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differences were observed between populations. No significant increase of genetic distance with geographic distance was observed. The estimates of gene flow between pairs of populations from different archipelagos, calculated under Wright's infinite island model, were homogeneous (average Nm ranging from 3.4 to 7.3). Moderate amounts of gene flow (i.e. effective migration) were thus inferred. These few successful migrants at each generation do not contribute much to recruitment. Hence, from the reef ecologist's point of view, island populations can be considered as primarily self-seeding, despite prior expectations of large oceanic transport in reef fish such as A. triostegus, inferred from their high passive dispersal capacities. In conrast, this moderate level of gene flow is enough to prevent the fixation of different alleles in the different archipelagos.

Keywords: Surgeonfish, manini, Acanthurus triostegus, allozymes, population genetics, F-statistics, gene flow, Pacific Ocean, French Polynesia, Moorea, Bora-Bora, Takapoto, Moruroa

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Geographic structure and gene flow in the manini (convict surgeonfish, *Acanthurus triostegus*) in the south-central Pacific

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Abstract

The geographic structure of the manini, Acanthurus triostegus, *a coral reef surgeonfish of Polynesia, was investigated using allozyme markers. Four samples, from Bora-Bora (Society Archipelago), Moorea (Society), Takapoto (Western Tuamotu) and Moruroa (Eastern Tuamotu), were studied at 10 polymorphic loci, and the data analysed using* F-*statistics and permutation tests. Single-locus and multiple-locus genotypic proportions in each sample did not differ from Hardy–Weinberg expectations, whereas significant differences were observed between populations. No significant increase of genetic distance with geographic distance was observed. The estimates of gene flow between pairs of populations from different archipelagos, calculated under Wright's infinite island model, were homogeneous (average* Nm *ranging from 3.4 to 7.3). Moderate amounts of gene flow (i.e. effective migration) were thus inferred. These few successful migrants at each generation do not contribute much to recruitment. Hence, from the reef ecologist's point of view, island populations can be*

considered as primarily self-seeding, despite prior expectations of large oceanic transport in reef fish such as A. triostegus, *inferred from their high passive dispersal capacities. In contrast, this moderate level of gene flow is enough to prevent the fixation of different alleles in the different archipelagos.*

2.4.1 Introduction

Most coral reef fishes have a pelagic larval phase lasting 10 days or more (Brothers, Williams and Sale, 1983; Victor, 1986; Wellington and Victor, 1989). Because of this, and because recruitment of larvae is very small relative to the great fecundity of adults (Talbot, Russell and Anderson, 1978; Sale, 1980; Williams, 1980; Victor, 1986), the prevailing view among reef fish ecologists is that larvae disperse widely and that populations of different reefs are interconnected by larval exchange (Sale, 1980; Mapstone and Fowler, 1988). However, some ecological data may also suggest that self-recruitment of reefs is a major process (Johannes, 1978; Sammarco and Andrews, 1988), enhanced by the occurrence of hydrodynamic eddies favouring particle retention (Lobel and Robinson, 1986; Hamner and Wolanski, 1988; Black, Moran and Hammond, 1991).

Genetic data available so far do not provide a clear-cut answer. Negligible differentiation has been found among samples of the damselfish *Stegastes fasciolatus* collected from reef islands of the Hawaiian archipelago up to 2500 km apart (Shaklee, 1984) and among populations of the Hawaiian snapper *Pristimoides filamentosus* (Shaklee and Samollow, 1984). In contrast, a high degree of differentiation has been reported between reef populations of the anemonefish *Amphiprion clarkii* (Bell, Moyer and Numachi, 1982) and of the damselfish *Stegastes partitus* (Lacson *et al.*, 1989) separated by a distance short enough to be within the potential dispersal range of larvae.

