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Genetic differentiation associated with commercial traffic in the Polynesian mosquito, *Aedes polynesiensis* Marks 1951

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The population structure of the Polynesian mosquito *Aedes polynesiensis* was investigated using electrophoretic data from two polymorphic protein loci. Considerable differentiation was observed both within and between islands in different archipelagos (Society, Tuamotu, Austral). Gene flow evaluated by F_{st} estimates was independent of geographic distance between islands but related to commercial traffic intensity. The results are discussed in view of recent findings on the variability of susceptibility to insecticides and of suitability as a vector for the nematode *Wuchereria bancrofti.*

ADDITIONAL KEY WORDS:—population genetics – gene flow – isolation by distance – French Polynesia.

CONTENTS

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INTRODUCTION

The Polynesian mosquito, *Aedes polynesiensis* (Marks, 1951) is an endemic species of the Polynesian region. It belongs to the *scutellaris* subgroup which, according to Marks (1954) and Belkin (1962), has colonized the south Pacific region from east to west concomitantly to man. This mosquito breeds in various artificial and natural biotopes (Jackowski, 1954). In the south Pacific region, two distinct races of *Wuchereria bancrofti* occur (nocturnally periodic and diurnally sub-periodic, according to their microfilaria periodicity in man). The diurnally sub-periodic form is mainly transmitted by *Ae. polynesiensis* (Rosen, 1955; Rageau, 1960; Iyengar, 1960). High incidences of filariasis have been reported in the Society islands since early times (see Iyengar's review, 1965). Thus, between 1950 and 1970, filariasis control by mass administration of Diethylcarbamazine (DEC) was carried out. Mosquito control using insecticides is impracticable because larval breeding sites are out of reach and adults distributed over large rural areas. MacDonald (1962) suggested that filariasis control could be achieved by replacing the natural vector populations by microfilaria-refractory populations. Whereas refractory mosquitoes could be obtained (Crampton *et al.*, 1993), how such insects will be able to replace natural populations remains a major problem. Recent studies on the variaiblity of competency as a vector for *Wuchereria bancrofti* (Failloux *et al.*, 1995) and of susceptibility toward various insecticides (Failloux *et al.*, 1994) have suggested that *Ae. polynesiensis* populations from different islands may exhibit substantial genetic differentiation. The present investigation was undertaken to investigate any differentiation in French Polynesia in order to examine how mosquito populations are structured within each island and ascertain the degree of gene flow between islands.

MATERIAL AND METHODS

Mosquito samples

Thirty-one samples were collected in 13 islands from four archipelagos (Fig. 1, Table 1). They are represented by mated females caught on human baits (F0) (Bonnet & Chapman, 1956) or their first laboratory generation (F1). The F0 adults were maintained in 30 × 30 × 30 cm cages and fed with a 10% sucrose solution. Females were allowed to feed on a restrained mouse to obtain eggs. After hatching, larvae were reared until imago (F1) in pans containing 1.5 litre of tap water and 0.5 mg of liver powder (INC Biomedicals Inc., USA.) at a density of 200–400 larvae per pan. All rearing experiments were conducted in an insectarium with a temperature of 25 ± 1°C, a relative humidity of 80 ± 10% and a photophase of 12 h. F0 and F1 imagoes were stored in liquid nitrogen until use.

Electrophoresis

Single adult homogenates were submitted to starch gel electrophoresis in TME 7.4 buffer systems (Pasteur *et al.*, 1988). From the twelve enzymatic systems resolved, five were selected because they provided clearly interpretable genotypes: esterases (Est, EC 3.1.1.1.), glutamate-oxaloacetate transaminases (Got, EC 2.6.1.1.), hexokinase (Hk, EC 2.7.1.1.), malate dehydrogenase (Mdh, EC 1.1.1.37.), and phosphoglucomutase (Pgm, EC 2.7.5.1.). A strain from Mangareva (Gambiers archipelago) was used as mobility control.

