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Genetic differentiation in relation to restricted larval dispersal of the convict surgeonfish *Acanthurus triostegus* in French Polynesia

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ABSTRACT: Genetic markers were used to study larval dispersal in coral reef fishes in order to investigate the impact of migration during the pelagic phase on island recruitment. Samples of *Acanthurus triostegus* were collected from 11 sites in French Polynesia in order to examine 3 different spatial scales (Island, Archipelago and Polynesia). To examine the effects of gene flow on population heterogeneity and population substructuring in *A. triostegus*, starch gel electrophoresis on 10 polymorphic loci encoding 10 enzymes was used [heterozygoty (H) = 0.325 ± 0.045; polymorphism level ($P_{0.95}$) = 0.323]. Nei's genetic distances calculated on the 10 polymorphic loci were very high (between 0.004 and 0.194 with an average of 0.058) and G-tests made on a single locus between pairwise samples showed 5 groups to be significantly different: 1 group comprised samples from Tiahura, Tubuai, Maiao, Tetiaroa, Pt. Paroa and Tahiti; 1 group comprised samples from Muroroa and Managreva and 3 other groups comprised the isolated samples from Takapoto, Bora-Bora and Nuku-Hiva respectively. Fixation index (F_{st}) values indicate significant differentiation between the 11 samples (F_{st} = 0.0886 on 11 populations), even between Bora-Bora and Moorea which are separated by 250 km. Estimates of gene flow (N_em: absolute numer of migrants at equilibrium), assuming equilibrium between the samples, were ≤10 individuals per generation, which is sufficient to ensure that the same alleles will be shared over long periods, but not sufficient to maintain identical allelic frequencies between populations. A hypothesis is proposed to illustrate the genetic structure of *A. triostegus* observed in French Polynesia based on ocean currents and the behaviour of the larval oceanic phase.

INTRODUCTION

The life history of most coral reef fishes is divided into 2 very dissimilar stages (Sale 1980): a relatively sedentary adult and juvenile stage and a planktonic egg and/or larval stage. Two reproductive strategies are also reported for coral reef fishes by Hourigan & Reese (1987). The first strategy is one whereby demersal eggs are protected by the adults, and is associated with low fecundity (25 to 10 000 eggs) and short larval duration (15 to 30 d). The second strategy is characterised by planktonic eggs, high fecundity (100 to 1 000 000 eggs) and a longer larval stage (from 20 to 80 d). Existence of a larval planktonic stage has led to the conclusion that there is considerable potential for dispersal and migration between geographically separated populations. The prevailing view is that reefs exist as spatially subdivided populations interconnected by pelagic larval exchanges (Mapstone & Fowler 1988). However, the distribution of coral reef fish in the Pacific suggests a high level of isolation between islands: only about 800 species occur in French Polynesia, compared to 1500 on the Australian Great Barrier Reef and 2180 in the Philippines (Sale 1980, Springer 1982, Randall 1985). Moreover, there is no direct relationship between the fish species occurring in French Polynesia and the larval duration of these species.

The aim of the present study was to evaluate the effect of larval dispersal on genetic homogeneity of

island populations of *Acanthurus triostegus* in French Polynesia. Two alternative hypotheses for the fate of larvae are proposed: (1) That larvae remain near the island where they were spawned and return to it before settling from the plankton. This is the local-recruitment concept. With local recruitment, and an absence of migration between islands, each population is isolated and inter-island genetic differentiation should develop with time. (2) That larvae are transported by currents and recruit to the first island they encounter. This is the random-recruitment concept. In this case, no genetic differentiation between islands is expected.

Of the published electrophoretic studies intended to assess subdivision of coral reef fish populations on a macrogeographic scale (Somero & Soulé 1974, Gorman & Kim 1977, Vawter et al. 1980, Bell et al. 1982, Shaklee 1984, Lacson 1992) only Bell et al. (1982) provide evidence for genetic differentiation between isolated populations. This study, made on *Amphiprion clarkii* along the coast of southern Japan, revealed an average genetic distance (Nei's distance) value of 0.008 and heterogeneity was found to be significant for 37 % of the tests carried out. Most of the differences were found between 5 sites on the Japanese coast and Bonin Islands, separated by about 1500 km; the 5 coastal sites did not show any evidence of differentiation. The other studies support the existence of a panmictic population sustained by larval migration.

This paper aimed to determine whether or not *Acanthurus triostegus* constitutes a single panmictic population in French Polynesia.

MATERIALS AND METHODS

The convict surgeonfish or manini *Acanthurus triostegus* is found throughout the tropical Indo-Pacific, including Madagascar, Australia, Japan, Hawaii and Polynesia, and the Gulf of Mexico. The sexes are separate and each female can lay more than 100 000 eggs each year (Randall 1961). The reproductive cycle varies with localities and shows seasonality in French Polynesia, associated with the warm period. Reproduction occurs during the day, in groups of hundreds of individuals, near channels through the reef. This species has pelagic eggs and a larval duration estimated at between 60 and 70 d. Their distribution during the oceanic stage is poorly documented. However, larvae are reported at about 50 m depth around Hawaii (Randall 1961) and the highest concentrations of larvae are found in 13 to 20 m depth in the Great Barrier Reef (Leis 1991). Competent postlarvae returning to the reef measure 20 to 25 mm before settlement. This species was chosen mainly because it is very abundant in French Polynesia and therefore presented no sampling problems. Moreover, its broad distribution was an advantage because a larger-scale study was planned.

