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Insights into the genetic makeup of French Polynesian peripheral populations of the small giant clam *Tridacna maxima*

Florentine Riquet[1,2] | Mathilde Horaud[1,2] | Vaimiti Dubousquet[3,4,5] | Josina Tiavouane[6] | Carmela Lopes[7] | Phila Raharivelomanana[4] | Véronique Berteaux-Lecellier[6] | Serge Planes[3] | Daphné Grulois[6] | Serge Andréfouët[8] | Simon Van Wynsberge[9] | Philippe Borsa[6] | Gaël Lecellier[6] | Cécile Fauvelot[1,2]

[1]UMR ENTROPIE (IRD, Université de La Réunion, CNRS, IFREMER, Université de la Nouvelle-Calédonie), Villefranche-sur-Mer, France

[2]CNRS, Laboratoire d'Océanographie de Villefranche, LOV, Sorbonne Université, Villefranche-sur-Mer, France

[3]PSL Research University: EPHE-UPVD-CNRS, USR CRIOBE, Université de Perpignan, Perpignan, France

[4]UMR EIO (IFREMER, ILM, IRD, Université de la Polynésie Française), Faaa, Tahiti, French Polynesia

[5]Délégation à la Recherche, Government of French Polynesia, Papeete, Tahiti, French Polynesia

[6]UMR ENTROPIE (IRD, Université de La Réunion, CNRS, IFREMER, Université de la Nouvelle-Calédonie), centre IRD de Nouméa, Nouméa, New Caledonia

[7]Département STS, Faaa, Université de Polynésie Française, Tahiti, French Polynesia

[8]C/O Ifremer/Centre Océanographique du Pacifique, Vairao, UMR ENTROPIE (IRD, Université de La Réunion, CNRS, IFREMER, Université de la Nouvelle-Calédonie), Tahiti, French Polynesia

[9]Ifremer, UMR 9220 ENTROPIE (IRD, Univ. Réunion, IFREMER, Univ. Nouvelle-Calédonie, CNRS), Nouméa, New Caledonia

Correspondence
Cecile Fauvelot, UMR ENTROPIE (IRD, Université de La Réunion, CNRS, IFREMER, Université de la Nouvelle-Calédonie),

Abstract

1. The small giant clam, *Tridacna maxima*, is distributed from the Red Sea and East African coast to French Polynesia. Across this widespread Indo-Pacific range, *T. maxima* shows strong population structure, in agreement with its limited dispersal abilities.
2. Peripheral populations may have smaller effective population sizes, increasing their vulnerability under any environmental changes. Understanding evolutionary processes at play in such regions located at the edges of *T. maxima* distribution is a prerequisite in the context of transfers and restocking programmes.
3. In this study, giant clams were sampled from 14 atolls and islands within four archipelagos in the peripheral region of French Polynesia, in 2001–2002 and/or in 2012–2013, then genotyped at the *COI* gene and at nine microsatellite loci.
4. Mitochondrial lineages of *T. maxima* from French Polynesia diverged from those sampled in Micronesia, Melanesia, the Coral Triangle and the Red Sea by 6.6–7.3%. Within French Polynesia, significant genetic structure was found, indicating restricted gene flow, and it was stable through time. Most of the genetic variation at microsatellite loci was between archipelagos. The most differentiated archipelago was the most geographically isolated (the Austral Islands).
5. The current patterns of genetic structuring of *T. maxima* in French Polynesia probably result from long-term genetic isolation with limited dispersal ability. In addition, these results underlined that sufficiently large populations of *T. maxima* have persisted in the Central Pacific during the last sea-level regression.
6. Strategies to optimize transfers and restocking programmes should be designed to preserve the genetic diversity and structure observed here, to avoid the risks

181 chemin du Lazaret, 06230 Villefranche-sur-Mer, France.
Email: cecile.fauvelot@ird.fr

Present address
Florentine Riquet, IFREMER, RBE-ASIM, Station de La Tremblade, La Tremblade, France.

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of altering the genetic structure, allele loss and/or introduction of maladapted alleles in the receiving populations.

KEYWORDS
COI gene, French Polynesia, genetic differentiation, glacial refugia, microsatellite, phylogeography, *Tridacna maxima*

1 | INTRODUCTION

While marine biodiversity hotspots are commonly recognized as regions of high conservation priority (Hughes, Bellwood & Connolly, 2002), centres of endemism receive less attention despite their role as a source of evolutionary novelty (Bowen et al., 2013; Bowen et al., 2016). A centre of endemism is defined as an area in which the ranges of restricted-range species overlap, or a specific area gathering a high occurrence of endemics. For most marine groups, such centres lie in peripheral species distribution (Bowen et al., 2016). Peripheral populations represent the geographic limit of the natural ranges of species and are of particular interest to evolutionary biologists because of their ecological and evolutionary singularity (e.g. lower effective population size, increased genetic differentiation and/or genetic drift, and variability in individual and population performance; Lesica & Allendorf, 1995; Sexton et al., 2009). The phylogeographic structure of marine species often aligns with taxonomy-based marine bioregions (Bowen et al., 2016), so that population-level genetic divergences between bioregions can be viewed as a starting point for macroevolutionary divergence. Therefore, examining phylogeographic patterns in peripheral bioregions should provide better insights into the evolutionary processes at play (Bellwood & Meyer, 2009). These data are needed to adapt current management strategy (i.e. restocking programs but also overfishing and commercial exchanges) in order to address conservation needs.

The vast majority of marine benthic organisms have a bipartite life history in which adults are sedentary and early larval stages are planktonic. A consequence of the planktonic phase is the possibility of exchanges of individuals (i.e. population connectivity) among habitat patches, as well as the possibility of colonizing suitable, vacant habitats, sometimes reachable only during rare events like hurricanes (Andréfouët et al., 2002; Levin, 2006). Patterns of connectivity are especially important for designing management strategies to restore and conserve marine populations (Hellberg, 2007). Indeed, regular exchanges of individuals maintain gene flow among populations, counterbalancing the effect of genetic drift, as allele frequencies vary over time owing to chance sampling events, with the intensity of genetic drift varying inversely with the number of breeding individuals in a population (Palumbi, 1994; Hellberg et al., 2002).

French Polynesia, which encompasses the Marquesas, Tuamotu, Society, Gambier and Austral Islands archipelagos, lies at the eastern periphery of the Indo-Polynesia province of the tropical Indo-West Pacific ensemble (Briggs & Bowen, 2012), and is hence an interesting region to study the colonization history of Indo-Pacific coral reef associated organisms. In addition, its present shallow-water habitats (lagoons) were subjected to eustatic sea-level changes in the late Quaternary glacial ages and disappeared during the low stands, adding a palaeogeographical component to the phylogeographic structure of reef communities (Hewitt, 2003; Pellissier et al., 2014). Specifically, sea-level regression in the Pleistocene resulted in severe reductions in shallow-water reef habitats (Lambeck & Chappell, 2001) or even local extinction of strictly lagoon resident coral reef species (Paulay, 1990; Arnaud-Haond, Bonhomme & Blanc, 2003; Fauvelot, Bernardi & Planes, 2003). Bivalves were particularly affected as about one-third of the species that inhabited the Central Pacific islands went extinct (Paulay, 1990). With the resurgence of lagoons during the Holocene sea-level transgression, the occurrence of strictly lagoonal species in French Polynesia should have resulted from postglacial colonization of individuals from western Pacific refugia. This was possibly the case of the small giant clam, *Tridacna maxima* (Röding, 1798).

Of the 12 currently known species of giant clams (Fauvelot et al., 2020; Tan, Neo & Huang, 2022), only two species of the genus *Tridacna* occur in French Polynesia, *Tridacna maxima* and *Tridacna squamosa*. Interestingly, these are the two species with the widest geographic distribution (Neo et al., 2017). *Tridacna squamosa* Lamarck, 1819 is rare and exclusively occurs on forereefs in three of the five archipelagos of French Polynesia, namely the Austral Islands, Tuamotu and Gambier island archipelagos (Andréfouët et al., 2014). In contrast, *T. maxima* occurs in more or less high densities in four of the five archipelagos of French Polynesia (it is absent or nearly absent in the Marquesas), which represents the extreme eastern range of this species (Neo et al., 2017). In French Polynesia, *T. maxima* preferentially occurs in shallow waters of lagoons (but see Van Wynsberge et al., 2016). In several atoll lagoons of the Tuamotu Archipelago, *T. maxima* grow and form large permanent aggregations of individuals (Gilbert et al., 2005), reaching the highest recorded densities over all of its range (Van Wynsberge et al., 2016).

The genetic characterization of *T. maxima* populations in French Polynesia is so far limited to very few studies. A mitochondrial DNA (mtDNA) divergence was observed between the Society Islands and the Western Pacific (Hui et al., 2016), with a 26-step mutation divergence equivalent to that found between the Central Pacific clade and the Indo-Malay clade (Gardner et al., 2012; Keyse et al., 2018). However, the relationship between French Polynesian and Central Pacific clades has not yet been established. Within French Polynesia, Laurent, Planes & Salvat (2002) observed significant genetic

differentiations between islands located within the Society and Tuamotu archipelagos and a significant correlation between genetic and geographic distances, suggesting a stepping-stone gene flow. Yet, as the observed genetic differentiation was mainly driven by a single locus under diverging selection, the relationship between neutral gene flow and geographic distance could not be assessed (Laurent, Planes & Salvat, 2002).

Conservation approaches to lessen the worldwide decline of wild giant clam populations involve implementing local management and enforcement efforts, as well as restocking of cultivated individuals to coral reefs (Tan, Neo & Huang, 2022). *Tridacna maxima* remains abundant over all of French Polynesia (Gilbert et al., 2006; Van Wynsberge et al., 2013): it is not a species threatened with extinction in any of the French Polynesia islands. Yet its abundance has significantly decreased in the past decades or even recent years in many areas, in particular owing to overfishing in the densely populated areas of the Society Islands (Van Wynsberge et al., 2016), and in some lagoons owing to massively lethal weather warming events (Van Wynsberge & Andréfouët, 2017; Andréfouët et al., 2018). In response to the overfishing problem, the local fishery management service (Direction des Ressources Marines) has imported specimens from well-stocked Tuamotu atoll lagoons to the depleted Society Island lagoons, in particular into Tahiti. However, clarification of the lineages existing in the region and clear assessment of the genetic differences of *T. maxima* between archipelagos and between islands is highly recommended before any transfers, and this information is still missing to date.

In this context, the objectives of this study were threefold: (1) to uncover the genetic relationships of French Polynesian *T. maxima* populations with *T. maxima* lineages from over the species' entire distribution; (2) to investigate the phylogeographic structure of *T. maxima* among archipelagos in French Polynesia and to infer its spatial scales of dispersal in this region; and (3) to investigate the demographic history of *T. maxima* populations in light of Holocene sea-level changes. This set of information helps clarify which conservation measures should be considered for the management of this emblematic species in French Polynesia.