Hardy-Weinberg equilibrium

Hardy-Weinberg proportions were first tested by the probability test proposed by Haldane (1954), using the GENEPOP software (version 2.0) of Raymond & Rousset (1995b). The overall significance of multiple tests for each locus or for each sample

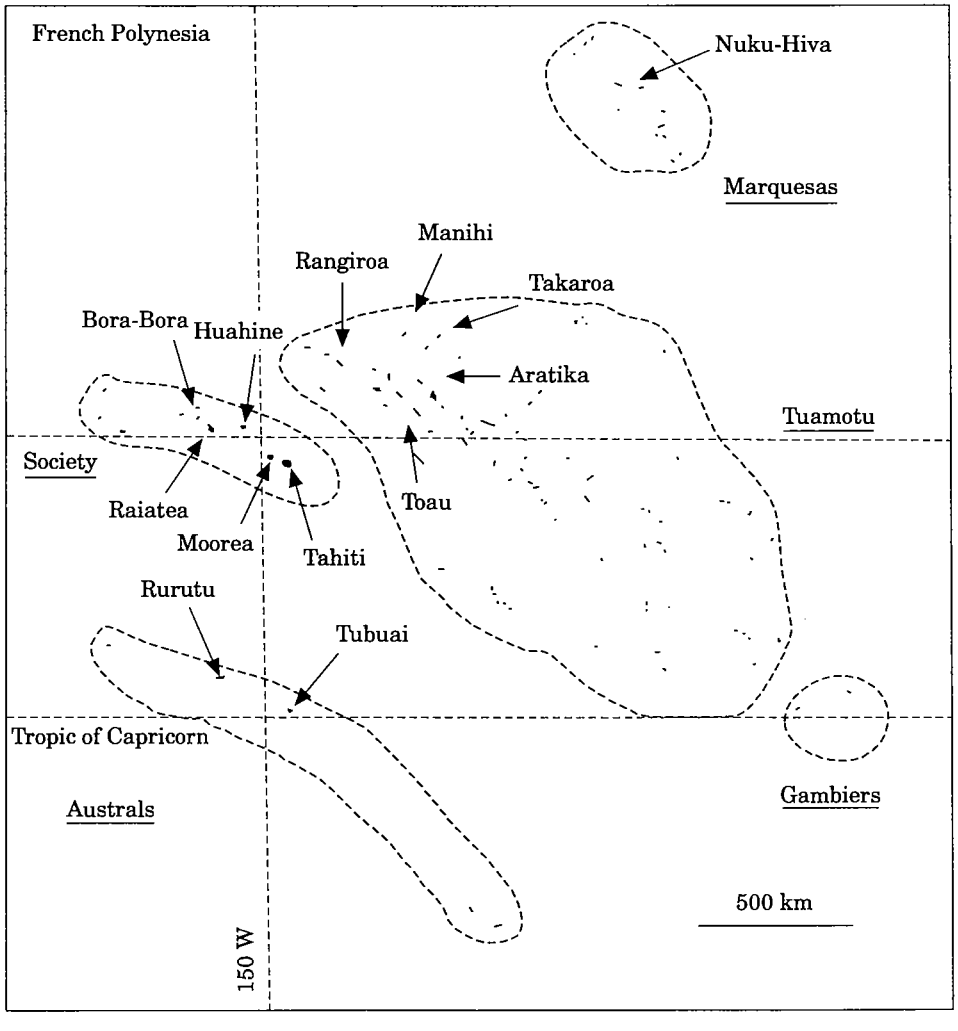

Figure 1. Map showing locations of mosquito strains collected in islands of French Polynesia.

was estimated by Fisher's combined probability test (Fisher, 1970). Hardy-Weinberg proportions were also tested assuming that the alternative hypothesis H1 is heterozygote deficiency or heterozygote excess according to Rousset & Raymond (1995b). Briefly, the statistic defining the rejection zone is chosen to maximize the power of the exact test when there is departure from H0 due to the heterozygote excess or deficiency. In this case, the global test of Rousset & Raymond (1995b) was used for testing multiple populations or multiple loci.

