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▶ **To cite this version:**

Cécile Fauvelot, Planes S. Understanding origins of present-day genetic structure in marine fish: biologically or historically driven patterns?. Marine Biology, 2002, 141, pp.773 - 788. 10.1007/s00227-002-0869-7 . ird-03044074

HAL Id: ird-03044074
https://ird.hal.science/ird-03044074

Submitted on 7 Dec 2020

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Marine Biology (2002) 141: 773–788
DOI 10.1007/s00227-002-0869-7

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Understanding origins of present-day genetic structure in marine fish: biologically or historically driven patterns?

Received: 20 January 2002 / Accepted: 3 May 2002 / Published online: 21 August 2002
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Abstract Determining the origin of genetic structure is of wide interest because of its use in stock discrimination in marine organisms. Schematically, genetic differentiation can result from historical patterns maintained over geological time or from present-day isolation attributable to biological characteristics of the species. We used a comparative approach to population genetic analysis based on allozyme polymorphism to determine the impact of reproductive strategy (i.e. biological origin) and habitat (i.e. historical origin) on the genetic structure of individuals sampled from five isolated islands in French Polynesia. Eight species of coral reef fishes from two families (Chaetodontidae and Pomacentridae) were selected to test the impact of sea-level change (historical origin) and reproductive strategy (biological origin) on genetic structure. Seven of the eight study species showed significant divergence in allelic frequencies computed over all sites. For these seven species, multilocus F_{st} values ranged from 0.0114 to 0.0287. None of the eight species showed a significant relationship between genetic divergence and geographical distance between sites. Significant divergence (difference in allozyme frequencies) between some pairs of sites occurred but was unrelated to distances between them. These results suggest that the genetic structure of coral reef fish in French Polynesia is likely to be driven according to an island model in which migrations between populations are rare and random in space and time. Overall, none of the species showed congruent genetic structures between sites sampled. Genetic structure of the eight species did not appear significantly related either to reproductive strategy or habitat preference. Genetic diversity (heterozygosity) was significantly correlated with these two factors, with species laying benthic eggs and/or inhabiting lagoons showing significantly higher multilocus heterozygosity than species laying pelagic eggs and/or living on the outer reef slope. Overall, the absence of differences according to habitat and/or reproductive strategy did not provide any conclusive pattern regarding the origin of the genetic structure, but the limited divergence in allelic frequencies suggests recent differentiations.

Communicated by S. A. Poulet, Roscoff

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Introduction

A central challenge with respect to marine species is to understand patterns of genetic differentiation, if any, in a fluid ecosystem that tends to homogenize populations (Palumbi 1994). Even for sedentary species, such as coral reef ones, for which adults are often confined to a limited area by their behaviour or the fragmentation of their habitat, the pelagic larval stage allows for migration and gene flow (Leis 1984). Such dispersal is not without benefit to animals that inhabit a patchy heterogeneous environment, and larval exchange is assumed, for most species, to be the only mechanism uniting spatially discrete populations (Bonhomme and Planes 2000). In this sense, coral reef fish provide a good model for investigating the impact of the pelagic larval stage on dispersal, since the fragmentation of their habitat restricts exchange to the larval stage that can be accurately estimated at least in time using the microstructure of otoliths (Wellington and Victor 1989). Initial models considered pelagic larvae as drifting propagules that matched oceanic current (Roberts 1997), but recent investigations demonstrated real swimming capabilities or swimming orientation at least for the latest stage (Leis et al. 1996; Leis and Carson-Ewart 1997; Stobutzki and Bellwood 1997). These oriented swimming capabilities

have been proposed as mechanisms that would explain retention and self-recruitment in very open areas, such as the Great Barrier Reef (Jones et al. 1999) or the Caribbean (Swearer et al. 1999).

Dispersal is among the most difficult problems to study empirically in the sea because of the impracticality of direct observations of larval stages. Besides plankton net surveys and/or otolith analysis, which provided significant results on dispersal (Leis and Miller 1976; Jones et al. 1999; Swearer et al. 1999), natural genetic markers have also produced significant results (reviews in Smith et al. 1990; Bohonak 1999). As early as 1975, Ehrlich suggested that assessment of allozymic variation among geographically remote populations of reef fish is the optimal approach for testing dispersal and migration capabilities of larvae. Allozyme electrophoresis has become a powerful technique to demonstrate genetic variation and has been widely used in coral reef fish surveys (Planes 2002). Analyses of genetic structure of coral reef fish populations were initiated in 1982 in Japan (Bell et al. 1982) and in 1984 in Hawaii (Shaklee 1984; Shaklee and Samollow 1984); both looked at allozyme variations. With the exception of a remote oceanic population, these first studies undertaken in the Pacific did not reveal significant genetic differentiation among populations. The straightforward conclusion and general belief during that period was that coral reef fish populations exchanged genes through the pelagic stage at rates sufficient to homogenize the genetic structure over broad geographical ranges. Since the early 1980s several other studies have been undertaken on coral reef fish and provided divergent outcomes, ranging from panmixis over large areas to local and regional differentiation (Ehrlich 1975; Bell et al. 1982; Waples 1987; Lacson et al. 1989; Lacson 1992; Planes 1993; Planes et al. 1993, 1997; Doherty et al. 1994, 1995). The origin of such discrepancies is probably manifold.

Detectable allelic frequencies can be used to estimate levels of migration if it can be assumed that these frequencies reflect a balance between the opposing forces of migration (gene flow) and random divergence of allelic frequencies (genetic drift). Of course, other forces, notably natural selection and historical contact, can influence allelic frequencies, and the relative importance of these forces in natural populations has been extremely difficult to evaluate directly. While this theory is silent about allopatric populations with identical genetic profiles (Shaklee et al. 1982), differentiation provides unequivocal evidence of reproductive isolation. The main problem when trying to summarize genetic data relating to larval dispersal is to be able to exclude all other factors likely to affect the genetic structure of populations, such as historical events. Historical factors may conflict with the current situation in areas affected by sea-level changes during the last glaciation events, creating reductions in the effective population size when suitable habitat disappeared. Such a hypothesis has been proposed to explain some contradictions between level of genetic differentiation and dispersal capabilities, in comparison of two species in French Polynesia (Planes et al. 1993). The species (*Dascyllus aruanus*) with reduced oceanic larval stage (i.e. dispersal stage) exhibited more or less genetic homogeneity within French Polynesia, while the other species (*Acanthurus triostegus*), with longer pelagic phase, showed genetically structured populations within the same region (Planes 1993). Such antagonistic results initiated the hypothesis tested in the present work, since the absence of common sampling protocols and the variety of geographical scales surveyed make it impossible to identify any general trends from the data available in the literature.

In the present work we used a comparative approach, based on a multispecific analysis, to evaluate the features influencing the genetic structure between populations of coral reef fish and to provide testable hypotheses. Previous work on the basis of a comparative approach in marine fish all focused on testing for and showing a significant relationship between potential larval dispersal and genetic structure (Waples 1987; Doherty et al. 1995; Gold and Richardson 1998). The present survey was intended to contrast the biological and historical features that mainly affect the genetic structure observed. This is of primary interest when genetic data are to be used for management and conservation, since we need to know whether we are looking at a present-day trend or an ancestral pattern. Regarding the biological features, we contrast species having pelagic eggs (generally linked to longer larval duration) to species with benthic attached eggs (generally associated with shorter larval duration) (Thresher 1984). As historical factors, we concentrated on testing the effect of sea-level changes and its consequence for habitats according to species, by comparing species showing stable habitat, whatever the sea level (outer slope inhabitants), to species experiencing removal of their habitat in low sea-level periods, leading to local extinction (lagoonal species).

For the comparative analysis, we collected individuals of eight species showing different biological (reproductive strategy) and ecological (habitat) features within a similar network of isolated islands, providing different spatial scales within French Polynesia. The aim of this study was then to evaluate the level of genetic structure of these species, using allozymes to detect clustering of species showing similar features. We addressed the following questions: (1) Do allozymes show genetic differentiation among geographically isolated benthic populations of coral reef fishes in French Polynesia? (2) Is the amount of genetic differentiation correlated with geographical separation? (3) Are single-species genetic patterns correlated with the type of egg? (4) Does the habitat of adults have an impact on single-species genetic structure?

Materials and methods

Sampling

The geomorphology of French Polynesian islands is of particular interest when investigating larval dispersal between reefs, since the

lack of reef continuum and the deep bottom between islands eliminate potential migration by adult movement (Duncan and McDougall 1976). Five isolated islands were sampled in French Polynesia (Fig. 1). One high volcanic island (Moorea) and one atoll (Tetiaroa) in the Society Archipelago were chosen, together with atolls from the Tuamotu Archipelago (Rangiroa, Takapoto and Marutea). Sites were selected according to the access facilities and the geographical distances between islands, in order to provide small (e.g. 60 km between Moorea and Tetiaroa), medium (about 250 km between Moorea and Takapoto), and large spatial scales (up to 1,550 km between Moorea and Marutea). Such distances were specifically chosen to test the relationship between genetic differentiation and geographical distance (cf. question 2, above).

Species were chosen from two different families in order to provide different reproductive strategies, based on egg type (Thresher 1991) and different habitats, to answer questions 3 and 4. The Chaetodontidae family provided species spawning pelagic eggs. Spawning in butterflyfishes involves large groups, with both sexes well represented (Allen et al. 1998). Eggs hatch in the open sea approximately 24 h after their release and larvae spend an average of 45 days in the pelagos before returning to reefs (Hourigan and Reese 1987). The second family (Pomacentridae) provided species spawning benthic eggs. Most damselfish species are highly territorial and several days prior to spawning, the male (or in some cases both partners) select the nesting site. Eggs are under care in the nest for a period ranging from 2 to 7 days until hatching (Allen 1992). Larvae are pelagic and remain in the water column about 25 days on average (Wellington and Victor 1989).

