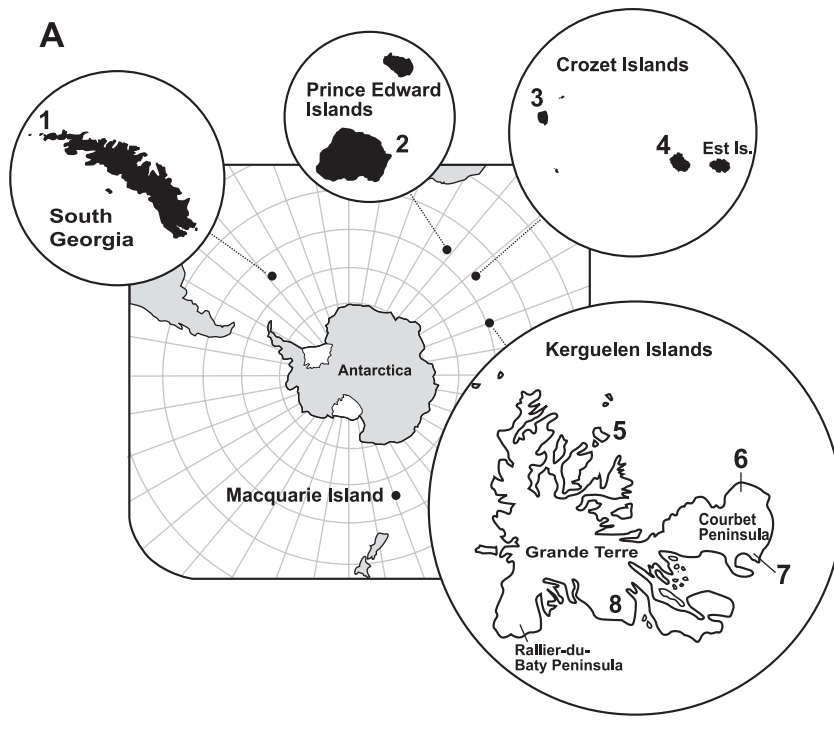
We examined genetic variation within *Diomedea exulans* according to recent taxonomic revisions (Robertson & Nunn 1998; Burg & Croxall 2004). A hierarchical sampling design was used to assess the genetic structure at different spatial levels. A first level involved comparisons among four archipelagos: Kerguelen (KER), Crozet (CRO), South Georgia (SG) and Prince Edward (PE) Islands (Fig. 1). A second level consisted of comparisons of colonies within two archipelagos: Crozet and Kerguelen. These two spatial levels corresponded, respectively, to the 'long' and 'short' distances to which dispersal movements are constrained. A total of 10 sites were sampled (see Fig. 1 for sample locations and sizes). Samples were collected between 2003 and 2005 on two

islands from Crozet: La Possession and Cochons. Sampling was extensive on La Possession where the three breeding areas were visited. Three out of four sectors harbouring wandering albatrosses at Kerguelen were visited in 2003. For Howe island and islets and Baie Larose, breeding densities were small so that one partner from each breeding pair was sampled during a single visit. Courbet is a vast peninsula with ~80 km of coastline. While nearly the whole coast is suitable to wandering albatrosses, nests are not distributed evenly. Two sites, Pointe Morne and North Courbet, of relatively high densities and separated by 50 km were sampled on Courbet. The Rallier-du-Baty peninsula in the western part of Kerguelen, which hosts approximately 750 pairs (Weimerskirch *et al.* 1989), could not be visited. A smaller number of samples from Marion Island in the Prince Edward Islands, and from Bird Island at South Georgia were obtained. The small colony of Macquarie Island (south of Australia) was not sampled (19 pairs in 2004; Terauds *et al.* 2006). Samples consisted of blood except for Marion Island where feathers were plucked off chicks. A total of 344 birds were sampled.

We chose AFLPs because they can easily be generated in large numbers (hundreds) compared to microsatellites (i.e. typically five to 20 loci). This is an advantage for studying species having reduced genetic diversity and for which the proportion of polymorphic loci is expected to be low. Since we intended to study genetic structure both at large and fine scales, we wanted to be able to adjust quickly the number of markers, in order to increase our chances of uncovering fine genetic differences, if present (see also Bensch & Akesson (2005) about advantages of AFLPs). Procedures for DNA extraction, the generation of AFLP markers, and genotyping error assessment have been described in Milot *et al.* (2007). Since wandering albatrosses are extremely depleted in nuclear genetic diversity (Milot *et al.* 2007), a large number of AFLP primer combinations had to be used in order to obtain enough polymorphic markers for the analyses (Table S1, Supplementary material). By generating a large number of markers, there is a reasonable chance of finding one or more sex-linked markers (Questiau *et al.* 2000). To identify potential sex-linked markers that may confound our population genetic analyses, we sexed all birds genetically using the method described in Fridolfsson & Ellegren (1999).

### *Genetic diversity*

Allele frequencies were computed with the Bayesian estimator of Zhivotovsky (1999) for dominant markers and expected heterozygosity with the unbiased estimator of Lynch & Milligan (1994), as implemented in AFLP-SURV (Vekemans *et al.* 2002). To assess whether genetic diversity differed among colonies, we used only polymorphic loci since our goal was to compare colonies relative to each other. Most



**Fig. 1** (A) Breeding islands of the wandering albatross across the Southern Ocean. Sampling locations are as follows, with DNA sample sizes/ approximate annual number of breeding pairs in brackets: 1. Bird Island (16/1300), South Georgia; 2. Marion Island (17/1800), Prince Edward Islands; 3. Cochons Island (20/1000), Crozet Islands; 4. La Possession Island (three colonies sampled, see panel B), Crozet Islands; 5. Howe island and islets (27/30), Kerguelen Islands; 6. Pointe Morne (50/54), Kerguelen Islands; 7. Courbet Nord (55/250), Kerguelen Islands; 8. Baie Larose (11/11), Kerguelen Islands (b) Close-up of La Possession Island showing the location of the three breeding zones of wandering albatrosses; sample/colony size were: Pointe Basse 55/200, Baie Américaine 46/25, Baie du Marin 47/160. Colony sizes are either from recent field counts (H. Weimerskirch and E. Milot, unpublished), or literature (Gales 1998; Tickell 2000).

population studies report their results in this manner. Hence, values of heterozygosity should not be viewed as genome-wide estimates of diversity as we previously reported in Milot *et al.* (2007).

#### Analysis of population genetic structure

We used two complementary approaches to infer population structure. The first one considers sampled colonies as candidate subpopulations that may be genetically distinct and allows for testing of specific hypotheses such as the existence of a hierarchical genetic structure or a pattern of isolation-by-distance. In this case, population-level parameters (e.g.  $F_{ST}$ ) were estimated. The second approach makes no a priori hypothesis about population subdivision: individual-based methods are used to detect the existence of genetic clusters within the sample and may reveal unsuspected patterns.