Genetic differentiation

Genetic differentiation between populations, or groups of populations, was tested using Fisher's exact test on RxC contingency tables for each locus. An unbiased estimate of the exact probability was obtained with a Markov chain method (Raymond & Rousset, 1995a), using the GENEPOP (version 2.0) software of Raymond & Rousset (1995b). For all tests, the Markov chain was set to at least 100 000 steps, and 1000 steps of dememorization (see Raymond & Rousset, 1995a

TABLE 1. Geographic origin of *Aedes polynesiensis* samples collected in French Polynesia between October 1992 and February 1993

Strain	Origin		Locality	Generation studied
	Island	Archipelago		
1. TA1	Tahiti	Society	Papeeno	F1
2. TA2	Tahiti	Society	Hitia	F1
3. TA3	Tahiti	Society	Papara	F1
4. TA4	Tahiti	Society	Punaauia	F1
5. TA5	Tahiti	Society	Papeete	F0
6. TA6	Tahiti	Society	Mataeia	F1
7. TA7	Tahiti	Society	Taravao	F1
8. TA8	Tahiti	Society	Vairao	F1
9. MO1	Moorea	Society	Haapiti	F1
10. MO2	Moorea	Society	Temae	F1
11. MO3	Moorea	Society	Titiroa	F1
12. HU1	Huahine	Society	Faau	F0
13. HU2	Huahine	Society	Fare	F1
14. HU3	Huahine	Society	Maroe	F0
15. RA1	Raiatea	Society	Taoru	F0
16. RA2	Raiatea	Society	Opoa	F0
17. RA3	Raiatea	Society	Puohine	F0
18. RA4	Raiatea	Society	Tevaitoa	F0
19. BO1	Bora-Bora	Soceity	Marata	F1
20. BO2	Bora-Bora	Society	Tereia	F0
21. AR2	Aratika	Tuamotu	Aratika	F1
22. TO1	Toau	Tuamotu	Toau	F1
23. RN1	Rangiroa	Tuamotu	Avatoru	F1
24. RN2	Rangiroa	Tuamotu	Avatoru	F1
25. RN3	Rangiroa	Tuamotu	Tiputa	F1
26. MA1	Manihi	Tuamotu	Kaina	F1
27. MA2	Manihi	Tuamotu	Turipaoa	F1
28. TK1	Takaroa	Tuamotu	Takaroa	F1
29. NU1	Nuku-Hiva	Marquesas	Taiohae	F0
30. RU1	Rurutu	Australs	Rurutu	F1
31. TU1	Tubuai	Australs	Tepu	F0

for details). The overall significance of multiple tests for each locus was estimated by Fisher's combined probability test (Fisher, 1970). F_{is} and F_{st} parameters were computed according to Weir & Cockerham (1984).

Linkage disequilibrium

For each population, the global disequilibrium between pairs of loci was tested using Fisher's test on RxC contingency tables (see above).

Effective migrants and isolation by distance

The number of effective migrants (Nm) was estimated from the F statistics according to the equation $Nm = (1/F_{st}-1)/4$ (Wright, 1969). This formula assumes the neutrality of the polymorphic genes and an island model of migration (see e.g. Hartl & Clark, 1989). Isolation by distance (Slatkin, 1993) was investigated in computing rank correlations between F_{st} estimates calculated between pairs of islands and various parameters: geographic distances and commercial exchanges between islands. Partial Mantel one-sided tests in which P values were determined by permutation procedures (Smouse, Long & Sokal, 1986; Leduc *et al.*, 1992) were used to estimate the significance of the various correlations. The intensity of commercial exchanges was measured by two series of indices as described by Pasteur *et al.* (1995). One evaluated air traffic based on the 1992 Air Tahiti and Air Moorea flight schedules, the other maritime traffic based on the 1992 records published by the Papeete Port Autonome. A global traffic index was built by summing up both air and maritime data.

Multiple tests

The significance level of each test was adjusted on the number of tests run by the sequential method of Bonferroni (Holm, 1979).