Sampling. A total of 406 surgeonfish (>60 mm total length) were captured from 11 sites during 15 November 1990 to 15 February 1991 using spear-fishing techniques. The fish were measured, then dissected in order to isolate the liver, the eyes and part of the dorsal muscle (a piece of 1 or 2 g). The tissues were stored at −80 °C in liquid nitrogen to prevent possible degradation of the enzymatic activity. The 11 sites were chosen to represent 3 spatial scales (Fig. 1). For the Island spatial scale, 2 samples (39 and 31 fish respectively) were collected from Pt. Paroa and Tiahura on Moorea Island. For the Archipelago spatial scale, 5 samples (39, 39, 32, 39 and 40 fish respectively) were caught off Moorea, Tetiaroa, Bora-Bora, Maiao and Tahiti, islands of the Society Archipelago. For the Polynesia spatial scale, 6 samples (40, 32, 39, 40, 39 and 36 fish respectively) were collected off Tahiti, Takapoto, Tubuai, Mangareva, Nuku-Hiva and Mururoa, islands from 5 different Polynesian archipelagoes. All fish were collected in the lagoon habitat, except for the atolls of Takapoto, Mururoa and Tetiaroa, where the fish were sampled on the ocean side of the reef, and Nuku-Hiva where there is no coral reef.

Enzyme analysis. Each piece of tissue was homogenised at 4 °C in an equal volume of Tris/EDTA/NADP buffer (pH 6.8). The homogenenates were centrifuged at 15 000 × *g* for 30 min at 4 °C. The supernatant was stored at −80 °C. The samples were then processed by routine electrophoresis. The protocol for enzyme electrophoresis on horizontal starch was essentially that of Pasteur et al. (1987), and the nomenclature of the enzymes followed Shaklee et al. (1990).

Thirty-one enzyme loci with clearly interpretable genetic variation were scored (see Table 1). A locus was considered polymorphic if the frequency of the most common allele was ≤0.95 in at least 1 population. Alleles at polymorphic loci were assigned numerical designations expressing the mobility of their respective protein products relative to the mobility of the most common allozyme (designated 100) among the samples.

Statistical analyses. Allele frequencies at polymorphic loci were determined. Genotypic frequencies at polymorphic loci were tested for conformity to Hardy-Weinberg expectations using Emigh's (1980) correction and adjusting the significance levels for multiple tests (Lessios 1992). The present study comprised 110 tests (11 populations × 10 loci) and the 0.05 adjusted significance level become 4.54×10^{-4}. The chi-square value for this level of significance was computed by