*Population-level analyses.* The dominant nature of AFLPs prevents the direct estimation of the inbreeding coefficient  $f$  (*sensu* system-of-mating inbreeding; Templeton 2006), which can undermine analyses of population structure. Specifically, when  $f > 0$ ,  $F_{ST}$  values obtained from dominant markers under the assumption of Hardy–Weinberg equilibrium (no inbreeding) will be downwardly biased. Therefore, we used the Bayesian approach developed by Holsinger *et al.* (2002) and Holsinger & Wallace (2004), which aims at estimating  $F_{ST}$  analogue (designated by  $\Theta^B$ ) from dominant markers while accounting for the uncertainty about the inbreeding coefficient. Models are fitted to the data under three hypotheses: (i) both  $\Theta^B$  and  $f$  are unknown and  $\geq 0$  (full model); (ii)  $\Theta^B$  is unknown but no inbreeding occurs ( $f = 0$  model); (iii) there is no genetic structure but  $f$  is unknown ( $\Theta^B = 0$  model). Depending on the model, either  $\Theta^B$ ,  $f$ , or both are estimated. The different models are then compared using a deviance information criterion

(DIC; see Holsinger & Wallace (2004) for details). We fitted models to albatross data as described above using the program HICKORY (Holsinger & Lewis 2005). We assumed a prior uniform distribution of  $f$  for the full and ' $\Theta^B = 0$ ' models. We used HICKORY default values for sampling and chain length parameters (burn-in = 50 000, sample = 250 000, thin = 50). Convergence of Markov chains generated by the program was confirmed using standard diagnostic tests implemented in the BOA program (Smith 2005).

We then computed pairwise  $F_{ST}$  between colonies with the program AFLP-SURV which allows an a priori value for  $f$  to be specified. For this purpose, allele frequencies were estimated with the square root and the Bayesian (Zhivotovsky 1999) methods. To test for hierarchical population structure, we performed an analysis of molecular variance (AMOVA; Excoffier *et al.* 1992) using ARLEQUIN 3.01 (Excoffier *et al.* 2005) on three hierarchical levels: among archipelagos, among colonies within archipelagos and within colonies. Within-individual component of the genetic variance could not be measured with AFLP. In such cases, ARLEQUIN partitions the phenotypic rather than the genetic variance by considering multilocus genotypes as haplotypes.

We did a Mantel test on pairwise values of  $F_{ST}$  and geographical distance to evaluate different population scenarios using the analytical framework of Hutchison & Templeton (1999). Specifically, this framework aims at discriminating among these four models: (I) a model of isolation by distance where populations are at migration–drift equilibrium; (II) a nonequilibrium model where gene flow is most influential at all distances; (III) a nonequilibrium model where local genetic drift is more influential than gene flow at all distances; and (IV) a nonequilibrium model where gene flow has a predominant influence at shorter distances only. This approach is thus well suited to test our predictions about demographic panmixia and isolation-by-distance models. We first conducted the Mantel test over the whole range of geographical distances. However, since there were large gaps in distances, we then divided this range into three classes corresponding, respectively, to the 'within archipelagos', the 'among archipelagos within the Indian Ocean', and the 'between South Georgia (Atlantic Ocean) and other archipelagos' scales. Admittedly, the test for the latter class has low statistical power because it involves the comparison of all South Indian colonies to the same colony (Bird Island) from South Georgia.

*Individual-based clustering.* We used the Bayesian method of Pritchard *et al.* (2000) to infer the number of populations from which albatross genotypes in our sample were derived. This was done with the algorithm for dominant markers implemented in STRUCTURE version 2.2 (Falush *et al.* 2007). We ran the model with admixture and correlated allele frequencies (Falush *et al.* 2003). Allele frequencies are expected to be correlated among populations that have diverged

recently, which is likely the case for wandering albatross colonies based on our results from population-level analyses (see Results). Also, we had no a priori reason to exclude the possibility that some individuals have mixed ancestry. After preliminary trials, we set the burn-in to 200 000 and subsequent run length to 1 million iterations. To ensure that Markov chains converged, we did three runs for each value (1–6) of  $K$ , the number of putative populations. We set 0.01 and 0.05 as priors for the average and standard deviation of  $F$  (drift within populations), respectively, as suggested by Falush *et al.* (2003). A uniform prior (0, 10) on the parameter  $\alpha$  shaping the distribution of admixture proportion was assumed. We used the log probability of the data given  $K$  ( $\ln P(X|K)$ ; Pritchard *et al.* 2000) as a criterion to infer the number of clusters represented by our sample. We also computed  $\Delta K$ , i.e. the second order rate of change of  $\ln P(X|K)$  as suggested by Evanno *et al.* (2005). We used both criteria because the latter, although more reliable, cannot be measured for  $K = 1$ , a possibility that could not be ruled out in our case (note that  $\Delta K$  also cannot be estimated for the maximal value of  $K$ -tested, i.e. a value of 6).

#### Demographic data

We compiled movements of albatrosses among breeding islands from banding data. This was possible because database managers from the different research teams working on sub-Antarctic islands exchange information about the foreign birds detected in their study colonies. We built up on previous work done by Cooper & Weimerskirch (2003) who reported movements between La Possession (CRO) and the Prince Edward archipelago, by updating their survey and extending the analysis to other islands. Monitoring of albatross populations has varied in intensity among colonies. All chicks and breeding adults at La Possession have been banded since 1966 and the identity of all breeders has subsequently been verified every year (Weimerskirch *et al.* 1997a). Similar protocols have been used to monitor populations at Marion Island (PE) since 1976 (Nel *et al.* 2003) and Macquarie Island since 1994 (Terauds *et al.* 2006). The small population on Macquarie Island was also monitored between 1955 and 1994 although less intensively: most chicks were banded but the survey (i.e. checking for leg bands) of all breeding adults was not systematic (Terauds *et al.* 2006). At South Georgia, most chicks born on Bird Island have been banded every year since 1976 (Croxall *et al.* 1990), and a banding effort was also carried out during a few breeding seasons between 1958 and 1976. On Kerguelen Islands, banding of adults and episodic recoveries started on the Courbet Peninsula in 1969, and a census has taken place since 1985 during which about half the breeding birds are checked annually for a band (Weimerskirch *et al.* 1997a). In addition, since 1988 all