RESULTS

Polymorphism of Aedes polynesiensis

Since some collections were represented only by females captured in the field (F0) and others only by the offspring (F1) of such females, a first series of analyses was conducted to determine how one generation reared in the laboratory might affect the results. These analyses included comparisons of allelic frequencies and population structures observed on the F0 and F1 of each sample when available. The results indicated that little change had occurred between F0 and F1 (data not shown), and the following analysis will be based on the F0 of samples when available, and if not, on F1 (Table 1).

Among the six loci investigated, three (*Got-1*, *Hk-1* and *Mdh-1*) were monomorphic for the same allele (A) in most samples; rare alleles were observed for *Got-1* in a single

sample (RA4 with allele B at a frequency of 0.02), for *Hk-1* in two samples (MO3 with allele B at 0.02, and TU1 with allele C at 0.02), and for *Mdh-1* in three samples (HU2 with alleles B and C at 0.02 and 0.03, respectively; RA1 with allele B at 0.01; and TO1 with allele C at 0.02).

Est-1, *Got-2* and *Pgm* segregated in all populations for three or more alleles. The following genetic analysis is based on those three loci.

Statistical independence

Genotypic associations between pairs of loci were rejected in all of the samples when taking into account multiple testing (Bonferroni sequential test, $P > 0.05$), suggesting that *Est-1*, *Got-2* and *Pgm* polymorphisms could be considered as statistically independent from each other.

Hardy-Weinberg proportions

Hardy-Weinberg was applied to each locus in each population using the probability test. *P*-values were combined (Fisher's method) for each locus across populations for an overall test: Hardy-Weinberg equilibrium was significantly ($P < 10^{-4}$) rejected only for *Est-1*. This discrepancy among loci is best explained by selection at *Est-1*, as significant deviations of Hardy-Weinberg at this locus were not due in all cases to heterozygote deficits (details not shown). The locus *Est-1* was not considered further in the analysis.

Hardy-Weinberg equilibrium (H0: random mating) was first testing assuming that the alternative hypothese H1 is heterozygote excess, in order to possibly detect some selective phenomenon such as overdominance. For each locus and overall population the null hypothesis was not rejected ($P > 0.05$, data not shown). Hardy-Weinberg equilibrium (H0) was also tested assuming that the alternative hypothesis H1 is heterozygote deficit. This particular H1 hypothesis was chosen because all phenomena of interest (e.g. inbreeding, Wahlund effect, presence of null alleles) generate heterozygote deficiency. Six tests were significant ($P < 0.05$), but only one remained so ($P < 0.05$) when multiple testing was taken into account (Table 2). Global tests considering all populations for each locus or considering all loci for each population were not significant (Table 2).

Population differentiation

The overall differentiation of the 31 samples was relatively high ($F_{st} = 0.12$) and highly significant ($P < 10^{-5}$). In order to analyse the organization of this differentiation, various groups of samples were analysed (Table 3).

Within each island, differences in allelic composition observed in the collected samples were significant ($P < 0.05$) and F_{st} varied from 0.016 to 0.053, with the exception of Huahine, Rangiroa and Manihi ($F_{st} < 0.02$, $P > 0.05$). This intra-island differentiation as sometimes associated with geographical barriers. In Moorea and Bora-Bora, for example, the samples collected north and south of the central relief were significantly different ($P < 10^{-4}$). In Raiatea, the RA1 sample collected on

TABLE 2. Allelic frequencies observed in populations of *Aedes polynesiensis* at the *Pgm* and *Got2* loci