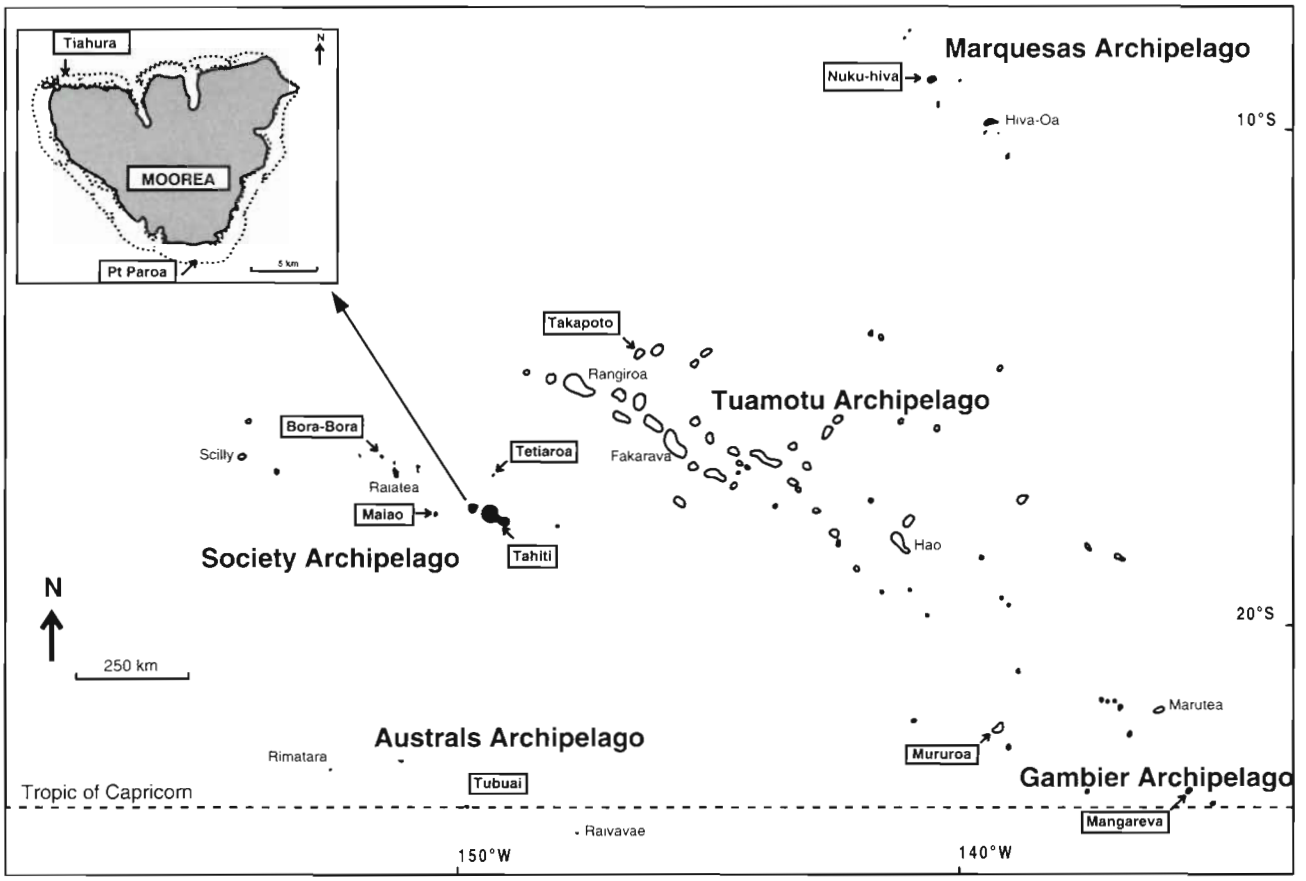

Fig. 1. *Acanthurus triostegus*. Sampling sites (denoted by rectangles)

randomising 10 000 values from the chi-square distribution. The 5th highest value was taken to represent the 0.0005 level of significance; the highest of 10 repeat computations was used in order to prevent Type I statistical errors.

Estimates of genetic divergence among samples were obtained using 2 different methods. (1) Comparisons of genetic differences among samples were assessed by *G*-test pairwise sample computations and genetic distances (*D*: Nei 1978) between the 11 populations, and the resulting matrix subjected to cluster analysis using the UPGMA algorithm (Sneath & Sokal 1973). Significance of the Nei's genetic distances and the UPGMA resulting was tested by determining the standard deviation of *D* (Nei 1987): variance of $D = (1 - I)/(In)$, where I = Nei's genetic identity and n = number of loci. For the *G*-test, the p-values were adjusted using the correction for multiple non-independent tests (Rice 1989), an α level of 0.05 becomes 0.0009 (corrected to 0.001). Analyses were performed using 'Genes in Populations', a computer program designed by B. May and C. C. Krueger and written by W. Eng (Cornell University, Ithaca, NY, USA).

(2) *F*-statistics were computed following the method of Weir & Cockerham (1984) using Eq. (10) for multiple loci and the algorithm described by Reynolds et al. (1983) for weighting of multiple alleles. A chi-square test (Workman & Niswander 1970) was used to evaluate the null hypothesis, $F_{st} = 0$: $\chi^2 = 2NF_{st}(k - 1)$; $df = (k - 1)(s - 1)$, where N is the total number of individuals sampled; k is the number of alleles at the locus; s is the number of populations.

Estimations of the absolute number of migrants at equilibrium [$N_em = (1 - F_{st})/4F_{st}$; Wright 1951] were calculated as an estimate of gene flow between populations. N_em was calculated from the F_{st} values from the Island model with a small level of migration. It represents the number of migrant individuals for each generation at equilibrium. The N_em estimates assume an equilibrium between drift and migration. Moreover, it is generally accepted that 1 migrant individual per local population per generation is sufficient to obscure the effect of genetic drift (Speith 1974). While this principle is correct, it is inappropriate when applied to the analysis of population structure at a single point in time; 1 migrant is sufficient to ensure that the same

allele will be shared over long periods of time, but is not sufficient to maintain identical allelic frequencies between populations (Allendorf & Phelps 1981).

RESULTS

Of the 31 loci examined, 16 were monomorphic in all the samples while 5 demonstrated infrequent allelic variation; the latter comprised *Idh-f*, *Idh-m*, *AAT-1*, *AAT-3* and *GPD* (Table 1). Finally, significant polymorphism was observed in 10 loci corresponding to a polymorphism level ($P_{0.95}$) of 0.323 (Table 2). The variation in allelic frequency of the most common allele in each locus was large and was not attributable to sampling errors. Variation was greatest at 8 loci: *PGI-1* where the frequency of the most common allele varied from 0.73 to 0.94, *AAT-2* (0.40 to 0.98), *ADH* (0.42 to 0.88), *SDH* (0.28 to 0.73), *ADA* (0.49 to 1.00), *GDA* (0.33 to 0.97), *MDH-2* (0.22 to 0.99) and *HPD* (0.12 to 0.59).

