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Existence of two novel and non-sectorized clades of the giant clam *Tridacna maxima* in French Polynesia: implications for connectivity and origin

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Abstract

Giant clams are widely depleted with the exception of French Polynesia, where the dominant species, *Tridacna maxima*, is still exploited. Here, we report the first genetic structure analysis of *T. maxima* samples, issued from 4 polynesian archipelagos and spread on a surface of about 4 millions square kilometers. This study was based on both mitochondrial (*COI* and *16S*) and nuclear (*18S*) sequences and led to the discovery of two new *T. maxima* clades, which diverged 1.5 millions of years before present. French Polynesian clades cohabite over a large area with a North-West South-East axis on either side of which, one of each clade is dominant. Contrary to the strong genetic structuration observed in the *T. maxima* population in Indo- and West Pacific, we show here that the populations are widely interconnected, except in Tuamotu archipelago. This is underlined by a high connectivity between distant islands and archipelagos, which is independent from the direction of the oceanic currents. Altogether our data bring growing evidences of a progression of both clades in French Polynesia, one south and one north.

Introduction

Giant clams are represented by two genus, *Tridacna* and *Hippopus*, which have diverged 15 million of years before present [1,2]. While *Hippopus* genus only consists of two species, *H. Hippopus* and *H. porcellanus*, *Tridacna* genus has recently extended from eight to nine described species [3]. Among these nine *Tridacna* species, except sparse *T. squamosa*, *T. maxima* is the unique representative of the genus in French Polynesia [4], while both of them are described widespread in Indian Ocean, Red sea and notably in West Pacific [3,5,6]. Only absent in Marquesas, *T. maxima* is spread in the four other Polynesian archipelagos, where it harbors high densities, even if its quantity can strongly differ between islands. Their highest densities are found in Tuamotu archipelagos [7], especially in Fangatau [8] and Reao [9] atolls, where the *T. maxima* clams grow and accumulate tightly against each other, giving rise to a particular “mapiko” structure, specific to French Polynesia [8,10]. High *T. maxima* densities are also found in other parts of French Polynesia, such as in Tubuai island (Australes archipelago, [11]).

However, with the exception of French Polynesia, giant clam stocks are widely depleted, and they are listed in the IUCN Redlist of threatened species since 1996. Many phylogenetic studies of giant clams have now been conducted in different oceans. They were performed with allozyme markers in the Pacific Region [12,13], as well as nuclear and/or mitochondrial markers in the red sea [5], in the Indo-Pacific region [3,14–18] and in the Pacific region [19]. Concerning *Tridacna maxima* species, the presence of four distinct lineages in the Indo-Pacific region and Red Sea, both considered as high spot of biodiversity, has been detected [17]. Regarding the East-Pacific region, considered as the end of the biodiversity gradient, only few studies rely on the giant clam populations.

Because of its very high densities in French Polynesia compared to the rest of the world [8,9,11], *T. maxima* exploitation for the local consumption and the exportation, as well as for the aquarium trade, is still allowed. Nevertheless, this exploitation is subject to an international standard set by the Washington Convention of 3 March 1973, and to a local standard which prohibits the exploitation of clams less than 12 cm length (Resolution No. 88-184/AT). Since 2001, different studies on giant clams have been undertaken by the Direction of Marine Resource of French Polynesia in partnership with the Research and Development Institute and the University of French Polynesia [7]. These studies mainly concentrate on stock assessment, with the objective to master the aquaculture of these bivalves. Associated restocking projects, consisting in the reintroduction of *T. maxima* in depleted places, might generate a risk of a genetic homogenization [20]. Moreover, genetic studies on *T. maxima* in French Polynesia are still in their infancy and, as far as we are concerned, except the work on *Tridacna squamosa* [4], no genetic study with mitochondrial or nuclear markers has been conducted on French Polynesian giant clams. Only one study, based on allozyme diversity, was performed [13]. The authors used ten polymorphic loci to study the genetic variation on nine populations from six French Polynesian islands, in the Society and Tuamotu archipelagos. While the confined environment provided by numerous lagoons of French Polynesia might provide a hot spot for genetic differentiation, a significant genetic difference between populations was only detected at the archipelagos level, and according to only one locus on the ten tested.

French Polynesia is a naturally fragmented structure composed of a set of 118 remote islands, distributed into five archipelagos, located on a 5.5 millions square kilometers surface area and therefore provides a good area to go deeper in the understanding of the intraspecific genetic divergence of *T. maxima* and of the origin of this divergence. To this purpose, we used three different genetic markers, the cytochrome c oxydase I gene (*COI*), the mitochondrial small ribosomal subunit *16S* RNA (*16S* rDNA) and the nuclear small ribosomal subunit *18S* RNA (*18S* rDNA) and determine the genetic structure and connectivity between *T. maxima* issued from 14 islands spread over the four archipelagos which possess giant clams, collectively representing an area of about 4 millions square kilometers.

Materials and Methods

Sample collection and DNA extraction

Giant clams from *T. maxima* species (n = 304) were sampled between the 1st February 2011 and the 2d of November 2013, in 14 islands distributed in four out of the five archipelagos of French Polynesia. The Australes archipelago is represented by Maria, Tubuai, Raivavae; the Gambier by Mangareva; the Tuamotu by Reao, Tatakoto, Hao, Makemo, Kauehi, Tikehau, Kaukura, Apataki and the Society by Tahiti and Moorea. In Tahiti, the biggest island of French Polynesia, *T. maxima* giant clams have been sampled over three regions: North, West and South.

Mantel samples were collected from *T. maxima* at 0.5-2 m depth, just by clipping a piece of mantle tissue immediately stored in 70% ethanol. Total genomic DNA was extracted from each mantle sample using the Wizard Genomic DNA Purification Kit (Promega), according to the manufacturer's instructions.

Amplification and sequencing

The genetic structure of *T. maxima* was studied using one nuclear genetic marker, the *18S* rDNA and two mitochondrial markers, the *16S* rDNA gene and the cytochrome c oxidase subunit 1 gene (*COI*). All corresponding DNA regions were amplified by polymerase chain reaction (PCR) using specific primers and the Promega GoTaq polymerase kit. DNA regions of the *18S* rDNA (800 bp) and of the *16S* rDNA (462 bp) were amplified with Canapa's specific primers [21] and Schneider's primers [1] respectively and according to the following PCR conditions: 35 cycles of 94°C (45 s), either 50°C (45 s) or 55°C (45 s) for the *18S* rDNA and the *16S* rDNA respectively, and 72°C (45 s). For *COI* gene, the primers were designed and allowed the amplification of a 658 bp DNA region. The forward primer, *COI* F (5'-cggtaaaacgacggccagtggtgataattcgaacagaa-3'), was modified from Kochzius' *COI* forward primer [15] and the *COI* reverse primer (*COI* R: 5'-ggagcggataacaatttcacacaggaacgaacgctgtaataacc-3') was designed from the highly conserved regions within the published sequences of *T. maxima* *COI* gene. The PCR reaction consisted of 7 cycles of 94°C (45 s), 40°C (45 s) and 72°C (45 s), followed by 30 cycles of 94°C (45 s), 50°C (45 s), and 72°C (45 s).