2 | METHODS

2.1 | Sampling

Note that each sample (i.e. the total number of individuals sampled in a specific location at a specific period of time) is labelled throughout the Results section based on the sampling site and sampling year, as follows: ARCHIPELAGO_SITE_YEAR. *Tridacna maxima* were sampled during two periods (2001–2002 and 2012–2013) at 14 islands' and atolls' lagoons across the four archipelagos of French Polynesia where the species occurs – Society Islands (SI), Tuamotu Archipelago (TU), Austral Islands (AI) and Gambier Islands (GI). Eleven islands were sampled only once, two islands were sampled in two different periods (Moorea (SI_MOO) and Tubuai (AI_TUB), Figure 1, Table 1) and one island, Raivavae, was sampled three times (AI_RAV, Figure 1, Table 1). Briefly, at each sampling site, from seven to 30 individuals were randomly sampled by scuba diving (Table 1). For each specimen sampled in 2001–2002, a piece of muscle or mantle was placed in an individual tube, stored in liquid nitrogen in the field and then at −80 °C back in the laboratory. For specimens sampled in 2012 and 2013, mantle biopsies were conducted and tissues were preserved in 80% ethanol for subsequent genetic analyses.

2.2 | DNA amplification, microsatellite genotyping and mitochondrial DNA sequencing

Total genomic DNA was extracted from each tissue sample using the Wizard Genomic DNA Purification Kit (Promega Corporation, Madison WI, USA) or the DNeasy Blood and Tissue Kit (Qiagen, Valencia CA) following manufacturers' protocols. All individuals were genotyped using 12 microsatellite markers specifically developed for *T. maxima* as described in Grulois et al. (2015). Amplified products were separated by electrophoresis on an ABI 3130xl DNA sequencer (Applied Biosystems, Carlsbad, CA, USA) at Plateforme Gentyane (INRA, Clermont-Ferrand, France). Alleles were scored using GeneMapper® v. 4.0 (Applied Biosystems) and checked visually. The reliability of genotyping was assessed by genotyping again 10% of the total number of individuals randomly chosen: all alleles were identically scored.

For a subset of individuals from 2012 and 2013 ($N = 128$, Table 1), the 5′-end fragment of the mitochondrial cytochrome c oxidase subunit I (*COI*) gene was amplified using primers CO1-Tricro-F and CO1-Tricro-R (Kochzius & Nuryanto, 2008), or the *COI*-F (5′-CGGTAAAACGACGGCCAGTGGGTGATAATTCGAACAGAA-3′) and *COI*-R (5′-GGAGCGGATAACAATTTCACACAGGAACGAACGCTGTAATACC-3′) primers, modified from Kochzius & Nuryanto (2008) and designed from the highly conserved regions within the published sequences of the *T. maxima COI* gene. The PCR analyses were carried out in a final volume of 25 µL containing 10–100 ng template DNA, 1× Green GoTaq® Flexi Buffer (Promega), 2 mM $MgCl_2$, 0.2 mM dNTPs, 0.8 µM forward and reverse primers and 1 U GoTaq® Flexi DNA Polymerase (Promega). The PCR reaction consisted of seven cycles of 45 s at 94°C, 45 s at 40°C and 45 s at 72°C, followed by 30 cycles of 45 s at 94°C, 45 s at 50°C and 45 s at 72°C. Amplified products were sent to GATC Biotech (Konstanz, Germany) for sequencing on an ABI 3730XL Genetic Analyzer (Applied Biosystems) using the forward primer. All sequences are available from Genbank, accession numbers MF167466–MF167499 and OR262491–OR262494 (Table S1).

2.3 | Mitochondrial data analysis

In addition to the 128 mitochondrial DNA (mtDNA) *COI* new sequences from this study, available *COI* sequences of *T. maxima* were downloaded from the NCBI Nucleotide database (https://www.ncbi.nlm.nih.gov/nucleotide/): DQ155301 (Tang, 2005), EU346365-68

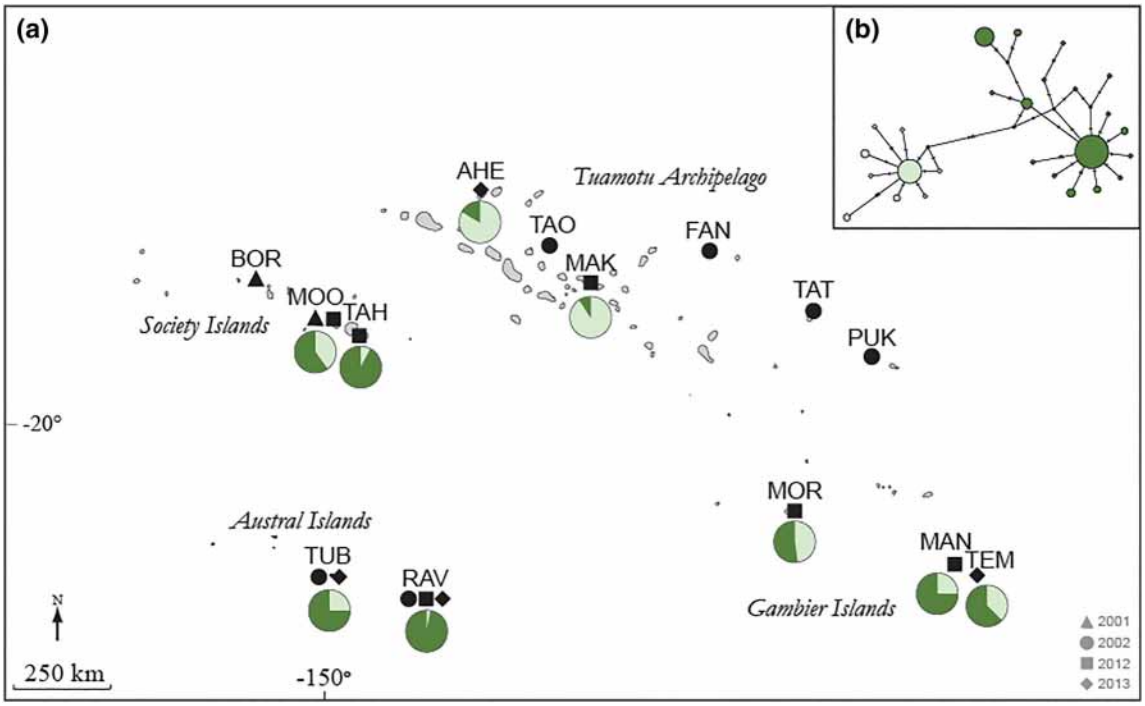

FIGURE 1 (a) Map of French Polynesia with sampling locations of *Tridacna maxima*. (b) Median-joining network based on *COI* haplotypes, with relative frequencies of Haplogroups 5a (dark green) and 5b (light green) presented as green pies on the map (see Figure 2 and Figure S1 for detailed network). AHE, Ahe; BOR, Bora Bora; FAN, Fangatau; MAK, Makemo; MAN, Mangareva; MOO, Moorea; MOR, Moruroa; RAV, Raivavae; PUK, Pukarua; TAH, Tahiti; TAO, Taiaro; TAT, Tatakoto; TEM, Temoe; TUB, Tubuai. Sampling details are provided in Table 1. Individuals sampled in 2001 represented by a triangle, those sampled in 2002 by circles, those sampled in 2012 by squares and those sampled in 2013 by diamonds.

(DeBoer et al., 2008), EU003610-14 (Nuryanto et al., 2007), FM244476-85 and FM244513-619 (Nuryanto & Kochzius, 2009), HE995454–87 (Hui et al., 2016), JX974926-44 (Huelsken et al., 2013), KF446329-515 (DeBoer et al., 2014), KY769524-25 (Findra et al., 2017), LC322934-76 (Ben Othmen et al., 2020), MG195196-278 (Neo et al., 2018), MG385346-480 (Keyse et al., 2018) and MN068731-87 (Fauvelot et al., 2020), as well as *COI* sequences from Tarawa Atoll (Republic of Kiribati) and Palmyra Atoll (Gardner et al., 2012; Keyse et al., 2018). Only sequences with non-ambiguous base calls were kept, totalling 657 published *COI* sequences (detailed list in Table S1). It should be noted that some of these sequences represent distinct haplotypes (e.g. Hui et al., 2016) while for some others, sequences correspond to specimens from one location (e.g. Keyse et al., 2018) that can share the same haplotype. All 785 sequences were visually aligned in Genedoc (Nicholas & Nicholas, 1997) and trimmed to a common length of 400 base pairs (bp).

To examine the phylogenetic relationships of *T. maxima* haplotypes from French Polynesia relative to the genetically distinct mtDNA clades already reported over its entire Indo-Pacific range, a median-joining network (Bandelt, Forster & Röhl, 1999) was constructed as implemented in PopArt (Leigh & Bryant, 2015) based on the 785 mtDNA *COI* gene sequences presented above. The ε value was set to 0 to reduce complexity introduced by reticulation in the network and the resulting network was manually arranged in Adobe Illustrator®. Mean net nucleotide divergences among distinct clades were estimated based on uncorrected *P*-distance in MEGA X (Kumar et al., 2018). To further explore the phylogenetic relationship of *T. maxima* lineages, a subset of sequences was selected to work on. Fourteen to 16 distinct haplotypes belonging to each clade were randomly chosen (see Results) which also coincides with the regional distribution. Note that for Clade 5, 24 distinct haplotypes belonging to the two haplogroups were selected (see Results). Bayesian inference was used, implemented in the software MrBayes 3.2.6 (Ronquist et al., 2012) through CIPRES Science Gateway V. 3.3 (Miller, Pfeiffer & Schwartz, 2010). Two *COI* gene sequences of *T. elongatissima* Bianconi, 1856 were used as outgroup (Fauvelot et al., 2020). The best fit model was selected according to the Bayesian information criterion in MEGA X, which favoured HKY + G (Hasegawa, Kishino & Yano, 1985). Starting trees for each chain were random and the default values of MrBayes software were chosen for all settings (including prior distributions). Each Metropolis-coupled Markov chain Monte Carlo (MCMC) was run for 10^8 generations (i.e. sufficient time for all chains to converge to stable likelihood values <0.001), with trees sampled every 5,000 generations and the first 25% discarded as burn-in. Convergence was checked for each parameter (all effective sample size [ESS] >> 200; all potential scale reduction factor [PSRF] = 1.0) using Tracer 1.7.1 (Rambaut et al., 2018). Posterior probabilities (PP) were used to assess clade support.

Within French Polynesia, genetic diversity for the mitochondrial gene was estimated within each sampling site as haplotype diversity (Nei, 1987), nucleotide diversity (Nei, 1987) and mean number of

TABLE 1 Sampling details and genetic diversity indices in *Tridacna maxima* for each samples based on a 400 bp fragment of the mtDNA *COI* gene and nine microsatellite loci.