Archipelago	Colony	Expected heterozygosity (SE)	%Var <sub>I</sub>	%Var <sub>L</sub>
South Georgia	Bird Island	0.206 (0.029)	8.9	91.1
Prince Edward	Marion Island	0.189 (0.026)	15.6	84.4
Crozet	Baie du Marin	0.199 (0.027)	4.7	95.3
	Baie Américaine	0.198 (0.025)	6.7	93.3
	Pointe Basse	0.202 (0.027)	4.2	95.8
	Cochons Island	0.202 (0.028)	8.7	91.3
Kerguelen	Pointe Morne	0.194 (0.027)	4.6	95.4
	North Courbet	0.187 (0.026)	4.5	95.5
	Howe island and islets	0.193 (0.026)	8.5	91.5
	Baie Larose	0.195 (0.025)	26.6	73.4
Average		0.196	9.3	90.7

**Table 1** Expected heterozygosity within albatross colonies and per cent of the total variance attributable to sampling of individuals (%Var<sub>I</sub>) and of loci (%Var<sub>L</sub>). Note that the population variance component (%Var<sub>P</sub>) was zero

chicks on the Courbet Peninsula have been banded shortly prior to fledging (H. Weimerskirch, unpublished). A study colony was set up at the Pointe Morne colony (KER) in 2000. Systematic search of banded birds were organized at Est Island (CRO; Fig. 1) in 1972, 1982, and 1988; Cochons Island (CRO) in 1976 and 2005; Rallier du Baty Peninsula (KER; Fig. 1) in 1986; Howe island and islets (KER) in 2003; and Baie Larose (KER) in 2003 (Weimerskirch *et al.* 1989; H. Weimerskirch and E. Milot, unpublished).

We considered a natal disperser to be a bird born on an island and who later moved to another island to attempt to breed for the first time. An adult that switched from one island to another between two breeding seasons was classified as a breeding disperser. Obtaining accurate estimates of dispersal rates would require the simultaneous estimation of other demographic parameters such as age-specific survival and recruitment, using a modelling approach. However, interisland movements by albatrosses were too rare to apply this approach. Nevertheless, given that monitoring has been exhaustive in several colonies and has covered numerous cohorts, we could at least estimate the number of migrants per generation between some colonies, and contrast the results to those obtained from genetic data.

## Results

A total of 697 AFLP fragments were amplified among which we first selected 52 loci that were polymorphic when considering the whole sample of 344 birds. However, five of these were sex-linked and thus eliminated from our data set (Table S1). We kept the remaining 47 markers for subsequent analyses. Among these, 29 were polymorphic under the 5% criterion (i.e. present in 5–95% of individuals). Seven additional markers (not included in the 47 above) were also polymorphic (5% criterion) but discarded in the first place because they were unclear for some samples. Therefore, a total of 36 (29 + 7) markers were polymorphic under the 5% criterion, and the level of polymorphism

( $P_{5\%} = 5.2\%$ ) was nearly identical to that previously reported for the species (5.1%; Milot *et al.* 2007). Among-colony differences in heterozygosity were minute (i.e. the largest being 0.019) and nonsignificant (normal approximation  $\chi^2 = 0.067$ ,  $P > 0.5$ ; Table 1). This is confirmed by the null population variance component (%Var<sub>P</sub> = 0; see Lynch & Milligan 1994 for details).

### Population genetic structure

Albatross populations were weakly structured across the species' range ( $\Theta^B < 0.05$  for all Bayesian models; Table 2). The model with population structure but no inbreeding ( $f = 0$ ) fitted the data best, having the lowest DIC value. Moreover,  $\Theta^B$  values from the full (0.0464) vs. the  $f = 0$  (0.0332) models differed significantly (comparison of posterior distributions: mean difference = 0.0156, 95% credible interval: 0.0022–0.0297). The fit of the  $\Theta^B = 0$  model was between that of the full and the  $f = 0$  models, the latter two having a nonzero  $\Theta^B$ . However, for the models with nonzero inbreeding, Bayesian estimates of  $f$  were unrealistically large ( $> 0.94$ ; Table 2), a level only reached in selfing species. Holsinger & Lewis (2005) warn that  $f$  values inferred from this Bayesian method may be unreliable due to weak identifiability of the inbreeding coefficient with dominant markers. To deal with such situations, they implemented a fourth model in HICKORY, the  $f$ -free model, in which the program selects  $f$  values from a prior (in our case uniform) distribution without generating a posterior distribution of  $f$ .  $\Theta^B$  values from the  $f$ -free vs. full models were not significantly different (mean diff. = 0.0006, 95% credible interval: -0.0168–0.0175), indicating that unrealistic  $f$  estimates should not have affected the estimation of  $\Theta^B$ . However, the model with no inbreeding ( $f = 0$ ) was still preferred (Table 2) and its  $\Theta^B$  was significantly lower than that from the  $f$ -free model (mean diff. = 0.0151, 95% credible interval: 0.0004–0.0307). Therefore, this analysis does not provide evidence for the occurrence of inbred mating in albatross populations or hidden genetic substructure.

**Table 2** Fitting of albatross AFLP data to Bayesian population models. Parameters estimated are the inbreeding coefficient  $f$ , and  $\Theta^B$  which is an  $F_{ST}$  analogue.  $\bar{D}$  expresses the deviance of the model,  $pD$  the estimated number of parameters and DIC is a measure of model fit similar to the widely used Akaike's information criterion

Model	$f$		$\Theta^B$		$\bar{D}$	$pD$	DIC
	Mean (SD)	95% CI	Mean (SD)	95% CI			
Full	0.9711 (0.0284)	0.8961–0.9992	0.0464 (0.0047)	0.0379–0.0564	2186.9634	323.9787	2510.9421
$f = 0$	—	—	0.0332 (0.0041)	0.0259–0.0419	1535.8348	233.5386	1769.3734
$\Theta^B = 0$	0.9422 (0.0577)	0.7868–0.9986	—	—	2258.7934	47.0829	2305.8763
$f$ –free	—	—	0.0482 (0.0065)	0.0363–0.0616	1567.7546	268.1787	1835.9333

**Table 3** Analysis of molecular variance on AFLP data of albatrosses from 10 colonies and four archipelagos

Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of variation	Fixation index	$P$
Among archipelagos	3	23.86	0.04	0.80	$F_{CT}$ : 0.008	0.0991
Among colonies within archipelago	6	34.93	0.04	0.77	$F_{SC}$ : 0.008	0.0016
Within colonies	334	1512.37	4.53	98.43	$F_{ST}$ : 0.016	< 0.0001
Total	343	1571.16	4.60			

**Table 4**  $F_{ST}$  between pairs of albatross colonies as computed from the square root (above diagonal) and Bayesian (below diagonal) estimates of allele frequencies. Significant values (0.05 level) are indicated by an asterisk. Values in bold remained significant upon applying a Benjamini–Yekutieli correction for multiple tests (Narum 2006)