	Pgm								*Got-2*						Over all loci	
	A	B	C	D	E	n^a	F_{is}	P^b	A	B	C	n^a	F_{is}	P^b	F_{is}	P^b
1. TA1	0.62	0	0.38	0	0	30	–0.18	0.92	0.88	0.12	0	30	+0.21	0.33	–0.06	0.42
2. TA2	0.76	0	0.24	0	0	29	–0.30	1.00	0.74	0.26	0	29	–0.15	0.91	–0.22	0.99
3. TA3	0.74	0	0.26	0	0	29	+0.03	0.62	0.73	0.27	0	30	–0.01	0.68	+0.01	0.51
4. TA4	0.42	0	0.58	0	0	30	+0.40	0.03	0.92	0.08	0	30	–0.07	1.00	+0.28	0.14
5. TA5	0.66	0	0.34	0	0	28	–0.02	0.69	0.87	0.13	0	27	+0.20	0.36	+0.05	0.33
6. TA6	0.65	0	0.35	0	0	30	–0.38	0.99	0.77	0.23	0	45	+0.20	0.04	–0.12	0.61
7. TA7	0.86	0	0.15	0	0	29	+0.10	0.52	0.70	0.30	0	30	+0.06	0.52	+0.08	0.33
8. TA8	0.58	0	0.42	0	0	30	–0.01	0.67	0.68	0.32	0	30	+0.02	0.63	+0.00	0.53
9. MO1	0.57	0	0.43	0	0	30	–0.76	1.00	0.78	0.22	0	30	–0.26	1.00	–0.55	1.00
10. MO2	0.43	0	0.57	0	0	30	–0.21	0.94	0.57	0.43	0	30	–0.21	0.94	+0.21	0.96
11. MO3	0.60	0	0.40	0	0	30	–0.09	0.55	0.75	0.25	0	30	+0.39	0.05	–0.12	0.12
12. HU1	0.63	0	0.37	0	0	30	+0.01	0.62	0.92	0.08	0	30	–0.07	1.00	–0.01	0.69
13. HU2	0.54	0	0.46	0	0	27	–0.25	0.96	0.98	0.02	0	29	—	—	–0.20	0.83
14. HU3	0.63	0	0.32	0.02	0.03	30	+0.21	0.11	0.98	0.02	0	30	—	—	+0.20	0.11
15. RA1	0.55	0	0.45	0	0	30	–0.26	0.86	0.50	0.47	0.03	15	+0.15	0.35	–0.04	0.77
16. RA2	0.76	0	0.24	0	0	25	–0.08	0.82	0.80	0.14	0.06	25	–0.17	1.00	–0.12	0.90
17. RA3	0.73	0	0.27	0	0	30	–0.35	1.00	0.85	0.15	0	30	–0.16	1.00	–0.27	1.00
18. RA4	0.67	0.02	0.31	0	0	30	+0.14	0.30	0.77	0.23	0	30	–0.29	1.00	–0.05	0.72
19. BO1	0.42	0	0.58	0	0	30	+0.40	0.03	0.75	0.25	0	28	+0.07	0.54	+0.25	0.05
20. BO2	0.58	0	0.40	0	0.017	30	–0.12	0.67	0.93	0.07	0	14	–0.04	1.00	–0.10	0.81
21. AR2	0.35	0	0.62	0.03	0	33	–0.09	0.78	0.87	0.13	0	75	+0.20	0.11	–0.00	0.16
22. TO1	0.82	0.03	0.15	0	0	30	–0.17	1.00	0.87	0.13	0	30	–0.14	1.00	–0.15	1.00
23. RN1	0.81	0	0.19	0	0	29	+0.23	0.24	0.63	0.37	0	30	–0.28	1.00	–0.07	0.55
24. RN2	0.90	0	0.10	0	0	30	–0.09	1.00	0.73	0.27	0	30	+0.16	0.32	+0.08	0.47
25. RN3	0.70	0	0.30	0	0	30	+0.38	0.05	0.73	0.27	0	30	+0.83	$<10^{-4c}$	+0.60	$<10^{-4}$
26. MA1	0.18	0	0.77	0.03	0.02	30	+0.04	0.46	0.93	0.07	0	30	–0.05	1.0	+0.02	0.51
27. MA2	0.31	0	0.69	0	0	8	–0.21	0.96	0.87	0.13	0	8	–0.02	1.0	–0.16	0.80
28. TK1	0	0	1.00	0	0	30	—	—	0.93	0.07	0	30	–0.05	1.00	–0.06	0.11
29. NU1	0.68	0.15	0.17	0	0	30	–0.02	0.54	0.82	0.18	0	30	+0.24	0.22	+0.08	0.27
30. RU1	0.84	0	0.16	0	0	29	–0.17	1.00	0.92	0.08	0	30	–0.07	1.00	–0.13	1.00
31. TU1	0.73	0	0.27	0	0	30	+0.16	0.32	1.00	0	0	30	—	—	+0.15	0.32
All samples[c]							–0.06	0.94					+0.04	0.14	–0.02	0.69

