Multiple origins define the genetic structure of tiger shrimp *Penaeus monodon* in the colombian Caribbean Sea

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A R T I C L E   I N F O

A B S T R A C T

The tiger shrimp *Penaeus monodon* is a native species of the Indo-Pacific Ocean that was introduced to promote its cultivation in several American countries, including Colombia. As a result of inappropriate aquaculture practices, it has established itself in the wild in almost all the Colombian Caribbean Sea. To evaluate the genetic diversity, population structure, and origin of the founder populations, samples from three sites in the Colombian Caribbean were analyzed from 10 microsatellite loci and the mitochondrial DNA Control Region. Genetic diversity similar to native populations was found to be present in three relatively discrete populations and their origin is related to natural populations from Thailand, the Philippines, Taiwan and China. We discuss how oceanographic conditions and culture systems of tiger shrimp facilitated the success of biological invasion processes in marine ecosystems of the Colombian Caribbean.

1. Introduction

The planet is currently facing a crisis of biological diversity loss, on such an enormous and accelerated scale that it has been called "the sixth extinction" [1], due to its magnitude compared to earlier ones. In this context, biological invasions have been considered the second cause of this crisis [2], and their effects in terms of economic and ecosystem losses are incalculable. However, despite the drastic nature of this scenario, the course of an invasion can be an excellent setting for investigating ecological and evolutionary processes in founder populations and help to understand their response to natural selection and genetic drift in new and changing environments [3,4]. Understanding these processes can play a crucial role in the implementation of invasive species prevention, management, and control plans, if factors such as the origin of the invasive population, the routes of introduction, the number of founder populations and their genetic structure and diversity are identified [5,6]. Understanding the ecological characteristics of the invasive population can also help predict dispersal and colonization mechanisms [7,8], identify critical phases during its life cycle, and define natural enemies for potential biological control [9].

Theoretically, the success of biological invasions is considered to be mediated by the gene pool of the invading population and the result of genotype-genotype and genotype-environment interaction during the invasion process. At the onset of any founder process only a fraction of the genetic variation of the original population participates [10]. However, this fraction may be reduced during the colonization and expansion phase as a consequence of bottlenecks and genetic drift [10–12], limiting the adaptive capacity of any invasive species. Despite the expected presumptions during invasion events, many species show congruence with the loss of genetic

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diversity, while others do not [4,13–15], and there are no studies that determine or describe the genetic changes that have occurred around this phenomenon [16].

Successful invasions with genetic diversity loss are possible (e.g. Betancur et al. [17]) if new allelic combinations appear due to epistasis or dominance interactions that promote additive genetic variation, facilitating adaptive changes in the invasive species [14, 18]. In addition, multiple introductions and/or a large introduction may be favorable because they provide a large amount of variation and new genetic combinations, minimizing the effect of bottlenecks and drift [19], while promoting accelerated rates of evolution and ranges of expansion [4].

The tiger shrimp *Penaeus monodon* is a species native to the Indo-Pacific whose native distribution covers the Indian Ocean and the southeastern Pacific Ocean, from Japan to Australia [20]. The tiger shrimp has been cultivated as a food source by coastal communities in some Indo-Pacific countries for more than a century and is the most important crustacean in the international market, undergoing significant expansion in developing Asian countries [21]. This production success favored its introduction into several countries in Africa, Europe, and America [22], leading to accidental escapes and subsequent establishment in the wild in West African countries [23,24] and in the southeastern USA, as far as the Gulf of Mexico [25]. In South America it has been recorded in the east coast of Brazil [26–30], Venezuela [31,32] and Colombia [22,33–35]. However, to date there is insufficient information to confirm its establishment as an invasive species in this area.