Archipelago Island	Year of sampling	Label	Mitochondrial DNA *COI* sequences						Microsatellite loci				
			N	*S*	*Hd*	*π*	*k*	*D*	*N*	N_{all}	A_r	H_e	F_{IS}
Society Islands (SI)													
Bora Bora	2001	BOR__01	–		–	–	–		18	8.3	5.3	0.758	0.024
Moorea	2001	MOO__01	–		–	–	–		16	7.1	4.9	0.749	0.129***
	2012	MOO__12	5	5	0.40	0.007	2.80	−1.161	7	4.8	4.0	0.699	0.137***
Tahiti	2012	TAH__12	25	12	0.60	0.007	2.67	−0.764	26	9.3	5.4	0.767	0.093**
Tuamotu (TU)													
Ahe	2013	AHE__13	6	8	0.60	0.007	2.67	−1.408	13	7.2	5.0	0.777	0.113**
Taiaro	2002	TAO__02	–		–	–	–		9	5.0	3.9	0.747	0.181***
Makemo	2012	MAK__12	11	11	0.67	0.006	2.25	−1.719	10	5.8	4.5	0.717	0.091
Fangatau	2002	FAN__02	–		–	–	–		28	10.1	5.5	0.738	0.082*
Tatakoto	2002	TAT__02	–		–	–	–		21	7.7	5.0	0.721	−0.010
Pukarua	2002	PUK__02	–		–	–	–		21	9.0	5.4	0.765	0.100**
Gambier Islands (GI)													
Moruroa	2012	MOR__12	23	15	0.77	0.013	5.17	0.971	22	8.9	5.5	0.778	0.082*
Mangareva	2012	MAN__12	8	8	0.61	0.008	3.25	0.257	8	6.4	5.1	0.758	0.015
Temoe	2013	TEM__13	8	7	0.54	0.009	3.75	1.851	10	6.9	4.8	0.715	0.116
Austral Islands (AI)													
Tubuai	2002	TUB__02	–		–	–	–		20	9.6	5.9	0.812	0.106**
	2013	TUB__13	12	15	0.92	0.012	4.83	−0.115	30	10.2	5.7	0.782	0.090**
Raivavae	2002	RAV__02	–		–	–	–		22	9.8	6.0	0.815	0.177***
	2012	RAV__12	–		–	–	–		12	7.7	5.5	0.767	0.086*
	2013	RAV__13	30	26	0.83	0.007	2.99	−1.843*	22	9.9	5.6	0.787	0.148

Note: Each sampling site is labelled as follows: ARCHIPELAGO_SITE_YEAR, with SI, TU, GI and AI for the Society Islands, Tuamotu, Gambier Islands and Austral Islands, respectively.

Abbreviations: A_r, allelic richness (based on six individuals); *D*, Tajima's *D* (1989); F_{IS}, fixation index; *Hd*, Haplotype diversity; H_e, expected heterozygosity; *k*, mean number of pairwise nucleotide differences between two individuals; *N*, number of analysed individuals; N_{all}, mean number of alleles per sample; *S*, number of segregating sites; *π*, nucleotide diversity.

*$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$.

pairwise nucleotide differences between individuals (Tajima, 1983) using DnaSP v6.12.03 (Rozas et al., 2017). A median-joining network was constructed based on the 128 *COI* gene sequences exclusively obtained from the sampled individuals, as described above. Mitochondrial DNA sequences were analysed using ARLEQUIN v. 3.5.2.2 (Excoffier & Lischer, 2010) to test the null hypothesis of mutation-drift equilibrium within sampling sites and archipelagos, using Tajima's *D* (Tajima, 1989). The observed *D* values were compared with the distribution expected under the infinite-site model without recombination, as generated by 1,000 coalescent simulations based on the observed number of segregating nucleotide sites (*S*). Fu's *Fs* test (Fu, 1997), which aims to identify an excess of substitutions caused by recent population growth, genetic hitch-hiking, or background selection, was also used. Demographic history within each of the four archipelagos was examined from the mismatch distribution based on the number of pairwise nucleotide site differences among individuals. Two theoretical distributions under DnaSP were also computed, the first one as expected for a population of constant population size at equilibrium, based on the observed theta values, and the second one as expected in growing and declining populations (Rogers & Harpending, 1992). To test whether one model fitted the observed data better than the other model, square deviations (SD) between frequencies of observed pairwise differences and their expectations under the two different models were estimated. A paired *t*-test was used to test for differences in SDs, as described in Peijnenburg, van Haastrecht & Fauvelot (2005). If significant, the model with the smaller sum of all SDs was assumed to best explain the data.

Genetic differentiation among sampling sites within French Polynesia was estimated from mtDNA nucleotide sequence divergences using Φ_{ST} in ARLEQUIN, based on the T92 + G nucleotide substitution model (Tamura, 1992) with $G = 0.07$, selected according to the Bayesian information criterion in MEGA. *P*-Values were estimated from the pseudo-distribution of Φ_{ST} generated by 10,000 random permutations on the original matrix of sequences. In addition, a hierarchical analysis of molecular variance (AMOVA;

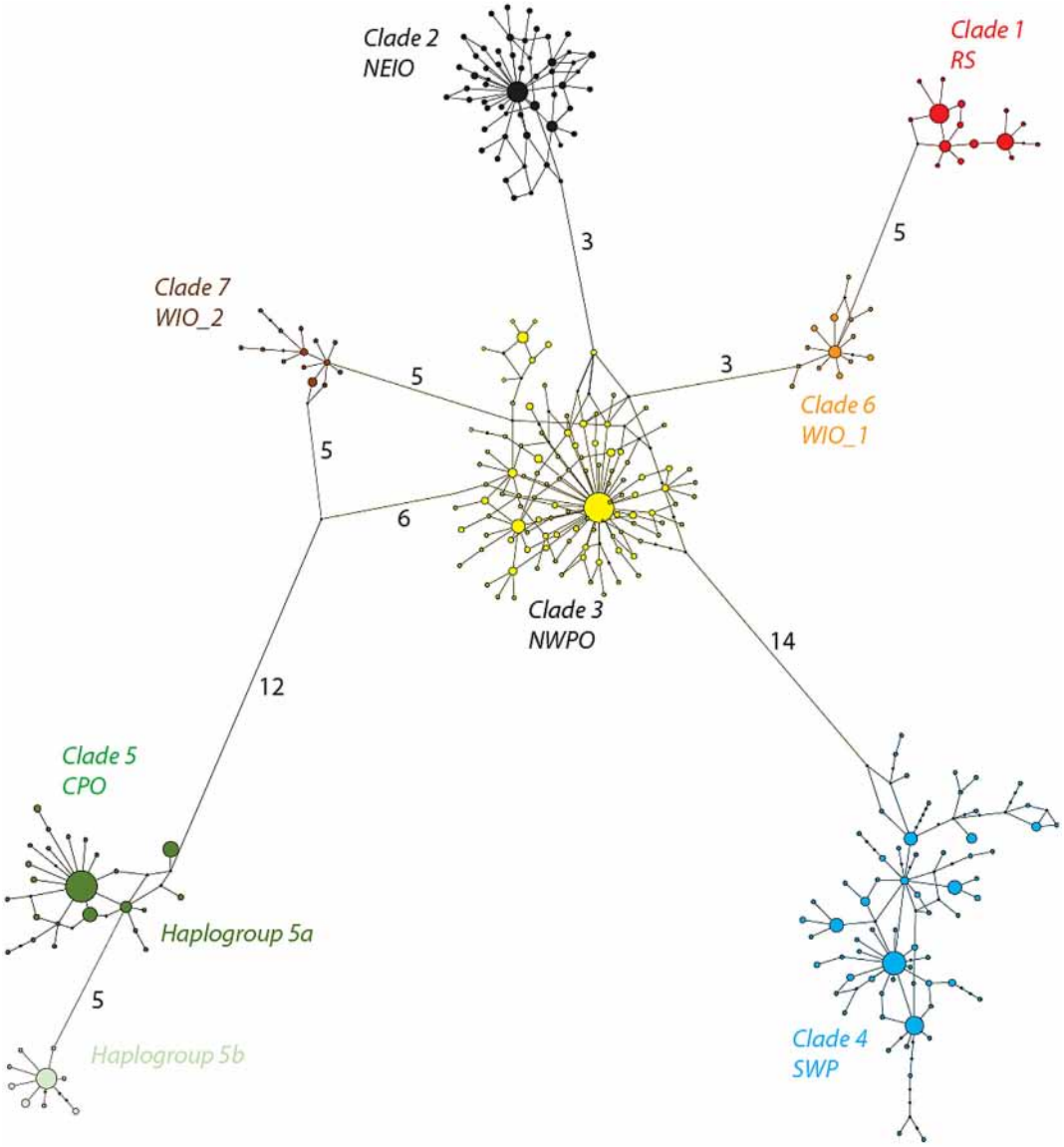

FIGURE 2 Median-joining haplotype network of *Tridacna maxima* based on 657 published *COI* gene sequences and 128 newly described sequences from French Polynesia. Haplogroups are designated as clades according to Fauvelot et al. (2020). CPO, Central Pacific Ocean; NEIO, Northeastern Indian Ocean; NWPO, North-western Pacific Ocean; RS, Red Sea; SWP, South-western Pacific; WIO, Western Indian Ocean. Circles represent unique *COI* haplotypes sized by frequency; connections among haplotypes represent one nucleotide substitution, unless specified by numbers equivalent to counts of nucleotide substitutions between haplotypes. Black dots represent missing haplotypes connecting haplotypes recovered in the sequence dataset. For French Polynesia samples, haplotype frequencies based on identity to Haplogroup 5a and 5b are shown by pie graphs on Figure 1.

Excoffier, Smouse & Quattro, 1992) was computed in ARLEQUIN, where sampling sites were grouped by archipelago to examine the partitioning of the total variance among the four archipelagos. The significance of the observed Φ_{ST} values and associated variance components was estimated by 10,000 random permutations.

2.4 | Nuclear data analysis

First, MICRO-CHECKER (Van Oosterhout, Weetman & Hutchinson, 2006) was used to detect the presence of null alleles in the microsatellite dataset. Loci that showed high null alleles frequencies were removed from the final dataset. Then, based on this final dataset, genetic diversity was estimated for each sample (i.e. each sampling site and temporal replicate) as the mean number of alleles per locus and allelic richness (i.e. the expected number of alleles corrected for sampling size, based on a rarefaction method) using the R package diveRsity (Keenan et al., 2013). GENEPOP 4.2. (Rousset, 2008) was used to estimate expected heterozygosity and fixation index (F_{IS}) and to test for departure from Hardy–Weinberg (HW) equilibrium in each sample (10,000 dememorization steps, 500 batches and 5,000 iterations per batch).