All PCR products were purified using Wizard SV Gel and PCR Clean-Up System (Promega) and sequenced (Eurofin and GATC, Germany). Sequences were edited, assembled and multi-alignment was performed using MEGA6 software [22]. Gene sequences were deposited in GenBank.

DNA Sequences

In addition to our *COI*, *16S* and *18S* new sequences issued from the 304 samples, 154 *COI* sequences, 15 *16S* sequences and 6 *18S* sequences of *Tridacna* species were extracted from the NCBI repository of the nucleotide sequences, mainly associated to the works of Huelsken et al. [3], DeBoer et al. [15] and Nuryanto et al. [16]. Outgroups from other species were also included (4 *COI* sequences, 3 *16S* sequences and 5 *18S* sequences). See Table S1.

Phylogenetic analysis

The phylogenetic analysis was realized using StarBeast v2.1.3 software [23]. The general procedure, treatment of each gene region and Priors for nodes defining species, was similar to the procedure mentioned by Huelsken et al. [3]. In addition to a general time reversible model, a Hasegawa-Kishino-Yano model with gamma distributed and invariant sites (G + I) was also applied to each gene, with an additional partitioning by codon position (1+2+3) for *COI*. Speciation was also modeled both as birth-death and Yules processes with the same parameters as those described in Huelsken et al. [3].

The phylogeographic patterns were assessed by examining an aggregation of 114 unique *COI* haplotypes (**Table S1**) after manually alignment and a heuristic maximum parsimony search, conducted in MEGA6.06 [22].

The software Figtree was used to graphics preparation of the trees (Rambaut: <http://tree.bio.ed.ac.uk/software/figtree/>).

Population genetic statistics

Molecular diversity measures for all populations were evaluated in Arlequin v3.5.1.2 [24], including haplotype diversity [25], nucleotide diversity [25,26] and pairwise sequence divergence, genetic signal of population equilibrium (Tajima's *D*-test statistic [27], Fu's *F*-test [28] and mismatch distribution for assessment of the demographic status of populations by sum of squared deviations (SSD; [29–32]) and Harpending's Raggedness Index (HRI; [33]). AMOVA were also performed in Arlequin v3.5.1.2.

A classical Multidimensional Scaling and hierarchical clustering with the Ward method were performed from the *F*_{st} pairwise differences of population with R version 3.1.1 (R Core Team 2014 <http://www.R-project.org/>).

Results

DNA Sequences

304 *T. maxima* were sampled over 14 islands spread on 4 out of 5 French Polynesian archipelagos (**Table 1**). Some of them were sequenced at three loci; 2 mitochondrial regions (*COI* n=304 and *16S* n=124) and 1 nuclear region (*18S* n=88). Alignment of these sequences allowed the identification of 59 distinct haplotypes for *COI*, 6 for the *16S* and 6 for the *18S*. All of them were novel haplotypes of *T. maxima*. The resulting alignment of *COI* sequences was 461 bp length. No double peaks nor in-frame stop codons were observed, indicating no evidence of heteroplasmy or nuclear copies of mitochondrial DNA. Aminoacid translation of the sequences yielded to 153 amino

acids and showed 9 non-synonymous substitutions among the 54 polymorphic sites and 58 base substitutions. These 9 substitutions were conservative changes and therefore didn't alter the characteristics of the protein domain. The resulting alignment of the *16S* sequences was 392 bp length and disclosed 5 base substitutions on 5 sites. The sequence alignment of the *18S* was 604 bp length with 7 base substitutions on 7 sites.

Table 1. *Tridacna maxima* sampling information and genetic indexes based on mitochondrial cytochrome c oxidase I sequences. Samples sites, geographic region, number of sequences (n), number of haplotypes (N_{hp}), haplotype diversity (h), nucleotide diversity (π), Tajima's D, Fu's *FS*, sum of square deviation (SSD) and Harpending's Raggedness index (HRI)

Site	Geographic regions	n	Genetic diversity		Neutrality tests			Mismatch distribution	
			N _{hp}	h	π (percentage)	D	Fu's <i>FS</i>	SSD	HRI
Maria	Australes	5	3	0.70 +/- 0.22	0.43 +/- 0.34	-1.12 ^{NS}	0.64 ^{NS}	0.09 ^{NS}	0.29 ^{NS}
Tubuai		5	4	0.90 +/- 0.16	0.65 +/- 0.48	-0.75 ^{NS}	-0.33 ^{NS}	0.17 ^{NS}	0.67*
Raivavae		27	11	0.70 +/- 0.10	0.61 +/- 0.37	-2.12**	-2.92 ^{NS}	0.55***	0.06 ^{NS}
Mangareva	Gambier	8	3	0.61 +/- 0.16	0.71 +/- 0.46	0.26 ^{NS}	2.75 ^{NS}	0.16 ^{NS}	0.29 ^{NS}
Reao	Tuamotu East	10	6	0.84 +/- 0.10	0.88 +/- 0.54	0.21 ^{NS}	-0.10 ^{NS}	0.10 ^{NS}	0.15 ^{NS}
Tatakoto		10	5	0.82 +/- 0.10	0.50 +/- 0.34	-1.53 ^{NS}	-0.27 ^{NS}	0.05 ^{NS}	0.19 ^{NS}
Hao		10	2	0.20 +/- 0.15	0.04 +/- 0.07	-1.11 ^{NS}	-0.34 ^{NS}	0.33 ^{NS}	0.4 ^{NS}
Makemo	Tuamotu West	11	4	0.67 +/- 0.12	0.49 +/- 0.33	-1.72*	1.05 ^{NS}	0.023 ^{NS}	0.07 ^{NS}
Kauehi		5	3	0.80 +/- 0.16	0.52 +/- 0.39	0 ^{NS}	0.95 ^{NS}	0.11 ^{NS}	0.36 ^{NS}
Tikehau		6	3	0.80 +/- 0.12	0.93 +/- 0.62	1.28 ^{NS}	2.58 ^{NS}	0.14 ^{NS}	0.22 ^{NS}
Kaukura		4	3	0.83 +/- 0.22	0.87 +/- 0.65	-0.82 ^{NS}	1.16 ^{NS}	0.16 ^{NS}	0.31 ^{NS}
Apataki		5	5	1.00 +/- 0.13	1.01 +/- 0.74	1.19 ^{NS}	-1.17 ^{NS}	0.12 ^{NS}	0.20 ^{NS}
Moorea	Society	7	3	0.67 +/- 0.16	1.18 +/- 0.74	1.77 ^{NS}	3.76 ^{NS}	0.21*	0.49*
Tahiti West		181	31	0.77 +/- 0.03	0.69 +/- 0.40	-1.18 ^{NS}	-13.96***	0.70 ^{NS}	0.18*
Tahiti South		8	3	0.46 +/- 0.20	0.43 +/- 0.31	-1.70*	1.57 ^{NS}	0.31***	0.23 ^{NS}
Tahiti North		12	5	0.58 +/- 0.16	0.63 +/- 0.40	-0.84 ^{NS}	0.69 ^{NS}	0.12 ^{NS}	0.34 ^{NS}

*0,05≥P≥0,01; **0,01>P≥0,001; ***P<0,001; NS, not significant.