Within these two families, eight species were selected according to their habitat, with species only found in the lagoon and species only found on the outer slope. Selection of species according to their habitat was based on previous studies of the fish communities (Galzin 1987; Galzin, personal communication): *Chaetodon citrinellus* as the butterflyfish inhabiting lagoons; *Chaetodon quadrimaculatus* and *Forcipiger flavissimus*, as butterflyfishes living on the outer slope; *Pomacentrus pavo*, *Chrysiptera glauca* and *Dascyllus aruanus*, as damselfishes inhabiting lagoons; and *Chromis xanthura* and *Plectroglyphidodon dickii*, as damselfishes living on the outer slope.

The standard sampling effort was 50 fishes per species per site, but some of the species could not be found or were rare in certain localities (Table 1): *Chaetodon citrinellus* was not found in Marutea, and *Plectroglyphidodon dickii* was absent at Moorea and Tetiaroa; *Chrysiptera glauca* was rare and difficult to collect at Moorea and Tetiaroa. A total of 1,662 individuals were collected either with a speargun or using an anaesthetic solution for smaller fishes, between March 1998 and December 2000.

Isoenzyme analysis

Fish were preserved in ice after collection until the liver and a piece of muscle were removed from each fish and placed separately in liquid nitrogen for long-term conservation. Individual pieces of tissues were homogenized at 4°C in an equal volume of Tris-HCl/EDTA/NADP buffer (pH 6.8). Homogeneous samples were centrifuged at 15,000×*g* for 30 min at 4°C, and the supernatant was removed and stored in individual labeled Eppendorf at –80°C until all electrophoretic determinations were completed. First, 12 individuals of each species were used in order to design a protocol: only loci with clearly interpretable patterns were scored. The samples were then processed by routine electrophoresis on horizontal starch gel, following Pasteur et al. (1987). Alleles at polymorphic loci were assigned numerical designations expressing the mobility of their respective protein products relative to the mobility of the most common allele (designated 100) among the samples. Enzyme names and numbers follow Shaklee et al. (1990).

Statistical analysis

Allelic and genotypic frequencies for the polymorphic loci were obtained by counting phenotypes directly from the gels using the Genetix 4.0 package (Bonhomme et al. 1993) available on: http://www.univ-montp2.fr/genome-pop/genetix.htm. Observed heterozygosity values were computed for each population from the genotypic frequencies, adding monomorphic loci for multilocus values (Nei 1973). Heterozygosity values were assessed with their estimates of variance and standard deviation generated by resampling over loci (available on the Genetix package). Significant differences in multilocus heterozygosity were analyzed by a *t*-test between species to test hypotheses on the impact of the reproductive strategy and/or the habitat. The fixation index (F_{is}) was used to represent the Mendelian equilibrium, and single and multilocus deviation from Hardy–Weinberg equilibrium was tested using the Markov chain reaction implemented in Genepop 3.1d (Raymond and Rousset 1995). Significance levels for statistical tests were adjusted, for each species separately, according to the sequential Bonferroni (Rice 1989).

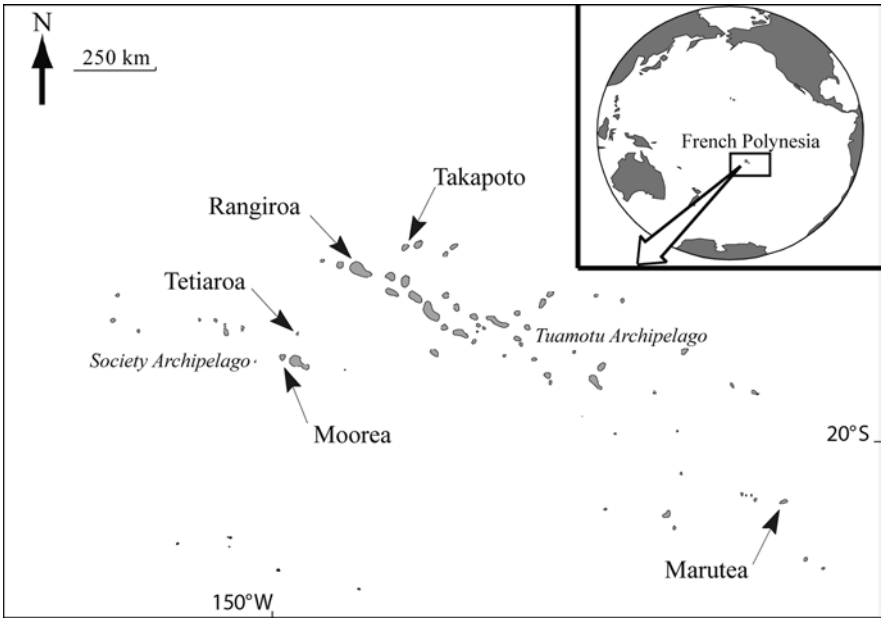


Fig. 1. Location of sampling sites of the eight fish species in French Polynesia. Details of sites are described in the text and sampling effort is detailed in Table 1

Table 1. Sampling effort by species and sites. *N* total number of individuals of each species collected from all sites; – no individuals

Fish taxon	Tuamotu Archipelago			Society Archipelago			
	Marutea	Rangiroa	Takapoto	Tetiaroa	Moorea	*N*	Habitat
Chaetodontidae (pelagic eggs)							
Chaetodon citrinellus	–	50	50	50	50	200	lagoon
Chaetodon quadrimaculatus	50	50	48	49	49	246	outer slope
Forcipiger flavissimus	50	50	50	49	39	238	outer slope
Pomacentridae (benthic eggs)							
Chrysiptera glauca	50	48	49	–	–	147	lagoon
Pomacentrus pavo	50	27	50	48	50	225	lagoon
Dascyllus aruanus	48	46	48	50	49	241	lagoon
Plectroglyphydodon dickii	48	48	47	–	–	143	outer slope
Chromis xanthura	49	49	48	31	45	222	outer slope

Wright's standardized variance in allelic frequencies (F_{st}; Wright 1969) was computed over all sites and between each pair of sites, following the Weir and Cockerham (1984) algorithm available on Genetix. Significant differences between allelic frequencies were tested using the Fisher exact test implemented in Genepop 3.1d. Significance levels for statistical tests were adjusted, for each species separately, according to the sequential Bonferroni (Rice 1989).

Correlation between geographical distance and genetic differentiation (multilocus F_{st}) was performed over all loci for each species using Mantel's test. We computed the normalized Mantel statistic, r (which takes values from –1 to +1), which was tested for significance through a permutation test at the 0.001 level (i.e. performing 999 random permutations of populations in one of the distance matrices), under the null hypothesis that both matrices are not linearly related. Mantel's tests were computed using the Mantel procedure of the Genetix package. In such correlations, we followed Hutchison and Templeton's (1999) model which directly links F_{st} and geographical distance. This recent approach removed the problems of relating the estimate of regional multilocus F_{st} to gene flow and the subsequent question linked to the genetic equilibrium assumed by the island model.

In addition to correlation between pairwise F_{st} values and geographical distances that only consider isolation by distance, we visualized the relationships among sites, based on the F_{st} values, using a multi-dimensional scaling analysis (MDS) as suggested by Lessa (1990). MDS analysis uses distances between objects (pairwise population F_{st} values in the present approach) and approximates those distances in a reduced number of dimensions through an iterative fitting procedure. A two-dimensional plot fitted to pairwise F_{st} values between sites was created for each species in XLStat v.4.3 (available on http://xlstat.com). The goodness of fit between the fitted and observed distances was measured by a stress test, with a zero stress value indicating a perfect fit between the fitted and observed distances (Kruskal and Wish 1978). Such a procedure was used to search for any structure between sites that has no direct link with the geographical distances, such as oceanic currents and geomorphology.

The last set of analyses compared results for the different species according to the hypothesis on their reproductive strategy or their habitat. To evaluate the level of correlation between genetic patterns exhibited by the different species, pairwise F_{st} values for each species were computed and Mantel's test was performed among species using the Mantel software (available on http://life.bio.sunysb.edu/morph). F_{st} values within each matrix were first standardized before computing the sum of the cross product; the result is divided by $(n–1)$ where n is the number of pairs of distances compared in the computation (Smouse et al. 1986). The Mantel statistic, r, is then equivalent to the computation of a Pearson correlation coefficient. Probabilities of this statistic were then computed by random permutations, using 10,000 permutations. Finally, in order to represent biological distances between species, a matrix of the Bray–Curtis dissimilarity coefficient (D) was calculated (where $D = 1–S$, and S is the Bray–Curtis similarity coefficient) from pairwise F_{st} values, using Progiciel R (Legendre and Vaudor 1991). The relationship among species was investigated using an MDS approach. A two-dimensional plot fitted to the Bray–Curtis dissimilarity coefficient (D) between species was created in XLStat v.4.3. The goodness of fit between the fitted and observed distances was measured by a stress test (Kruskal and Wish 1978).