Significant deviation of genotypic frequencies from the Hardy-Weinberg equilibrium was observed in only 3 instances: *ADH* and *MDH* presented a slight excess of heterozygotes in Pt. Paroa and Mururoa respectively and *GDA* in Maiao exhibited a significant deviation corresponding to a deficiency of heterozygotes (chi-square = 16.57, df = 1, $p < 0.005$). For the remaining loci, large chi-square values resulted from low expected frequencies of genotypes observed in 1 or 2 individuals. Those deviations represented only 2.7% of the 110 tests carried out and thus can be considered as a sampling error. Data from all the different samples were pooled and conformity to Hardy-Weinberg expectations was tested. Six loci presented significant deviation: *PGI-1* (chi-square = 12.373, df = 2, $p < 0.005$), *AAT-2* (chi-square = 5.26, df = 1, $p < 0.025$), *SDH* (chi-

Table 1. *Acanthurus triostegus*. Enzyme systems with corresponding tissues and buffers. *: polymorphic enzymatic system; A: discontinuous buffer Tris-citrate-borate (TCB, pH 8.7); B: discontinuous buffer Tris-HCl (pH 8.5); C: continuous buffer Tris-citrate (TC, pH 6.7); D: continuous buffer Tris-citrate (TC, pH 8.0)

Enzymes	Locus	Buffer	Tissue
Lactate dehydrogenase	*Ldh-1*	A	Eyes
	Ldh-2	A	Eyes
	Ldh-3	A	Eyes
Malate dehydrogenase	*Mdh-1*	D	Eyes
	*Mdh-2**	D	Eyes
Isocitrate dehydrogenase	*Idh-f**	C	Liver
	*Idh-m**	C	Muscle
6 Phosphogluconate dehydrogenase	*6PGD*	C	Eyes
α-Glycerophosphate dehydrogenase	*GPD**	D	Muscle
Sorbitol dehydrogenase	*Sdh**	B	Liver
Alcohol dehydrogenase	*Adh**	A	Liver
Hexose phosphate dehydrogenase	*HPD**	A	Liver
Glucose phosphate isomerase	*PGI-1**	A	Eyes
	*PGI-2**	A	Eyes
Phosphoglucomutase	*PGM**	C	Muscle
Malic enzyme	*Me-1*	D	Muscle
	Me-2	D	Muscle
Mannose 6 phosphate isomerase	*MPI*	C	Muscle
Super oxide dismutase	*Sod-1*	A	Liver
	Sod-2	A	Liver
Fumarase	*Fum*	A	Muscle
Adenosine diaminase	*ADA**	C	Muscle
Guanine deaminase	*GDA**	C	Liver
Aspartate aminotransferase	*AAT-1**	C	Liver
	*AAT-2**	C	Liver
	*AAT-3**	C	Muscle
Adenylate kinase	*AK*	D	Eyes
Creatine kinase	*CK*	C	Liver
Glyoxylase-I	*GLO*	A	Liver
Leucine aminopeptidase	*Lap*	D	Muscle
Esterases	*Est*	B	Liver

Table 2. *Acanthurus triostegus*. Allele frequencies at 10 polymorphic loci for 11 sites. The most common allele is designated 100. N: number of alleles analysed at each locus