Phylogenetic analyses

As expected, the tree topologies for single *COI*, *16S* and *18S* gene datasets (**Fig. 1**) were strongly similar to the tree topologies published by Huelsken et al. [3]. The only significant difference is the appearance of 2 new clades in the *T. maxima* taxon. The similarity between the trees supports a consistent phylogenetic signal. These undescribed new clades sequences were distinct from the other species with an average pairwise *COI* sequence divergence (uncorrected pairwise distances) of 13.7% with *T. crocea*, 16.8% with *T. derasa*, 16.2% with *T. sp*, 14.3% with *T. squamosa* and 9.0% with *T. maxima* as compared to 10.4% between *T. squamosa* and *T. crocea*. Between both clades, the average pairwise distance is 3.3%.

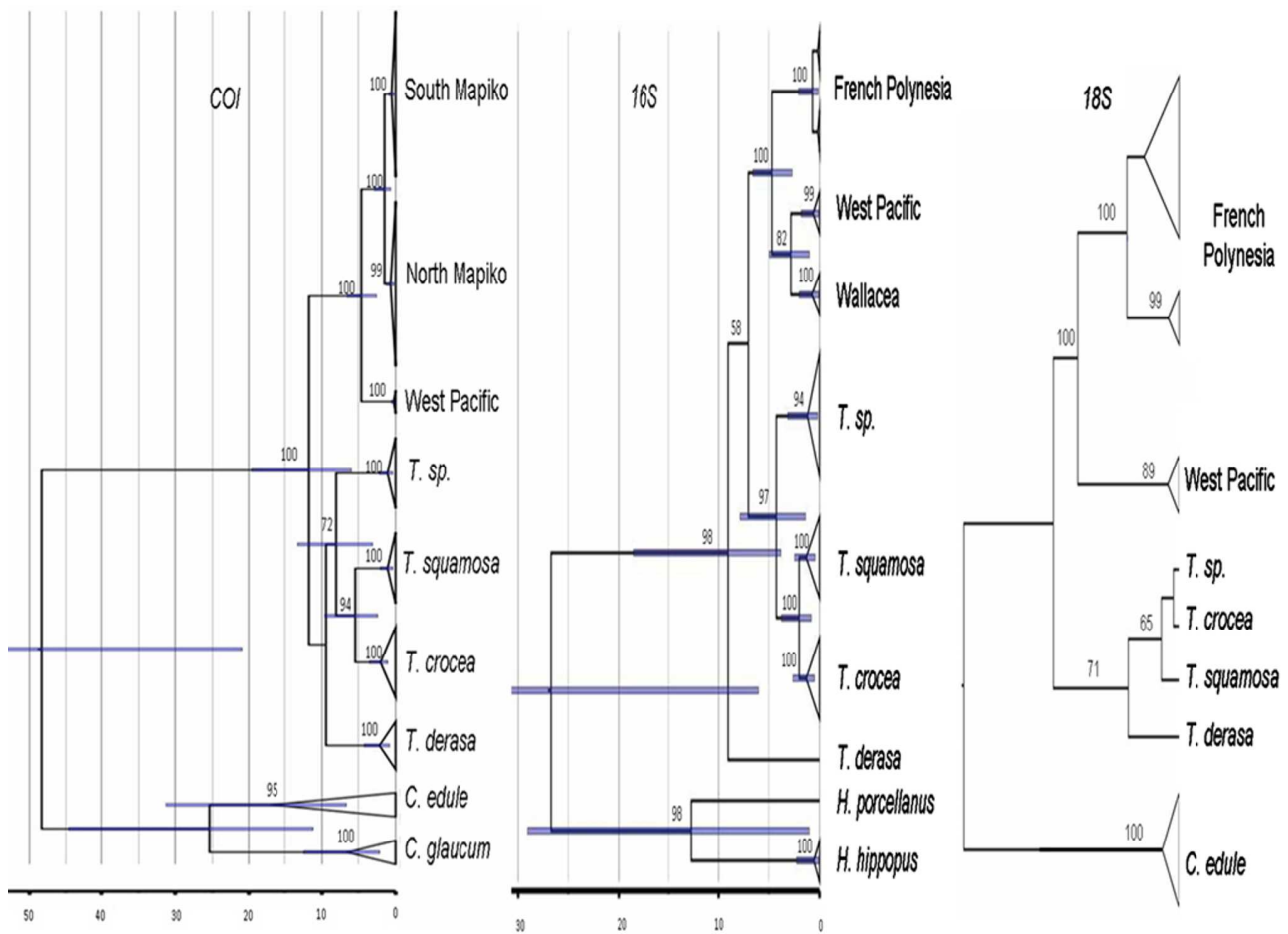


Figure 1 : Species relationships within *Tridacna* based on Bayesian phylogenetic trees for mitochondrial *COI*, *16S* or *18S*. The topology is a time calibrated maximum clade credibility tree under a birth-death model. Bayesian posterior probabilities are above the branches. The 95% heights of nodes are drawn in blue rectangle on significant nodes.

Time calibrated gene trees for *COI* and *16S* also showed similar estimations of the ages of nodes in agreement with the fossil dates. The divergence date for *T. squamosa* is estimated at 1.06 millions of years before present (My BP) with *COI* tree and 1.28 My BP with *16S*. For *T. crocea*, the estimations are 1.99 My and 1.3 My BP respectively. The divergent date for the new clades are estimated at 1.5 My BP (0.66 – 2.77, 95% HPD), each of them diverging since 0.5 My (0.18 - 0.96, 95% HPD).

Intraspecific phylogeographic patterns with *COI* region of *T. maxima* was explored with French Polynesia new clades (**Fig. 2**). The pattern highlighted two monophyletic “East.Pacific” clades, configuring a third expansion between “Wallacea” and “West Pacific” clades.