Genetic structure among samples at microsatellite loci was assessed using: (1) estimates of F_{ST} (Weir & Cockerham, 1984); (2) principal component analysis (PCA; Pearson, 1901) computed on the matrix of genotypes; (3) an individual-based Bayesian clustering method; and (4) AMOVAs. Comparing results from these different analyses using different statistical approaches allows solid assumptions about the genetic structure to be made. First, estimates of F_{ST} were calculated using GENEPOP. Exact tests for population differentiation (10,000 dememorization steps, 500 batches and 5,000 iterations per batch) were carried out to test for differences in allele distributions across samples and between pairwise samples. Isolation-by-distance was tested by investigating the relationship between pairwise matrices of linearized genetic distances ($F_{ST}/1 - F_{ST}$) and the natural logarithm of shortest path geographic distances with Mantel tests implemented in GENEPOP. The shortest path geographic distance among sampling sites was estimated as the shortest geographic distances, excluding landmasses, using the R package geosphere (Hijmans, 2012). Then, in order to graphically visualize the overall genetic distance between samples, the genetic structure was also depicted using a PCA, performed using the R package adegenet 1.4–2 (Jombart, 2008; Jombart & Ahmed, 2011), a distance-based approach for which few (nearly no) assumptions may be violated. The individual-based Bayesian clustering analysis was performed with the software STRUCTURE 2.3.4 (Pritchard, Stephens & Donnelly, 2000; Falush, Stephens & Pritchard, 2007). This method contrasted with the two other approaches as STRUCTURE is a model-based approach with strong priors and hypotheses (HW equilibrium, linkage equilibrium; Jombart, Devillard & Balloux, 2010). Identifying the 'true' number of genetic clusters (K) can be challenging, the ΔK approach tending to underestimate genetic structure (Janes et al., 2017). In this context, different values of K were explored (up to 20) following a hierarchical analysis. For each value of K, five replicate chains of 200,000 MCMC iterations were run after discarding 25,000 burn-in iterations. Following Wang's (2017) recommendations, several models were tested: with and without an admixture model, and for both models, with and without uncorrelated allele frequencies. Besides, for each of these four models, different values of the initial alpha parameter, from 1/10 (i.e. with a 'true' K of 10) to 1 ($K = 1$, suggesting one panmictic population) were tested. Since all models tested led to very similar results, results with $\alpha = ½$ (i.e. with a 'true' $K = 2$) were thereafter presented when all samples were analysed, and with alpha = 1 (i.e. with a 'true' $K = 1$) when five or 14 samples were analysed (see below). To determine individual ancestry proportions (q-values) that best matched across all replicate runs, CLUMPP (Jakobsson & Rosenberg, 2007) was used and individuals' assignments visualized in the R software (R Core Team, 2017). Finally, a hierarchical AMOVA was performed using the R package poppr (Kamvar, Tabima & Grünwald, 2014), with 10,000 permutations to assess significance among and within sampling periods, then archipelagos. This approach, making no assumptions about HW equilibrium, aims to assess population differentiation by evaluating where the most variation exists in a hierarchical population structure (here, period or archipelago, i.e. temporal vs. spatial genetic structure).

BayesAss 3.0.4 (Wilson & Rannala, 2003) was used to estimate recent levels of gene flow among sampling sites, we used. As recommended, this involved: (1) manually conducteing exploratory runs using the default value of each mixing parameter (i.e. migration rates, allele frequencies and inbreeding coefficients of 0.1); (2) evaluating the resulting acceptance rates of these parameters; and (3) repeating the process by adjusting mixing parameter values for subsequent runs until acceptance rates fall within a desired range (Wilson & Rannala, 2003). The MCMC was run for 100×10^6 iterations, discarding the first 25×10^6 iterations, with mixing parameters of 0.75. Convergence was checked using Tracer 1.7.1 (Rambaut et al., 2018).

Finally, to test for evidence of a recent reduction in effective population size, the microsatellite data set was analysed using BOTTLENECK 1.2.02 (Cornuet & Luikart, 1996; Piry, Luikart & Cornuet, 1999). This test detects significant differences between the gene diversity (HExp) and the expected equilibrium heterozygosity (HEq) calculated through simulations from the observed number of alleles at each locus, under various mutation models (Luikart & Cornuet, 1998). A significant excess or deficiency of HExp compared with the HEq can be interpreted as a signature of a recent change in population size (Luikart & Cornuet, 1998). The HEq was calculated under the stepwise mutation model (SMM) and the two-phase mutation model (TPM) with 95% single-step mutations in each sample with $N > 10$. Significant differences between HExp and HEq were estimated with the Wilcoxon signed-rank test.

3 | RESULTS

3.1 | Setting the scene at the Indo-Pacific scale

The results addressed in this section are based on mtDNA sequences, focusing on the sampling sites, regardless of the sampling period, and aiming to analyse the genetic diversity of French Polynesian *T. maxima* with regards to all Indo-Pacific *T. maxima*.

The 785 *Tridacna maxima COI* gene sequences were assigned to 296 distinct haplotypes belonging to seven distinct haplogroups (Figure 2, Table S1). All 128 new sequences of French Polynesia *T. maxima* represented 26 haplotypes, all grouped in Haplogroup 5, together with six published haplotypes from the Society Islands (Hui et al., 2016) and 33 published sequences from Palmyra and Tarawa atolls (Gardner et al., 2012; Keyse et al., 2018). A minimum of 19 substitutions separated Haplogroup 5 from another haplogroup previously designated Clade 3, containing sequences from the tropical North-western Pacific, or from Clade 7, exclusive to the western Indian Ocean (Hui et al., 2016; Fauvelot et al., 2020). Mean net nucleotide divergence among clades varied from 1.62 ± 0.64 to 7.73 ± 1.12% (Table S2). Haplogroup 5 was nearly equally divergent from all other clades, with uncorrected *P*-distances at the *COI* gene ranging from 6.3 (with Clade 3 or Clade 7) to 7.7% (with Clade 4; Table S2). Haplogroup 5 was further divided into two haplogroups (Haplogroup 5a and 5b) diverging from each other by five nucleotide

substitutions (Figure 2, Figure S1). All sequences from Tarawa and Palmyra (Gardner et al., 2012) clustered into Haplogroup 5a, except two sequences from Tarawa that were found in Clade 3 (Table S1).

The Bayesian analysis retrieved seven more or less supported (PP = 0.79–1.0) *T. maxima* clades, with Clade 5 being strongly (PP = 1.0) supported (Figure S2). Clade 5, which encompassed Haplogroups 5a and 5b was sister to a strongly supported (PP = 1.0) clade comprising five *T. maxima* clades: the three West Indian Ocean and Red Sea clades, the Northeastern Indian Ocean clade (Clade 2 of Keyse et al., 2018) and the North-western Pacific Ocean clade (Figure S2). The South-western Pacific clade (Clade 4) was placed at the base of the *T. maxima* phylogenetic tree.

3.2 | Setting the scene at the regional scale: within French Polynesia

3.2.1 | *Genetic diversity of T. maxima within French Polynesia*

Mitochondrial *COI* genetic diversity was uneven across samples (Table 1), with haplotype diversity ranging from 0.40 (SI_MOO_12) to 0.92 (AI_TUB_13), and nucleotide diversity ranging from 0.6% (TU_MAK_12) to 1.3% (SI_MOR_12). The mean number of pairwise nucleotide differences varied from 2.25 (TU_MAK_12) to 5.17 (SI_MOR_12). While Haplogroups 5a and 5b were represented at all sites across French Polynesia, their frequencies strongly differed among sites (Figure 1, Figure S1). Haplogroup 5a comprised 18 haplotypes which were found at relatively high frequencies in the sites sampled in the Society (86.7%) and Austral islands (90.5%). Haplogroup 5b comprised nine haplotypes which were predominant (88%) in two atolls of the Tuamotu Archipelago (Ahe and Makemo). In the Gambier Islands, the two haplogroups were found in 59 and 41% for Haplogroup 5a and Haplogroup 5b, respectively. The genetic diversity within Haplogroup 5a was more than twice that found in Haplogroup 5b ($\pi = 0.53\%$ and $k = 2.12$ for Haplogroup 5a, $\pi = 0.2\%$ and $k = 0.87$ for Haplogroup 5b).

Using nuclear data, MICRO-CHECKER suggested the presence of null alleles at three microsatellite loci that showed a high percentage of missing data (Tm_025349, 31.11%; Tm_018921, 14.92%; and Tm_024224, 11.43%; Figure S3). These three loci were removed from further analysis. Genotyping was attempted for a total of 341 individuals using nine microsatellite markers (each with less than 10% of missing data per locus; Figure S3), and 307 individuals were successfully amplified (3.7% missing data, seven to 34 alleles/locus). Mean allelic richness per locus per sample and expected heterozygosity across samples ranged from 3.9 (TU_TAO_02) to 6.0 (AI_RAV_02) and from 0.699 (SI_MOO_12) to 0.815 (AI_RAV_02), respectively (Table 1). Hardy–Weinberg equilibrium at all microsatellite loci was not rejected for five samples; all the other samples showed significant departure from HW equilibrium at one to three microsatellite loci, but not consistently the same three loci (Figure S4). Genotype frequencies at one microsatellite locus (Tm_01666) were consistent with HW equilibrium in all samples; at the eight other microsatellite loci, HW equilibrium was rejected for at least one sample (Figure S4). When combining loci, departure from HW equilibrium was found in 13 samples, all owing to a deficit in heterozygotes. Note that the null hypothesis of HW equilibrium was not rejected for sample SI_BOR_01 when combining loci, despite the presence of one locus showing HW disequilibrium. In addition, genotype frequencies in sample AI_RAV_12 did not depart from HW equilibrium over all nine loci, despite HW equilibrium being rejected for one of the nine loci.

3.2.2 | *Genetic structure of T. maxima within French Polynesia*

Significant genetic heterogeneity was observed at the mitochondrial locus (overall $\Phi_{ST} = 0.265$, *P*-value < 0.0001). Significant pairwise Φ_{ST} values generally involved the TU_MAK_12 and AI_RAV_12 samples (Table 2). Samples within archipelagos were not significantly different from one another (all *P*-values >0.05). When samples were pooled by archipelago, all pairwise comparisons were significant, except the one between the Society vs. Austral island archipelagos ($\Phi_{ST} = -0.014$). The highest mtDNA genetic divergence was observed between the Society Islands and the Tuamotu Archipelago ($\Phi_{ST} = 0.611$, $P < 0.0001$), followed by the one observed between the Tuamotu Archipelago and Gambier Islands ($\Phi_{ST} = 0.541$, $P < 0.0001$). The AMOVA indicated that variation between the four archipelagos represented a significant proportion of the total molecular variance (24.7%, $P = 0.03$), while sampling sites within an archipelago did not significantly contribute to the total variance. However, genetic diversity was mainly assigned to differences within sampling sites (73.47%, $P = 10^{-3}$, Table 3).