The chronological occurrence of tiger shrimp in the western Atlantic Ocean suggests the existence of at least two foci of introduction and dispersal of its invasion: one in the south, on the east coast of Brazil, where it was first recorded in 1987 [26] and was progressively reported northward through Venezuela and Colombia; and another in the north, on the southeast coast of the USA, where it was reported in 1988 as a consequence of an accidental escape from farming systems, and then was recorded towards Central America through Mexico, Belize and Guatemala, reaching the islands of Jamaica, Cuba, the Dominican Republic and Puerto Rico [25, 35–38]; (Fig. 1, Supplement 2). Although this hypothesis has not been tested, this scenario may favor and facilitate their ability to adapt, colonize and expand as a result of mixing genotypes with different origins, improving their genetic condition and reducing the negative effect inherent to any founding process. For example, Aguirre-Pabón et al. [22] found evidence suggesting that specimens collected in the Gulf of Salamanca (Colombia) were related to at least two different sectors of their native habitat in the Indo-Pacific; this information was consistent with batches introduced from Taiwan and the Philippines to Brazil in the 1970s and 1980s for farming purposes [39,40]. In addition, the increase in capture frequencies and abundances demonstrate the adaptive capacity of this animal to
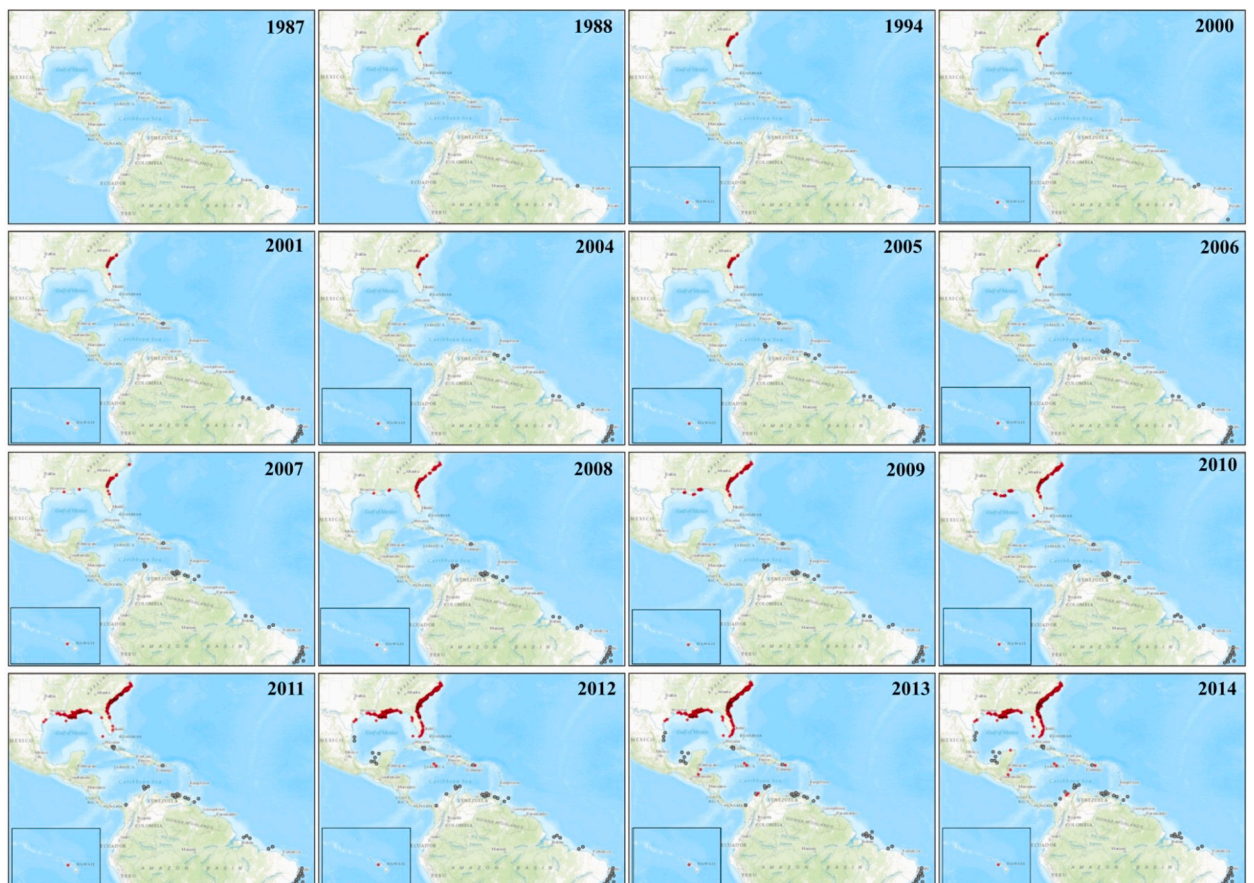