While the above ecological problem focuses on the importance of larval migration between populations and subsequent allorecruitment on reefs, the estimates of gene flow inferred from population structure are expected to give an answer concerning effective migration, which is another concept. The genetic impact of allorecruitment operates at an evolutionary scale, not at the ecological scale. A small amount of gene flow, mediated by the successful recruitment of a small proportion of foreign larvae (i.e. small amounts of allorecruitment), can suffice to prevent differentiation between islands. As stressed by Slatkin (1987), the comparison of gene flow data with knowledge of life-history (dispersal capacity in particular) may prove a fruitful approach in population biology studies. The comparison of effective migration rate with dispersal capacity is also an important issue in the current debate about patterns of structure and processes of regulation in coral reef fish assemblages, and more generally in supply-side ecology (Underwood and Fairweather, 1989; Ayre, 1990).

The purpose of the present study was to provide preliminary information on the genetic structure and gene flow of Polynesian populations of the manini (convict surgeonfish, *Acanthurus triostegus*), a reef fish present throughout the Pacific, whose biology has been investigated (Randall, 1961a,b) and whose larval stage is estimated as being relatively long (up to 70 days). We thereby intended to test self-recruitment versus allorecruitment in coral reef fish from the southern Pacific.

2.4.2 Materials and methods

(a) Sampling

Acanthurus triostegus L. is one of the most abundant surgeonfishes in the reef habitat of the Pacific. Thirty-two to 36 individuals were caught by spear-fishing between February and

April 1990 in each of four islands of French Polynesia (Figure 2.4.1): Moorea (Society Archipelago), Bora-Bora (Society), Takapoto (Western Tuamotu) and Moruroa (Eastern Tuamotu). Moorea and Bora-Bora are two oceanic islands 250 km apart. Takapoto is a closed atoll, 650 km from Moorea. Moruroa is an open atoll, 1200 km from Moorea. Fish were collected inside the lagoon, except in Takapoto, where collection was on the oceanic side of the reef in order to compare with the other samples, all from an open habitat. The fish were dissected on site. Samples of tissue (liver, eyes and about 2 g of dorsal muscle) were kept in liquid nitrogen until storage at –80 °C in the laboratory.

(b) Enzyme electrophoresis

The samples of tissue were homogenized at 0–4 °C in an equal volume of Tris-EDTA-NADP, pH 6.8 buffer (Pasteur *et al.*, 1988) using an Ultraturrax homogenizer. The homogenates were centrifuged at 22 000*g* for 30 min at 4 °C and the supernatant, used as a source of soluble enzymes, was stored for a few weeks to a few months at –80 °C until electrophoresis. Horizontal starch gel electrophoresis and subsequent enzyme staining were performed according to Pasteur *et al.* (1988). The enzyme systems amenable to interpretation are listed in Table 2.4.1.

(c) Data analysis

Single-locus F-statistics were estimated using the parameters F, f and θ of Weir and Cockerham (1984), which in Wright's notation correspond to F_{it}, F_{is} and F_{st}, respectively. Their standard deviations over loci were estimated using a jackknife procedure. Weighted averages of F, f and θ (Weir and Cockerham, 1984) were then compared to zero using a t-test (Sokal and Rohlf, 1981). Genetic distances based on the coancestry coefficient (θ) were computed as $D = -\ln (1 - \theta)$ (Reynolds, Weir and Cockerham, 1983). The correlation of genetic distance with geographic distance was tested using Mantel's test of the association of two parameters in data matrices with internal correlation (Manly, 1985). Dixon's test for detecting outliers in a normal population (Sokal and Rohlf, 1981, p. 413) was used on the sets of single-locus f and θ. The reason for discarding outliers was that consistency is necessary for considering the information at different loci as replicates. The occurrence of a locus presenting large differences between populations (large θ values), among loci at which differences are consistently smaller, can be interpreted in terms of selection on this or a closely linked locus (Slatkin, 1987). Where Mendelian inheritance of allozyme phenotypes has not been formally established, as is the case here, it is also wise to discard those loci at which within-population phenotypic frequencies obviously depart from Mendelian expectations for codominant alleles and/or interpopulation differences are not consistent with those at other loci.