Results

Genetic variation within species

A total of 39 loci were screened and the number of loci showing activity varied from 20 (for *Dascyllus aruanus*) to 27 (for *Chaetodon quadrimaculatus* and *Plectroglyphidodon dickii*) (Tables 2, 3). Protocols and details are available from the authors. The number of polymorphic loci varied between 8 and 14 when considering a frequency ≤ 0.95 for the most common allele, and between 9 and 18 when considering a frequency ≤ 0.99 for the most common allele. Overall population multilocus heterozygosity varied from 0.0785 for *Chaetodon quadrimaculatus* to 0.1557 for *Dascyllus aruanus*.

All polymorphic loci were tested for deviations from Hardy–Weinberg equilibrium within each site. For all species, 12 single loci (out of 479 tested) deviated from the equilibrium predictions ($P < 0.05$), but once the probability level was corrected according to a sequential Bonferroni (distinct correction for each species), none of the deviations remained significant. Multilocus F_{is} values, analyzed separately for each site within each species, ranged between –0.0532 (in Marutea for *Plectroglyphidodon dickii*) and 0.1635 (in Takapoto for *Pomacentrus pavo*). No species at any site showed significant multilocus deviation from Hardy–Weinberg equilibrium. This result presumes that, for each species, each sample from one site can be attributed to individuals from the same population and that each site provides a good estimation of the population.

With the exception of *Plectroglyphidodon dickii*, exact tests computed over all samples within each species showed significant divergence in allelic frequencies for all species in French Polynesia (Table 4). Multilocus F_{st}

Table 2. Summary (part 1) of the electrophoretic results for each species, for each population, for each locus and over all loci. *N* number of fishes sampled; H_{obs} observed heterozygosity; F_{is} fixation index (Weir and Cockerham 1984), *M* monomorphic loci; – no activity of this locus for the species; $P_{(0.95)}$ and $P_{(0.99)}$ are percentages of polymorphic loci within each population. Significant deviation from Hardy–Weinberg equilibrium is denoted by* ($P < 0.05$) following F_{is} values. *Ma* Marutea, *Te* Tetiaroa, *Mo* Moorea, *R* Rangiroa and *Ta* Takapoto

Locus	*C. citrinellus*				*C. quadrimaculatus*					*F. flavissimus*				
	Ra	Ta	Te	Mo	Ma	Ra	Ta	Te	Mo	Ma	Ra	Ta	Te	Mo
N	50	50	50	50	50	50	48	49	49	50	50	50	49	39
*AAT-1**														
H_{obs}	0.260	0.280	0.200	0.260	0.020	M	M	M	M	0.060	0.120	0.060	0.082	0.077
F_{is}	0.175	0.072	0.188	–0.140	0	M	M	M	M	–0.021	0.039	–0.021	0.299	–0.027
*AAT-2**														
H_{obs}	0.200	0.220	0.240	0.220	0.020	M	0.063	M	0.020	0.120	0.130	0.120	0.204	0.026
F_{is}	0.091	–0.102	–0.126	0.056	0	M	–0.022	M	0	–0.033	–0.025	–0.039	–0.064	0
*ADA**														
H_{obs}	0.429	0.420	0.480	0.500	M	M	M	0.020	M	0.200	M	0.080	M	M
F_{is}	0.185	0.198	–0.009	0.038	M	M	M	0	M	0.093	M	–0.032	M	M
*ADH**														
H_{obs}	–	–	–	–	–	–	–	–	–	0.020	M	M	0.020	M
F_{is}	–	–	–	–	–	–	–	–	–	0	M	M	0	M
*CK**														
H_{obs}	M	M	M	M	M	M	M	M	M	M	M	M	0.020	M
F_{is}	M	M	M	M	M	M	M	M	M	M	M	M	0	M
*Est1**														
H_{obs}	–	–	–	–	0.360	0.220	0.229	0.225	0.429	0.540	0.420	0.580	0.571	0.462
F_{is}	–	–	–	–	–0.026	–0.114	0.380*	0.291	–0.018	–0.048	0.167	–0.092	–0.133	0.010
*Est2**														
H_{obs}	0.360	0.380	0.320	0.440	0.140	0.080	0.042	0.061	0.020	0.200	0.260	0.140	0.265	0.077
F_{is}	0.277	0.195	0.274	0.147	–0.065	–0.032	–0.011	–0.021	0	0.091	0.108	0.163	0.016	0.544*
*Est3**														
H_{obs}	–	–	–	–	0.380	0.460	0.479	0.367	0.510	–	–	–	–	–
F_{is}	–	–	–	–	0.122	0.081	0.017	0.145	–0.075	–	–	–	–	–
*EstD**														
H_{obs}	–	–	–	–	–	–	–	–	–	0.080	0.080	M	0.041	0.026
F_{is}	–	–	–	–	–	–	–	–	–	–0.023	–0.032	M	–0.011	0
*GDA**														
H_{obs}	0.200	0.260	0.400	0.380	0.300	0.300	0.313	0.245	0.286	–	–	–	–	–
F_{is}	0.073	0.284	0.071	–0.025	0.035	0.22	0.337*	0.259	0.09	–	–	–	–	–
*GDH**														
H_{obs}	–	–	–	–	–	–	–	–	–	0.280	0.320	0.220	0.184	0.231
F_{is}	–	–	–	–	–	–	–	–	–	0.102	–0.028	0.071	0.321*	0.095
*GPD-1**														
H_{obs}	M	0.040	0.040	M	0.020	M	0.042	M	0.020	0.020	0.020	M	0.041	M
F_{is}	M	–0.010	–0.010	M	0	M	–0.011	M	0	0	0	M	–0.011	M
*GPD-2**														
H_{obs}	–	–	–	–	–	–	–	–	–	M	M	0.04	M	M
F_{is}	–	–	–	–	–	–	–	–	–	M	M	–0.005	M	M
*GPI-1**														
H_{obs}	0.020	0.100	0.120	0.040	0.060	0.100	0.104	0.102	0.225	0.020	M	0.020	0.020	M
F_{is}	0.662*	–0.029	–0.037	–0.005	–0.014	–0.029	–0.044	0.241	–0.089	0	M	0	0	M
*GPI-2**														
H_{obs}	0.020	0.020	0.040	M	0.040	M	0.021	M	0.041	0.100	0.020	0.020	0.082	0.501
F_{is}	0	0	–0.010	M	–0.010	M	0	M	–0.011	–0.043	0	0	–0.021	–0.007
*IDH-1**														
H_{obs}	0.460	0.360	0.340	0.420	0.020	M	0.021	M	M	M	M	M	0.020	0.026
F_{is}	–0.157	0.117	–0.095	–0.011	0	M	0	M	M	M	M	M	0	0
*IDH-2**														
H_{obs}	M	M	M	M	M	0.020	0.042	0.020	M	0.060	0.040	0.100	0.245	0.184
F_{is}	M	M	M	M	M	0	–0.005	0	M	–0.021	–0.010	–0.029	0.030	0.177
*LDH**														
H_{obs}	0.080	0.240	0.080	0.120	M	M	M	M	M	M	M	M	0.041	0.026
F_{is}	–0.032	–0.126	–0.032	–0.054	M	M	M	M	M	M	M	M	–0.011	0
*MDH-1**														
H_{obs}	M	M	M	M	M	0.020	M	M	M	–	–	–	–	–
F_{is}	M	M	M	M	M	0	M	M	M	–	–	–	–	–
*MDH-2**														
H_{obs}	M	M	M	M	M	M	M	M	0.041	0.020	M	M	M	M
F_{is}	M	M	M	M	M	M	M	M	–0.011	0	M	M	M	M

Table 2. Contd.

Locus	*C. citrinellus*				*C. quadrimaculatus*					*F. flavissimus*				
	Ra	Ta	Te	Mo	Ma	Ra	Ta	Te	Mo	Ma	Ra	Ta	Te	Mo
*MEP-1**														
H_{obs}	0.100	0.080	0.100	M	0.120	0.080	0.042	0.612	0.041	M	0.040	0.020	M	M
F_{is}	–0.043	–0.032	–0.034	M	–0.054	–0.032	0.486	0.382	–0.011	M	–0.005	0	M	M
*MEP-2**														
H_{obs}	M	M	M	M	0.220	0.280	0.250	0.408	0.143	0.020	M	M	M	M
F_{is}	M	M	M	M	–0.080	–0.153	0.130	–0.045	–0.047	0	M	M	M	M
*MPI**														
H_{obs}	M	M	M	M	0.040	M	M	M	M	0.140	0.020	0.060	0.041	0.026
F_{is}	M	M	M	M	0	M	M	M	M	–0.065	0	–0.021	–0.011	0
*PEPB-1**														
H_{obs}	M	M	M	M	M	M	M	M	M	M	M	0.020	M	0.026
F_{is}	M	M	M	M	M	M	M	M	M	M	M	0	M	0
*PEPB-2**														
H_{obs}	0.140	0.300	0.040	0.180	0.100	0.040	M	0.082	0.020	–	–	–	–	–
F_{is}	0.155	0.072	–0.010	0.091	–0.034	–0.010	M	–0.033	0	–	–	–	–	–
*PEPD**														
H_{obs}	0.360	0.440	0.360	0.260	M	M	M	M	0.020	0.220	0.100	0.120	0.143	0.077
F_{is}	0.075	0.116	0.086	0.197	M	M	M	M	0	0.303	–0.034	–0.044	–0.067	–0.018
*PGAM**														
H_{obs}	M	M	M	M	M	M	0.021	M	M	–	–	–	–	–
F_{is}	M	M	M	M	M	M	0	M	M	–	–	–	–	–
*PGDH**														
H_{obs}	0.080	0.060	0.180	0.020	0.320	0.260	0.438	0.388	0.510	0.100	0.040	0.020	M	0.026
F_{is}	0.300	–0.014	0.100	0	0.178	0.165	–0.110	0.003	–0.101	–0.027	–0.010	0	M	0
*PGM**														
H_{obs}	0.300	0.200	0.240	0.260	M	M	0.021	M	M	0.300	0.300	0.320	0.449	0.539
F_{is}	–0.022	0.179	–0.040	0.063	M	M	0	M	M	–0.142	0.163	–0.074	0.044	–0.09
*SOD-1**														
H_{obs}	M	M	M	M	0.020	M	0.021	M	M	M	M	M	0.020	M
F_{is}	M	M	M	M	0	M	0	M	M	M	M	M	0	M
*SOD-2**														
H_{obs}	–	–	–	–	0.020	0.020	0.021	M	M	–	–	–	–	–
F_{is}	–	–	–	–	0	0	0	M	M	–	–	–	–	–
Overall														
H_{obs}	0.1254	0.1417	0.1325	0.1292	0.0815	0.0704	0.0802	0.0733	0.0869	0.1000	0.0752	0.0776	0.0996	0.0738
F_{is}	0.1119	0.1144	0.0510	0.0368	0.0384	0.0540	0.1336	0.1274	–0.0368	0.0445	0.0829	–0.0431	0.0100	0.0489
$P_{(0.95)}$	0.4583	0.4583	0.4583	0.4167	0.2963	0.2222	0.2222	0.2593	0.2222	0.4000	0.2800	0.2800	0.3200	0.2000
$P_{(0.99)}$	0.5417	0.5833	0.6250	0.4583	0.4074	0.3704	0.6296	0.4074	0.5556	0.5200	0.4400	0.4400	0.7200	0.6000