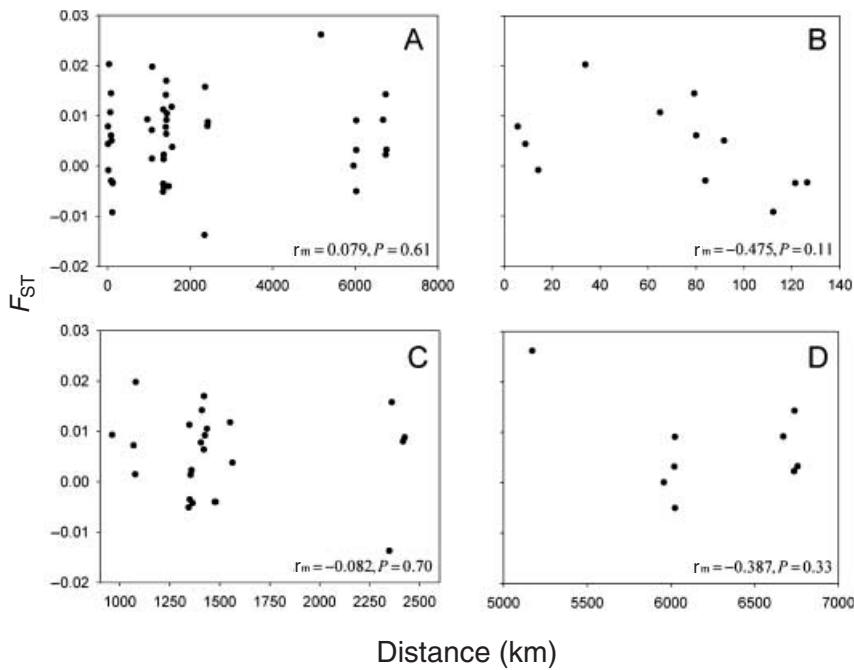
Archipelago	Colony†	NC	PM	HO	BL	BM	BA	PB	IC	MA	BI
Kerguelen	NC	—	<b>0.0246*</b>	0.0143	0.0241	0.0079	0.0152*	0.0108	0.0043	0.0173	0.0011
	PM	<b>0.0203*</b>	—	0.0109	0.0535*	<b>0.0217*</b>	0.0127	0.0172*	0.0182	0.0281	0.0154
	HO	0.0107	0.0051	—	0.0420	–0.0040	0.0140	0.0051	0.0024	0.0312	0.0048
	BL	–0.0029	0.0145	0.0061	—	0.0308	0.0269	0.0273	0.0261	–0.0184	0.0514
Crozet	BM	0.0078	<b>0.0170*</b>	–0.0051	–0.0035	—	0.0085	0.0028	–0.0014	0.0338*	–0.0067
	BA	<b>0.0142*</b>	0.0092	0.0113	0.0014	0.0079	—	0.0087	–0.0018	0.0089	0.0075
	PB	0.0064	0.0105*	0.0023	–0.0042	–0.0008	0.0044	—	–0.0029	0.0221	0.0080
	IC	0.0038	0.0118	–0.0040	–0.0040	–0.0033	–0.0034	–0.0092	—	0.0202	0.0017
Prince Edward	MA	0.0080	0.0088	0.0158	–0.0137	0.0198*	0.0015	0.0072	0.0093	—	0.0407
South Georgia	BI	0.0033	0.0143	0.0023	0.0092	–0.0050	0.0091	0.0032	0.0001	0.0262*	—

†NC, North Courbet; PM, Pointe Morne; HO, Howe island and islets; BL, Baie Larose; BM, Baie du Marin; BA, Baie Américaine; PB, Pointe Basse; IC, Cochons Island; MA, Marion Island; BI, Bird Island.

Wandering albatrosses exhibited a nonhierarchical population structure across their range. Thus, in the AMOVA, only a weak (0.80%) and nonsignificant proportion of the AFLP phenotypic variance was partitioned among archipelagos (Table 3). The variance among colonies within archipelago was also extremely small (0.77%) but significant ( $P = 0.0016$ ). This coincides with the occurrence of small but significant  $F_{ST}$  values between a few pairs of colonies (below). Other groupings did not yield significant hierarchical components to the genetic variance. These include the grouping of colonies according to their island [i.e. a

hierarchical level was added for the colonies located on La Possession at Crozet and Grande Terre at Kerguelen (Fig. 1)], and the further grouping of two colonies (Pointe Morne and North Courbet) located on the same peninsula.

Since no evidence for inbred mating was found, we assumed  $f = 0$  in the calculations of pairwise  $F_{ST}$ , which ranged from negative values ( $\equiv 0$ ) to a maximum of 0.0535 (Table 4). Seven out of 45 comparisons were significant, five both with the square root and Bayesian allele frequency estimates. Four comparisons involved the Pointe Morne colony, two with other colonies from the Kerguelen Islands



**Fig. 2** Pairwise  $F_{ST}$  values (from Bayesian allele frequency estimates) plotted against geographical distances. Panel A: data for the complete geographical range. The data for three classes of distances are shown separately for the remaining panels: within archipelagos (B), among archipelagos of the Indian Ocean (C) and between South Georgia and other archipelagos (D). Mantel correlation coefficients and  $P$  values are indicated at the bottom right of each panel.

(North Courbet and Baie Larose) and two with colonies from the Crozet Islands (Baie du Marin and Pointe Basse). The three other pairs that differed significantly were North Courbet (KER) vs. Baie Américaine (CRO), Baie du Marin (CRO) vs. Marion Island (PE), and Marion Island vs. Bird Island (SG). Thus, two significant comparisons involved colonies located on the same island [Grande Terre (KER)]. In only two cases was the  $F_{ST}$  significant with one method and not the other (Pointe Morne–Baie Larose, Marion Island–Bird Island). The smallest  $P$  value was found for the North Courbet–Pointe Morne dyad. This is remarkable because these two sites are probably the least geographically isolated from each other, with wandering albatrosses nesting at varying densities along the coast separating them. To account for multiple testing, we applied a Benjamini–Yekutieli correction based on the false discovery rate approach (Narum 2006). Three and two  $F_{ST}$  values remained significant with the square root and Bayesian method, respectively (Table 4). The correlation between  $F_{ST}$  values from the square root and Bayesian methods was only 0.59. However, this poor fit was mostly due to pairwise comparisons involving Baie Larose, which is the colony with the smallest sample size ( $n = 11$ ). Removing this site raised the correlation value to 0.90. Note that the square-root estimator is biased and may thus perform poorly when the sample size is very small (Lynch & Milligan 1994; Zhivotovsky 1999).

No evidence was found for an isolation-by-distance pattern with the Mantel test (Fig. 2). Moreover, when we regressed the residuals against geographical distance, the slope ( $b = 2 \times 10^{-11}$ ) was very close to, and not significantly different from, zero. Thus, the spread of pairwise  $F_{ST}$  values

did not increase with distance, contrary to what is expected under a migration–drift equilibrium model of isolation by distance, or under a nonequilibrium model where gene flow has a predominant influence at shorter distances only (Hutchison & Templeton 1999). Thus, our results are consistent with a nonequilibrium model characterized by either extensive gene flow among all colonies or a model where local genetic drift is the most influential force at all geographical distances [Hutchison & Templeton 1999 (cases II and III)].