Locus / Alleles	Tubuai	Nuku-Hiva	Manga-reva	Taka-poto	Mururoa	Tahiti	Bora-Bora	Tetiaroa	Maiao	Pt. Paroa	Tiahura	Total
PGI-1												
120	–	0.01	0.01	–	0.01	–	–	–	–	–	–	< 0.01
100	0.76	0.95	0.83	0.71	0.81	0.81	0.81	0.81	0.78	0.82	0.83	0.81
70	0.24	0.04	0.16	0.29	0.18	0.19	0.19	0.19	0.22	0.18	0.17	0.19
PGI-2												
120	0.06	0.18	0.05	0.06	0.04	0.08	0.02	0.06	0.03	0.01	0.08	0.07
100	0.94	0.82	0.94	0.92	0.95	0.91	0.98	0.94	0.97	0.99	0.92	0.93
70	–	–	0.01	0.02	0.03	0.01	–	–	–	–	–	< 0.01
AAT-2												
140	0.24	0.01	0.50	0.33	0.60	0.23	0.27	0.19	0.24	0.11	0.30	0.28
100	0.76	0.98	0.50	0.65	0.40	0.77	0.73	0.81	0.76	0.89	0.70	0.72
70	–	0.01	–	0.02	–	–	–	–	–	–	–	0.01
ADH												
100	0.50	0.10	0.44	0.59	0.58	0.44	0.39	0.38	0.44	0.56	0.42	0.44
50	0.50	0.90	0.56	0.41	0.42	0.56	0.61	0.62	0.56	0.44	0.58	0.56
SDH												
100	0.55	0.72	0.71	0.61	0.33	0.27	0.50	0.50	0.64	0.48	0.56	0.53
20	0.45	0.28	0.29	0.39	0.67	0.73	0.50	0.50	0.36	0.52	0.44	0.47
PGM												
110	–	–	0.02	–	–	0.01	–	0.01	–	–	–	< 0.01
100	1.00	1.00	0.89	1.00	0.96	0.97	0.91	0.94	0.96	0.94	0.97	0.96
60	–	–	0.09	–	0.03	0.01	0.09	0.04	0.04	0.06	0.03	0.04
20	–	–	–	–	0.01	0.01	–	0.01	–	–	–	< 0.01
ADA												
100	0.63	1.00	0.49	0.50	0.61	0.84	0.67	0.66	0.69	0.71	0.73	0.69
90	0.31	–	0.50	0.48	0.38	0.15	0.33	0.33	0.30	0.25	0.25	0.29
60	0.06	–	0.01	0.02	0.01	0.01	–	0.01	0.01	0.04	0.02	0.02
GDA												
140	0.27	0.21	0.06	0.44	0.03	0.06	0.67	0.03	0.18	0.16	0.23	0.23
100	0.70	0.79	0.94	0.56	0.97	0.94	0.33	0.96	0.82	0.84	0.77	0.77
70	0.03	–	–	–	–	–	–	0.01	–	–	–	< 0.01
MDH												
100	0.54	0.01	0.59	0.62	0.54	0.78	0.64	0.72	0.60	0.71	0.56	0.58
50	0.46	0.99	0.41	0.38	0.46	0.22	0.36	0.28	0.40	0.29	0.44	0.42
HPD												
120	0.56	0.45	0.51	0.88	0.56	0.54	0.42	0.53	0.41	0.54	0.59	0.54
100	0.44	0.55	0.49	0.12	0.44	0.46	0.58	0.47	0.59	0.46	0.41	0.46
N	78	78	80	64	72	80	64	78	78	78	62	812

square = 6.34, df = 1, $p < 0.025$), *ADA* (chi-square = 15.93, df = 3, $p < 0.005$), *GDA* (chi-square = 50.12, df = 3, $p < 0.005$) and *HPD* (chi-square = 7.31, df = 1, $p < 0.01$). Pooling of all the samples introduced disequilibrium to the population due to differences between samples.

Nei's genetic distances (D) were estimated using 31 loci (Table 3), and the dendrogram was constructed based on these genetic distances (Fig. 2). The major branch of the dendrogram separates Nuku-Hiva from all the other samples; and the G-test realised for single loci shows that divergences are caused mainly by 4 loci (*AAT-2*, *ADH*, *ADA* and *MDH*) and leave no doubt as to the discreteness of this origin. The dendrogram also separates Takapoto and Bora-Bora from Mururoa and Mangareva and from a group mainly comprising Society Archipelago samples. However, because distortion can occur when clustering, the UPGMA dendrogram cannot be used as a definitive analysis to separate populations. Using the estimation of the variance of D, the value of 0.032 appears as the limit of significance. According to that limit, the UPGMA tree shows 6 groups to be significantly different: 1 group comprised samples from Tiahura, Tubuai, Maiao, Tetiaroa, Pt. Paroa and Tahiti and 5 other groups each comprised a single sample. However, because the nodes between

Table 3. Matrix of Nei's genetic distances ± standard deviation, among samples from 11 sites (above the diagonal). Single locus *G*-test results between each sample are also presented (below the diagonal). The table shows loci exhibiting significant variation between the 2 samples compared. Significance levels have been corrected according to Rice (1989) for multiple tests and the adjusted probability of 0.05 for 55 tests; –: no loci presenting significant divergence