values ranged from 0 for *Plectroglyphidodon dickii* to 0.0287 for *Chaetodon quadrimaculatus*, with an average value of 0.0163 over all eight species. For single-locus tests, the percentage of loci showing significant divergence ranged from 15% for *Chrysiptera glauca* to 62% for *Dascyllus aruanus*, with an average of 28% over all species (excluding *P. dickii* which showed no significant divergence). Altogether, about one polymorphic locus in three contributed to significant divergence among populations.

Considering each species separately, the highest pairwise multilocus F_{st} value was found in *Chaetodon quadrimaculatus* between Tetiaroa and Moorea (Table 4, $F_{st} = 0.0536$, $P = 0.0070$). *Chromis xanthura* and *Plectroglyphidodon dickii*, two species with benthic eggs and inhabiting the outer slope, both showed low F_{st} values, with no significant divergence among any pairs of populations tested. Significant divergence and higher F_{st} values did not show any obvious pattern in relation to the distance of site separation, except for *Forcipiger flavissimus*, which showed higher F_{st} values and significant divergences for the most geographically distant population pairs. Finally, relationships computed between F_{st} values and geographical distances were not significant for any of the species analyzed (Table 4). The normalized Mantel statistic, *r*, obtained from a Mantel's test between genetic and geographical distances, ranged from –0.429 ($P = 0.840$) for *Chromis xanthura* to 0.571 ($P = 0.146$) for *Forcipiger flavissimus*. Some species (*Chaetodon citrinellus*, *Chaetodon quadrimaculatus* and *Dascyllus aruanus*) even exhibited highest F_{st} values for the comparison of the two sites separated by the smallest distances (Moorea–Tetiaroa).

Graphs of MDS analysis using pairwise multilocus F_{st} values did not reveal any congruent pattern among the six species analyzed (Fig. 2). Only six species of the eight could be analyzed, because the two remaining (*Chrysiptera glauca* and *Plectroglyphidodon dickii*) had insufficient sites to provide enough data for MDS computations. *Forcipiger flavissimus* showed a distribution of island populations in accordance with geographical distances and archipelago structure. The first

Table 3. Summary (part 2) of the electrophoretic results for each species, for each population, for each locus and over all loci. *N* number of fishes sampled; H_{obs} observed heterozygosity; F_{is} fixation index (Weir and Cockerham 1984), *M* monomorphic loci; – no activity of this locus for the species; $P_{(0.95)}$ and $P_{(0.99)}$ are percentages of polymorphic loci within each population. Significant deviation from Hardy–Weinberg equilibrium is denoted by* ($P < 0.05$) following F_{is} values. *Ma* Marutea, *Te* Tetiaroa, *Mo* Moorea, *R* Rangiroa and *Ta* Takapoto

Locus	*P. pavo*					*C. glauca*			*P. dickii*			*C. xanthura*					*D. aruanus*				
	Ma	R	Ta	Te	Mo	Ma	R	Ta	Ma	R	Ta	Ma	R	Te	Ta	Mo	Ma	R	Ta	Mo	Te
N	50	27	50	48	50	50	48	49	48	48	47	49	49	31	48	45	48	46	48	49	50
*AAT-1**																					
H_{obs}	M	M	M	M	M	–	–	–	M	M	M	M	M	M	M	M	M	M	M	M	M
F_{is}	M	M	M	M	M	–	–	–	M	M	M	M	M	M	M	M	M	M	M	M	M
*AAT-2**																					
H_{obs}	M	M	M	M	M	0.460	0.417	0.388	0.542	0.479	0.617	0.061	0.102	0.226	0.042	0.044	0.229	0.174	0.229	0.143	0.160
F_{is}	M	M	M	M	M	–0.03	0.100	0.166	–0.104	0.031	–0.209	–0.021	–0.034	–0.094	–0.011	–0.011	0.032	0.244	–0.119	0.154	0.121
*ADA-1**																					
H_{obs}	M	M	0.020	M	M	0.520	0.458	0.490	0.146	0.125	0.106	0.429	0.408	0.387	0.347	0.341	0.146	0.044	0.188	0.347	0.080
F_{is}	M	M	0	M	M	0.093	0.160	–0.073	–0.044	–0.046	0.246	0.050	0.164	0.190	0.299	0.314*	–0.068	–0.011	0.086	0.208	–0.032
*ADA-2**																					
H_{obs}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
F_{is}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*CK**																					
H_{obs}	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
F_{is}	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
*DIA**																					
H_{obs}	–	–	–	–	–	–	–	–	M	M	M	–	–	–	–	–	–	–	–	–	–
F_{is}	–	–	–	–	–	–	–	–	M	M	M	–	–	–	–	–	–	–	–	–	–
*Est1**																					
H_{obs}	0.320	0.148	0.180	0.316	0.340	–	–	–	0.438	0.625	0.447	0.429	0.449	0.355	0.396	0.378	0.292	0.413	0.229	0.388	0.340
F_{is}	0.041	0.268	0.100	–0.161	0.018	–	–	–	0.192	–0.124	0.192*	0.174	0.109	0.302	0.175	0.216	0.083	–0.004	–0.119	0.093	0.125
*Est2**																					
H_{obs}	0.400	0.185	0.140	0.125	0.180	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
F_{is}	–0.086	0.350	0.396*	0.192	–0.089	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*Est3**																					
H_{obs}	–	–	–	–	–	0.220	0.021	M	–	–	–	–	–	–	–	–	–	–	–	–	–
F_{is}	–	–	–	–	–	–0.114	0	M	–	–	–	–	–	–	–	–	–	–	–	–	–
*EstD**																					
H_{obs}	–	–	–	–	–	0.360	0.250	0.429	–	–	–	–	–	–	–	–	–	–	–	–	–
F_{is}	–	–	–	–	–	–0.115	0.302*	0.051	–	–	–	–	–	–	–	–	–	–	–	–	–
*GDA**																					
H_{obs}	–	–	–	–	–	–	–	–	0.521	0.438	0.447	–	–	–	–	–	–	–	–	–	–
F_{is}	–	–	–	–	–	–	–	–	–0.163	0.087	–0.081	–	–	–	–	–	–	–	–	–	–
*GPD-1**																					
H_{obs}	–	–	–	–	–	M	M	M	–	–	-	0.327	0.286	0.258	0.333	0.356	0.292	0.326	0.208	0.225	0.040
F_{is}	–	–	–	–	–	M	M	M	–	–	–	0.127	0.058	0.277	0.166	0.102	0.053	–0.071	0.260	0.035	–0.010
*GPD-2**																					
H_{obs}	0.440	0.407	0.320	0.375	0.300	M	0.021	M	0.396	0.479	0.447	0.143	0.122	0.032	0.208	0.178	0.021	0.044	0.063	0.122	0.060
F_{is}	–0.081	0.125	0.248	0.061	0.248	M	0	M	–0.017	–0.217	–0.036	–0.047	–0.045	0	–0.085	–0.075	0	–0.011	–0.022	–0.055	–0.021
*GPI-1**																					
H_{obs}	0.020	M	M	M	M	0.040	0.042	0.082	M	M	M	0.041	0.021	M	0.021	0.044	0.500	0.478	0.458	0.388	0.520
F_{is}	0	M	M	M	M	–0.010	–0.005	–0.024	M	M	M	–0.011	0	M	0	–0.006	0.046	0.017	–0.005	0.164	–0.056
*GPI-2**																					
H_{obs}	M	M	M	M	M	0.020	M	0.020	M	M	M	M	M	M	M	M	0.083	0.044	0.021	0.041	0.020
F_{is}	M	M	M	M	M	0	M	0	M	M	M	M	M	M	M	M	–0.033	–0.011	0	–0.011	0

Table 3. Contd.