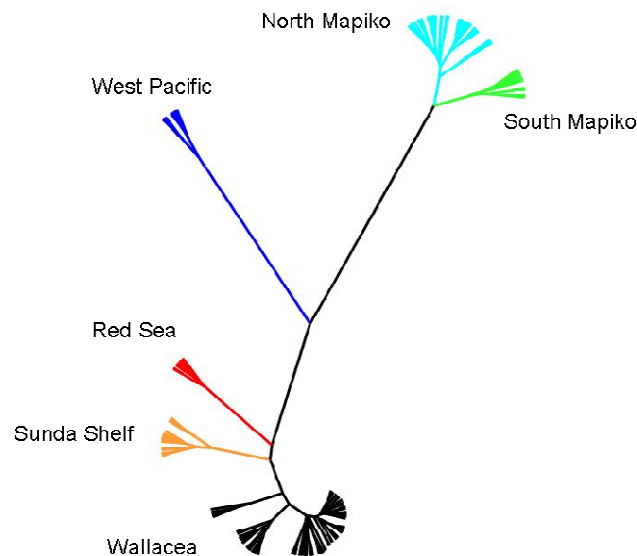


Figure 2: Unrooted parsimony tree for mitochondrial COI of *Tridacna maxima* according to the sampling locations. Major lineages are colored: turquoise for South Mapiko, green for North Mapiko, dark blue for West Pacific, red for Red Sea, orange for Sunda Strait and black for Indonesia, Singapore, western New Guinea and Taiwan (Wallacea).

BECAUSE OF THE LOW NUMBER OF THE 105 AND 103 HAPLOTYPES, ONLY COI REGION WAS ANALYZED.

Genetic diversity (**Table 1**) showed that the lower haplotypic and nucleotidic diversity was observed in Hao island ($h=0.20$ and $\pi=0.04$) and in South Tahiti ($h=0.46$ and $\pi=0.43$) while the h and π values were about 0.80 and 0.65 respectively for the others populations. The Tajima's D test and Fu's F_s test for each sample did not reject the null hypothesis of neutral evolution for the majority of the samples. Only Raivavae, Makemo and South Tahiti have a significant negative Tajima's D value and West Tahiti for Fu's F_s . This suggested a population size expansion or selection within these populations. The population expansion hypothesis was supported by non significant SSD and HRI in Makemo population. Concerning the two remaining populations South Tahiti and Raivavae, there is a significant deviation to expected SSD or HRI distribution. These values suggest that the demographic expansion model does not provide a particularly good fit to these data. However, we observed that the mismatch distributions were multimodal, consistent with old stationary populations. As a result, the agreement with neutrality could not be rejected.

Spatial Structure of genetic variation

To determine the partition of the genetic variation into regions, we analyzed the population pairwise F_{st} differences in a first time. The first axis of a multi-dimensional scaling from these evaluated differences discriminated the islands of Tuamotu from the other islands (**Fig. 3**). Furthermore, a strong amalgamation of Society, Australes and Gambiers islands was observed (low F_{st} differences, **Table S2**). Among this group, Moorea was discriminated with a lower F_{st} difference with the North Tuamotu islands. On the contrary, the West Tahiti site was significantly isolated from the other sites. In the Tuamotu archipelago, two distinct groups were observed: North–West Tuamotu and East Tuamotu.

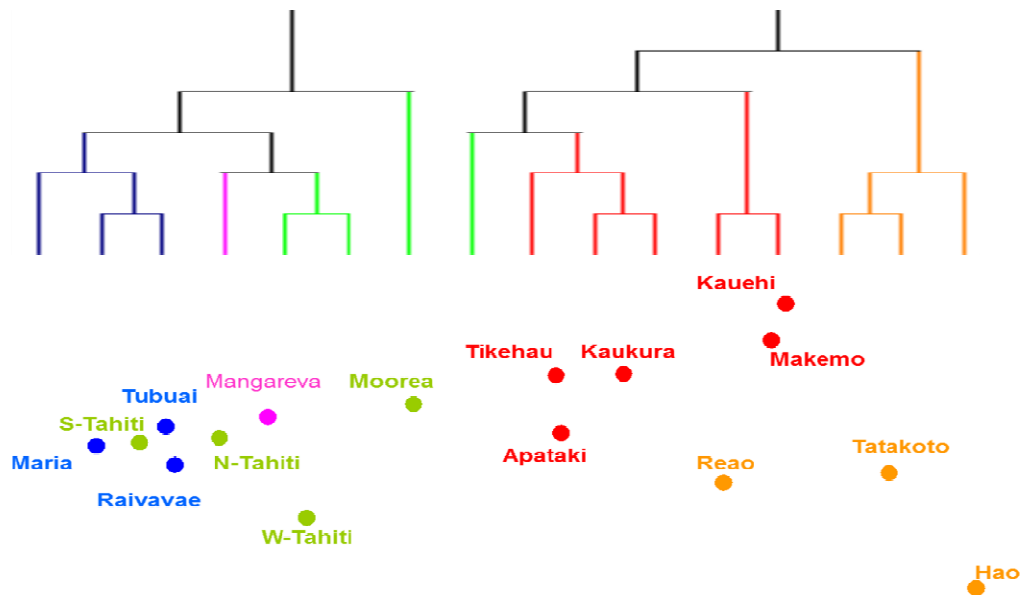


Figure 3 : Multi-dimensional scaling associated to the hierarchical clustering of the population pairwise F_{st} differences. Axis 1 and 2 of the MDS represent 68.7% and 24.1% of the total variance respectively. The geographic groups are symbolized by colors, red for West Tuamotu, orange for East Tuamotu, pink for Gambier, green for Society and blue for Australes. The legend of the plots indicates the corresponding island or site of the samplings. For Tahiti Island, sites of samplings are noted: N for North, S for South and W for West.

Using AMOVA, we found a significant genetic structure into the different regions (**Table S3**). There was a significant structure between geographic archipelagos ($F_{CT} = 0.3404$, p -value = 0.005) and the level of structure was maximized when Tuamotu populations were split into two (North and East) and three groups: North-West, Middle and East and the other islands were grouped ($F_{CT} = 0.47293$ and 0.47327 respectively, p -value=0).

Genetic population structure and gene flow

The proportion of the two French Polynesian clades at each sample site and principal gene flows between geographic groups was studied (**Fig. 4**).

We clearly observed an opposition between the proportions of the two clades on either side of a North-West/South-East axis, North Society-Gambier archipelagos. At the North of this axis, the frequency of one clade highly prevails over the other clade, until 100% in some sites. Conversely, the inverse proportions were observed at the South of this axis. This geographic discrimination led to name these clades North Mapiko and South Mapiko.