Individual-based clustering failed to reveal significant structuring since  $K = 1$  was the most likely number of clusters under the  $\text{Ln}P(X/K)$  criterion, while two clusters were preferred under the  $\Delta K$  criterion (however,  $\Delta K$  cannot be measured for  $K = 1$ ) (Table S2, Supplementary material). However, in runs where  $K = 2$ , individuals from all colonies were considered to be highly admixed, having approximately half of their genotypes assigned to each of the two clusters. Overall, these results best supported the existence of a single population.

#### Demographic data

Since monitoring programmes began on the sub-Antarctic islands, a total of 89 wandering albatrosses have been observed on more than one island. Among these, 30 were confirmed as natal dispersers (eight males, 10 females, 12 unknown) and eight as breeding dispersers (three males, four females, one unknown) (Table 5). The remaining birds (51) were considered as visitors and belonged to one of the following categories: (i) birds banded either as adults or as immature and seen on two islands, being either nonbreeders

**Table 5** Known movements of wandering albatrosses among the islands of the Southern Ocean for the period extending from ~1960–2006

Status	Origin*		Location of settlement (dispersers) or visited								
			Kerguelen		Crozet			Prince Edward		South Georgia	
			Courbet Peninsula/ Howe‡	La Possession	Cochons Island	Est Island	Marion Islands	Prince Edward Island	Bird Island	Other islands	
Natal dispersers	Kerguelen	Courbet Peninsula	—	1	0	0	0	0	0	0	
		Crozet	7	—	1	0	19	0	0	1	
	Prince Edward	Cochons Island	0	0	—	0	0	0	0	0	
		Est Island	0	0	0	—	0	0	0	0	
		Marion Island	0	1	0	0	—	0	0	0	
		Prince Edward Island	0	0	0	0	0	—	0	0	
	South Georgia	Bird Island	0	0	0	0	0	0	—	0	
		Other islands	0	0	0	0	0	0	0	—	
	Breeding dispersers	Kerguelen	Courbet Peninsula	—	1	0	0	0	0	0	0
			Crozet	1	—	0	0	4	0	0	0
Prince Edward		Cochons Island	0	0	—	0	0	0	0	0	
		Est Island	0	1	0	—	0	0	0	0	
		Marion Island	0	1	0	0	—	0	0	0	
		Prince Edward Island	0	0	0	0	0	—	0	0	
South Georgia		Bird Island	0	0	0	0	0	0	—	0	
		Other islands	0	0	0	0	0	0	0	—	
Visitors†		Kerguelen	Courbet Peninsula	—	2	0	0	0	0	0	0
			Crozet	6	—	2	0	37	2	1	0
	Prince Edward	Cochons Island	0	0	—	0	0	0	0	0	
		Est Island	0	1	0	—	0	0	0	0	
		Marion Island	0	0	0	0	—	0	0	0	
		Prince Edward Island	0	0	0	0	0	—	0	0	
	South Georgia	Bird Island	0	0	0	0	0	0	—	0	
		Other islands	0	0	0	0	0	0	0	—	

For natal dispersers the origin corresponds to their natal ground as these birds were banded as chicks on their nest; for breeding dispersers, the origin indicates where they were first found to breed; for visitors, this is the location where they were banded; †see text for a definition of visitors; ‡all Kerguelen immigrants and visitors settled on the Courbet Peninsula except for one bird at Howe islands and islets. Courbet Peninsula includes the Pointe Morne and North Courbet colonies, as well as the coastline between these two sites.

on both islands (13) or breeders on a single island (24); and (ii) birds banded as chicks on one island and later seen as nonbreeders (14) on another island. Some individuals in this latter category returned to their natal island to breed. Note that some visitors could be true dispersers. For instance, a bird banded as an immature or an adult on La Possession and subsequently found breeding on Marion could be a natal or a breeding disperser, yet since that bird was not observed as a chick or because we ignore its previous breeding history, inference about its dispersal status cannot be made.

Dispersal movements among archipelagos were highly asymmetric ( $\chi^2 = 148, 57, \text{d.f.} = 11, P < 0.001$ ). A majority of natal (63%) and breeding (57%) dispersers left La Possession (CRO) to settle on Marion Island (PE), while one chick (3%) and one adult breeder (14%) from Marion eventually nested on La Possession (Table 5). These data are essentially

the same as those reported by Cooper & Weimerskirch (2003), except for one additional case of natal dispersal and two of breeding dispersal documented since the work of these authors. Likewise, seven natal (23%) and one breeding (14%) dispersers moved from La Possession to Kerguelen Islands and only one natal disperser (3%) did so in the opposite direction. However, since the banding programme at Kerguelen began later, fewer birds have been banded there to date than at La Possession. This may explain why fewer birds banded at Kerguelen were later seen at Crozet than the reverse, despite the fact that the number of breeding pairs in the two monitored populations is similar. Only a single case of (natal) dispersal was identified between La Possession and South Georgia, but this bird was not found on Bird Island (i.e. the island where the long-term monitoring has taken place in South Georgia). No dispersal events are known to have occurred between South Georgia and either

**Table 6** Number of migrants per generation ( $Nm$ ) as estimated from CMR data, along with  $F_{ST}$  values from AFLP data. Only pairs of colonies for which a reliable  $Nm$  estimate could be obtained are included

Pair	From*	To	$Nm$ one direction†	$Nm$ both directions‡§	$F_{ST}$ (square root estimator)	$F_{ST}$ (Bayesian estimator)
1	La Possession (CRO)	Marion (PE)	10.6	~5	0.0232	0.0090
	Marion (PE)	La Possession (CRO)	< 1	.	.	.
2	La Possession (CRO)	Bird (SG)	< 1	< 1	0.0005	0.0012
	Bird (SG)	La Possession (CRO)	< 1	.	.	.
3	Marion (PE)	Bird (SG)	< 1	< 1	0.0407	0.0262
	Bird (SG)	Marion (PE)	< 1	.	.	.
4	Baie du Marin (Poss.)	Baie Américaine (Poss.)	16	14	0.0085	0.0079
	Baie Américaine (Poss.)	Baie du Marin (Poss.)	12	.	.	.
5	Baie du Marin (Poss.)	Pointe Basse (Poss.)	21	14	0.0028	-0.0008
	Pointe Basse (Poss.)	Baie du Marin (Poss.)	7	.	.	.
6	Baie Américaine (Poss.)	Pointe Basse (Poss.)	2	3	0.0087	0.0044
	Pointe Basse (Poss.)	Baie Américaine (Poss.)	4	.	.	.