	Tubuai	Nuku-Hiva	Mangareva	Takapoto	Mururoa	Tahiti	Bora-Bora	Tetiaroa	Maiao	Pt. Paroa	Tiahura
Tubuai		0.094 (± 0.056)	0.031 (± 0.032)	0.033 (± 0.032)	0.040 (± 0.036)	0.033 (± 0.032)	0.035 (± 0.034)	0.018 (± 0.024)	0.014 (± 0.021)	0.013 (± 0.021)	0.004 (± 0.011)
Nuku-Hiva	*PGH, AAT2, ADH, ADA, MDH*		0.139 (± 0.069)	0.194 (± 0.083)	0.175 (± 0.079)	0.141 (± 0.070)	0.136 (± 0.069)	0.116 (± 0.063)	0.108 (± 0.061)	0.124 (± 0.065)	0.082 (± 0.053)
Mangareva	*AAT2, GDA*	*AAT2, ADH, ADA, MDH*		0.079 (± 0.051)	0.032 (± 0.032)	0.066 (± 0.047)	0.086 (± 0.054)	0.029 (± 0.031)	0.042 (± 0.037)	0.048 (± 0.040)	0.027 (± 0.030)
Takapoto	*GDA, HPD*	*PGH, AAT2, ADH, ADA, GDA, MDH, HPD*	*GDA, HPD*		0.094 (± 0.056)	0.102 (± 0.059)	0.052 (± 0.041)	0.082 (± 0.053)	0.080 (± 0.052)	0.064 (± 0.046)	0.047 (± 0.039)
Mururoa	*AAT2, GDA*	*AAT2, ADH, SDH, ADA, GDA, MDH*	*SDH*	*AAT2, GDA, HPD*		0.041 (± 0.037)	0.102 (± 0.059)	0.041 (± 0.037)	0.032 (± 0.032)	0.049 (± 0.040)	0.036 (± 0.034)
Tahiti	*SDH, GDA*	*AAT2, ADH, SDH, ADA, MDH*	*AAT2, SDH, ADA*	*SDH, ADA, GDA, HPD*	*AAT2*		0.076 (± 0.050)	0.014 (± 0.021)	0.014 (± 0.021)	0.015 (± 0.022)	0.026 (± 0.029)
Bora-Bora	*GDA*	*PGI2, AAT2, ADH, ADA, GDA, MDH*	*GDA*	*HPD*	*AAT2, GDA*	*GDA*		0.069 (± 0.048)	0.043 (± 0.038)	0.052 (± 0.041)	0.040 (± 0.036)
Tetiaroa	*GDA*	*AAT2, ADH, ADA, GDA, MDH*	*AAT2*	*GDA, HPD*	*AAT2*	–	*GDA*		0.012 (± 0.020)	0.010 (± 0.018)	0.014 (± 0.021)
Maiao	–	*PGI1, AAT2, ADH, SDH, ADA, MDH*	*AAT2, SDH*	*GDA, HPD*	*AAT2*	–	*GDA*	–		0.012 (± 0.020)	0.014 (± 0.021)
Pt. Paroa	–	*PGI2, ADH, ADA, MDH*	*AAT2*	*GDA, HPD*	*AAT2*	–	*GDA*	–	–		0.015 (± 0.022)
Tiahura	–	*AAT2, ADH, ADA, MDH*	–	*GDA, HPD*	*AAT2, GDA*	*SDH*	*GDA*	*GDA*	–	–	

Mururoa and Mangareva are located just at the limit of significance, it seems reasonable to consider those 2 samples as a unique group. This will lead to the differentiation of 5 groups from *D* and the UPGMA analysis.

The *G*-test was used to test for statistically significant differences in the allele frequencies of each single locus between each pairwise comparison (Table 2). Thirteen pairwise comparisons between sample sites did not show any significant divergence in any locus. The nonsignificant comparisons were mainly between Tahiti, Tubuai, Tetiaroa, Maiao and Moorea (Pt. Paroa and Tiahura) samples. However, some unexpected results were found in the pairwise comparions, such as the absence of differentiation between Mangareva and Tiahura or the significant divergence between Tiahura and Tahiti or Tiahura and Tetiaroa. From the single locus *G*-test, *GDA* appears as the most variable locus responsible for the divergence of Bora-Bora from the other sample of the Society Archipelago. Finally, the *G*-tests performed over single loci confirm the results found previously in the analysis of *D*, by resulting in the same groups. In this case the samples from Mururoa and Mangareva are divergent in only 1 locus (*SDH*) of the 10 and no conclusion can be drawn about the differentiation of the 2 samples because of sampling error.

The mean fixation indices (F_{st}) were calculated for different clusters that were established by the sequential removal of samples that introduced variability (Table 4). Global F_{st} on 11 populations was estimated as 0.089 from Weir & Cockerham's (1984) methods and was highly significant. A specific estimation between Moorea (pooling the 2 Moorea samples) and Tahiti, 2 islands only 17 km apart, showed a significant F_{st} of 0.025 indicating a significant divergence between the 2 islands. However, difference between Maiao, Tetiaroa and Moorea was not significant (F_{st} = 0.007). Estimates of the number of migrants exchanged between the French Polynesian populations per generation (N_em) were greater than 1, $N_em > 2.57$ (Table 4), and because they are directly related to F_{st}, they follow the results shown with F_{st}.

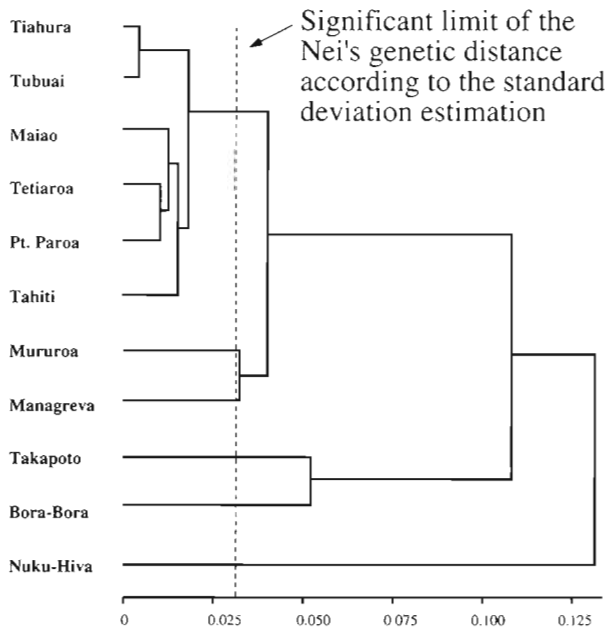

Fig. 2. *Acanthurus triostegus*. Dendrogram based on genetic distances between the 11 populations surveyed (see Table 3), using UPGMA clustering