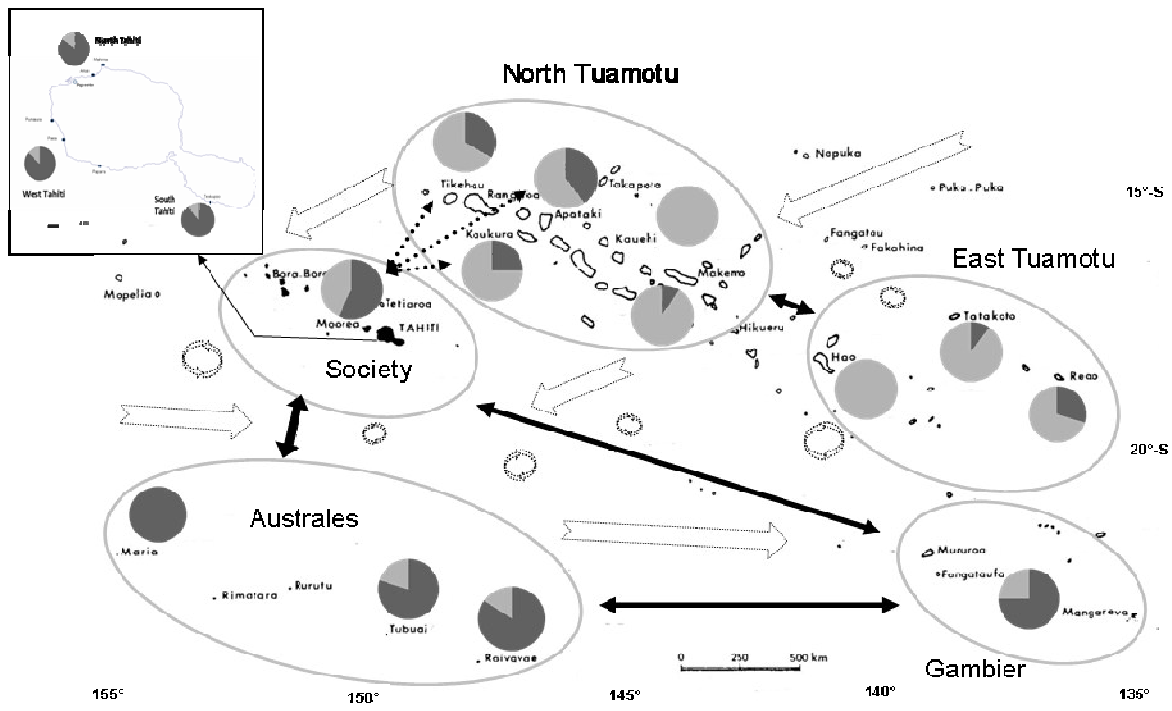


Figure 4 : Map of French Polynesia showing the frequencies between the 2 Mapiko COI clades and the connectivity between 5 geographic locations. Geographic groups are represented by ellipses. For Tahiti Island, a zoom picture is included at the bottom left of the map. Frequencies are illustrated in light grey for North Mapiko and strong grey for South Mapiko. Solid line arrows indicate non significant values of F_{st} differences between the corresponding geographic groups and dotted line arrows between two sites. Open arrows indicate the present oceanic surface currents and the swirling currents.

The estimated migrant values led to the same geographic groups as those previously obtained with the population pairwise F_{st} , providing a robust connectivity network (**Table S4**). They exhibited a strong relationship between islands within each geographic group of the North and East Tuamotu, Society, Australes and Gambier archipelagos. Moorea island also displayed a relationship with the islands of the North of the Tuamotu archipelago. At the geographic groups level, the East Tuamotu group displayed only relationship with the North Tuamotu group whereas the three other groups (Society, Australes, Gambier) are interconnected. The study of shared haplotypes consolidated these different geographic groups. Two on the 59 haplotypes were largely distributed all over French Polynesia. One haplotype was only absent from the East group of Tuamotu island (Hao, Tatakoto and Reao) and the second one was absent from both the East Tuamotu and the Australes archipelagos. It was interesting to note that the first haplotype, also shared with Australes, was present only in the three Islands at the North of the North-West Tuamotu group (Tikehau, Apataki and Kaukura) whereas the second haplotype, absent in Australes, was shared between all Islands of the North-West Tuamotu group. In the East Tuamotu group, only 2 on 8 haplotypes were shared with the North Tuamotu group. In the Australes group, 11 on 14 haplotypes were only present within this group, 3 shared with the Society group among which one is shared with the Gambier group corresponding to the largely shared haplotype. The directions intra- or inter-groups of these relationships did not systematically follow the flow direction of the present oceanic currents, which are mainly perpendicular.

Discussion

Our study, conducted in French Polynesia, disclosed two novel clades of *T. maxima*. These two clades, which do not extend towards the West Pacific, represent a novel *T. maxima* genetic

break, between the middle of South Pacific and the West Pacific. This is in line with the strong genetic population structure of *T. maxima* and other sessile marine species observed across the Indo-Pacific Ocean, even on small areas, and associated with a highly restricted gene flow [15,17,34]. These two clades are restricted to French Polynesia and do not extend into the West Pacific.

Our data allow to estimate the age of the divergence of the giant clam populations of French Polynesia, at 1.5 ± 0.5 My BP. At least two hypotheses can account for these observations: either these two clades existed before their arrival in French Polynesia or they diverged from a common ancestor after their arrival. During Pleistocene (2 My BP), the frequency of sea level variation increased significantly [35]. In course of the last glaciations peaks (21 000 years BP), the sea level of the Indo-Pacific region decreased to -120 m under the actual sea level [36,37], and led to a complete or partial dry for most of the lagoons. In French Polynesia this event probably led to local extinctions or reductions of giant clams population size, as proposed for *Pinctada margaritifera* (Arnaud-Haond et al., 2003). 11 500 years BP, the melting of the ice led to the increase of sea level until more than 1 m above the present sea level, and for 1 500 years, the sea level decreased until the present sea level [38]. Nuclear and mitochondrial markers have shown signs of recent bottlenecks and founder effects in *P. margaritifera* populations in Tuamotu, Gambier and Society archipelagos, which have been related to sea level fluctuations during the last glaciations period [39]. As *P. margaritifera*, giant clam genetic structure can also be explained by an important population decrease, or maybe extinction, which occurred during the last glaciations, following by either their successive reinvasions, from the Pacific region, one at the North of French Polynesia and another one at the South, or by the presence of two distinct founder niches, one in Tuamotu and the other one in Australes. Studies of the genetic structure of *T. maxima*, issued from the insular surroundings of French Polynesia (Fiji, Samoa, Tonga, Cooks islands), should allow to discriminate between these two hypotheses.