Fig. 1. Reports tiger shrimp

invade foreign habitats. Fuller et al. [25], reported captures of 678 specimens from North Carolina to Texas (USA) during 2011, while Sandoval et al. [34] recorded 397 specimens in the Gulf of Urabá (Colombia) during an eight-month period. Added to this evidence is the absence of evolutionarily adapted predators for its biological control in foreign environments and an advantageous life history shaped by its large size (~33 cm), wide tolerance to changes in environmental conditions, high fertility rate (500,000 to 750,000 eggs), occupation of numerous ecosystems and its predatory habit [41,42]. These attributes are what make it a successful organism capable of invading new habitats and niches whilst at the same time establishing itself with ease.

To date, its presence has only been documented in the western Atlantic by means of reports and studies of annual catches (see Fig. 1, Supplement 2). In Colombia, its presence has been recorded since 2008 [33], as well as distribution and abundance studies in the Gulf of Urabá in 2011 [34] and a first approach to determine its origin and genetic diversity in samples from the Gulf of Salamanca [22]. As in the rest of the Atlantic, aspects of the diversity and genetic structure of the invasive population, the number of introductions, and the routes that led to it are still unknown, which are necessary in order to generate baseline information to better understand the invasion process and help take measures to try to mitigate and control its impact on native biodiversity. Therefore, the purpose of the present study was to: i) evaluate its genetic diversity, ii) determine the population structure, and iii) identify the origin of the invasive tiger shrimp *Penaeus monodon* in the Colombian Caribbean Sea.

2. Materials and methods

2.1. Collection of tiger shrimp samples and DNA extraction

Between August 2013 and May 2014, 90 specimens of tiger shrimp were collected in three localities in the Caribbean Sea of Colombia: the Gulf of Morrosquillo (GM; N = 30), the Ciénaga Grande de Santa Marta (CGSM; N = 30) and the coastal area of the municipality of Dibulla in the department (state) of La Guajira (GUA; N = 30). Samples were obtained from catches made by artisanal fishermen who carry out their activities in these areas. These sites were strategically selected in order to cover the largest possible area with presence of tiger shrimp in the Caribbean Sea of Colombia [33,43].

Samples from the caudal peduncle of the shrimp were fixed in absolute ethanol, and DNA was isolated with the QIAGEN DNeasy® Blood & Tissue kit following the manufacturer's instructions. DNA quality was checked in a BioDoc-It® Imaging System UVP photodocumenter and its concentration was quantified in a NanoDrop (Thermo Scientific®).

2.2. Microsatellite and mtDNA-CR amplification

A system of 10 microsatellite loci (Supplement 1) described by Li et al. (2007) were amplified in a 10 µL reaction volume using the following final concentration: $1\times$ Buffer (Applied Biological Materials Inc., Canada), 2 mM $MgCl_2$, 0.2 mM dNTPs, 0.5 µM Primers, 0.2U *Taq* DNA Polymerase ABM (Applied Biological Materials Inc., Canada) and 1.5 µL template DNA. Temperature profiles were programmed on a BIO-RAD S100TM Thermal Cycler as follows: initial denaturation at 95 °C for 5 min, followed by 30 cycles at 94 °C for 30 s, hybridization temperature for 30 s, 72 °C for 90 s and final extension at 72 °C for 30 min. The products were visualized on a 2% agarose gel.