\*'Poss.' indicates a colony located on La Possession Island, Crozet; †dispersal data for pairs 4, 5 and 6 from Bried *et al.* (2006); ‡' $Nm$  both directions' is the average of the two  $Nm$  values (one in each direction) observed for a pair of colonies/islands. It is shown here because  $F_{ST}$  values also refer implicitly to genetic differentiation 'in both directions'; §' $Nm$  both directions' and  $F_{ST}$  are reported only once for each pair; thus, a dot indicates that the value is the same as for the line above.

Prince Edward Islands or the Kerguelen Islands, nor between the latter two. One bird banded as a nonbreeder on Macquarie Island was found breeding on Heard, an island to the southeast of Kerguelen which has sporadically harboured one pair (Johnstone 1980). A visit to Cochons Island (CRO) in 2005 led to the discovery of one bird born at La Possession. Finally, a single adult among those banded during sporadic field trips at Est Island was later found nesting at La Possession. No bird was found to have left La Possession to breed on Est despite the fact that both islands are only 16 km apart and well in sight range of each other. Interestingly, the pattern of visitors did not differ from that of confirmed dispersers ( $G = 5.52$ , d.f. = 4,  $P > 0.1$ ; test for goodness of fit conducted on categories in Table 5 with at least one observation). Hence, the number of immigrants that settle on a given island to breed could be proportional to the total number of foreign birds that visit the island.

#### *Nm estimates from demographic data vs. $F_{ST}$ values*

Given the time span of monitoring programmes, about one bird per annual cohort (i.e. 38 birds over 30–45 years of monitoring, depending on the island) was observed dispersing among islands across the species' range. An estimate of the number of migrants per generation can be calculated between some colony pairs by considering a generation time of 17 years for the wandering albatross, i.e. the average age of breeders as determined by fecundity and survival at different ages (demographic rates from La Possession; Weimerskirch *et al.* 1997a, 2005; E. Milot, unpublished). For instance, our data from La Possession cover the cohorts

born between 1966 and 2006. However, because wandering albatrosses start breeding on average at 10 years old, we assumed that no birds born after 1996 could have been observed as natal dispersers by 2006, so that our coverage of cohorts is defined between 1966 and 1996, which is approximately 1.8 albatross generations (in fact all natal dispersers identified in our database were born before 1996). Therefore, the 19 natal dispersers that left La Possession to settle on Marion represented an average of 10.6 migrants per generation. The four breeding dispersers corresponded to 1.7 migrants per generation for the period 1966–2006. However, other movements based on extensive long-term monitoring efforts indicate that less than one migrant per generation has dispersed between islands (accounting for the time span of monitorings in each case) (Table 6). Although conclusions remain hypothetical for other colonies that have been monitored less intensively, the data available strongly suggest that movements were also similarly restricted. One exception might be the eight birds from La Possession that moved to the Courbet Peninsula (KER) (but only one in the opposite direction). We also report the results of Bried *et al.* (2006) who examined the annual cohorts born at La Possession during a 17-years period (1968–85, i.e. one albatross generation) (Table 6). Sixty-two chicks from these cohorts eventually became natal dispersers. Specifically, they settled in a colony on La Possession which was not their natal colony. Table E shows that  $F_{ST}$  values are not indicative of the pattern of contemporary dispersal from CMR data, for the six colony pairs compared. In other words, higher  $F_{ST}$  values are not necessarily found between colonies that have exchanged fewer migrants over the last one or two generations.

## Discussion

We have previously reported that wandering albatrosses are extremely depleted in genetic diversity across their genome (Milot *et al.* 2007), a result corroborated by the larger number of markers screened in this study. A comparison with the Amsterdam albatross suggested that this low diversity was a trait inherited from a common ancestor (Milot *et al.* 2007). In addition, low to moderate levels of genetic diversity has been uncovered at microsatellite markers (Burg & Croxall 2004; Dubois *et al.* 2005; Bried *et al.* 2006). The present study further revealed that albatross populations exhibit little genetic structuring at the 47 polymorphic markers detected, a result contrasting sharply with the limited interisland dispersal movements revealed by CMR data.

### *Migration–drift disequilibrium*

The pattern of pairwise  $F_{ST}$  values against geographical distances is consistent with a nonequilibrium model where either gene flow (Hutchison & Templeton 1999, case II scenario) or random genetic drift (case III scenario) has been the predominant evolutionary force at all distances. Indeed, unless migration rates are similar among all colonies (island model), which is apparently not the case according to CMR data, such a homogeneous pattern of low pairwise  $F_{ST}$  values is unlikely to occur in populations at equilibrium.

It is well known that the  $F_{ST}$  value reflects the balance between gene flow and genetic drift over some evolutionary time and that it may not strictly reflect ongoing gene flow. When populations are not at equilibrium, low pairwise  $F_{ST}$  values over all geographical distances may be consistent with several scenarios. First, it may reflect the historical association of genes that persist after a colonization of new habitats occurred (i.e. between sources and newly founded populations). This is a plausible possibility for a pelagic seabird like the wandering albatross that breeds in relatively small colonies on dispersed islands, and whose range has likely shifted in response to past climatic fluctuations. Second, low pairwise  $F_{ST}$  values across the species may be maintained by recurrent gene flow among islands, probably through rare long-distance dispersal, as suggested by CMR data. Theoretical population genetic models indicate that rare long-distance dispersal can have a tremendous effect on the level of population structure comparatively to more frequent short-distance (e.g. within island) dispersal (Templeton 2006). Sporadic movements such as those uncovered from CMR data between some island pairs could have been sufficient to prevent or delay the genetic differentiation of populations if they have been recurrent in the history of albatross populations. Third, levels of demographic exchanges may have varied through evolutionary

time. In this case, an  $F_{ST}$  estimate will summarize into a single measure the average effect of varying gene flow through time. These three scenarios are not mutually exclusive and may all have contributed to various degrees in keeping albatross populations weakly structured. They are further discussed in the next section within the context of the different population models tested. The departure from migration–drift equilibrium identified using Hutchinson and Templeton's framework may explain the discordance between patterns of dispersal and of genetic differentiation among colonies (Table 6). However, since our  $Nm$  estimates from CMR data cover a short time span (one to two albatross generations), it is unsure whether they are representative of contemporary dispersal over a broader timescale.