Surprisingly, our results also show that both clades are not sectorized and distributed nearly all over French Polynesia, contrary to what it is observed in the other regions of the Indo-Pacific and West Pacific [17,34]. The genetic integrity of species living in fragmented habitats depends on many factors, including their dispersal abilities and the oceanic currents [40]. Giant clams have a pelagic phase of 9 days during their larval stage. Therefore, the flow has certainly highly contributed to their genetic history in French Polynesia. The frequencies of each of the two clades show an inverse gradient from North to South, suggesting that opposite flows can be used for migration in the founder niches hypothesis or that a clade overruns French Polynesia at the expense to the other clade. East Tuamotu are the more isolated islands, only connected with North-East Tuamotu islands. A privileged relationship between North-West Tuamotu and Moorea Island in the Society Archipelago is also observed. This relationship can be consistent with the surface oceanic current which goes from North-East to South-West. In this consideration, North Mapiko could have invaded French Polynesia from North to South. However, the presence of a strong connectivity between Society and Gambier archipelagos, Society and Australes archipelagos, cannot be explained by the present surface streams. The observed connectivity can be in the same direction or perpendicular to the present currents. Such a configuration was also described in West Pacific [12]. However, during exceptional events as El Niño or La Niña, flows are changed and can be inversed [40,41]. Thus, we suggest that in French Polynesia such changes are responsible for the high connectivity observed between the different islands.

Our results also provide information to improve the management plan of giant clams established by the Marine Resource Direction since 2001, and can thus contribute to the preservation of this important resource. As both clades already cohabit in numerous islands in the four archipelagos, transplantations from an island to the other one do not seem to present a dramatic environmental hazard. The high connectivity observed between Society islands, Australes and Gambier confer a natural mixing independently of the human manipulation.

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Author Contributions

Conceived and designed the experiments: VD, VBL, CL, PR, GL. Performed the experiments: VD, GL. Analyzed the data: VD, VBL, GL. Contributed reagents/ materials/analysis tools: VD, VBL, CL, PR, GL. Wrote the manuscript: VD, VBL, PR, GL.

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Supporting Information Legends

Table S1. Genbank accession numbers for all sequences used in this work (XLS)

COI

Study Source	Acc No	Locality	Name used in study	Putative species	Latitude (decimal degrees)	Longitude (decimal degrees)
Ladhar-Chaabouni et al., 2010.	FJ179506			Cerastoderma glaucum		
Ladhar-Chaabouni et al., 2010.	FJ179507			Cerastoderma glaucum		
Ladhar-Chaabouni et al., 2010.	FJ179499			Cerastoderma edule		
Ladhar-Chaabouni et al., 2010.	FJ179500			Cerastoderma edule		
DeBoer et al. 2008	EU341354	Indonesia	TSD_24	crocea		
Neo & Todd 2012	JN392066	Singapore	NML_61	crocea		
Huelsken et al. 2013	JX974945	Torres Strait, Australia	ET1879_TOR_croc	crocea	-10.54	142.35
Huelsken et al. 2013	JX974956	Lizard Island, Australia	ET544_LIZ_croc	crocea	-14.65	145.45
Plazza & Passamont 2010	GQ166591	?		derasa		
Lizano & Santos 2010	KJ202112	Philippines		derasa		
Huelsken et al. 2013	JX974957	Australia	ET356	derasa		
Huelsken et al. 2013	JX974919	Solomon Islands	ET2339_SOL_spp	sp.	-8.37	157.51
		Ningaloo, Western Australia	ET918_NIN_spp	sp.	-23.17	113.76
Huelsken et al. 2013	JX974910	Australia	ET920_NIN_spp	sp.	-23.17	113.76
Tang & Chen, unpublished	DQ168140	Taiwan	Tridacna sp.	sp.		
DeBoer et al. unpublished	EU346363	Indonesia	TSD52	squamosa		
Neo & Todd 2012	JN392038	Singapore	NML_23	squamosa		
		Torres Strait, Australia	ET1961_TOR_squa	squamosa	-10.42	142.25
Huelsken et al. 2013	JX974925	Lihou Reef, Coral Sea, Australia	ET358_LIH_squa	squamosa	-17.41	151.88
Nuryanto & Kochzius 2009	FM244476	Red Sea	Hap_1_Red	maxima		
Nuryanto & Kochzius 2009	FM244477	Red Sea	Hap_2_Red	maxima		
Nuryanto & Kochzius 2009	FM244478	Red Sea	Hap_3_Red	maxima		
Nuryanto & Kochzius 2009	FM244479	Red Sea	Hap_4_Red	maxima		
Nuryanto & Kochzius 2009	FM244480	Red Sea	Hap_5_Red	maxima		
Nuryanto & Kochzius 2009	FM244481	Red Sea	Hap_6_Red	maxima		
Nuryanto & Kochzius 2009	FM244482	Red Sea	Hap_7_Red	maxima		
Nuryanto & Kochzius 2009	FM244483	Red Sea	Hap_8_Red	maxima		
Nuryanto & Kochzius 2009	FM244484	Red Sea	Hap_9_Red	maxima		
Nuryanto & Kochzius 2009	FM244485	Red Sea	Hap_10_Red	maxima		
Nuryanto & Kochzius 2009	FM244513	Java & Sumatra	Hap_11_orange	maxima		
Nuryanto & Kochzius 2009	FM244514	Java & Sumatra	Hap_12_orange	maxima		
Nuryanto & Kochzius 2009	FM244515	Java & Sumatra	Hap_13_orange	maxima		
Nuryanto & Kochzius 2009	FM244516	Java & Sumatra	Hap_14_orange	maxima		
Nuryanto & Kochzius 2009	FM244517	Java & Sumatra	Hap_15_orange	maxima		
Nuryanto & Kochzius 2009	FM244518	Java & Sumatra	Hap_16_orange	maxima		
Nuryanto & Kochzius 2009	FM244519	Java & Sumatra	Hap_17_orange	maxima		
Nuryanto & Kochzius	FM244520	Java & Sumatra	Hap_18_orange	maxima		

2009

Nuryanto & Kochzius 2009	FM244521	Java & Sumatra	Hap_19_orange	maxima
Nuryanto & Kochzius 2009	FM244522	Java & Sumatra	Hap_20_orange	maxima
Nuryanto & Kochzius 2009	FM244523	Java & Sumatra	Hap_21_orange	maxima
Nuryanto & Kochzius 2009	FM244524	Java & Sumatra	Hap_22_orange	maxima
Nuryanto & Kochzius 2009	FM244525	Java & Sumatra	Hap_23_orange	maxima
Nuryanto & Kochzius 2009	FM244526	Java & Sumatra	Hap_24_orange	maxima
Nuryanto & Kochzius 2009	FM244527	Java & Sumatra	Hap_25_orange	maxima
Nuryanto & Kochzius 2009	FM244528	Java & Sumatra	Hap_26_orange	maxima
Nuryanto & Kochzius 2009	FM244529	Java & Sumatra	Hap_27_orange	maxima
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Nuryanto & Kochzius 2009	FM244532	Java & Sumatra	Hap_30_orange	maxima
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Nuryanto & Kochzius 2009	FM244534	Java & Sumatra	Hap_32_orange	maxima
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Nuryanto & Kochzius 2009	FM244537	Central Indonesia	Hap_35	maxima
Nuryanto & Kochzius 2009	FM244538	Central Indonesia	Hap_36	maxima
Nuryanto & Kochzius 2009	FM244539	Central Indonesia	Hap_37	maxima
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2009