Estimates of gene flow were calculated from the estimates of coancestry coefficients assuming an infinite island model at equilibrium as $Nm = (1 - \theta)/4\theta$ (Wright, 1969).

Additionally, departure from panmixis was assessed using a multiple-locus resampling test (Mathieu *et al.*, 1990), which is expected to point out genotypic disequilibria *sensu* Weir (1990). For this, a dispersion index for the natural sample was computed and compared to the distribution obtained for the collection of randomized replicates (Mathieu *et al.*, 1990). This test, based on permutations on contingency tables of individual X multiple-locus genotype, allows evaluation at the same time of both inter- and intralocus departures from the panmictic equilibrium.

F-statistics, Mantel's test and permutation tests were performed using the FST, MANTEL and PERMU procedures of the GENETIX package (Bonhomme *et al.*, 1993).

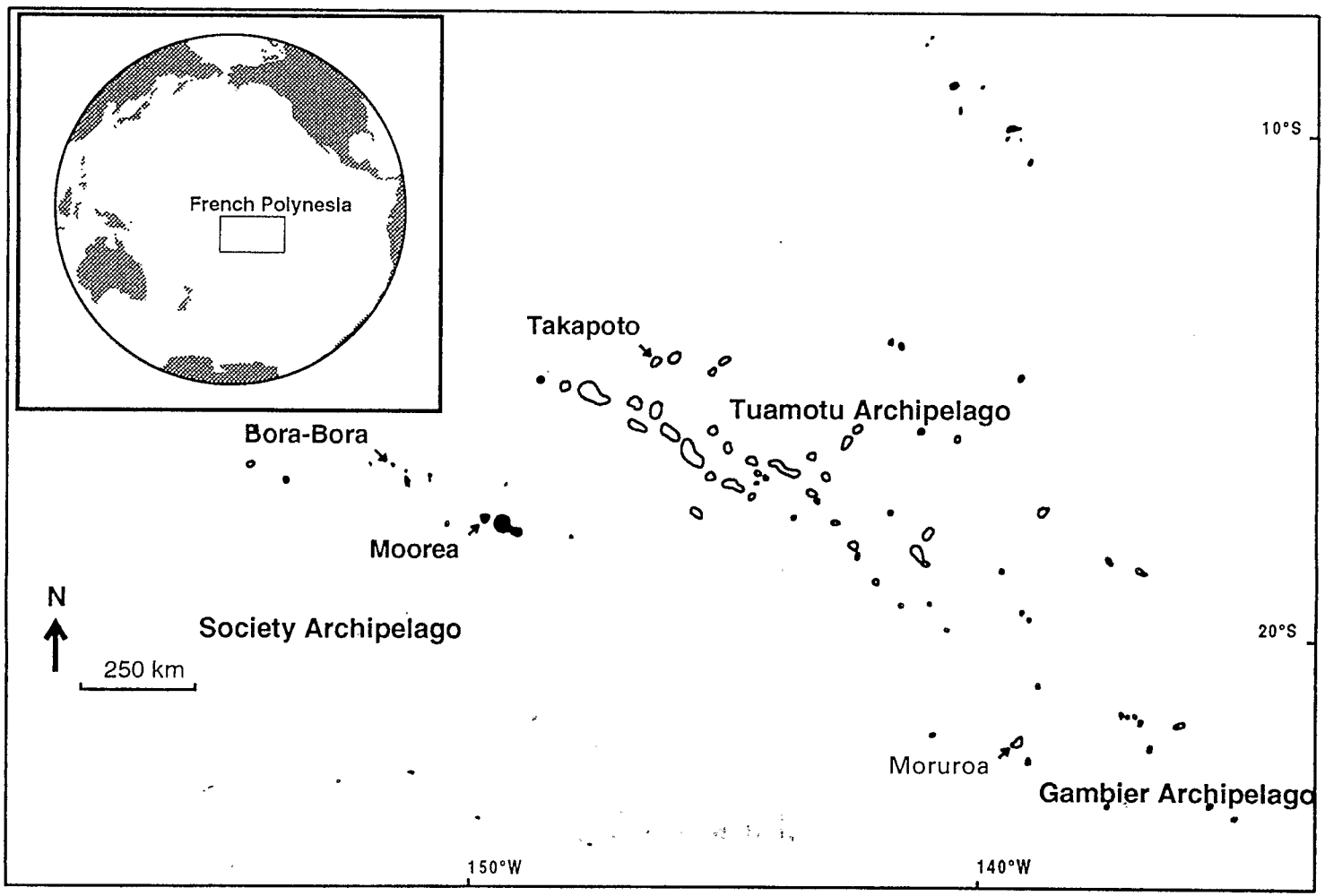

Figure 2.4.1 Islands of the south-central Pacific sampled for *Acanthurus triostegus*.

Table 2.4.1 Enzyme systems and presumptive loci scored in *Acanthurus triostegus*

Enzyme system	*Tissue*	*Buffer*	*Locus*	*Polymorphism*
Adenosine deaminase	Muscle	C	*Ada*	+
Adenylate kinase	Eye	D	*Ak*	–
Alcohol dehydrogenase	Liver	A	*Adh*	+
Aspartate aminotransferase	Liver	C	*Aat-1*	+
	Liver	C	*Aat-2*	+
	Muscle	C	*Aat-3*	–
Creatine kinase	Liver	C	*Ck*	–
Fumarase	Muscle	A	*Fum*	–
Glucose phosphate isomerase	Eye	A	*Gpi-1*	+
	Eye	A	*Gpi-2*	+
α-Glycerophosphate dehydrogenase	Muscle	D	*αGpd*	–