Based on the microsatellite dataset, significant differences were observed in allele frequencies among all samples, regardless of the sampling period and sampling site (18 samples, $F_{ST} = 0.027$, $P < 10^{-3}$).

Pairwise F_{ST} values at nuclear loci were significant in 54 comparisons over the 65 comparisons involving one sample from the Austral Islands Archipelago on the one hand and all other samples on the other hand, with the highest value estimated between AI_RAV_12 and SI_MOO_12 ($F_{ST} = 0.075$, $P < 0.001$; Table 2). In line with F_{ST} estimates, the STRUCTURE analysis revealed clear differences between the Austral Islands' samples on the one hand, and all other samples on the other hand (Figure 3a). The value $K = 2$ provided the best meaningful result, not only using the Evanno et al. (2005) method, but also by cross-checking these results with PCA (Figure 3b,c) and F_{ST} estimates, i.e. congruent results based on different analyses. No recent migration event was estimated using BayesAss between the Austral Islands on the one hand and the Society Islands, Tuamotu Archipelago and Gambier Islands on the other hand (Figure 4).

Within the Austral Islands, no additional genetic substructure was observed using STRUCTURE (Figure S5a), with the PCA analysis (Figure S5b) and based on F_{ST} estimates ($F_{ST} = 0.00$, $P = 0.15$;

TABLE 2 Genetic structure of *Tridacna maxima* (pairwise F_{ST} estimates in the lower diagonal and pairwise Φ_{ST} in the upper diagonal) between all sampling sites in French Polynesia. Significant *P*-values ($<10^{-3}$) are in bold. F_{ST} and Φ_{ST} estimates highlighted in light grey represent values within each of the four archipelagos. Temporal F_{ST} estimates were highlighted in dark grey.

	Society Islands				Tuamotu Islands						Gambier Islands			Austral Islands			
	BOR__01	MOO__01	MOO__12	TAH__12	AHE__13	TAO__02	MAK__12	FAN__02	TAT__02	PUK__02	MOR__12	MAN__12	TEM__13	TUB__02	TUB__13	RAV__02	RAV__12
MOO__01	−0.004		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
MOO__12	0.019	0.011		−0.015	0.462	–	0.576	–	–	–	0.063	−0.180	−0.110	–	−0.036	–	−0.038
TAH__12	−0.003	−0.006	0.016		**0.578**	–	**0.639**	–	–	–	0.215	0.050	0.141	–	0.038	–	−0.006
AHE__13	0.021	0.011	0.025	0.023		–	−0.063	–	–	–	0.079	0.399	0.236	–	0.311	–	**0.567**
TAO__02	0.029	0.015	0.037	0.029	−0.005			–	–	–	–	–	–	–	–	–	–
MAK__12	0.018	0.019	0.021	0.019	0.008	0.002		–	–	–	0.184	**0.519**	**0.384**	–	**0.419**	–	**0.633**
FAN__02	0.007	0.017	0.034	0.020	0.012	0.007	−0.002		–	–	–	–	–	–	–	–	–
TAT__02	**0.039**	**0.040**	**0.062**	**0.040**	**0.026**	0.021	0.030	**0.021**		–	–	–	–	–	–	–	–
PUK__02	**0.023**	**0.023**	**0.059**	**0.024**	0.021	0.017	0.029	0.017	0.016		–	–	–	–	–	–	–
MOR__12	0.011	0.010	0.041	0.010	0.010	0.007	0.000	0.003	0.017	0.011		0.062	−0.015	–	0.027	–	**0.246**
MAN__12	0.032	0.014	0.049	0.021	0.009	0.014	0.030	0.026	**0.043**	0.007	0.019		−0.098	–	−0.004	–	0.036
TEM__13	0.038	0.029	0.072	0.034	0.013	0.020	0.032	0.031	**0.040**	0.030	0.007	0.043		–	−0.008	–	0.136
TU_B_02	**0.038**	**0.029**	**0.0259**	**0.025**	**0.028**	**0.032**	0.029	**0.040**	**0.064**	**0.039**	**0.019**	0.036	0.030	–	–	–	
TUB__13	**0.043**	**0.042**	**0.067**	**0.031**	**0.026**	**0.044**	**0.032**	**0.040**	**0.069**	**0.049**	**0.026**	**0.054**	**0.028**	−0.005		–	0.074
RAV__02	**0.040**	**0.035**	**0.061**	**0.033**	**0.018**	0.028	**0.038**	**0.046**	**0.065**	**0.053**	**0.021**	**0.051**	0.027	0.003	0.010		–
RAV__12	**0.050**	**0.034**	**0.075**	**0.031**	0.019	**0.040**	**0.041**	**0.047**	**0.072**	**0.051**	**0.025**	**0.047**	0.023	0.000	0.003	−0.006	
RAV__13	**0.038**	**0.032**	**0.060**	**0.029**	**0.025**	0.034	0.028	**0.035**	**0.065**	**0.050**	**0.018**	0.040	0.027	−0.009	0.001	0.001	−0.008

Source of variation	Degrees of freedom (D.f.)	Variance (%)	*P*-Value
Among archipelagos	3	24.70	0.03
Among sampling sites within archipelagos	5	1.83	0.22
Within sampling sites	119	73.47	$<10^{-3}$
Total	127	100	

TABLE 3 Distribution of genetic diversity in *Tridacna maxima* across French Polynesia inferred through AMOVA using mtDNA *COI* gene sequences.

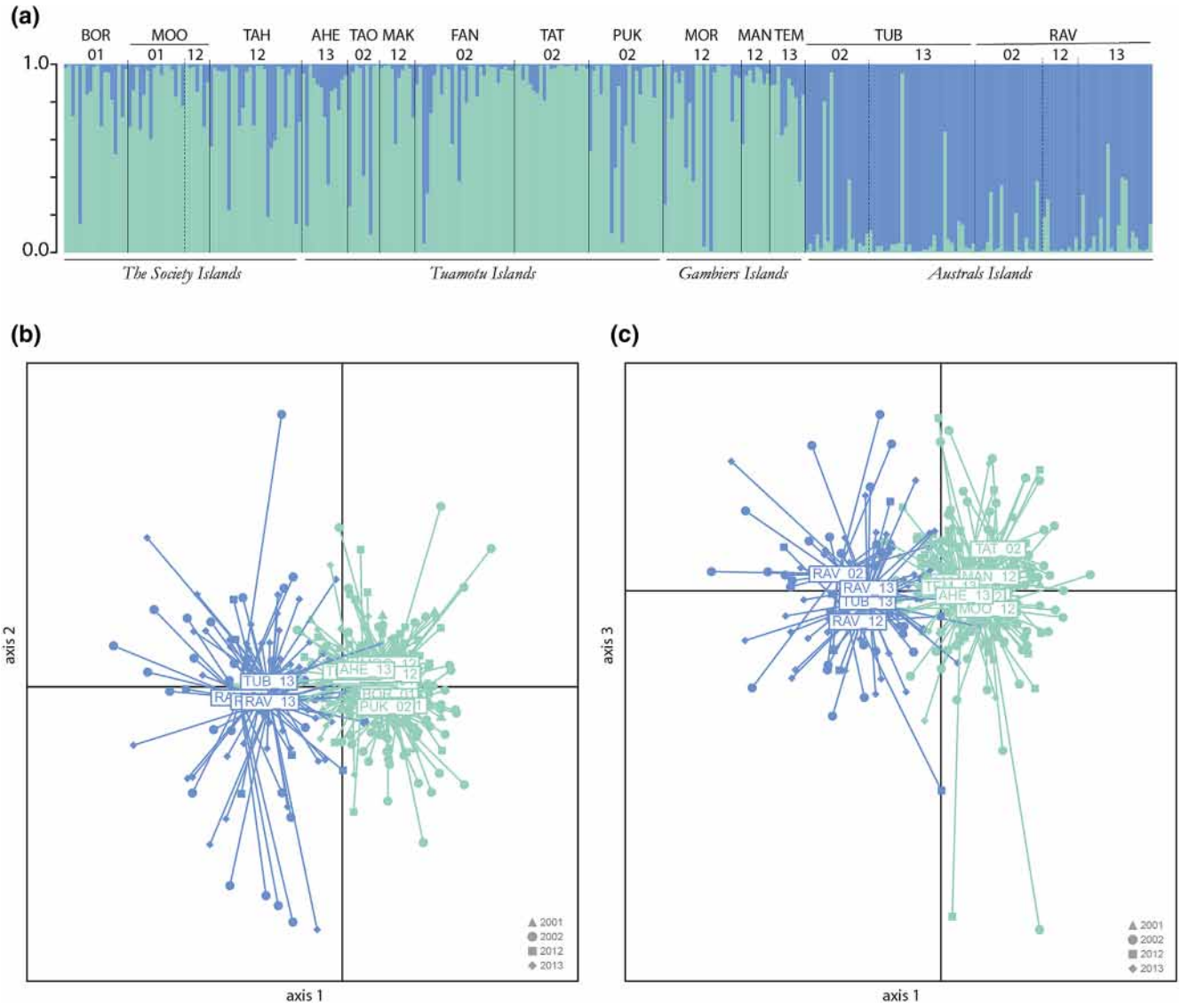

FIGURE 3 Population genetic structure of *Tridacna maxima* across French Polynesia based on individual genotypes at nine microsatellite loci. (a) STRUCTURE plot presenting individual percentage of membership (in percent) to each of the two genetic clusters (lagoon green, and blue). (b, c) Principal component analysis (PCA) with labels indicating the baricentres of respective samples. Labels and symbols are the same as for Figure 1 and Table 1.

pairwise F_{ST} estimates all non-significant, Table 2): no distinct group emerged within the Austral Islands. High self-recruitment was inferred in Raivavae (92%, Figure 4), a site that was also estimated as an important source site for Tubuai, with 25.3% of Tubuai's individuals originating from Raivavae (Figure 4) and probably contributing to the high gene flow observed between the two sampling sites of the Austral Islands.