[a] n=sample size. [b] Probability for rejecting Hardy-Weinberg equilibrium when H1=heterozygote deficit. [c] Underlined value remains significant when considering all samples.

TABLE 3. Population structure of *Aedes polynesiensis* in French Polynesia

		Probability of homogeneity			F_{st}			
	n^a	*Got-2*	*Pgm*	Total	*Got-2*	*Pgm*	Total	Nm
Between samples								
All samples	31	$<10^{-4}$	$<10^{-4}$	$<10^{-5}$	0.074	0.158	0.124	1.8
Tahiti	8	0.004	$<10^{-4}$	$<10^{-5}$	0.029	0.059	0.046	5.2
Moorea	3	0.03	0.16	0.03	0.08	0.020	0.033	7.4
Huahine	3	0.23	0.27	0.23	0.023	0.001	0.005	51
Raiatea	4	0.004	0.08	0.003	0.076	0.025	0.047	5.1
Bora-Bora	2	0.08	0.06	0.03	0.072	0.041	0.053	4.5
Rangiroa	3	0.45	0.03	0.07	–0.005	0.043	0.016	15
Manihi	2	0.60	0.68	0.77	–0.004	0.002	0.005	47
Between islands								
All islands	13	$<10^{-4}$	$<10^{-4}$	$<10^{-5}$	0.056	0.151	0.113	2.0
Society	5	$<10^{-4}$	$<10^{-4}$	$<10^{-5}$	0.045	0.017	0.028	8.7
Tuamotu	5	$<10^{-4}$	$<10^{-4}$	$<10^{-5}$	0.071	0.406	0.290	0.6
Australs	2	0.06	0.18	0.06	0.069	0.019	0.028	8.7
Between archipelagos								
All archipelagos	4	0.0004	$<10^{-4}$	$<10^{-4}$	0.018	0.028	0.024	10.2

[a]Number of samples

a small island (or '*motu*') of the coral barrier was significantly ($P < 10^{-4}$) differentiated from the three samples collected on the main island (RA2, RA3 and RA4). However, in other situations, as in Tahiti, intra-island differentiation could not be associated with a particular geographical barrier.

The differentiation between islands was investigated after pooling samples (Table 3). It was relatively elevated ($F_{st} = 0.113$) and significant ($P < 10^{-5}$) between all 13 islands, as well as between the islands of each archipelago. The only exception was the Australs archipelago, where differentiation between Rurutu and Tubuai was only marginally not significant ($P = 0.06$). The largest archipelago, Tuamotu, displayed the largest differentiation ($F_{st} = 0.29$). Differentiation between the four archipelagos ($F_{st} = 0.024$) was not greater than within each archipelago, and was significant ($P < 10^{-4}$).

Genetic exchanges

The importance of genetic exchanges between populations or groups of populations was estimated by computing the number of effective migrants (Table 3) from the F_{st} estimates of Weir & Cockerham (1984) using the formula $Nm = (1/F_{st} - 1)/4$ (Wright, 1969). Nm values displayed large variations within each island, from Nm = 51 in Huahine where no differentiation was observed to Nm = 4.5 in Bora-Bora where a significant differentiation between samples was observed. Between islands, Nm was equal to 2.0 when considering the 13 islands, and there were large differences when considering islands of the different archipelagos: Nm was equal to 8.7 between the five Society islands or the two Austral islands, and to 0.61 between the five Tuamotu islands.