Genotyping of PCR products was performed by capillary electrophoresis with the QIAGEN QIAxcel Advanced kit, using the high resolution cartridge (QIAxcel DNA High Resolution Kit). The size of each amplification was determined with QIAxcel ScreenGel version 1.0 software, using an alignment marker between 15 and 1000bp that migrates with each sample. Samples were considered heterozygous when the maximum height of the minor peak was greater than 70% of the maximum height of the major peak, whereas when only one peak was present they were considered homozygous (Butler, 2001). Mitochondrial DNA Control Region (mtDNA-CR) amplification was performed based on primers proposed by Chu et al. (2003) in a reaction volume of 25 µL using the following final concentration: $1\times$ Buffer, 2 mM $MgCl_2$, 0.2 mM dNTPs, 0.3 µM of primers, 0.05U of *Taq* DNA Polymerase and 2 µL of template DNA. The temperature profiles included initial denaturation at 95 °C for 5 min, followed by 30 cycles at 94 °C for 60 s, 58 °C for 30 s, 72 °C for 30 s and final extension at 72 °C for 5 min. Sequencing was performed using ABI's BigDye Terminator chemistry and run on an Applied Biosystems 3500 Genetic Analyzer with read capacity for sequences of approximately 1000 base pairs.

2.3. Data analysis

2.3.1. Genetic diversity

Prior to the genetic diversity analysis, the presence of null alleles at each locus was evaluated using Micro-Checker [44] and estimating the frequency in FreeNA [45]. In addition, the exact linkage disequilibrium test [46] was used to determine the independence of the genotypes among the loci and to avoid redundancy in the information obtained. Genetic diversity was evaluated by calculating the following indices: allele frequencies, number of alleles (Na), private alleles (Ap), allelic richness (Ar), observed (Ho) and expected (He) heterozygosity and the level of inbreeding (Fis [47]); estimating confidence intervals with 1000 replicates of resampling in the computer package GENETIX v.4.05 [48]. The GENEPOP v.3.4 program [46] was used to examine the deviation from Hardy-Weinberg equilibrium (*E*-HW) in each population, and the heterozygote deficit across loci and between populations was evaluated globally.

For mtDNA-CR, 98 tiger shrimp sequences (including 16 sequences from Ref. [22]) were edited and aligned employing the program MEGA v.5.02 [49], inspecting the alignment quality visually. Nucleotide diversity (π), haplotype diversity (HD), polymorphic sites (S) and the average number of nucleotide differences (k) analyses were performed in the program ARLEQUIN v.3.5.2.2 [50].

The detection of recent demographic changes (bottlenecks) in the invasive tiger shrimp population was done in two ways: 1) the Wilcoxon test was used in the program BOTTLENECK v.1.2.02 [51], where the observed allele frequency distribution was compared to a population in mutation-drift equilibrium using the IAM, SSM and TPM models (at a ratio of 70:30 and with 10,000 iterations; and 2) the Garza- Williamson M-ratio index [52] was estimated using the ARLEQUIN v.3.5.2.2 program, finding the average ratio between the number of alleles at a given locus and the range in allelic size (M = k/r), where k is the number of alleles and r is the allelic range [50]. According to the interpretation of [52], for seven loci or more, the critical value Mc < 0.68 indicates a recent reduction in population size.

Regarding past demographic history (population expansion), we first evaluated whether each set of sequences per site fit the neutral evolution model using Tajima's D-test [53] and Fu's Fs [54], which allows detecting signs of model deviation (population expansion) when the index presents significantly negative values ARLEQUIN v.3.5.2.2 [50].

2.3.2. Genetic structure

Initially, an exploration of the degree of population differentiation was performed using i) the Fst statistic and gene flow (Nm = ¼ (1/Fst-1)), which permits comparison between sampling sites and estimation of the degree sof differentiation between them; ii) hierarchical analysis of molecular variance (AMOVA) to find out which of the components within and between comparisons explain genetic variation (ARLEQUIN v.3.1.1 [50], and iii) a Discriminant Analysis of Principal Components (DAPC; ADEGENET v.2.1.0 [55]). Subsequently, a Bayesian structure analysis (STRUCTURE v.2.3.3 [56]) was performed, which assigns individuals according to the probability of belonging to one or more groups when the population is genetically admixed. For this purpose, a starting period of 10^5 steps was used to minimize the effect of the starting configuration and 10^6 simulation runs (MCMC), using 10 replicates for each K examined (1–3 + 3, as proposed by Evanno et al. [57], and assuming the effect of null alleles/homozygotes. The number of most likely groups or populations was determined using the method proposed by Evanno et al. [57], based on Delta K (rate of change of Ln (X/K) among successive values of K) with the help of STRUCTURE SELECTOR [58].