Likewise, no additional genetic substructure was observed within the second genetic cluster gathering all the samples from the Society Islands, Tuamotu Archipelago and Gambier Islands, based on either STRUCTURE or PCA analyses (Figure S6). Self-recruitment was estimated at 68% in most samples, except in Tahiti (86%) and Fangatau (80%), two sampling sites that were also estimated as important sources throughout the three archipelagos, and especially

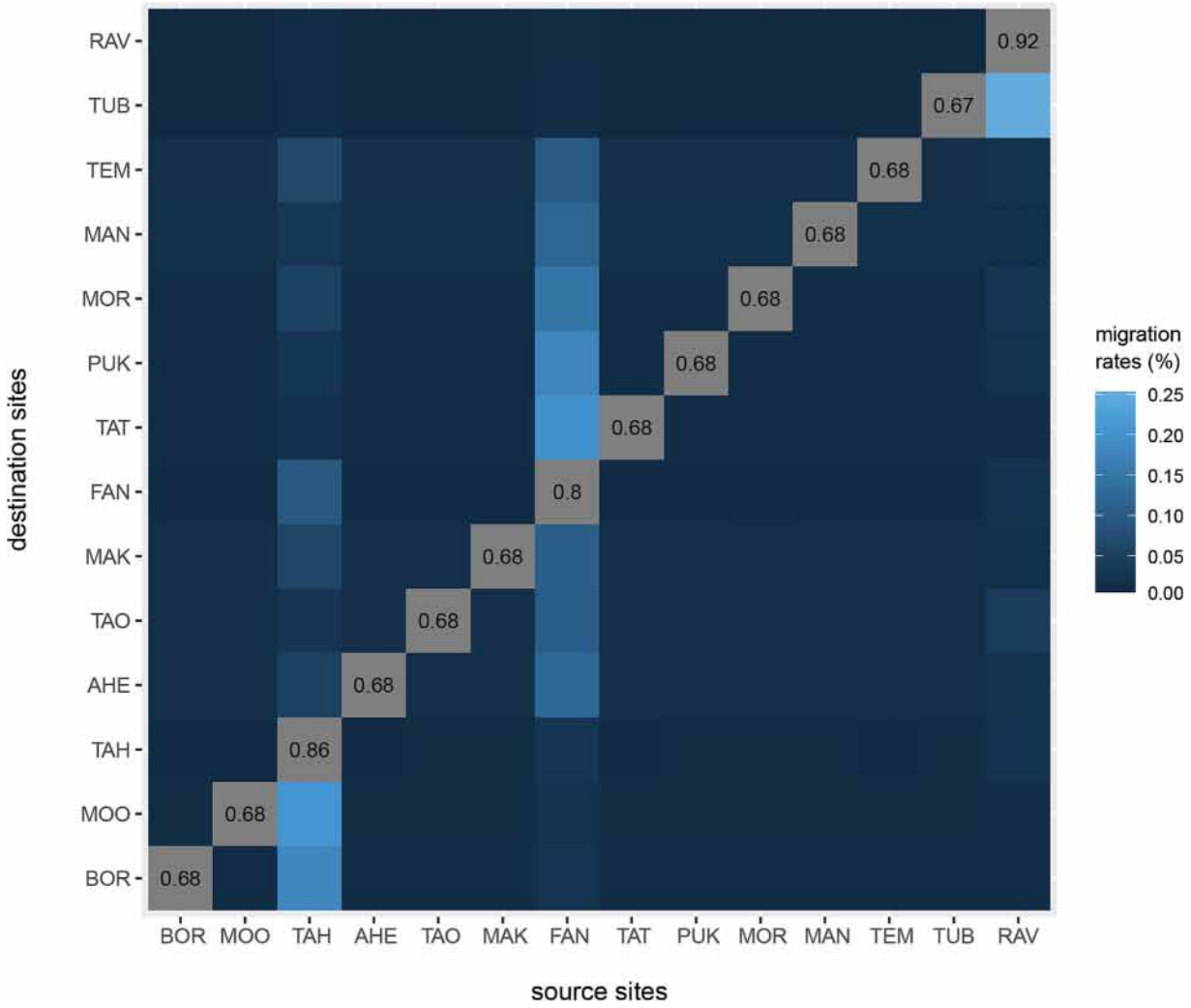

FIGURE 4 Recent migration between *Tridacna maxima* sampled populations in French Polynesia as inferred by BayesAss. Source sampling sites are plotted along the *x*-axis and sink sampling sites are plotted along the *y*-axis. Pairwise gene flow estimates are represented using a blue palette, the lighter the higher.

in the neighbouring sampling sites (Figure 4). Yet a significant global F_{ST} estimate was found when analysing all samples from these three archipelagos (i.e. removing the Austral Islands' samples, $F_{ST} = 0.191$, $P < 10^{-3}$). This significant genetic structure was mainly owing to two samples from the Tuamotu (TU_TAT and TU_PUK) for which pairwise estimates were high and significant with samples from the Society Islands and the Gambier Islands (Table 2).

Nuclear genetic variation between the four archipelagos represented a significant proportion of the total molecular variance (AMOVA test: 2.3%, $P = 10^{-3}$). Furthermore, genetic variation was significantly explained by differences between samples within an archipelago (although only a very small, but significant portion of the variance, 1.1%), between samples within sampling sites and within samples (91.8%, $P = 10^{-3}$, Table 4b).

When considering the two sampling periods separately, similar results were found. Significant overall genetic structure was observed at nuclear loci, although slightly smaller for the second period ($F_{ST\text{-}2001\text{-}2002} = 0.031$, $F_{ST\text{-}2012\text{-}2013} = 0.024$, $P < 10^{-3}$). For the 2001–2002 sampling period (three archipelagos sampled), 2.98% of the total variance was explained by differences between archipelagos ($P = 0.002$, Table S3) and for the 2012–2013 sampling period (four archipelagos sampled), 2.01% ($P = 0.001$) of the total variance was explained by differences between archipelagos (Table S3).

For each sampling period, significant correlation was found between genetic and shortest path geographic distances (Figure 5, 2001–2002: $R^2 = 0.40$, $P = 0.015$, 2012–2013: $R^2 = 0.04$, $P = 0.025$). When mixing samples regardless of the sampling period and considering samples of the same sampling site as replicates, this isolation by distance across the four archipelagos remained significant ($R^2 = 0.17$, $P < 10^{-3}$), suggesting no contribution of temporal variation. Indeed, the period of sampling did not contribute to any molecular variance (Table 4a, $P = 0.16$), a result congruent with the overall lack of significant genetic structure observed over time (Table 2, Figure S5 and S6), and similar pairwise F_{ST} estimates when analysing the two sampling periods (2001–2002 and 2012–2013). Instead, the majority of variation was found among sampling sites within a period of sampling (2.5%,

Source of variation	Df	Variance (%)	*P*-Value
A-			
Between sampling periods	3	0.40	0.16
Between sampling sites within sampling periods	14	2.54	$<10^{-3}$
Between samples within sampling sites	289	4.84	$<10^{-3}$
Within samples	307	92.22	$<10^{-3}$
Total	613	100	
B-			
Between archipelagos	3	2.33	$<10^{-3}$
Between sampling sites within archipelagos	10	1.09	$<10^{-3}$
Between samples within sampling sites	293	4.79	$<10^{-3}$
Within samples	307	91.79	$<10^{-3}$
Total	613	100	

TABLE 4 Components of genetic diversity at various levels of organization in *Tridacna maxima* from French Polynesia based on individual genotypes at nine microsatellite loci and inferred through AMOVA, considering the sampling period (A-) and archipelagos sampled (B-).

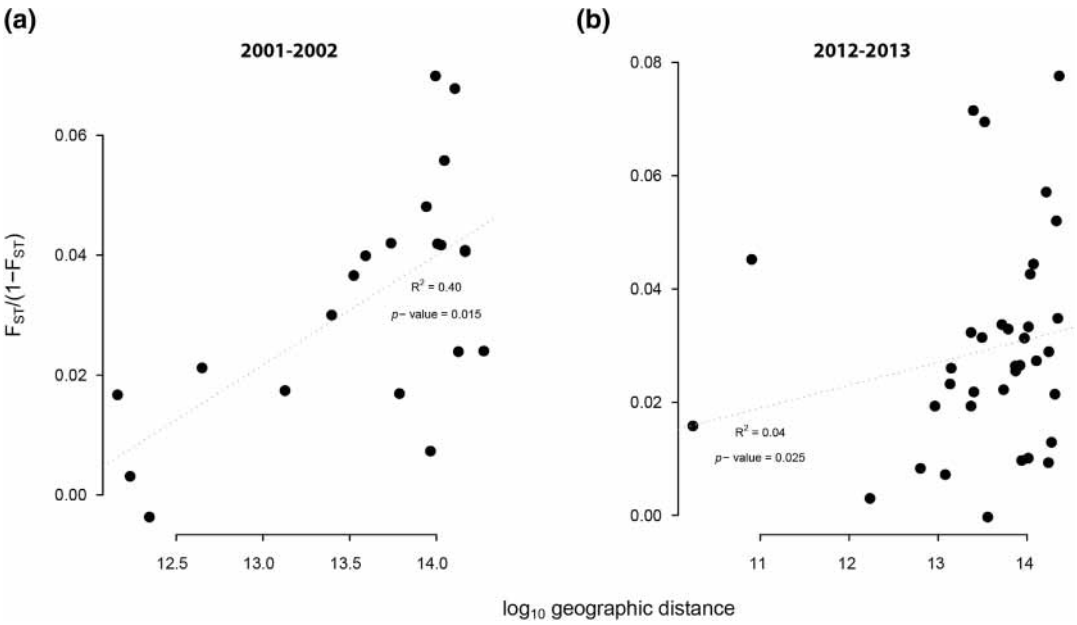

FIGURE 5 Plot of genetic distance (pairwise ($F_{ST}/1 - F_{ST}$) based on nine microsatellite loci; *y*-axis) against the natural logarithm of shortest path geographic distance (*x*-axis) among *Tridacna maxima* sampling sites of French Polynesia. The dotted line represents a regression trend. (a) From the 2001–2002 dataset; (b) from the 2012–2013 dataset.

$P = 0.01$, Table 4a), among samples within sampling sites (i.e. when samples from a single site were pooled whatever the period of sampling) and within samples (92.2%, $P = 0.01$, Table 4a).

3.2.3 | *Demographic history of T. maxima within French Polynesia*

Based on the mtDNA marker, Tajima's *D* was significant for Haplogroup 5b (−2040, $P < 0.01$) when pooling all sampling sites. Within sampling sites, Tajima's *D* was significant for AI_RAV_13 ($D = -1.84$, $P < 0.01$), which is dominated by Haplogroup 5a, as well as for TU_MAK_12 ($D = -1.72$, $P < 0.05$), which is dominated by Haplogroup 5b. When sampling sites were pooled by archipelagos, none of the Tajima's *D* values were significant. Only the Austral Islands samples showed negative values of *Fs*, and none were significant (all *P*-values >0.05). Within each archipelago, pairwise mismatch distributions presented two modes (Figure 6). The first mode mainly corresponded to within-haplogroup comparisons and the second mainly to between-haplogroup comparisons. Within each archipelago, no significant difference was found between the fit of the observed data and that expected under a stable population size model, or the sudden expansion model (paired *t*-test, all *P*-values >0.05). As none of these models better fit the observed data, the sudden expansion hypothesis can be rejected in all four archipelagos.