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Huelsken et al. 2013	JX974929	Torres Strait, Australia	ET2015_TOR_max	maxima	-10.45	142.22	
Huelsken et al. 2013	JX974930	Solomon Islands	ET2145_SOL_max	maxima	-8.35	157.37	
Huelsken et al. 2013	JX974931	Solomon Islands	ET2348_SOL_max	maxima	-8.10	156.87	
Huelsken et al. 2013	JX974932	Solomon Islands	ET2386_SOL_max	maxima	-8.30	157.52	
Huelsken et al. 2013	JX974933	Solomon Islands	ET2395_SOL_max	maxima	-8.75	158.22	
Huelsken et al. 2013	JX974935	Lizard Island, Australia	ET2793_LIZ_max	maxima	-14.70	145.45	
Dubousquet et al. (present study)	MF167466	French Polynesia	COI_PF01	maxima			
Dubousquet et al. (present study)	MF167467	French Polynesia	COI_PF02	maxima			
Dubousquet et al. (present study)	MF167468	French Polynesia	COI_PF03	maxima			
Dubousquet et al. (present study)	MF167469	French Polynesia	COI_PF04	maxima			

Dubousquet et al. (present study)	MF167510	French Polynesia	COI_PF45	maxima
Dubousquet et al. (present study)	MF167511	French Polynesia	COI_PF46	maxima
Dubousquet et al. (present study)	MF167512	French Polynesia	COI_PF47	maxima
Dubousquet et al. (present study)	MF167513	French Polynesia	COI_PF48	maxima
Dubousquet et al. (present study)	MF167514	French Polynesia	COI_PF49	maxima
Dubousquet et al. (present study)	MF167515	French Polynesia	COI_PF50	maxima
Dubousquet et al. (present study)	MF167516	French Polynesia	COI_PF51	maxima
Dubousquet et al. (present study)	MF167517	French Polynesia	COI_PF52	maxima
Dubousquet et al. (present study)	MF167518	French Polynesia	COI_PF53	maxima
Dubousquet et al. (present study)	MF167519	French Polynesia	COI_PF54	maxima
Dubousquet et al. (present study)	MF167520	French Polynesia	COI_PF55	maxima
Dubousquet et al. (present study)	MF167521	French Polynesia	COI_PF56	maxima
Dubousquet et al. (present study)	MF167522	French Polynesia	COI_PF57	maxima
Dubousquet et al. (present study)	MF167523	French Polynesia	COI_PF58	maxima
Dubousquet et al. (present study)	MF167524	French Polynesia	COI_PF59	maxima

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Study Source	Acc No	Locality	Name used in study	Putative species	Latitude (decimal degrees)	Longitude (decimal degrees)
Richter et al. 2008	AM909765	Indonesia		Hippopus hippopus		
Lizano & Santos 2014	KJ508348	Philippines		Hippopus hippopus		
Schneider & O'Foighil 1999	AF122974	aquarium store		Hippopus porcellanus		
DeBoer et al. 2008	EU341346	Indonesia	TSD_16 (white)	crocea		
Huelsken et al. (present study)	JX974861	Torres Strait, Australia	ET1879	crocea	-10.54	142.35
Huelsken et al. (present study)	JX974872	Lizard Island, Australia	ET544	crocea	-14.65	145.45
Richter et al. 2008	AM909753	Jordan (RedSea)	Tsqua17	squamosa		
Huelsken et al. (present study)	JX974840	Torres Strait, Australia	ET1961	squamosa	-10.42	142.25
Huelsken et al. (present study)	JX974841	Lihou Reef, Coral Sea, Australia	ET358	squamosa	-17.41	151.88
Tang & Chen unpub	DQ119339	Taiwan	YCT-2005	sp		
Huelsken et al. (present study)	JX974879	Ningaloo, Western Australia	ET920	sp	-23.17	113.76
Huelsken et al. (present study)	JX974878	Ningaloo, Western Australia	ET918	sp	-23.17	113.76
Huelsken et al. (present study)	JX974895	Solomon Islands	ET2339	sp	-8.37	157.51
Huelsken et al. (present study)	JX974902	Lihou Reef, Coral Sea, Australia	ET356	derasa	-17.41	151.88
Richter et al. 2008	AM909743	Jordan (RedSea)	Tmax04	maxima		
Tang & Chen unpub	DQ115320	Taiwan		maxima		
Huelsken et al. (present study)	JX974849	Solomon Islands	ET2386	maxima	-8.30	157.52
Huelsken et al. (present study)	JX974855	Lihou Reef, Coral Sea, Australia	ET303	maxima	-17.59	151.50
Dubousquet et al. (present study)	MF167525	French Polynesia	16S_PF01	maxima		
Dubousquet et al. (present study)	MF167526	French Polynesia	16S_PF03	maxima		
Dubousquet et al. (present study)	MF167527	French Polynesia	16S_PF04	maxima		
Dubousquet et al. (present study)	MF167528	French Polynesia	16S_PF05	maxima		
Dubousquet et al. (present study)	MF167529	French Polynesia	16S_PF06	maxima		

ITS

Study Source	Acc No	Name used in study	Putative species	Locality
Pradillon et al. 2006	AM182282		Cerastoderma edule	Germany
Taylor et al. 2007	AM774520		Cerastoderma edule	United Kingdom
Sharma et al. 2013	KC429384		Cerastoderma edule	?
Maruyama et al. 1998	D84660		Hippopus hippopus	?
Maruyama et al. 1998	D84661		Hippopus hippopus	?
Winnepenninckx et al. 1996	X91972		sp	?
Maruyama et al. 1998	D84190		squamosa	?
Maruyama et al. 1998	D84658		derasa	?
Maruyama et al. 1998	D88908		crocea	?
Maruyama et al. 1998	D84659		maxima	?
Taylor et al. 2007	AM774523		maxima	Australia
Dubousquet et al. (present study)		18S-PF01	maxima	French Polynesia
Dubousquet et al. (present study)		18S-PF02	maxima	French Polynesia
Dubousquet et al. (present study)		18S-PF03	maxima	French Polynesia
Dubousquet et al. (present study)		18S-PF04	maxima	French Polynesia
Dubousquet et al. (present study)		18S-PF05	maxima	French Polynesia
Dubousquet et al. (present study)		18S-PF06	maxima	French Polynesia