Glyoxalase-I	Liver	A	*Glo*	–
Guanine deaminase	Liver	C	*Gda*	+
Hexose phosphate dehydrogenase	Liver	A	*Hpd*	+
Isocitrate dehydrogenase	Liver	C	*Idh-L*	–
	Muscle	C	*Idh-M*	–
Lactate dehydrogenase	Eye	A	*Ldh-1*	–
	Eye	A	*Ldh-2*	–
	Eye	A	*Ldh-3*	–
Leucine aminopeptidase	Muscle	D	*Lap*	–
Malate dehydrogenase	Eye	D	*Mdh-1*	–
	Eye	D	*Mdh-2*	+
Malic enzyme	Muscle	D	*Me-1*	–
	Muscle	D	*Me-2*	–
Mannose phosphate isomerase	Muscle	C	*Mpi*	–
Phosphoglucomutase	Muscle	C	*Pgm*	+
6-Phosphogluconate dehydrogenase	Eye	C	*6-Pgd*	–
Sorbitol dehydrogenase	Liver	B	*Sdh*	+
Superoxide dismutase	Liver	A	*Sod*	–

+ = Locus polymorphic (frequency of the commonest electromorph < 0.95 in at least one population); – = sample monomorphism; A = discontinuous Tris-citrate-borate, pH 8.7 buffer; B = discontinuous Tris-HCl, pH 8.5 buffer; C = continuous Tris-citrate, pH 6.7 buffer; D = continuous Tris-citrate, pH 8.0 buffer. Loci *Aat-1* and *Aat-3* were scored on samples other than those of the present study (Planes, 1992).

2.4.3 Results

The estimates of single-locus F-statistics from genotype counts (see Appendix) are given in Table 2.4.2. Assuming that N has a normal distribution under the null hypothesis of Hardy–Weinberg equilibrium (Brown, 1970), no single-locus f value was significantly different from zero ($N = 33$; $p > 0.10$ at each locus). Neither could multilocus f values be considered different from zero. Therefore, agreement with Hardy–Weinberg proportions in each population was not rejected.