To better understand the forces driving genetic exchange, variations in F_{st} value were examined in relation to geographic distance separating islands, and to

commercial traffic between islands. The relationship between F_{st} and geographic distance can be visualized by the rank correlation between F_{st} and log distance (Slatkin, 1993). This correlation was positive when considering the 13 islands (+ 0.25), suggesting that genetic differentiation increases with distance. However, geographical distance and commercial traffic indices were significantly correlated (Mantel test, global traffic vs geographical distance: $r = -0.66$, $P < 10^{-3}$; air vs boat traffic: $r = 0.45$, $P < 10^{-4}$). In order to test the correlation between geographical distance and F_{st} independently of commercial traffic, the residual of the regression of F_{st} on the global traffic index was used (Fig. 2A). The resulting correlation ($r = 0.031$) was not significant (Partial Mantel test, $P > 0.36$). Similarly, the correlation between F_{st} and traffic indices was computed after removing the effect of geographic distance (Fig. 2B). The global traffic index was significantly correlated with F_{st} (Partial Mantel test, $r = -0.23$, $P = 0.03$). This was mainly due to the effect of air traffic (F_{st} vs air traffic: $r = -0.19$; F_{st} vs boat traffic: $r = -0.082$). These results indicate that the

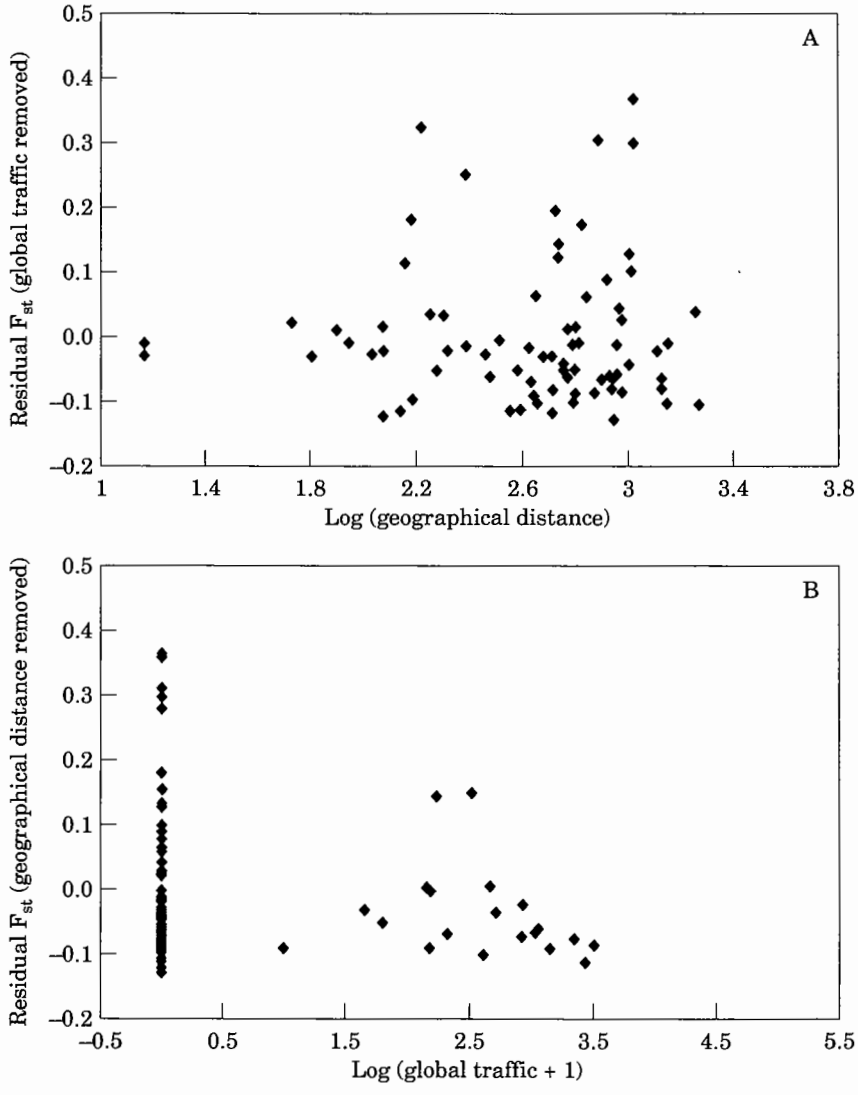

Figure 2. Genetic exchanges of *Aedes polynesiensis*. A, role of geographical distance and B, global traffic.

genetic differentiation in *Ae. polynesiensis* is globally more important between islands with important commercial exchanges than between those with a low intensity of commercial exchanges.