According to the analytical framework of Hutchison & Templeton (1999), an absence of relationship between  $F_{ST}$  and geographical distances may also be a sign of the predominant effect of random genetic drift (case III scenario). For example, a species may rapidly colonize a newly available geographical area, followed by reduced or no gene flow among the local populations just founded. Another example is provided when rapid habitat fragmentation divides a population into several isolates. After some period of divergence, local populations or isolates will exhibit significant genetic differences owing to genetic drift, although the pattern will not correlate to geography. The only difference in the pattern of pairwise  $F_{ST}$  expected between Hutchison and Templeton's cases II and III scenarios is one of magnitude in the variation of  $F_{ST}$  values. Under both scenarios, the slope of the regression line between geographical and genetic distances should be zero, but when drift is more influential than gene flow (case III),  $F_{ST}$  values should be relatively variable and overdispersed around the regression line. Considering the pattern observed for the wandering albatross,  $F_{ST}$  values show little variation, almost all of them being nonsignificantly different from zero. Thus, this global pattern is similar to that expected when gene flow is most influential (case II).

### *Population dynamics in the wandering albatross*

CMR data clearly rejected the hypothesis of global demographic panmixia. Analyses for three colonies on La Possession also revealed that even at small scale (< 20 km), populations are not panmictic (Bried *et al.* 2006; G. Gauthier, E. Milot, H. Weimerskirch, in preparation; Table 6). Therefore, the lack of genetic structure is not equivalent to demographic panmixia in the wandering albatross. The expression 'genetic panmixia' is often used as a synonym of a lack of structuring, which clearly does not always imply demographic panmixia, as shown here. Unfortunately, in the population genetic literature the word 'panmixia' is often used without specifying explicitly to which of these two concepts the authors are

referring. This can bring much confusion about whether authors interpret their results in terms of gene flow or in terms of random mating.

The observed genetic and CMR patterns are also not consistent with an isolation-by-distance model either. Rather, our system appears to bear the signature of a metapopulation dynamics, as suggested by the low demographic connectivity among most islands for which CMR data are sufficient for allowing some inference; even for the La Possession–Marion island pair, more frequent unidirectional movements represent about 10 birds per generation out of several hundred breeders. Below we discuss more precisely what type of metapopulation dynamics may have prevailed.

First consider CMR data. Dispersal movements among islands are not symmetric at least for one pair (La Possession–Marion, accounting for census size on both islands). Dispersal rates are also asymmetric among the three colonies on La Possession (G. Gauthier, E. Milot, H. Weimerskirch, in prep.). These results are more consistent with a source-sink model than an island model of metapopulation. Inchausti & Weimerskirch (2002) built a matrix population model based on CMR data to investigate the short-term (200 years) dynamics in the wandering albatross. Their model supported a source-sink model across the species' range where migration has an influence on the persistence of individual colonies. However, as the authors admitted, their underlying (symmetric) dispersal model was simplified because they had to extrapolate movements for the whole range of geographical distances by fitting a nonlinear function to the data available for a single island (La Possession). Our study shows that such extrapolation from intra- to inter-island dispersal movements, including the assumption of symmetry, may not be correct.

Now consider the genetic data. The weak level of population structure could be the consequence of (nearly) complete interbreeding among colonies. However, as mentioned above, this hypothesis is not supported by the contemporary pattern observed with CMR data. More likely, occasional long-distance dispersal (such as the movements detected with CMR data) contributed to maintain genetic panmixia. Although this conclusion is in agreement with a metapopulation dynamics in a broad sense, it still does not inform about the exact type of dynamics involved. Recall, however, that in addition to exhibiting a weak level of genetic structure, wandering albatrosses are also depauperate in genetic diversity compared to other vertebrates (Milot *et al.* 2007). In theory, a colony turnover resulting from recurrent colonizations and extinctions can reduce much the genetic diversity within local demes and in the whole metapopulation (Pannell & Charlesworth 1999). However, the resulting effect on  $F_{ST}$  is difficult to predict because it will largely depend on whether colonization proceeds through propagule pools (all founders being from the same

source population) or migrant pools (founders are drawn from the entire metapopulation; Pannell & Charlesworth 1999). In the latter case,  $F_{ST}$  can be severely reduced relative to that expected in a metapopulation without population turnover. These conclusions, however, are based on theoretical models assuming metapopulation equilibrium (constant turnover rate) and a large number of demes, two assumptions that may not fit well to wandering albatross populations. They also strongly depend on parameters such as the number of founders and the migration rate, and they generally imply that a proportion of demes become extinct at each generation while others are being founded. Therefore, it is difficult to identify, based on those theoretical models, what conditions may be causing such a reduction both in overall genetic diversity and structure in albatrosses. Nevertheless, the hypothesis that colonizations and extinctions are important determinants of the genetic makeup of wandering albatross populations is suggested by the exceptionally low genetic diversity at AFLPs, which also indicates that the long-term effective population size ( $N_e$ ) has been very small (Milot *et al.* 2007). Whitlock & Barton (1997) showed that, contrary to the classic island model where  $N_e$  is expected to increase relative to a panmictic population, systems where demes do not contribute equally to the whole gene pool and where population turnover occurs may have a much reduced  $N_e$ .

Putting our albatross data back into the context of past climatic fluctuations (Hall 2002), it is plausible that several breeding sites have been occupied only recently (in terms of evolutionary time) through a sequence of (postglacial) colonization of several islands from only one or a few ancestral colonies. The support for a single cluster in the STRUCTURE analysis may be the imprint of such an ancestral population that has not faded out yet, implying that this system of populations is probably young and has originated from a single source. Interestingly, the genetic (nucleotide) diversity is expected to take a long time to reach and stabilize at equilibrium values after a sudden increase in the number of demes (Pannell & Charlesworth 1999). Thus, the similarly low levels of genetic diversity, both in the entire species and within local demes (Table 1; Milot *et al.* 2007) suggest that colonies across the species' range may have derived recently from a range expansion from a genetically poor ancestral source. As mentioned by Pannell & Charlesworth (1999), 'the time scales over which such equilibration [of total nucleotide diversity] takes place may greatly exceed the age of a metapopulation in any given landscape, except under the most stable geoclimatic conditions'. This might explain why we previously found evidence for the maintenance of low levels of genetic diversity in the wandering and Amsterdam albatrosses since their speciation, although other factors such as low mutation rates might also be involved (Milot *et al.* 2007).

The above scenario does not make any assumption about the level of gene flow that has occurred between existing colonies after the hypothesized colonization events. In accordance with the diversity of contemporary dispersal rates revealed by CMR data, various patterns of gene flow may have existed. Therefore, our two data sets provide ambiguous support regarding the exact type of population dynamics in the wandering albatross, a situation that probably reflects complex population history and geographically variable patterns. Yet, both data sets support the hypothesis that dispersal has been sufficient to keep populations genetically panmictic (but not demographically panmictic), despite the fact that only a small proportion of birds were found to disperse among islands. Indeed, CMR data suggest that at least one or a few migrants could be exchanged every generation between some colony pairs. Overall, a mixed scenario, with recent colonizations, ongoing and recurrent long-distance dispersal and source-sink dynamics between some island pairs have probably shaped the current genetic signature that we observe today.