2.3.3. Genetic relationships with native populations of the Indo-Pacific Ocean (mtDNA-CR)

To evaluate the genetic relationships of invasive specimens of tiger shrimp collected throughout the Caribbean coasts of Colombia with native populations in the Indo-Pacific Ocean and thus infer a possible origin, 341 sequences from Indo-Pacific populations (Ky: Kenya, Mg: Madagascar, Ind: India, Th: Thailand, VN: Vietnam, Ch: China, Ta: Taiwan, Ph: Philippines and Aus: Australia) were obtained from GenBank with accession numbers EU426576 - EU426831, J226007 - FJ226027, EU368046 - EU368113 and DQ311142.

The editing and analysis of this set of sequences was carried out in the same way as in the previous section, determining genetic diversity indices in native and invasive populations, as well as their population structure relationships. A genetic distance matrix Fst [10], was obtained, and a hierarchical analysis of molecular variance (AMOVA) was performed based on the genetic distance relationships Fst of the native and invasive populations. This analysis consisted of assuming the origin of the invasive sequences in a single population in the Indo-Pacific and excluding sites in order to reduce the level of population differentiation until the sites with which the invasive population has the highest genetic relationship were found. To complement this analysis, a frequency matrix of shared haplotypes was obtained to illustrate the relationships between sites with native populations of tiger shrimp and its invasive

Table 1
Genetic diversity of the invasive tiger shrimp in the Colombian Caribbean, using microsatellite loci and the control region of mitochondrial DNA (mtDNA-RC). GM: Golfo de Morrosquillo, CGSM: Ciénaga Grande de Santa Marta, GUA: La Guajira.

Genetic diversity with all loci microsatellites			
Parameter	GM (30)	CGSM (30)	GUA (24)	GLOBAL (84)
Na	136	129	120	**170**
Ap	23	13	7	**43**
Ho	0.574	0.462	0.500	**0.512 ± 0.186**
He	0.894	0.892	0.881	**0.889 ± 0.041**
Fis	0.352	0.473	0.418	**0.415 ± 0.205**
Genetic diversity using loci microsatellites < 20% of null alleles			
Na	82	52	69	**120**
Ap	14	13	7	**25**
Ho	0.678	0.688	0.569	**0.634 ± 0.121**
He	0.90	0.91	0.86	**0.888 ± 0.037**
Fis	0.238	0.309	0.326	**0.267 ± 0.127**
Genetic diversity with mtDNA-RC			
Parameter	GM (27)	CGSM (41)	GUA (30)	GLOBAL (98)
NH	2	2	3	**3**
S	76	4	77	**77**
π (%)	1.42	0.08	1.14	**0.72**
DH	0.074	0.095	0.133	**0.099**
k	6.53	0.38	6.12	**3.3**
Fu	13.113	1.284	10.02	**10.1**
D	−2.755*	−1.4075	−2.752*	**−2.539***

counterpart in the Caribbean Sea of Colombia. These analyses were performed by calculating the nucleotide substitution model (GTR + I + G; Gamma = 0.51) in MRMODELTEST v.3.06 [59], which was simplified to Tamura-Nei (TN + G) due to the simplicity of the models used by the ARLEQUIN v.3.1.1 program and because this is the model most similar to GTR + I + G.

3. Results

3.1. Genetic diversity

The 10 microsatellite loci were highly polymorphic (170 alleles in total) and showed no linkage disequilibrium (p = 0.847), suggesting an independent distribution of alleles at the different loci. Allelic richness was high (RA = 11.8–12.7, average RA = 12.2 ± 2.653), with a large number of private alleles per site, mainly in GM (23/17%) and CGSM (13/10%). Moderate values of observed heterozygosity (average Ho: 0.512 ± 0.186) and inbreeding (average Fis: 0.415 ± 0.205) were observed with all microsatellite loci (Table 1, Supplement 1). However, these values were higher (average Ho: 0.640 ± 0.121; average Fis: 0.268 ± 0.129) when genetic diversity was estimated considering only loci with less than 20% null alleles (Table 1, Supplement 1).