DISCUSSION

The significant genetic differentiation of *Ae. polynesiensis* observed between islands is consistent with the variations observed in previous investigations (Failloux *et al.*, 1994, 1995). In particular, it was shown that the variations in insecticide tolerance were not associated with insecticide use, and that suitability as a vector for *W. bancrofti* microfilariae from Tahiti was significantly greater in mosquitoes from Tahiti and Raiatea than in those from Tuamotu and the Marquesas, Gambiers and Australs. Here we show that genetic differentiation was highly significant when considering all islands or the islands of the Society or Tuamotu archipelagos, and only marginally significant when considering the two Australs. This differentiation was independent of the geographic distance separating the islands, but significantly correlated to the intensity of global commercial traffic between islands. Thus, the genetic differentiation of *Ae. polynesiensis* populations appears to decrease as commercial traffic intensity increases, and air traffic seems to play a more important role than maritime traffic since its contribution to the correlation was shown to be higher. The large difference in gene flow observed between islands in the Society ($Nm = 8.7$) and the Tuamotu ($Nm = 0.6$) archipelagos is in good agreement with the present status of commercial exchanges within French Polynesia. Air transportation, which began to be developed in the early 1960s, has been stable since 1979 (Atlas de la Polynésie française, 1993) and is concentrated in the Society archipelago where the islands of Tahiti, Moorea, Huahine, Raiatea and Bora-Bora have developed important tourism infrastructures. In contrast, maritime traffic is still the only way to reach many islands of the other archipelagos. From the 78 islands of Tuamotu (and not taking into account Mururoa and Fangataufa where the French army is based), Rangiroa is the most visited atoll due to the development of tourism and the black pearl industry. The other islands are less developed: Manihi and Takaroa are less touristic, and Aratika and Toau are extremely isolated without any air link.

The absence of significant correlation between genetic differentiation and geographic distance in *Ae. polynesiensis* is in sharp contrast with observations done on *Culex pipiens quinquesfasciatus* from the same islands. In the latter species, genetic differentiation increases significantly ($P < 0.01$) with geographic distance (Pasteur *et al.*, 1995). Not only is the biology of the two species very different, but also the history of colonization. If we accept Jackowski's hypothesis (1954) that *Ae. polynesiensis* colonized the Pacific region concomitantly with man, the species has been present in French Polynesia for the last 1500–3000 years (Atlas de la Polynésie française, 1993). It has adapted to the potential breeding sites specific to these islands at a time when inter-island communications were very limited and prevented migration. It is likely that these conditions favoured the patchy differentiation observed in populations from different islands. In contrast, *Cx. p. quinquefasciatus* arrived in the area at the beginning of this century and has remained strictly dependent on man-made breeding sites. Thus, the different patterns of geographic differentiation in the two species may be, at least partially, related to the length of colonization. The significant

correlation between commercial exchange and the importance of genetic differentiation of island populations suggests that the modern intensification of maritime and air travel is presently disturbing the original pattern of differentiation in *Ae. polynesiensis*. To confirm this hypothesis, more extensive sampling of isolated islands may be needed. Furthermore, it will be important to determine in the future how this may affect Bancroft filariasis epidemiology (Failloux *et al.*, 1995).

The differentiation observed in the small islands of Moorea (130 km^2), Bora-Bora (30 km^2), and Raiatea (171 km^2) was associated with the position of the sampled localities: north or south of the central mountain for Moorea and Bora-Bora, and a small island of the coral barrier for Raiatea. It is possible that a close characterization of the biotopes in Tahiti has accounted for the differentiation observed in this large island (1042 km^2).

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