Table S2. Pairwise population FST differences and significant level

pairwise population Fst differences between samplings and p-value

Archipelago	Australes		Gambier		Society			Tuamotu								
Islands	Maria	Tubuai	Raivavae	Mangareva	East Tahiti	South Tahiti	West Tahiti	Moorea	Tikehau	Apataki	Kaukura	Reao	Tatakoto	Hao	Makemo	Kauehi
Maria	-	-	-	-	-	-	+	-	-	-	-	+++	+++	+++	++	++
Tubuai	-0.02459	-	-	-	-	-	++	-	-	-	+	++	+++	+++	+++	+++
Raivavae	-0.03015	-0.06325	-	-	-	-	+++	+	+++	+++	+++	+++	+++	+++	+++	+++
Mangareva	0.01718	-0.01944	0.02721	-	-	-	+++	-	-	-	-	+	+++	+++	+++	++
East Tahiti	-0.03672	-0.03489	0.00269	-0.07716	-	-	+++	-	+	+	+	+++	+++	+++	+++	+++
South Tahiti	-0.03896	-0.02564	-0.03747	-0.07692	-0.08182	-	++	-	-	+	++	+++	+++	+++	+++	+++
West Tahiti	0.20452	0.21303	0.22638	0.19779	0.20132	0.18391		+++	+++	-	+++	+++	+++	+++	+++	+++
Moorea	0.1609	0.07599	0.20405	-0.02949	0.07665	0.10624	0.3119		-	-	-	++	+++	+++	+++	-
Tikehau	0.42659	0.32004	0.42895	0.17998	0.30233	0.37294	0.4523	-0.00114		-	-	+	++	+++	-	-
Apataki	0.34932	0.2637	0.39495	0.13601	0.25575	0.31152	0.29753	-0.0095	-0.06782		-	-	-	++	+	+
Kaukura	0.52096	0.41463	0.49837	0.25294	0.37846	0.47208	0.46597	0.01154	-0.18343	-0.17889		-	-	+++	-	-
Reao	0.55824	0.50337	0.57516	0.41724	0.49139	0.53333	0.40442	0.28528	0.22584	0.0064	0.12171		-	-	+++	++
Tatakoto	0.73946	0.68714	0.68927	0.59246	0.64483	0.70767	0.5576	0.42765	0.31453	0.14894	0.18772	0.00347		-	+++	+++
Hao	0.91851	0.87759	0.78706	0.79053	0.79829	0.88047	0.63506	0.65037	0.61251	0.47596	0.61132	0.17949	0.03419		+++	+++
Makemo	0.70384	0.63675	0.6454	0.51839	0.58727	0.66071	0.61328	0.31139	0.02112	0.18752	-0.04487	0.35961	0.33938	0.60833		-
Kauehi	0.75	0.67233	0.68849	0.57105	0.63607	0.71814	0.66088	0.34768	0.11168	0.23077	0.07376	0.37987	0.38262	0.71852	0.01916	

upper: not significant (-), 0.01<p<0.05 (+), 0.001<p<0.01 (++) , p<0.001 (+++)

lower: pairwise population Fst differences

Table S3. AMOVA

	Among populations						Fst	Fct	Fct p-value
	Among groups		within groups		Withing populations				
	Var	%Var	Var	%Var	Var	%Var			
No barriers			1.06638	40.64	1.55735	59.36	0.40644		
Tuamotu vs Society vs Australes vs Gambiers	0.98568	34.04	0.37924	13.1	1.53051	52.86	0.4714	0.34043	**
East Tuamotu vs North Tuamotu vs Society vs Australes vs Gambier	1.14196	39.43	0.22403	7.73	1.53051	52.84	0.4716	0.39426	***
East Tuamotu vs North Tuamotu vs Society vs South Polynesia	1.17381	40.29	0.20905	7.18	1.53051	52.53	0.47466	0.4029	***
East Tuamotu vs North Tuamotu vs Tahiti vs Moorea vs Australes vs Gambiers	1.15741	40.63	0.16079	5.64	1.53051	53.73	0.46274	0.40629	***
East Tuamotu vs North Tuamotu vs South Polynesia	1.65013	47.29	0.30849	8.84	1.53051	43.87	0.56135	0.47293	***
East Tuamotu vs North Tuamotu vs South vs Centre Tuamotu	1.64408	47.33	0.29928	8.62	1.53051	44.06	0.55942	0.47327	***

p<0.001 (***) p<0.005 (**), p<0.05 (*)

Table S4. Migrant values

	Archipelago		Australes		Gambier		Society				Tuamotu						
	Island	Maria	Tubuai	Raivavae	Mangareva	East Tahiti	South Tahiti	West Tahiti	Moorea	Tikehau	Apataki	Kaukura	Reao	Tatakoto	Hao	Makemo	Kauehi
	Maria																
Australes	Tubuai	inf															
	Raivavae	inf	inf														
Gambier	Mangareva	28.60465	inf	17.87854													
	East Tahiti	inf	inf	185.47826	inf												
Society	South Tahiti	inf	inf	inf	inf	inf											
	West Tahiti	1.94472	1.84711	1.70867	2.0279	1.98359	2.21879										
	Moorea	2.60756	6.08018	1.95033	inf	6.02284	4.20645	1.10307									
	Tikehau	0.6721	1.06232	0.66562	2.27813	1.15385	0.84071	0.60545	inf								
	Apataki	0.93137	1.3961	0.76598	3.17622	1.45506	1.10504	1.18052	inf	inf							
	Kaukura	0.45977	0.70588	0.50328	1.47676	0.82115	0.55914	0.57303	42.82353	inf	inf						
Tuamotu	Reao	0.39567	0.4933	0.36932	0.69835	0.51751	0.43751	0.73633	1.25266	1.714	77.63158	3.60802					
	Tatakoto	0.17617	0.22765	0.22541	0.34394	0.2754	0.20654	0.39671	0.66918	1.08966	2.85714	2.16359	143.5				
	Hao	0.04436	0.06974	0.13527	0.13249	0.12634	0.06788	0.28733	0.2688	0.31632	0.5505	0.3179	2.28571	14.125			
	Makemo	0.21039	0.28524	0.27471	0.46452	0.35139	0.25676	0.31529	1.10572	23.17362	2.16635	inf	0.89039	0.97328	0.32192		
	Kauehi	0.16667	0.24368	0.22623	0.37557	0.28608	0.19624	0.25657	0.93811	3.97714	1.66667	6.27907	0.81625	0.80679	0.19588	25.58947	