Locus	*P. pavo*					*C. glauca*			*P. dickii*			*C. xanthura*					*D. aruanus*				
	Ma	R	Ta	Te	Mo	Ma	R	Ta	Ma	R	Ta	Ma	R	Te	Ta	Mo	Ma	R	Ta	Mo	Te
*IDH-1**																					
H_{obs}	M	M	M	M	M	M	M	M	M	0.021	M	M	0.020	M	M	M	0.083	0.130	0.104	0.163	0.100
F_{is}	M	M	M	M	M	M	M	M	M	0	M	M	0	M	M	M	–0.033	–0.059	–0.044	–0.079	0.241
*IDH-2**																					
H_{obs}	0.140	0.111	0.100	0.104	0.100	0.460	0.542	0.327	0.042	M	M	M	0.020	M	0.042	0.022	0.083	0.044	0.063	0.204	0.120
F_{is}	–0.065	–0.040	–0.043	–0.044	–0.043	–0.157	–0.301*	0.307	–0.011	M	M	M	0	M	–0.011	0	–0.025	–0.011	–0.022	0.177	–0.054
*LDH**																					
H_{obs}	M	M	M	M	M	M	M	M	M	M	M	M	M	M	0.021	M	–	–	–	–	–
F_{is}	M	M	M	M	M	M	M	M	M	M	M	M	M	M	0	M	–	–	–	–	–
*MDH-1**																					
H_{obs}	M	M	M	M	M	M	M	M	M	M	M	–	–	–	–	–	–	–	–	–	–
F_{is}	M	M	M	M	M	M	M	M	M	M	M	–	–	–	–	–	–	–	–	–	–
*MDH-2**																					
H_{obs}	–	–	–	–	–	0.020	M	M	M	0.021	M	M	M	M	M	M	0.125	0.152	0.042	0.102	0.140
F_{is}	–	–	–	–	–	0	M	M	M	0	M	M	M	M	M	M	–0.056	–0.071	–0.011	–0.043	–0.065
*MEP-1**																					
H_{obs}	M	M	0.020	M	0.020	0.060	0.042	0.061	–	–	–	0.020	0.061	0.032	M	M	0.208	0.261	0.188	0.245	0.200
F_{is}	M	M	0	M	0	–0.021	–0.005	–0.021	–	–	–	0	–0.014	0	M	M	0.174	0.303	0.096	0.043	0.179
*MEP-2**																					
H_{obs}	–	–	–	–	–	–	–	–	0.021	0.021	0.021	M	0.020	0.032	M	M	M	M	M	M	M
F_{is}	–	–	–	–	–	–	–	–	0	0	0	M	0	0	M	M	M	M	M	M	M
*MPI**																					
H_{obs}	0.060	M	0.020	M	0.020	–	–	–	M	M	M	M	M	M	0.021	M	–	–	–	–	–
F_{is}	–0.010	M	0	M	0	–	–	–	M	M	M	M	M	M	0	M	–	–	–	–	–
*PEPA**																					
H_{obs}	–	–	–	–	–	–	–	–	M	M	M	0.102	0.041	0.065	M	M	–	–	–	–	–
F_{is}	–	–	–	–	–	–	–	–	M	M	M	–0.043	–0.011	–0.017	M	M	–	–	–	–	–
*PEPB-1**																					
H_{obs}	0.020	M	M	0.021	M	–	–	–	0.271	0.188	0.149	0.041	0.041	0.065	0.021	M	0.500	0.500	0.333	0.265	0.340
F_{is}	0	M	M	0	M	–	–	–	–0.113	–0.074	–0.051	–0.011	–0.005	–0.017	0	M	–0.223	–0.076	0.144	0.311	–0.060
*PEPB-2**																					
H_{obs}	M	M	M	M	0.020	0.020	0.042	M	–	–	–	–	–	–	–	–	–	–	–	–	–
F_{is}	M	M	M	M	0	0	–0.005	M	–	–	–	–	–	–	–	–	–	–	–	–	–
*PEPD-1**																					
H_{obs}	0.020	0.037	M	0.021	M	–	–	–	–	–	–	0.041	0.102	0.097	0.083	0.022	0.083	0.130	0.313	0.204	0.460
F_{is}	0	0	M	0	M	–	–	–	–	–	–	–0.005	–0.030	–0.034	–0.019	0	0.305	–0.049	0.155	0.079	0.005
*PEPD-2**																					
H_{obs}	0.340	0.407	0.360	0.292	0.200	–	–	–	0.021	M	M	–	–	–	–	–	–	–	–	–	–
F_{is}	0.241	0.003	0.075	0.053	–0.101	–	–	–	0	M	M	–	–	–	–	–	–	–	–	–	–
*PGAM-1**																					
H_{obs}	–	–	–	–	–	–	–	–	M	M	M	M	M	M	M	M	–	–	–	–	–
F_{is}	–	–	–	–	–	–	–	–	M	M	M	M	M	M	M	M	–	–	–	–	–
*PGAM-2**																					
H_{obs}	0.400	0.482	0.340	0.250	0.360	0.340	0.271	0.429	–	–	–	0.571	0.469	0.581	0.417	0.444	–	–	–	–	–
F_{is}	–0.156	0.051	0.184	0.252	0.023	–0.095	–0.017	0.098	–	–	–	–0.194	–0.297*	–0.156	0.121	0.122	–	–	–	–	–
*PGDH**																					
H_{obs}	–	–	–	–	–	M	0.021	0.041	M	M	M	M	M	0.032	0.042	0.044	M	M	M	M	M
F_{is}	–	–	–	–	–	M	0	–0.011	M	M	M	M	M	0	–0.011	–0.011	M	M	M	M	M

*PGM-1**																						
H_{obs}	–	–	–	–	–	–	–	–	0.688	0.646	0.702	0.306	0.367	0.226	0.354	0.333	0.188	0.087	0.104	0.163	0.060
F_{is}	–	–	–	–	–	–	–	–	–0.135	–0.122	–0.176	0.260*	0.160	0.143	0.189	0.191	–0.093	–0.034	–0.044	–0.068	0.377
*PGM-2**																						
H_{obs}	M	0.037	M	M	M	0.020	M	M	0.021	M	M	0.020	M	0.065	M	M	–	–	–	–	–
F_{is}	M	0	M	M	M	0	M	M	0	M	M	0	M	–0.017	M	M	–	–	–	–	–
*SDH**																						
H_{obs}	–	–	–	–	–	M	M	M	0.188	0.146	0.128	0.429	0.286	0.452	0.375	0.356	0.229	0.152	0.167	0.225	0.120
F_{is}	–	–	–	–	–	M	M	M	–0.093	0.152	0.191	–0.144	0.086	–0.190	–0.019	–0.035	0.043	–0.061	0.117	0.035	0.195
*SOD**																						
H_{obs}	M	M	M	M	M	M	M	M	M	M	M	–	–	–	–	–	–	–	–	–	–	
F_{is}	M	M	M	M	M	M	M	M	M	M	M	–	–	–	–	–	–	–	–	–	–	
*XO**																						
H_{obs}	0.280	0.074	0.200	0.208	0.200	0.200	0.167	0.102	0.208	0.021	0.085	–	–	–	–	–	–	–	–	–	–	
F_{is}	0.029	0.475	0.063	–0.106	–0.101	0.211	–0.062	–0.034	–0.094	0	–0.034	–	–	–	–	–	–	–	–	–	–	
Overall																						
H_{obs}	0.1061	0.0821	0.0739	0.0743	0.0757	0.1245	0.1042	0.1076	0.1296	0.1188	0.1166	0.1184	0.1127	0.1161	0.1083	0.1031	0.1687	0.1663	0.1333	0.1500	0.1600	
F_{is}	0.0008	0.1378	0.1635	0.0484	0.0325	–0.0222	0.0422	0.0959	–0.0532	–0.0523	–0.0329	0.0353	0.0437	0.0659	0.1304	0.1407	0.0200	0.0348	0.1336	0.1136	0.0322	
P(0.95)	0.3043	0.3043	0.3043	0.3043	0.3043	0.3182	0.2727	0.2727	0.3333	0.2963	0.2963	0.3200	0.3600	0.2800	0.2800	0.2800	0.5500	0.5500	0.5500	0.7000	0.6000	
P(0.99)	0.3478	0.3913	0.3043	0.3913	0.3043	0.4091	0.5455	0.4545	0.4815	0.4444	0.3704	0.5600	0.6400	0.600	0.600	0.4800	0.7500	0.7500	0.7500	0.7500	0.7000	

Table 4. Multilocus genetic variation of each population pair for each species (F_{st}: Weir and Cockerham 1984). Distances separating islands of a pair shown in kilometres. *Ma* Marutea, *Te* Tetiaroa, *Mo* Moorea, *R* Rangiroa and *Ta* Takapoto. Significant differences in allelic frequencies between populations ($P < 0.05$) are followed by their probabilities. *Bold characters* show significant differences after the sequential Bonferroni correction (Rice 1989); – not calculated. Normalized Mantel statistic, *r*, is followed by its probability. Mantel's tests were not performed for *C. glauca* and *P. dickii* because the number (three) of sampled populations was too small