Differences in genetic composition between samples, expressed as large θ values, were observed. Assuming a normal distribution, the average multilocus θ value (0.0439) could be considered significantly different from zero (Student's t-test; 8 d.f.; $p = 0.038$). The *Gda* locus was discarded for the above calculations because the θ value at this locus departed significantly from the distribution of all other single-locus θs (Dixon's test: $p = 0.02$).

Permutation tests on matrices of genotypic data from each population did not result in the detection of multiple-locus genotypic disequilibria whereas significant departure from random expectations was evident for the pool of all samples (Figure 2.4.2).

Pairwise coancestry coefficients (θ) and genetic distances (D) between populations are presented in Table 2.4.3. D values did not show a clear increase with geographic distance

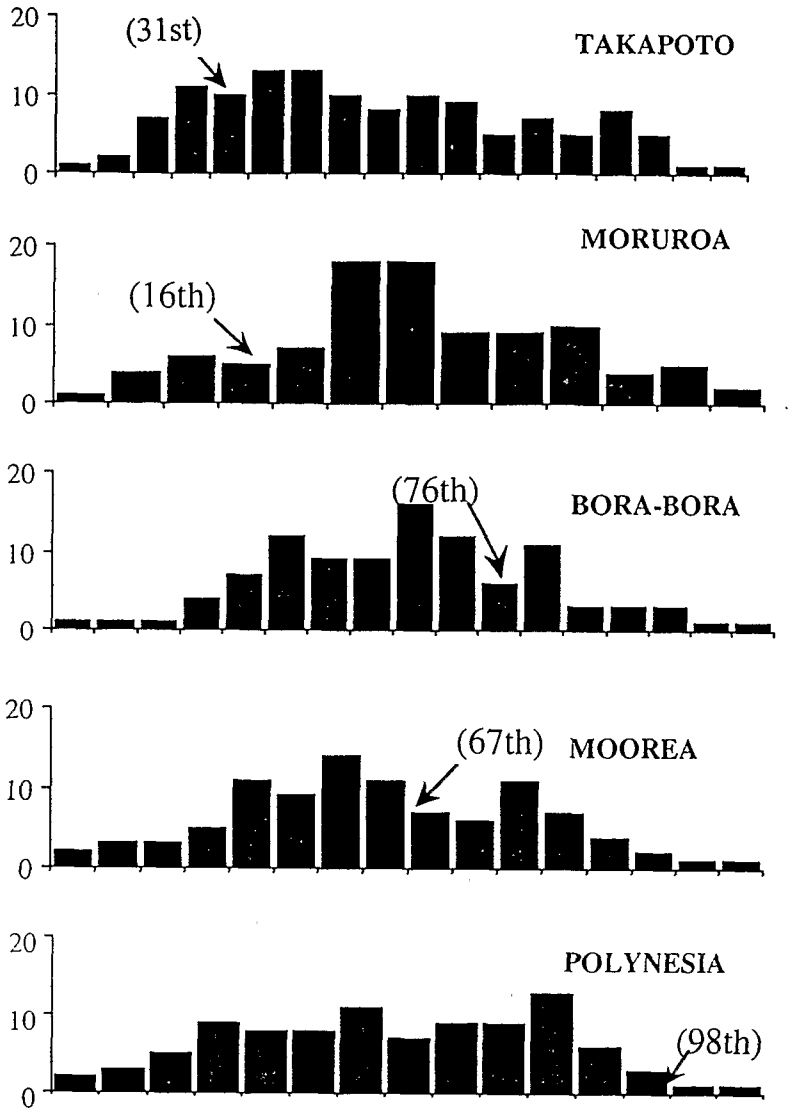

Figure 2.4.2 Distributions of dispersion indices from permutation tests (100 random permutations) on the matrices of individual X multiple-locus genotypes for each of four populations of *Acanthurus triostegus* and on the matrix of pooled data. Abscissa: percentiles of total range. Ordinate: frequencies. Arrow: dispersion index value of the wild sample (rank in brackets) among the random distribution.