As for the mtDNA-CR sequences, the final array was 460bp long and only three haplotypes were detected out of the 98 sequences examined, recording two for GM and CGSM, and 3 for GUA (Table 1). Nucleotide and haplotype diversity was low (GM: μ(%) = 0.142 and HD = 0.074; CGSM: μ(%) = 0.080 and HD = 0.095, GUA: μ(%) = 0.114 and HD = 0.133), with CGSM being the poorest site with only four polymorphic sites (S), compared to GM = 76 and GUA = 77 (Table 1). Deviation was also detected in the neutrality model according to Tajima's D test (D = −2.593 ± 0.00; Table 1).

The analysis performed to evaluate signs of recent drastic reductions (bottleneck) was significant according to the Wilcoxon test in the infinite allele models (IAM) and two-phase models (TPM) for the three sites studied (Table 2). This result was supported by the M-ratio index, where all values were below the threshold established for populations with significant reductions (M-ratio <0.68) and relatively low population sizes (LDNe) at the GM and GUA sites (Table 2).

3.2. Genetic structure

The hierarchical analysis of molecular variance (AMOVA) using the three study sites in the Colombian Caribbean Sea was significant only with microsatellite loci (Fst = 0.018, p = 0.011, variance = 1.8%). The Bayesian structuring analysis and Principal Component Discriminant Analysis (DAPC) showed the existence of three populations, with a higher relationship between CGSM and GUA (green population: 93% and blue population: 51%, respectively; Fig. 2: A, B and C), and a third population in GM (red population: 72%) that seems to have a higher relationship with GUA (blue color: 23%)

3.3. Genetic relationships with native populations of the Indo-Pacific Ocean (mtDNA-CR)

A total of 439 mtDNA-CR sequences were obtained, with a length of 411bp and originating from 10 different countries. The 98 sequences from the invasive population in the Colombian Caribbean Sea were represented by only three haplotypes and showed the lowest values of genetic diversity (μ (%) = 0.75, DH = 0.099; Table 3) compared to sites representative of their native habitat in the Indo-Pacific Ocean (1.74 < μ (%) > 9.58, DH > 0.9; Table 3).

High differentiation (Fst) was found with the Indian Ocean sites (Kenya, Madagascar and India; Fst >0.950), and in lower proportion with the Pacific Ocean sites (China: 0.298, Taiwan: 0.373, Philippines: 0.468 and Vietnam: 0.400; Fig. 3: A and B), that compose a relatively homogeneous group (Fst <0.089, p = 0.000, Fig. 3B). The degree of divergence between the invasive population in the Caribbean Sea of Colombia and the Pacific Ocean sites may be related to the mixing of at least two populations with different origin and genetic information (as suggested in Fig. 3: A and B), causing an increase in the degree of divergence.

Of the three haplotypes found in the invasive population of tiger shrimp in the Caribbean Sea of Colombia, the most frequent (H1 = 93.3% in GUA, 95% in CGSM, 96.3% in GM) was related to sequences originating from Taiwan; a second less frequent (H2 = 3.3% in GUA, 5% in CGSM) was related to sequences from China, the Philippines and Thailand; while the third (H3 = 3.3% in GUA, 3.7% in GM) was not recorded in the set of sequences from the Indo-Pacific Ocean (Fig. 2B and 4, Supplement 4). These results suggest at least two sources of the invasive population of tiger shrimp in the Colombian Caribbean Sea, and it is likely that H1, due to its high frequency, is the precursor haplotype of the founding process in the Colombian Caribbean Sea.

Table 2

Demographic changes (bottlenecks) in invasive tiger shrimp in the Caribbean of Colombia, by evaluating the mutation/drift balance and using the mutation models: infinite alleles (AMI), step-by-step (SSM) and two phases (TPM = IAM + SSM); the Garza-Williamson index (reduction when M-ratio <0.68) and the effective population size (LDNe). GM: Golfo de Morrosquillo, CG: Ciénaga Grande de Santa Marta, LG: La Guajira.