Based on the analyses of the microsatellite dataset, recent changes in effective population size ($P < 0.05$) were detected through

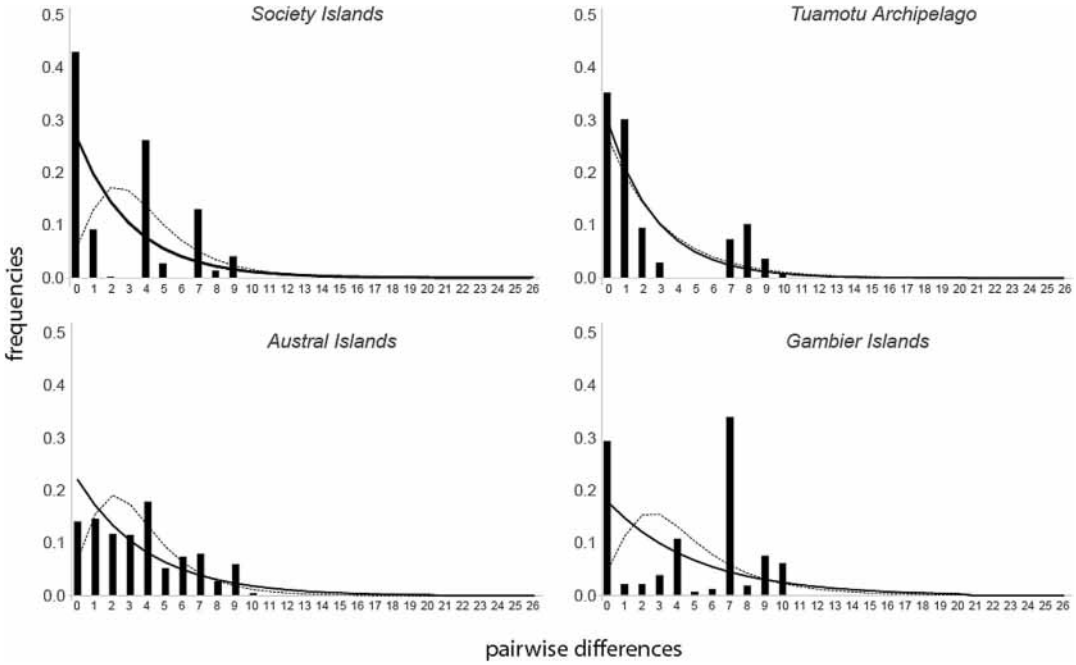

FIGURE 6 Observed (histogram) and expected (line) mismatch distributions for *Tridacna maxima* in four archipelagos of French Polynesia, based on mitochondrial DNA *COI* sequences. The solid line represents the expected distribution under a model of constant population size and the dotted line represents the distribution expected in a population having experienced recent demographic change.

heterozygote deficiencies under the SMM in SI_BOR_01, TAH12, TU_FAN_02, TU_PUK_02, GI_TEM_13, AI_RAV_02, and AI_RAV_13, and under both SMM and TPM in AI_RAV_12 (Table 5).

4 | DISCUSSION

The small giant clam *T. maxima* lineages from French Polynesia were highly differentiated from all known mitochondrial lineages across the geographic range of the species, except from two locations: the atolls of Tarawa (Kiribati) and Palmyra. Within French Polynesia, two mitochondrial haplogroups and two nuclear genetic clusters were found, with varying frequencies across islands and archipelagos, resulting in significant genetic structure of *T. maxima* within French Polynesia, with a clear genetic distinction of the Austral Islands.

4.1 | *Evolutionary history of T. maxima in French Polynesia*

Because in French Polynesia, *T. maxima* is more abundant in shallow lagoon waters, these populations were expected to show: (1) reduced genetic diversity as a result of recent (re)colonization events following severe reduction in shallow-water reef habitat and the exondation of 40–70 m deep atoll lagoons during the last glaciations; and (2) genetic homogeneity consecutive to the recent (re)colonization of these habitats (Planes, Bonhomme & Galzin, 1993; Fauvelot, Bernardi & Planes, 2003). Levels of haplotype and nucleotide diversities observed within French Polynesia populations were indeed lower than observed within the Coral Triangle, a region where, at least, two highly divergent clades are observed in sympatry (Nuryanto & Kochzius, 2009; Huelsken et al., 2013; DeBoer et al., 2014; Hui et al., 2016; Keyse et al., 2018). The low level of French Polynesian mtDNA diversity is in agreement with the hypothesis of recent reduction in population size, a result also observed in other French Polynesian lagoonal species (e.g. in *Pinctada margaritifera* (Arnaud-Haond, Bonhomme & Blanc, 2003), *Pomacentrus pavo*, *Chrysiptera glauca*, *Dascyllus aruanus* and *Chaetodon citrinellus* (Fauvelot, Bernardi & Planes, 2003)). Nevertheless, nucleotide diversity over all French Polynesia samples was not as low as observed in Red Sea *T. maxima*, which is located on the western limit of the species range (Ben Othmen et al., 2020; Lim et al., 2020). Likewise, using nuclear markers, genetic diversity estimates of all *T. maxima* French Polynesian samples (0.758 ± 0.031) were lower than those estimated across New Caledonia and Vanuatu archipelagos in the South-western Pacific (0.815 ± 0.018; Van Wynsberge et al., 2017a), but higher than those estimated in the Comoros Islands, Western Indian Ocean (0.703 ± 0.011; Mohamed et al., 2016), using the same nuclear markers. Although a reduced genetic diversity was observed in the peripherical French Polynesian populations, the non-significant values of Tajima's *D* estimated within nearly all samples along with the stable population size model within each archipelago do not support the recent population bottleneck hypothesis: *T. maxima* populations did not seem to have recently (re)colonized French Polynesia lagoons after the last sea-level regression. Genetic diversity tends to decline with distance from the Coral Triangle, both latitudinally and

TABLE 5 Results of the Wilcoxon signed-rank tests computed using BOTTLENECK (Piry, Luikart & Cornuet, 1999) for heterozygosity excess or deficiency under the two-phased mutation model (TPM) and the stepwise mutation model (SMM) for *Tridacna maxima* populations sampled across French Polynesia at different time periods. Significant *P*-values are represented in bold.

	Number of loci		*P*-Value	
	TPM	SMM	TPM	SMM
BOR01				
Deficiency	5	6	0.632	**0.019**
Excess	4	3	0.410	—
MOO01				
Deficiency	2	6	0.898	0.285
Excess	7	3	0.125	0.751
TAH12				
Deficiency	5	6	0.544	**0.024**
Excess	4	3	0.500	—
AHE13				
Deficiency	3	6	0.751	0.125
Excess	6	3	0.285	0.898
MAK12				
Deficiency	3	7	0.751	0.082
Excess	6	2	0.285	0.935
FAN02				
Deficiency	4	8	0.285	**0.002**
Excess	5	1	0.751	—
TAT02				
Deficiency	6	6	0.367	0.064
Excess	3	3	0.673	0.975
PUK02				
Deficiency	3	9	0.673	**0.001**
Excess	6	0	0.367	—
MOR12				
Deficiency	4	4	0.632	0.248
Excess	5	5	0.410	0.787
TEM13				
Deficiency	6	6	0.150	**0.014**
Excess	3	3	0.875	—
TUB02				
Deficiency	6	8	0.150	**0.005**
Excess	3	1	0.875	—
TUB13				
Deficiency	4	7	0.367	**0.001**
Excess	5	2	0.673	—
RAV02				
Deficiency	3	7	0.714	**0.018**
Excess	6	2	0.326	—
RAV12				
Deficiency	9	9	0.0009	**0.001**
Excess	0	0	—	—

TABLE 5 (Continued)

	Number of loci		*P*-Value	
	TPM	SMM	TPM	SMM
RAV13				
Deficiency	5	7	0.150	**0.007**
Excess	4	2	0.875	—

longitudinally (Messmer et al., 2012). This is a common pattern observed in other coral reef associated organisms (Messmer et al., 2012; Gaither & Rocha, 2013) that can be explained by the geological history of Indo-Pacific coral reefs that similarly shaped both species and genetic diversity patterns through evolutionary time (Bellwood & Wainwright, 2002; Barber & Bellwood, 2005).

The geographic isolation of the French Polynesia archipelago cannot alone explain the observed genetic pattern in *T. maxima*. *Tridacna maxima* populations in French Polynesia host a Central Pacific clade (Clade 5) deeply divergent from those of the Coral Triangle and Western Pacific regions, supporting the genetic differentiation of Central Pacific populations inferred using allozymes from all other clades (Benzie & Williams, 1997). This Central Pacific clade was also encountered in Tarawa (Gilbert Islands) and encompassed Palmyra atoll (Gardner et al., 2012) as well as four of the five French Polynesian archipelagos (Hui et al., 2016; present study). Yet an additional clade (Clade 3) was also reported in Tarawa, in sympatry with the Polynesian clade (Gardner et al., 2012; Keyse et al., 2018, Table S1). Given the geographic distances separating French Polynesia and Tarawa atoll (ca. 2500 nautical miles), the Central Pacific clade may encompass all islands located between these two (e.g. Cook Islands, Tokelau, Samoa) and therefore probably covers the Eastern Indo-Pacific realm (Beger et al., 2020). Alternatively, the Central Pacific clade occurring in Tarawa may have been introduced by anthropogenic translocation, and thus may not be observed in all islands located between these two. Programmes to re-establish or supplement depleted populations of giant clams have been conducted across the Pacific Island nations (Bell et al., 2005) with numerous translocations of giant clams occurring during the 1980s and 1990s throughout the Pacific (Teitelbaum & Friedman, 2008; Kinch & Teitelbaum, 2009). Additional sampling and analysis of *T. maxima* across Central Pacific Islands will probably help to explore this scenario.

The occurrence of strongly differentiated mitochondrial clades in the Central Pacific has also been observed in two other species of Tridacninae. A strongly divergent clade was found in *Tridacna noae* in the eastern part of its currently known distribution, in sampled populations from Wallis Island and from Western Samoa (Fauvelot et al., 2019). Likewise, the analysis of a mtDNA *COI* fragment from two French Polynesia *Tridacna squamosa* revealed a clade clearly distinct from the sequences of Indonesian specimens (Andréfouët et al., 2014). Such distinction of Central Pacific populations has previously been reported in other coral reef associated organisms (Messmer et al., 2012; Crandall et al., 2019). Even if the sampling in the current study was not of high enough resolution to infer the exact location of the genetic break, the observed pattern in *T. maxima* confirms this break being located between the Central Indo-Pacific and the Eastern Indo-Pacific (Vermeij, 1987; Crandall et al., 2019). This break may correspond to a gap in the geographic distribution of many reef species owing to the loss of shallow reefs, with distances between suitable habitats being greater than the dispersal capacity of several taxa. This lack of favourable habitats probably hinders regular larval dispersal and gene flow to occur between these two provinces, contributing to the diversification of the Indo-Pacific marine fauna (Crandall et al., 2019).