Table 2.4.2 *F*-statistics on French Polynesian *Acanthurus triostegus* data

Locus	*f*	*θ*	*F*
Ada	0.1630	0.0250	0.1839
Adh	–0.1082	0.0247	–0.0808
Aat-2	0.0314	0.0855	0.1142
Gpi-1	0.1739	–0.0070	0.1681
Gpi-2	0.0207	0.0005	0.0212
Gda	–0.0216	0.3140[a]	0.2992
Hpd	0.1879	0.1275	0.2915
Mdh-2	–0.2483	–0.0019	–0.2506
Pgm	–0.0577	0.0275	–0.0286
Sdh	–0.0190	0.0481	0.0300
Multilocus (all 10 loci)	0.0101	0.0771[b]	0.0864
SD	0.0547	0.0361	0.0663
Multilocus (*Gda* excluded)	0.0132	0.0439[c]	0.0565
SD	0.0600	0.0173	0.0678

[a]Value detected as outlier ($p = 0.02$); [b]$p = 0.064$; [c]$p = 0.038$.
SD = standard deviation (jackknife).

Table 2.4.3 Estimates of genetic distance (D) and gene flow (Nm, with SD confidence intervals) derived from coancestry coefficients (average values over the nine loci of Table 2.4.2) between pairs of *Acanthurus triostegus* populations

Pairwise comparison	*Geographic distance (km)*	$\theta \pm SD$	D	Nm	
Bora-Bora/Moorea	210	0.0031 ± 0.0100	0.0031	80.4	$(18.8, \infty)$
Bora-Bora/Takapoto	755	0.0686 ± 0.0557	0.0711	3.4	(1.8, 19.2)
Bora-Bora/Moruroa	1450	0.0480 ± 0.0283	0.0492	5.0	(3.0, 12.4)
Moorea/Takapoto	665	0.0329 ± 0.0224	0.0335	7.3	(4.3, 23.6)
Moorea/Moruroa	1200	0.0423 ± 0.0245	0.0432	5.7	(3.5, 13.8)
Takapoto/Moruroa	1035	0.0629 ± 0.0300	0.0650	3.7	(2.4, 7.4)

(Mantel's test; $g = 1.25$; $p = 0.083$). Hence, consistency of these results with the expectations of an island model was not rejected. Estimates of gene flow between pairs of populations from different archipelagos, calculated for an island model at equilibrium (Nm; Table 2.4.3.), ranged from 3.4 to 7.3 migrants per generation, an array of values which can be considered as quite homogeneous. In contrast, the estimate of migration between Bora-Bora and Moorea (same archipelago) was $Nm = 80.4$.

2.4.4 Discussion

The present genetic study of *Acanthurus triostegus* in French Polynesia, the first one in coral reef fishes in this region of the Pacific, yielded results of both biogeographic and ecological interest.

Island populations at the scale of the whole of French Polynesia were significantly different from each other, whereas populations were not found to be internally structured, and hence could be considered as separate panmictic units. The model of one single population for the whole region, which could be expected from the passive dispersal capacities of *A. triostegus*, has therefore to be rejected.

The lack of correlation, on our limited sampling, between genetic distance and geographic distance indicates that the patterns observed may fit an island model, although the genetic distance estimate available for islands within the same archipelago (i.e. Moorea and Bora-Bora) was smaller. Further data encompassing a large number of samples from island within archipelagos should provide more precise information on the genetic structure of *A. triostegus*. These should also allow the testing of some current models of population genetic structure for reef fishes (e.g. island model versus two-dimensional stepping-stone model).

From a population genetic perspective, the values of effective migration rates were moderately large, i.e. small enough to allow significant divergence of gene frequencies between islands, although large enough (> 1) to counteract the effect of genetic drift if one assumes an infinite island model. From the ecologist's point of view, the meaning of these results is that unexpectedly low effective migration (see Section 2.4.1) occurs between islands, even within the same archipelago. Even though larval transport between islands cannot be determined directly from gene flow data on samples of recruited individuals (many larvae arriving on a reef are not necessarily recruited), the present results show that most of the population of recruits is contributed by self-recruitment in the reef fish *A. triostegus*.