		Pelagic eggs						Benthic eggs							
Pairwise		Lagoon		Outer slope				Lagoon						Outer slope	
Islands	Distances	*C. citrinellus*		*C. quadrimaculatus*		*F. flavissimus*		*P. pavo*		*C. glauca*		*D. aruanus*		*C. xanthura*	*P. dickii*
Ma/Te	1550	–		**0.0139**	**(0.0000)**	**0.0323**	**(0.0003)**	0.0136		–		**0.0228**	**(0.0000)**	0	–
Ma/Mo	1548	–		**0.0505**	**(0.0000)**	**0.0462**	**(0.0015)**	**0.0368**	**(0.0023)**	–		**0.0354**	**(0.0000)**	0.0080	–
Ma/R	1425	–		**0.0473**	**(0.0000)**	**0.0212**	**(0.0051)**	0.0221		0.0042		0.0059		0.0300	0
Ma/Ta	1270	–		0.0040		0.0136		0.0042		**0.0289**	**(0.0076)**	0.0109		0	0.0002
Ta/Mo	566	0.0132	(0.0256)	0.0273		0.0401		0.0164	(0.0302)	–		**0.0186**	**(0.0012)**	0.0036	–
Ta/Te	520	**0.0139**	**(0.0083)**	0.0092		0.0165		0		–		0.0125		0.0047	–
R/Mo	365	0.0024		**0.0326**	**(0.0025)**	0.0308		0.0446	(0.0075)	–		**0.0185**	**(0.0035)**	0.0263	–
R/Te	310	0.0112		0.0281	(0.0180)	0.0087		0.0298		–		**0.0309**	**(0.0000)**	0.0385	–
R/Ta	226	0.0011		0.0199	(0.0406)	0		0.0017		0.0192		0.0135	(0.0226)	0.0247	0.0021
Te/Mo	60	**0.0269**	**(0.000)**	**0.0536**	**(0.0070)**	0.0036		**0.0070**	**(0.0000)**	–		**0.0412**	**(0.0000)**	0.0144	(0.0391)	–
	Overall	**0.0114**	**(0.0000)**	**0.0287**	**(0.0000)**	**0.0208**	**(0.0000)**	**0.0162**	**(0.0000)**	**0.0178**	**(0.0000)**	**0.0215**	**(0.0000)**	**0.0145**	**(0.0000)**	0
	Mantel's test	–0.286	(0.705)	–0.039	(0.704)	0.571	(0.146)	0.154	(0.461)			–0.220	(0.692)	–0.429	(0.840)	

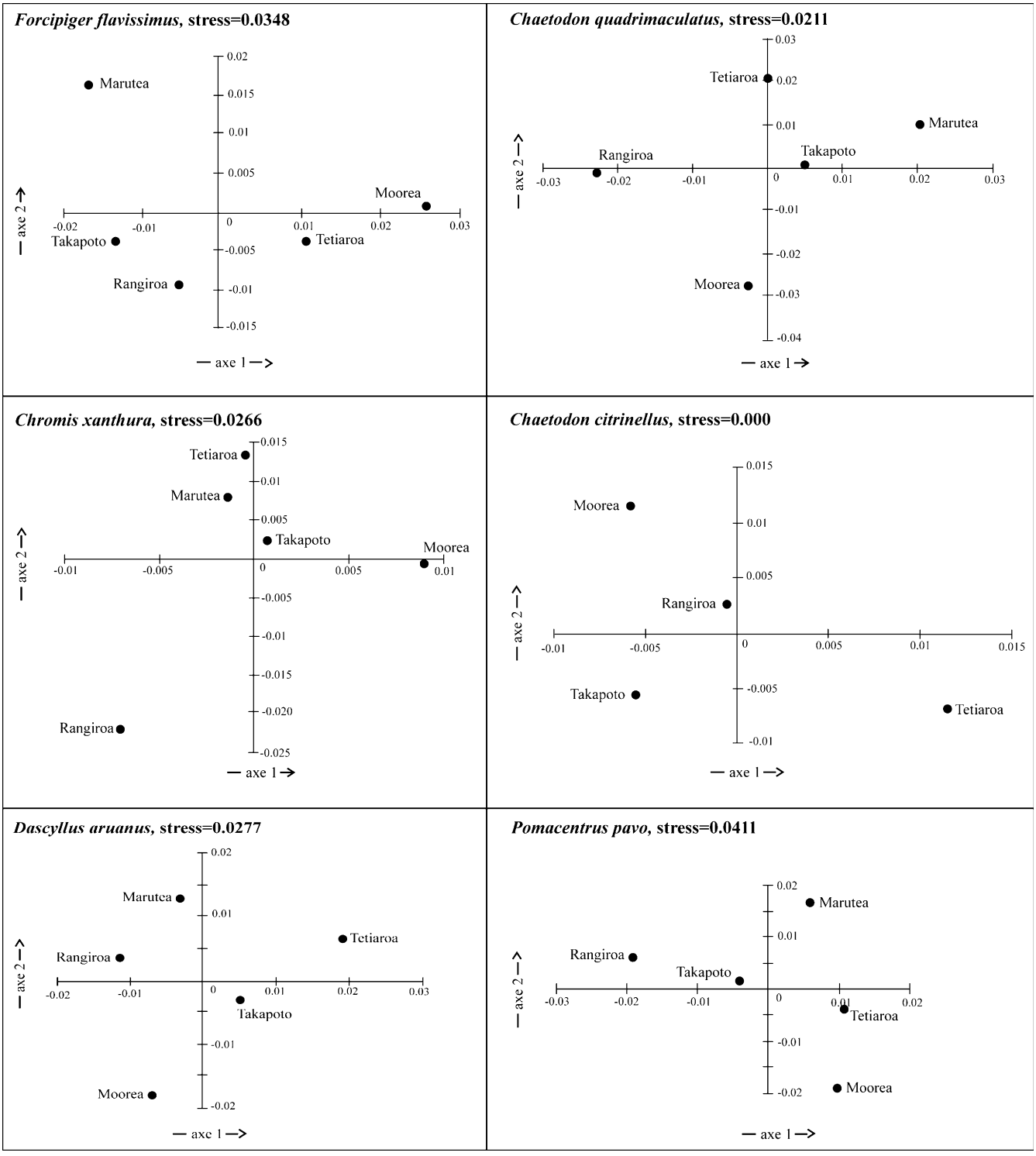


Fig. 2. Multidimensional scaling plots of sites computed for each species based on pairwise F_{st} matrices. *Plectroglyphidodon dickii* and *Chrysiptera glauca* are missing because the small number of sites (3) did not allow analysis by MDS

axis differentiated closest sites (Moorea, Tetiaroa, Rangiroa and Takapoto) from the furthest site, Marutea; the second axis segregated populations of the Society Archipelago (Moorea and Tetiaroa) from populations of the Tuamotu (Rangiroa and Takapoto) Archipelago. However, such structure was uniquely observed for a single species. Overall, some species, such as *Forcipiger flavissimus, Chaetodon citrinellus*, and *Chromis xanthura*, showed one isolated island (Marutea, Tetiaroa and Rangiroa, respectively) relative to all other sites remaining together, while the other species had a more spread out distribution of islands. No generalization could be made relative to the historical origin, the geomorphological structure of the islands, or even their

location in relation to oceanic currents, latitude or longitude.

Genetic variation among species

Species with benthic eggs showed significantly higher multilocus heterozygosity than species with pelagic eggs ($H_{benthic} = 0.117 \pm 0.025$ versus $H_{pelagic} = 0.096 \pm 0.028$; $t = 2.188$, $P = 0.0358$). Species inhabiting lagoons exhibited significantly higher multilocus heterozygosity levels than species found on the outer slope ($H_{lagoon} = 0.121 \pm 0.032$ versus $H_{slope} = 0.097 \pm 0.019$; $t = 2.725$, $P = 0.0102$).

Analysis of genetic differentiation (F_{st} values) relative to reproductive strategy or habitat did not reveal any significant difference. Mantel's test performed for comparison of F_{st} values between species did not show any significant association of species with similar biological features (Table 5). *Plectroglyphidodon dickii* and *Chrysiptera glauca* were excluded from these comparisons since only three samples were collected and they could not be compared (cf. Table 1). All populations of Marutea were excluded in correlations comparing *Chaetodon citrinellus* with other species, because of missing samples (cf. Table 1). The normalized Mantel statistic, r, ranged from –0.412 ($P = 0.0775$) between *Chaetodon citrinellus* and *Chromis xanthura* to 0.733 ($P = 0.0678$) between *Chaetodon citrinellus* and *Dascyllus aruanus*, but none of these correlations was significant.

Two MDS analyses were made: one using six species (without *Plectroglyphidodon dickii* and *Chrysiptera glauca*) and omitting Marutea data, and a second using only five species (excluding *Chaetodon citrinellus*) with all locations (Table 6; Fig. 3). Prior to computing the MDS, we estimated Bray–Curtis distances based on the dissimilarity between species in the F_{st}-values distribution. These distances ranged from 0.1555 between *Dascyllus aruanus* and *Chaetodon quadrimaculatus* to 0.5925 for *Pomacentrus pavo* and *Chaetodon citrinellus*, omitting Marutea from the analysis. After excluding *Chaetodon citrinellus* and reconsidering all sites, distances appeared similar to the previous estimates ($t = 0.273$; $P = 0.791$), suggesting that most of the divergence in genetic structure between species was due to F_{st} values observed between the closest islands (Moorea, Tetiaroa, Rangiroa and Takapoto). Finally, we did ANOVAs on Bray–Curtis distances to test for variation in the genetic structure between species showing different reproductive strategies and/or habitats. None of the factors (reproductive strategy and/or habitat) had significant influence on the genetic structure ($P > 0.8$ for all ANOVAs on both data sets of Table 6 and tested for reproductive strategy and habitat, respectively).