The occurrence of a distinct *T. maxima* mitochondrial clade in the Central Pacific, strongly differentiated from the clades co-occurring within the Coral Triangle and Western Pacific region (a major potential refuge for inner-reef specialists; Paulay, 1990), further suggests that *T. maxima* has not recently colonized French Polynesia (and Central Pacific islands) from the Coral Triangle. This result also supports the hypothesis that sufficiently large populations of *T. maxima* have persisted during the last sea-level low in the Central Pacific under two non-exclusive scenarios: (1) *T. maxima* has persisted on the outer reefs of French Polynesia islands and atolls, a scenario supported by the observations of *T. maxima* presently inhabiting outer reefs (Van Wynsberge et al., 2016); and (2) *T. maxima* may have persisted in another recognized refugia for inner-reef specialists of the Pacific islands. Indeed, according to Paulay (1990), the Austral and Marquesas islands lack developed reef systems similar to those of the Central Pacific islands and instead have extensive embayments dominated by unconsolidated sediments which harbour several typical inner-reef species. *Tridacna maxima* is absent from the Marquesas (with no fossil records; Cabioch et al., 2008, although it seems to occur at low densities, M. Pahuatini pers. obs.), but it is abundant in the Austral Islands. The Austral Islands Archipelago may well have been a Central Pacific refugee during the last sea-level low.

4.2 | *Genetic structure and connectivity of T. maxima in French Polynesia*

Within French Polynesia, different patterns of genetic structure were observed in *T. maxima* depending on the two types of genetic markers used in this study. Nevertheless, both markers highlighted a clear distinction of the Austral Islands Archipelago, regardless of the period of sampling. Physiologically, *T. maxima* in the Austral Islands also have different growth rates than in Tuamotu, which was first ascribed to

different environmental conditions (Van Wynsberge et al., 2017b). However, genetic processes may also be at play. The highest F_{ST} values in the Tuamotu Archipelago were found for the three semi-closed East Tuamotu atolls – Tatakoto, Pukarua and Fangatau – for which high retention of *T. maxima* larvae can be expected considering the atolls' geomorphology, combined with limited recruitment from outside owing to their oceanic isolation.

Discrepancies between types of markers are not rare and have already been observed, notably in species studied in this same region and thus probably sharing similar evolutionary histories (Arnaud-Haond, Bonhomme & Blanc, 2003; Fauvelot et al., 2007). Levels of differentiation estimated from mitochondrial and nuclear loci are expected to differ at equilibrium. Mitochondrial DNA is maternally inherited, displaying reduced effective population size compared with nuclear DNA, and generally lacking recombination between mtDNA molecules (Allendorf, 2017). Additionally, mtDNA is coding for genes and displays a slower rate of evolution than microsatellite markers. Mitochondrial markers often have their diversity more strongly affected by historical events such as founder effects or bottlenecks (Arnaud-Haond, Bonhomme & Blanc, 2003). In *T. maxima*, the genetic structure pattern at the mtDNA locus is driven by the differing frequencies of the two haplogroups co-occurring in French Polynesia. Regarding the specific proprieties of the mtDNA, the observed pattern probably results from past migration rather than present gene flow, reflecting the evolutionary history of *T. maxima* in French Polynesia. The two haplogroups probably originated from two refuge areas in which individuals would have evolved independently for a sufficient amount of time for genetic divergence to occur. The short duration of the larval phase of *T. maxima* (9–10 days; Jameson, 1976; Dumas et al., 2014; Lucas, 2014), combined with a large distance between suitable habitats within the vast and fragmented French Polynesia archipelagos, make this scenario very likely. The present data do not allow for the identification of such refuge areas, but the continued existence of these two haplogroups indicates that they have not yet been erased by present-day gene flow and/or that gene flow levels have remained moderate.

The nuclear loci revealed the occurrence of two genetic clusters in *T. maxima* across the four archipelagos, the first one comprising the individuals from the Austral Islands, and the second one encompassing the other sampled sites. Genetic differentiation was high between these two groups, and no recent migration was inferred between them, a pattern stable over time (i.e. over 10 years). This result contrasts with the genetic homogeneity found using nine microsatellite loci between populations of the black-lipped pearl oyster *P. margaritifera* sampled in Raivavae (Austral Islands) and the three populations sampled from the Tuamotu Islands (Reisser et al., 2019). These differences in genetic structure between *T. maxima* and *P. margaritifera* across French Polynesia may be attributed to differences in their population sizes (abundant for *T. maxima* (Richard, 1982; Laurent, 2001; Gilbert et al., 2006; Andréfouët et al., 2009; Van Wynsberge et al., 2013)), several orders of magnitude lower (SA and SVW pers. obs.) for *P. margaritifera*, as well as differences in pelagic larval durations (9–10 days in *T. maxima* but typically ≥20 days in *P. margaritifera* (Sangare et al., 2020)), and possibly, different histories with regards to artificial translocations. Indeed, translocation of *P. margaritifera* across islands of French Polynesia for black pearl production have artificially inflated gene flow among natural populations (Lemer & Planes, 2012), exacerbating the differences observed between the two species using the same genetic markers over the same region.

In *T. maxima*, the genetic distinctiveness of Tubuai and Raivavae populations agrees with the geographic location of the Austral Islands, being the most distant (apart from the Marquesas that were not included in the present study) and the most oceanographically isolated archipelago. The Austral Islands are under the influence of the South Pacific Current, while the three other archipelagos are mainly influenced by the South Equatorial Current, with some variations across seasons (Martinez et al., 2006; Martinez et al., 2009).

Gene flow was also low between the remaining three archipelagos. This confirms earlier results between the Society and Tuamotu island populations analysed using allozyme variation (Laurent, Planes & Salvat, 2002), although this differentiation was observed at a single locus. Within each archipelago, populations were not significantly differentiated, suggesting that stepping-stone gene flow ensured by the planktonic larvae connects the different islands of an archipelago.

Finally, the genetic divergence in *T. maxima* over French Polynesian populations was 10-fold the divergence estimated over 23 locations sampled across New Caledonia, Chesterfields and Vanuatu (Van Wynsberge et al., 2017a) using the same genetic markers, a contrasting finding probably attributable to the differences in spatial scales. Yet the genetic differentiation estimates between the most distant sites (separated by ca. 2000 km in French Polynesia, against ca. 1000 km in New Caledonia) were comparable among studies/areas (Van Wynsberge et al., 2017a). This pattern may suggest reduced gene flow among populations in French Polynesia compared with New Caledonia, that could be related to differences in potential for larval dispersal and/or habitat availability. However, because in New Caledonia most of the study sites were located in the lagoon around Grande Terre, made from a nearly continuous reef resulting in near genetic homogenization among all sampled populations, the most probable explanation of the differences among studies is the uneven number of long-distance comparisons among geographically isolated patch reefs used in the two studies.

4.3 | Implications for giant clam conservation in French Polynesia

The results found in this study have several important consequences for fishery and aquaculture management, and for the conservation of *T. maxima*. The local fishery management service (Direction des Ressources Marines) has already restocked specimens from well-stocked Tuamotu atoll lagoons to the depleted Society Island lagoons. Several hundreds to thousands of individuals from Reao atoll (eastern

Tuamotu Archipelago) were translocated in 2018 (i.e. after the sampling of the present study) to Tautira lagoon (Tahiti, Society Archipelago). In addition, lagoon populations that have suffered from mass mortality have received specimens from healthy lagoons: for instance, in 2020, Tatakoto atoll was restocked with clams from the nearby Reao atoll. Because no evidence of strong genetic differentiation was found at the scale of one archipelago, the present results suggest that translocations can occur between islands within the same archipelago. In addition, since genetic differentiation between the Tuamotu, the Gambier and the Society Islands archipelagos were found to be low, the current results suggest that translocations can also occur between islands of these three archipelagos. However, the present results advocate that no translocation should occur between the Austral Islands and the rest of French Polynesia. To our knowledge, no large restocking programmes in the Society Islands or Tuamotu have used giant clams from Austral Islands.

In French Polynesia, restocking is also performed at a smaller scale but much more frequently for private business, for instance for tourism purposes to generate giant clam gardens near hotels. For this, local providers based in Tahiti raise clams in aquaria but the specimens may initially come from Tuamotu and Austral island lagoons. Live specimens are held in open circuit aquaculture basins, or they can also be left acclimatizing to new conditions in the Tahiti lagoon for a while before their actual transplantation to a final destination. The same process is also used for the aquarium trade, and in this case the specimens are not reintroduced in a local lagoon but eventually are sent to international retailers in the USA and Europe. Whatever the aquaculture facility setting, the spawn of imported giant clams can potentially be broadcast in nearby lagoons during the acclimatization stage or final relocation stage, with potential genetic consequences. Another motivation for restocking is ecosystem restoration and bioremediation of degraded areas. Restocking of giant clams has not yet occurred for this purpose in French Polynesia or elsewhere to our knowledge, but this activity is becoming increasingly popular (Carranza & zu Ermgassen, 2020) and could occur in the near future considering the beneficial traits and services brought by giant clams (Neo et al., 2015). Regardless of the reasons motivating the restocking of giant clams, these results show that should clams be translocated from the Austral Islands to other archipelagos (or the other way around), the authorities will have to bear in mind the risk of local population genetic structure loss and introduction of maladapted alleles if such import–exports are authorized.

In terms of fishery management, and beyond the aforementioned restocking actions, the genetic distinctiveness between the Austral Islands and the other archipelagos suggests that two distinct stocks exist, which therefore, theoretically, call for specific assessment and management plans. Giant clam fishery regulations are currently implemented at the scale of the whole French Polynesia. In fact, collecting clams under 12 cm is forbidden across French Polynesian Islands. In addition, the catch in some specific islands/lagoons in Tuamotu or the Austral islands has been limited by quotas (Van Wynsberge et al., 2013). However, no intermediate measures exist that are specific to an entire archipelago, which would represent a management scale between the whole of French Polynesia and a specific lagoon. Notably, the same minimum size limit for catch (currently fixed at 12 cm) for all archipelagos may be questioned, considering (1) the different growth curves reported between individuals of Austral vs. Tuamotu Islands archipelagos (Van Wynsberge et al., 2017b) and (2) the existence of distinct stocks, mainly fuelled by self-recruitment as evidenced in the present study. In conclusion, transfers and restocking programmes between islands and archipelagos should be conducted with much caution and the present study justifies distinct assessment and management plans between French Polynesia archipelagos, especially for the Austral Islands.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Philippe Borsa https://orcid.org/0000-0001-9469-8304
Cécile Fauvelot https://orcid.org/0000-0003-0806-1222

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