As stressed by Le Fèvre and Bourget (1992), larval dispersal is determined not only by the duration of the larval stage, but also by hydrodynamic conditions and larval behaviour. Larvae of *A. triostegus* have been captured at relatively large depths; 50 m in Hawaii (Randall, 1961b) and more than 20 m in the Great Barrier Reef lagoon (Leis, 1991), depths at which wind-induced Ekman surface currents are much attenuated and retention is therefore favoured. Because of obvious sampling constraints, little more is known about the

larval behaviour of *A. triostegus*, but there is some indication that larvae of other fish species are able to resist passive transport offshore by selective vertical movements (e.g. Rijnsdorp, Van Stralen and Van der Veer, 1985). The manini, like the majority of the coral reef species, disperses its eggs and larvae toward the ocean. Adult manini congregate in the pass of the reef for spawning (Randall, 1961*b*), where currents are stronger and supposedly export the eggs offshore. Such behaviour would be expected to impede larval homing, so active larval behaviour favouring inshore movement seems likely.

Up to now, gene flow data have only answered the question of how much allorecruitment occurs in *A. triostegus*. Investigations on the genetic structure of larval populations before settlement, now accessible through the refinement of sampling methods such as networks of larval traps (Doherty, 1987), and the advent of miniaturized techniques such as PCR, should contribute to a better understanding of the pre-recruitment stage in reef fish.

We showed that equilibrium-effective migration rates do not support the hypothesis of massive larval dispersal and inter-island transportation in the manini surgeonfish in the south-central Pacific. Even within the same archipelago, the absolute number of successful migrants is very small and does not contribute significantly to the population of the recruited larvae, which thus results almost entirely from self-recruitment. One can then ask why a long larval stage is

2.4.5 Appendix. Genotype numbers at 10 loci in four populations of *Acanthurus triostegus*: Takapoto, Moruroa, Bora-Bora and Moorea

Locus	*Genotype*	*Takapoto* $N = 32$	*Moruroa* $N = 36$	*Bora-Bora* $N = 32$	*Moorea* $N = 32$
Ada	090/090	9	7	4	3
	100/060	1	1	0	2
	100/090	13	13	13	9
	100/100	9	15	15	18
Adh	050/050	5	5	10	11
	100/050	18	20	19	15
	100/100	9	11	3	6
Aat-2	100/070	1	0	0	0
	100/100	14	5	18	16
	140/100	13	19	11	13
	140/140	4	12	3	3
Gpi-1	070/070	4	2	2	1
	100/070	9	9	8	9
	100/100	19	24	22	22
	120/100	0	1	0	0
Gpi-2	100/070	2	0	0	0
	100/100	27	32	31	27
	120/100	3	4	1	5
Gda	100/100	8	34	3	20
	140/100	19	2	15	9
	140/140	5	0	14	3
Hpd	100/100	2	9	10	7
	120/100	4	14	17	11
	120/120	26	13	5	14
Mdh-2	050/050	5	3	2	4
	100/050	14	27	19	20
	100/100	13	6	11	8
Pgm	100/060	0	2	6	2
	100/100	32	34	26	30
Sdh	020/020	6	15	8	6
	100/020	14	19	16	16
	100/100	12	2	8	10

N = sample size.

maintained over an evolutionary timescale in the manini, if there are no short-term advantages to maintaining a pelagic phase with dispersal capacities. In our opinion, the classical extinction–recolonization hypothesis of metapopulation models (Levins, 1971; Olivieri, Couvet and Gouyon, 1990) is not adequate for explaining the maintenance of a long larval stage in reef fish such as the manini, since the reef environment of oceanic islands, most of them being millions of years old, appears to have been stable over large periods of time, and the presence of coral reef communities on the reef's outer slope is not known to have been interrupted. Further ecological or genetic hypotheses are therefore needed to address the question.

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