The MDS graph computed from Bray–Curtis distances of six species, excluding all Marutea comparisons, segregated Chaetodontidae from Pomacentridae (Fig. 3A). However, this pattern was not maintained when excluding one species and introducing Marutea samples (Fig. 3B). Neither of the MDS graphs reveals any structure related to reproductive strategy and/or habitat.

Discussion and conclusions

The allozyme survey conducted on eight species sampled at similar sites within French Polynesia showed significant divergences between populations (except for *Plectroglyphidodon dickii*), with a similar range of multilocus

Table 5. Correlation between genetic distance matrices (pairwise F_{st} values) for each species pairs. Normalized Mantel statistics are indicated above the diagonal, and probabilities tested by random permutations are given below the diagonal

	C. citrinellus	*F. flavissimus*	*C. quadrimaculatus*	*P . pavo*	*D. aruanus*	*C. xanthura*
C. citrinellus		–0.153	0.565	–0.354	0.733	–0.412
F. flavissimus	0.6458		0.175	0.567	0.069	–0.398
C. quadrimaculatus	0.1270	0.3070		0.501	0.543	0.396
P . pavo	0.7690	0.0520	0.0925		0.280	0.432
D. aruanus	0.0678	0.4210	0.0740	0.2312		0.021
C. xanthura	0.0775	0.8670	0.1630	0.1500	0.4796	

Table 6. Bray–Curtis dissimilarity coefficients between each species, computed from comparisons of pairwise F_{st} matrices. *Plectroglyphidodon dickii* and *Chrysiptera glauca* were not included in this analysis because sample size was too small. Distance coefficients above the diagonal were calculated for all six species, excluding all Marutea data. Distance coefficients below the diagonal are comparisons of pairwise F_{st} matrices obtained with all pairwise islands, but excluding *C. citrinellus*, since the Marutea sample was missing for this species

	C. citrinellus	*F. flavissimus*	*C. quadrimaculatus*	*P. pavo*	*D. aruanus*	*C. xanthura*
C. citrinellus		0.5031	0.4645	0.5925	0.3393	0.5868
F. flavissimus	–		0.4110	0.3974	0.4725	0.5568
C. quadrimaculatus	–	0.3395		0.3725	0.1555	0.3141
P. pavo	–	0.3051	0.2981		0.3835	0.3638
D. aruanus	–	0.3528	0.2414	0.3148		0.3079
C. xanthura	–	0.5807	0.3818	0.3963	0.4479	

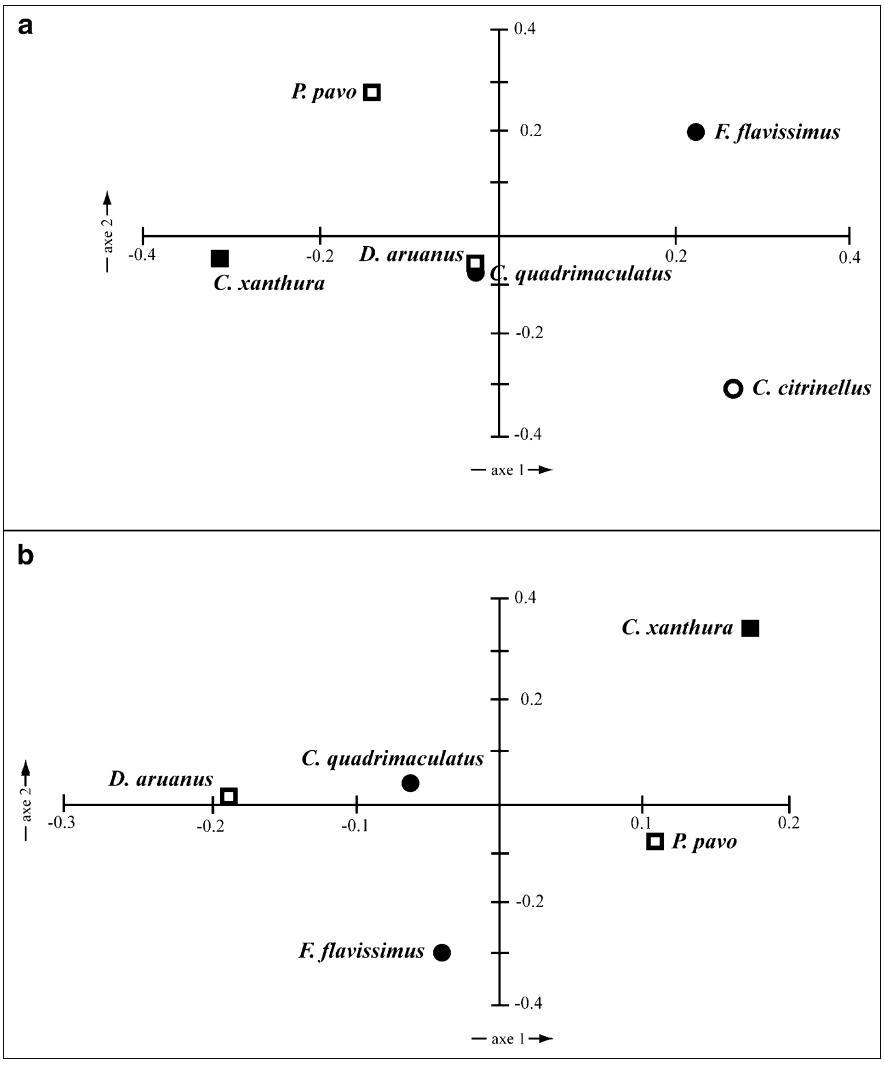


Fig. 3A, B. Multidimensional scaling plots of species based on Bray–Curtis dissimilarity coefficient (*D*) between pairs of species. *Plectroglyphidodon dickii* and *Chrysiptera glauca* are not included because of their smaller sample size. *Squares* represent species with benthic eggs; *circles* represent species with pelagic eggs. *Solid symbols* represent species living on the outer slope; *open symbols* show species inhabiting lagoons. **A** The MDS including *Chaetodon citrinellus* in the analysis, but without Marutea populations for all the other species. **B** The MDS including Marutea in the pairwise F_{st} matrices used to compute the Bray–Curtis dissimilarity coefficient, but excluding *Chaetodon citrinellus*

F_{st} values (from 0.0114 to 0.0287). The genetic structure of each of the eight species was not significantly correlated with the geographical distance between sites. Such a standardized sampling protocol provided a unique test for the impact of reproductive strategy and habitat on the genetic structure of isolated island populations, as well as the relationship with geographical distances. Regarding the main questions addressed, we found no impact of reproductive strategy and/or habitat on genetic structure, whereas heterozygosity showed significant differences.

Variation in genetic diversity

Gene flow and genetic drift should equally affect neutral loci, whereas selection is more likely to be locus specific (Lewontin and Krakauer 1973). The role of selection in maintaining genetic polymorphisms at allozyme loci has been reported in diverse marine species (Koehn et al. 1980; Pogson et al. 1995; Powers and Schulte 1998; Lemaire et al. 2000). However, such a force has been found to act on allelic frequencies depending on heterogeneous environmental conditions (mostly through temperature and/or salinity gradients). Moreover, assumptions necessary to infer gene flow from allozyme-frequency data (i.e., effective neutrality, weak mutation rate, approximate migration–drift equilibrium) seem in general to be valid (Baer 1999). Our data did not demonstrate evidence of a locus-specific process, such as a Hardy–Weinberg disequilibrium. While not conclusive regarding selection, we considered that migration and genetic drift were the two main evolutionary forces acting on allelic frequencies of allozyme loci.

In the present work we found significant difference in heterozygosity, with species laying benthic eggs and/or inhabiting lagoons showing higher values than species laying pelagic eggs and/or occurring on the outer slope. Considering the neutral theory of evolution (Kimura 1983; Nei and Graur 1984), heterozygosity is a direct function of the effective population size (N_e) and the mutation rate ($\mu = 10^{-6}$ for allozymes; Voelker et al. 1980) according to the model $H = 4N_e\mu/(4N_e\mu + 1)$, with mutation rate being related to the time and the number

of generations. Regarding the present survey, Pomacentridae and Chaetodontidae species occurring on the outer slope have experienced more stable effective population size and may be derived from much older origins than species inhabiting lagoons that were dry during each sea-level transgression. Therefore, in theory, we expect species from the outer slope to show higher heterozygosity than species inhabiting lagoons, because they did not experience local extinction or bottlenecks during low sea level.

Regarding fecundity, species laying pelagic eggs are usually the ones showing higher individual fecundity compared to benthic spawners (Thresher 1984). Species showing high individual fecundity being subject to strong variability in reproductive success (Hedgecock 1994), such as marine fish, will therefore express limited effective population size, because a limited number of adults can provide much of the new generation of offspring. This process has been proposed as the origin of genetic drift signal (i.e., chaotic patchiness or microgeographic differentiation) in marine organisms (Johnson and Black 1984). Overall, under the neutral theory of evolution, the characteristics of coral reef fish would lead to the prediction of higher heterozygosity in species laying benthic eggs and occurring on the outer slope, although our results are somewhat different.

Several other hypotheses, mostly based on selectionistic models, have also been proposed to predict differences in genetic diversity among species. Various models have been described based on: stability in environmental heterogeneity (Levins 1968); time of divergence between species (Soulé 1972); size and mobility variation (Selander and Kaufman 1973); predictability of trophic resources (Valentine and Ayala 1975); and ecological heterogeneity between habitats and niche specialist or generalist species (Nevo 1978; Smith and Fujio 1982). Most of the previous models gave a single causative explanation for the variation in genetic diversity. When applied to our data, we can always propose some hypothesis that will fit with previous models, such as species inhabiting lagoons experiencing more heterogeneous environments compared to the outer slope, or species with benthic eggs being less mobile than species laying pelagic eggs.