#### *Congruence with other wandering albatross genetic studies*

Burg & Croxall (2004) examined the population structure and taxonomy of the wandering albatross species complex. A nested clade analysis on mtDNA data from *Diomedea exulans* (*sensu* Robertson & Nunn 1998) suggested a historic model of long-range dispersal, underlining the important role that this type of movement may play in this system. Pairwise  $F_{ST}$  values at mtDNA and microsatellite data among South Georgia, Prince Edward and Crozet Islands were nonsignificant (Burg & Croxall 2004). Alderman *et al.* (2005) confirmed the affinity of Macquarie Island birds with other *D. exulans* populations (PE, CRO, SG) in nested clade and cluster analyses on mtDNA, while a significant pairwise  $F_{ST}$  was found between Macquarie Island and South Georgia but not other archipelagos. Results from these two studies agree with the type of general pattern uncovered in this study.

Bried *et al.* (2006) used microsatellites to investigate genetic structuring among three wandering albatross colonies. Like us, they found Baie du Marin to be undifferentiated from Pointe Basse, while these two La Possession colonies differed significantly from Pointe Morne on the Kerguelen Islands. Thus, microsatellites and AFLPs provide a congruent picture for these three colonies. These authors also reported that among the chicks born on La Possession between 1968 and 1985 and that later recruited to this island, 62 (~6%) bred in a colony different from their natal colony (Table 6). This amount of within-island dispersal is higher than values among islands reported here, yet far from panmixia. Bried *et al.* concluded that the '... genetic and demographic

estimates of dispersal are therefore consistent', and further suggested that two colonies from the same archipelago should be more genetically similar than if they were located on distinct archipelagos. Our results based on 10 rather than three colonies show that the reality is more complex. First, populations are not at migration–drift equilibrium. Second, dispersal rates at short distances could vary by orders of magnitude, as suggested by the failure to find any La Possession banded albatross during visits to Est Island, although both islands are separated by a short distance (comparable to that between Baie du Marin and Pointe Basse). Third, our most significant pairwise  $F_{ST}$  was found between the two least geographically isolated colonies (Pointe Morne and North Courbet).

#### *Population structure in seabirds*

Friesen *et al.* (2007) reviewed the barriers that have promoted genetic divergence in seabirds. In a meta-analysis, two barriers clearly stood out by their effect on both population genetic and phylogeographical structure. The first one is the nonbreeding distribution, with species being year-round residents nearby their breeding colonies or having population-specific nonbreeding grounds exhibiting a higher level of population/phylogeographical structuring than those undertaking long-distance migration or dispersing without heading toward specific nonbreeding areas (note: these authors classified the wandering albatross in the latter category although individual birds do use specific nonbreeding areas (Weimerskirch & Wilson 2000)). Friesen *et al.* also reported a limited support for an effect of foraging range during the breeding season on population structure. Burg & Croxall (2001) uncovered pronounced genetic structure in the black-browed albatross (*Thalassarche melanophris*) but not in the grey-headed albatross (*Thalassarche chrysostoma*), and suggested that this difference may result from the distinctive foraging habits of these species.

This role of at-sea distribution as a 'barrier' is consistent with our hypothesis that foraging patterns may limit the opportunities for interarchipelago dispersal. However, this may not necessarily result in a pronounced genetic structure at the species level where metapopulation dynamics may have delayed or prevented its development (recall also that rare but recurrent long-distance dispersal can strongly reduce genetic structuring). Given current data on the genetics and demography of wandering albatrosses, this is a conceivable scenario to explain the weak global population structure ( $\Theta^B < 0.05$ ) if the populations are young and not in equilibrium. This leads to the second important barrier identified by Friesen *et al.* (2007): climate zone. In their analysis, species or populations inhabiting polar and temperate regions were less often genetically structured, or showed weaker structuring, than those from tropical regions. This observation was attributed to the greater exposure of

polar and temperate species to climatic fluctuations than tropical species whose ranges and populations show greater temporal stability in general. Consequently, a sub-Antarctic species like the wandering albatross would be less likely to have achieved equilibrium conditions and complete lineage sorting compared to tropical species.

The same picture might hold for other albatross species exhibiting little genetic structure, such as the grey-headed albatross mentioned earlier. In the Buller's albatross (*Thalassarche bulleri*), Van Bekkum *et al.* (2006) found a complete absence of genetic structure at microsatellites between the only two existing populations, although CMR data from one population indicate a high philopatry in this species as well. Little genetic structuring also exists among three colonies of waved albatrosses (*Phoebastria irrorata*) from the island of Española in the Galápagos Islands (Huyvaert & Parker 2006), although the small geographical scale involved makes this system more comparable to the La Possession Island rather than the whole wandering albatross population. Finally, a role for colonization events through rare long-distance dispersal is indirectly supported by evidence for peripatric speciation in the white-capped/shy albatross complex (Abbott & Double 2003) and the occurrence of two distinct evolutionary lineages (species) occupying restricted ranges, within the wandering albatross species complex (Burg & Croxall 2004).

## Conclusion

A lack of genetic variation is often perceived as an impediment to population genetic studies. At first sight, our study seemed doomed to inconclusive results as a consequence of the extreme monomorphism at hundreds of molecular markers. Yet, one has to keep in mind that here, nearly 50 polymorphic diallelic markers were still available. Moreover, our study shows that systems with low genetic diversity may provide insights into important population processes, especially when comparisons with other sources of information, such as demographic data, are possible.

The least we can say is that the 'paradox' between mobility and philopatry is not apparent in the genetic structure. Although a single population dynamic model could not be identified, the comparison between genetic and CMR data suggest that several factors including ongoing and recurrent long-distance dispersal, colonizations and source-sink dynamics may have been involved to different extents in shaping current patterns of population structure and the evolutionary trajectory of the wandering albatross. One key finding is the departure from migration-drift equilibrium. Therefore, using  $F_{ST}$  values to identify which colony pairs are exchanging fewer migrants would be unwarranted in our case, in particular for conservation purposes. This conclusion may hold for other seabird species having comparable population dynamics.

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This work was part of Emmanuel Milot's PhD thesis on albatross population genetics. He is also interested in life history evolution and in the genetic consequences of 'slow' life-history strategies. Henri Weimerskirch studies foraging ecology, energetics, reproductive biology and population biology of marine top predators in their relationship with environmental variability. Louis Bernatchez's major research interests are in understanding patterns and processes of molecular and organismal evolution, as well as their significance to conservation.

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### Supplementary materials

The following supplementary material is available for this article:

**Table S1** Primer combinations used in selective amplification of AFLPs, and number of polymorphic markers selected for each combination

**Table S2** Inference of the number of clusters (populations) from which the albatross genotypes sampled are drawn

This material is available as part of the online article from:

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