DISCUSSION

The electrophoretic data and analyses demonstrate that populations of *Acanthurus triostegus* in French Polynesia do not represent a genetically homogeneous assemblage, with different units being discernable from the allelic data. According to the various analyses, 5 groups appear to be significantly different: 1 group comprised samples from Tiahura, Tubuai, Maiao, Tetiaroa, Pt. Paroa and Tahiti, 1 group comprised samples from Mururoa and Managreva and 3 other groups comprised the isolated samples from Takapoto, Bora-Bora and Nuku-Hiva. Using the Island model, the estimation of the number of effective migrants per generation is between 2.57 and 38.21. These values, however, probably do not represent the ecological reality. An effective migrant is an individual that migrates to a

Table 4. F_{st} values and jackknife SD estimates (multilocus; Weir & Cockerham's 1984) for different hierarchical sample groups. Estimates of N_em were derived from the F_{st} values using formulae given in the text. n: number of individuals

	n	F_{st}	SD (jackknife)	N_em
Polynesia (11 populations)	409	0.0886	0.0200	2.57
Global without Nuku-Hiva	370	0.0536	0.0200	4.41
Society Archipelago (6 populations)	222	0.0401	0.0265	5.98
Society Archipelago (without Bora-Bora)	190	0.0213	0.0100	11.47
Tahiti – Moorea	110	0.0250	0.0173	9.75
Tetiaroa – Moorea – Maiao	150	0.0065	0.0100	38.21
Moorea Island (2 populations)	72	0.0164	0.0283	14.99