Overall, it is difficult to find any clear origin that would explain the variation in heterozygosity, even when using a comparative analysis of several species collected according to standardized sampling protocol. Therefore, a significant difference in heterozygosity cannot be used to understand ecological and/or biological features. In addition, the heterozygosity encountered in a previous survey of *Dascyllus aruanus* (Planes et al. 1993) was very low compared to our present value (0.065 versus 0.1557), because some monomorphic loci were not scored in the present survey. Therefore, we arrive at the problem of how comparative genetic surveys can be related to heterozygosity and how we need to standardize sampling and genetic protocols (Planes 1997).

Variation in the genetic structure

Over all populations, multilocus F_{st} values computed for the eight species of this survey showed concordant ranges with values usually obtained for species with high dispersal capabilities on the same spatial scale (except *Plectroglyphidodon dickii*). The present research strategy was developed from results of previous genetic surveys that examined *Acanthurus triostegus* (Planes 1993) and *Dascyllus aruanus* (Planes et al. 1993) in French Polynesia. Both species showed significant genetic differences among populations. *Dascyllus aruanus* populations appeared almost homogeneous across Polynesia (minor genetic differences could be detected only when comparing remote archipelagoes; overall $F_{st} = 0.01$). In contrast, *Acanthurus triostegus* populations were highly structured, with large genetic differences between islands (overall $F_{st} = 0.09$) and the genetic structure was concordant with the major oceanic currents in the area. Comparison of results obtained for *Dascyllus aruanus* and *Acanthurus triostegus* did not fit the idea that species with long pelagic larval stages exhibit greater dispersal and consequently show higher gene flow between populations (Waples 1987; Doherty et al. 1995). In fact, *Dascyllus aruanus* larvae spend about 25 days in the ocean, whereas *Acanthurus triostegus* larvae remain in the plankton for 60 days. At that time, it was proposed that this contradiction (species with longer larval duration showing restricted gene flow) was due to historical factors. During the last glaciations, 15 to 20 thousand years BP (Bard et al. 1996), sea level was 120 m below present-day sea level, and lagoons of classic Darwinian atolls that are 50–70 m deep at the most were completely dry. Because *Dascyllus aruanus* only inhabits lagoons, and such habitats were not available in French Polynesia during the last glaciations, the authors proposed that the species became extinct in this region during this period. Therefore, the present population is a result of recent recolonizations, occurring when the present sea level was reached (5 to 8 thousand years BP; Bard et al. 1996). Consequently, there has not been enough generations for the appearance of genetic structure due to genetic drift. In contrast, *Acanthurus triostegus* is more ubiquitous and inhabits lagoons as well as oceanic slopes. Because this species could be maintained on oceanic slopes when the sea level was lower, the structure of *Acanthurus triostegus* populations is older and expresses longer evolution more likely to show a genetic differentiation due to long-term genetic drift together with limited gene flow. These studies suggested that oceanic currents, as well as historical events, affect the population structure between oceanic islands. In these interpretations, historical factors played a more crucial role than the pelagic larval duration and this suggests that the present-day genetic structure cannot be directly interpreted as a pattern of dispersal.

The present protocol intended to confirm these hypotheses by comparing the genetic structure of species showing different reproductive strategies and different

habitats. The reproductive strategy was used to represent the potential biological dispersal, since species with benthic eggs exhibit statistically much shorter pelagic periods compared to species that lay pelagic eggs (Thresher 1991). Furthermore, benthic eggs themselves do not participate in the dispersal phase, which reduces potential dispersal even more. The difference in habitats indirectly tested for the impact of historical factors (Nelson et al. 2000; Hickerson and Ross 2001), since we assumed that species restricted to lagoonal habitats experienced severe changes in the effective population size with potential extinction and recolonization in some lagoons following sea-level changes during the Holocene (Pirazzoli and Montaggioni 1988; Bard et al. 1996). Such a test can only be carried out using comparative approaches, since it requires standardized protocol and we cannot use published data conducted in different areas, with different protocols (Waples 1987; Doherty et al. 1995; Gold and Richardson 1998). Genetic structure of the eight species did not appear significantly related either to the reproductive strategy or to the habitat preference (cf. *t*-test on global multilocus F_{st} and MDS analyses) and none of the species showed a significant relationship between genetic structure and geographical distance. Overall, the genetic structure of each species appeared variably determined by the genetic difference among closest and/or most-distant islands (except for *Chaetodon citrinellus*) emphasizing some chaotic patterns among species, with variations in genetic structure occurring over large spatial scales, as well as small ones, within and among species. Such spatially random genetic differentiation accommodates Wright's island model in the sense that each individual issued from one population is equally likely to move to any other population (Wright 1931). In such a model, no relationship between the geographical distance and genetic differentiation is expected. The genetic similarity between islands (i.e., populations) will be a function of the regularity of the migrations, assuming that they are very infrequent in time. Biologically, such a model requires that populations be mostly self-recruiting and that pelagic larval flux between islands be very rare, so that it cannot counterbalance genetic drift (a very slow process when acting on large effective population sizes). These features have been partly demonstrated in coral reef fish in which self-recruitment has been observed (Jones et al. 1999; Swearer et al. 1999), and where larval fluxes appear to be unpredictable and largely chaotic (Dixon et al. 1999). The island model satisfies most of our genetic results but not the previous data on *Acanthurus triostegus*, which demonstrated a significant relationship between genetic differentiation and geographical distance favoring isolation by distance (Planes et al. 1996).

The genetic structure of two species was notable. *Plectroglyphidodon dickii* stands out from other species, appearing homogeneous between the three sampled populations that are separated by more than 1,000 km, even if it shows a larval duration of about 27 days (Wellington and Victor 1989), similar to most Pomacentridae analyzed. While showing genetic homogeneity over a large spatial scale, this species appeared absent (or very rare) in islands of the Society Archipelago such as Tetiaroa or Moorea sampled in the present survey, as well as in other islands not sampled (Galzin 1987; Galzin personal communication). Such absence (or rarity) in some islands, independently of the presence of suitable habitats (Galzin 1987), suggests that migration is a rare event in the insular model we investigated.

The other notable result arises from the observed genetic structure of *Dascyllus aruanus*, which is similar to other species analyzed in this study, but differs from previous data (Planes et al. 1993). F_{st} values have increased significantly (from 0.0076 in 1990 to 0.0215 in 2000) over a short period of time for the same localities. Temporal change in genetic structure has already been observed in marine fish (Lacson and Morizot 1991; Gold et al. 1993) as well as marine invertebrates, and there is a growing belief that such variations arise from variance in reproductive success (Hedgecock 1994; Ruzzante et al. 1996; Herbinger et al. 1997; Lenfant and Planes 2002). Such variance in reproductive success among cohorts was suggested by the chaotic genetic patchiness model that has been proposed to explain genetic variations in new recruits of marine invertebrates (Johnson and Black 1982, 1984; Watts et al. 1990). In the present data, multilocus F_{st} values for each species over all sites ranged from 0.0114 to 0.0287; a similar range of values was found between groups of new recruits of sea urchins (Watts et al. 1990) or between cohorts of temperate sea bream (Lenfant and Planes 2002). Similarly, the level of genetic variation we observed in coral reef fish throughout French Polynesia could partially reflect variable recruitment within a large panmictic population, rather than genetic differences due to isolation (Bernardi et al. 2001). Overall, it appears almost impossible to generate a single theory to explain the genetic structure after having analyzed about ten species through time on the same spatial scale. Such research effort is considerable when considering the total number of species, individuals, and sites surveyed; but even with such effort, we could not elucidate any generalized model. The underlying reasons are to be found in the number of factors potentially affecting the model, as emphasized in some recent surveys (McGlashan and Hughes 2001; Riginos and Nachman 2001). Therefore, it is reasonable to consider that a multifactorial process is driving the genetic structure of populations. It is almost impossible to disentangle and identify which parameters have most effect on the system, assuming that each parameter is likely to affect differently each species, depending on its origin. Finally, when conducting a standardized sampling protocol, it seems that the ecology of the species, the geography of the area and the history of the species do not individually explain the genetic structure of coral reef fish in French Polynesia. However, we have shown that, for most species, French Polynesia cannot be considered as a single panmictic population. The randomly variable genetic structure

observed among species fits the idea that coral reef fish species in French Polynesia are likely to follow an island model in which migrations between populations are randomly driven in space and time. Nevertheless, the chaotic genetic pattern found for most species in a context of limited genetic differentiation (all F_{st} values were lower than 3%) may also result from temporal variation in reproductive success, which may drive the small genetic differences observed between locations. Further analysis combining temporal and spatial sampling should now be undertaken to validate definitively the origin of the genetic structure in such an insular model.

Acknowledgements We thank anonymous reviewers for their helpful comments. Special thanks go to François Bonhomme who greatly contributed through discussion to set up this work. We gratefully acknowledge the assistance in sampling specimens: René Galzin and Yannick Chancerelle for collecting specimens from Tetiaroa and additional ones from Takapoto; Robert Wan for the facilities he offered in Marutea; Pierre Remoissonet and Yves Leduc for providing SRM facilities in Rangiroa and Takapoto. This study was supported by grants from PNDB (French National Program on Biodiversity) and by the TOTAL-ELF-FINA foundation.

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