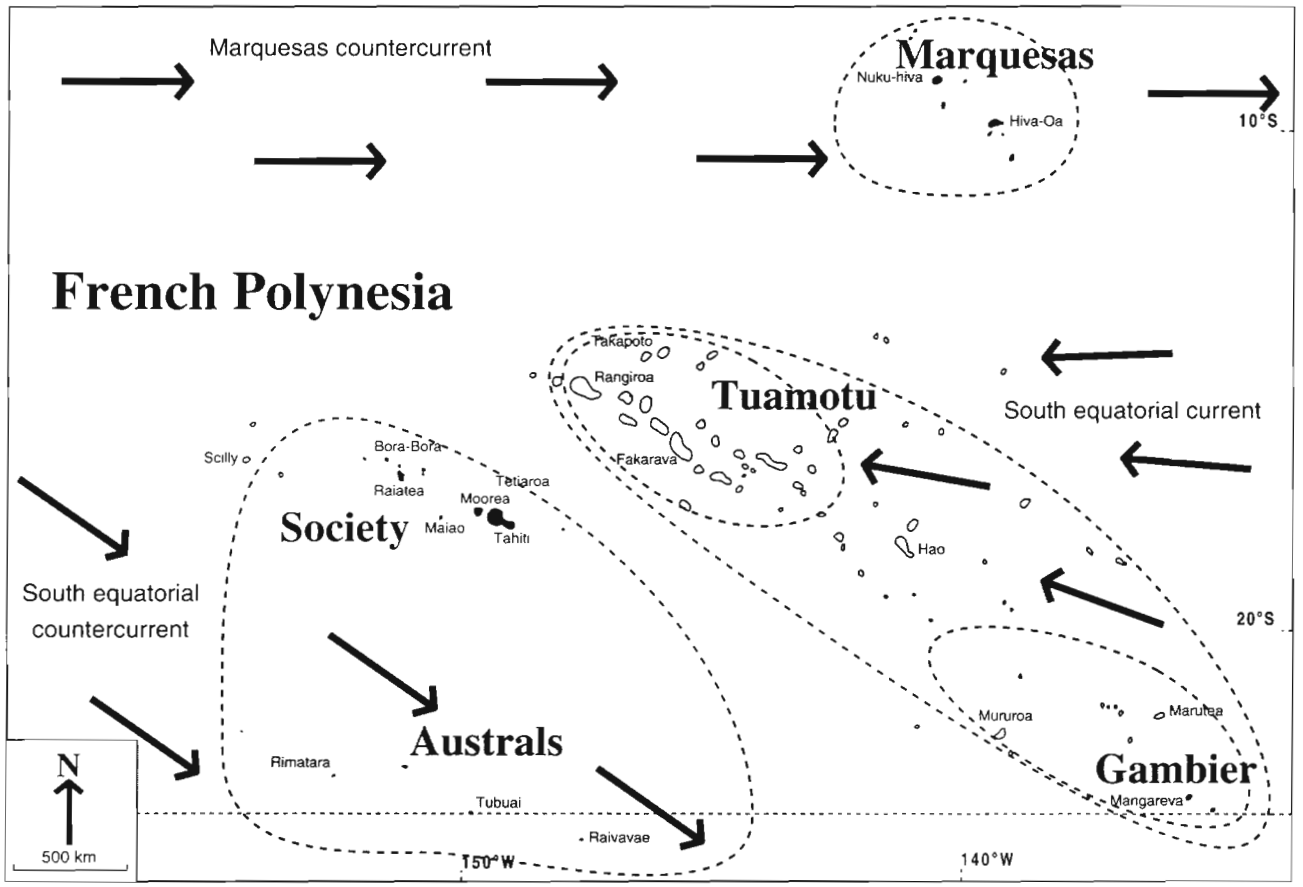

Fig. 3. *Acanthurus triostegus*. Superimposition of hydrodynamic data and genetic structure of *A. triostegus* in French Polynesia. Dotted lines encircle homogeneous genetic groups

different population and reproduces. This ensures that its genes are incorporated into future generations. Consequently, the real number of migrants is likely to be higher than the estimation suggests. Moreover, we used the Island model commonly used in population genetics, but which does not relate to the ecological data. The stepping-stone model, which required complicated mathematical analysis, would probably be more appropriate and show a higher number of migrants because of restricted gene flow between neighbouring populations (Slatkin 1989). The comparison of these 2 models and the development of mathematical solutions are the subject of a paper in preparation. The estimations of N_em in the present paper give a comparison with other studies.

The genetic consequences of larval dispersal are characterised by the balance between the forces of gene flow (which tend to make gene frequencies uniform among populations) and those of genetic drift and natural selection (which both act to diversify populations) (Wright 1931). Therefore, the observed variation in allelic frequencies in populations of *Acanthurus triostegus* could be the result of selection, genetic drift or both. The analysis used cannot discern which of selection and genetic drift is the main force causing the observed differentiation. It is assumed, however, that the pattern of biochemical genetic variation observed among populations of *A. triostegus* in French Polynesia is most likely to be the product of genetic drift.

This hypothesis fits the prevailing currents in the area (Rancher & Rougerie 1992) (Fig. 3). Fig. 3 superimposes currents and genetic data in the Polynesia area. The Marquesas countercurrent is very regular throughout the year. Opposition between this current and the South Equatorial current could explain the strong divergence of the Marquesas population, the border between these 2 currents constituting a barrier for larvae (Vermeij 1987). The genetic differentiation between the Tuamotu-Gambier assemblage and the Society and Australs archipelagoes is weaker, possibly because the border between the South Equatorial current and the South Equatorial countercurrent is more variable during the year and allows larval migration at some times. Since the highest concentrations of acan-

thurid larvae occur at depths of 13 to 20 m during the day (Leis 1991), they are likely to be affected by the current system described by Rancher & Rougerie (1992) in the Polynesian region.

In that context, the significant difference found between Bora-Bora and Moorea, separated by about 250 km, is surprising, as is that between Moorea and Tahiti, both situated in the same archipelago and water mass. The first divergence appears relatively strong because both samples from Moorea (Tiahura and Pt. Paroa) showed a significant difference from Bora-Bora in the allelic frequencies of *GDA*. However, the divergence between Tahiti and Moorea seems weaker because one sample from Moorea (Tiahura) shows a difference in *SDH* locus with Tahiti, while the other sample (Pt. Paroa) appears similar to Tahiti. Because of this variability, and even if the F_{st} between Moorea (pooling Tiahura and Pt. Paroa) and Tahiti shows a significant divergence, no conclusion can be made about the genetic differentiation between Moorea and Tahiti. More samples with greater numbers of individuals will be needed for further studies.

Assuming that differentiation is the result of genetic drift alone, the differentiation between Moorea and Bora-Bora described for *Acanthurus triostegus* seems to support the hypothesis developed by Johannes (1978) concerning the reproductive strategy of coral reef fish. His observations have shown that many species spawn at times of the year when prevailing winds or currents are at their weakest, and that spawning is concentrated in the vicinity of nearshore gyres which can increase the return of larvae to their natal area. This suggests that larval dispersal is not an adaptation for dispersal of species, but perhaps an evolutionary response to reduce the intense predation pressure of the reefs by transporting larvae offshore (Johannes 1978). Recent studies of larval colonisation have shown that only postflexion larvae are sampled in the reef front (Dufour 1991), suggesting that larvae return to the lagoon when they are competent to settle. Results of the genetic structure of the population of *A. triostegus*, a species with larval duration of 60 to 70 d, favour the hypothesis of local-recruitment to each island; the existence of gyres around the islands (Lobel & Robinson 1986, Wolanski & Hamner 1988) provides the mechanism for this to occur. This hypothesis could cause controversy by changing the current view regarding the evolutionary significance of the oceanic phase of reef fish. However, this situation may also be the result of the unique geomorphology of the Polynesian system, which features very isolated islands without continental plates in-between. Consequently, further studies would be necessary to complete the description of the genetic structure and the gene flow through French Polynesia as well as other locations with different geomorphology.

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