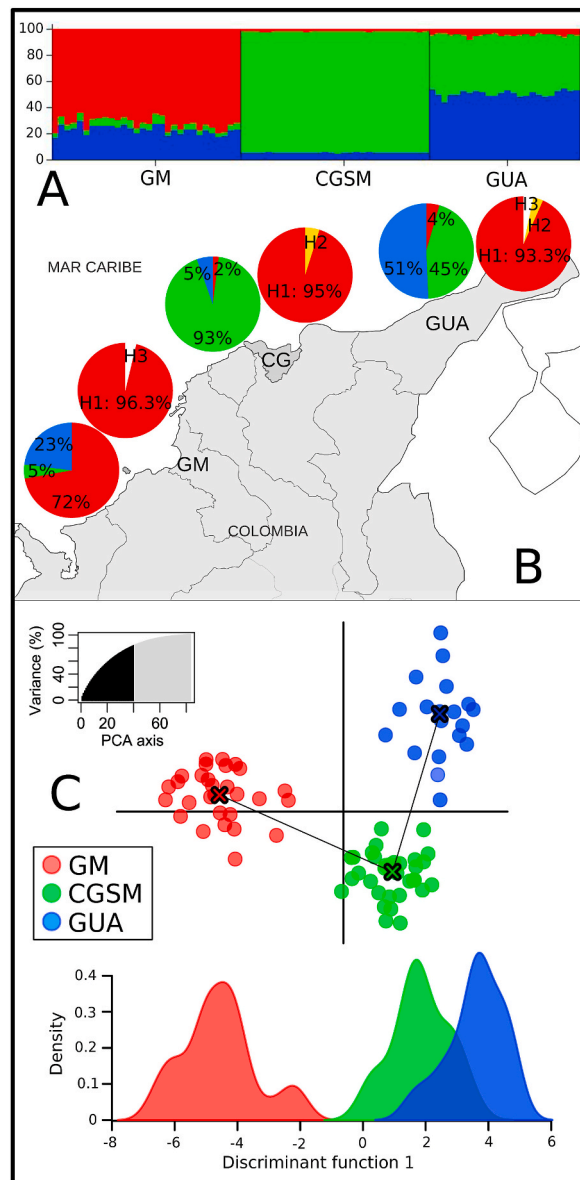| Places	I.A.M	T.P.M	S.M.M	M-ratio	Ne (LDNe)
GM	0.0005	0.0068	0.6152	0.65	437
CGSM	0.0005	0.0010	0.2158	0.63	Infinite
GUA	0.0005	0.0068	0.4609	0.61	391.9

Fig. 2. Structure and DAPC

Table 3
Genetic diversity parameters of the invasive tiger shrimp in the Colombian Caribbean and of native populations of the Indo-Pacific.

Region	Country	N	NH	S	π (%)	DH	k	Fs	D
Caribbean Sea	**Colombia**	98	3	71	0.75	0.099	3.06	9.37	−2.50*
Pacific Ocean	**Australia**	28	28	65	3.32	1.000	13.35	−18.17*	−0.92
	Philippines	35	32	79	3.41	0.993	13.71	−16.63*	−1.10
	Thailand	59	51	129	9.58	0.994	38.79	−11.71*	1.15
	Taiwan	60	53	121	3.45	0.993	13.96	−24.30*	−1.60*
	Vietnam	34	31	102	8.10	0.995	32.82	−6.35*	1.10
	China	68	62	136	7.45	0.997	30.47	−24.70*	0.24
Indian Ocean	**India**	20	16	52	1.74	0.978	7.08	−5.91*	−1.86*
	Kenya	12	12	41	2.27	1.000	9.17	−5.28*	−1.46
	Madagascar	25	24	57	2.54	0.997	10.22	−14.53*	−1.25

N: Number of individuals, NH: Number of haplotypes, S: Polymorphic sites, π: Nucleotide diversity, DH: Haplotype diversity, k: Average number of nucleotide differences, D: Tajima test, Fs: Fu value test statistically significant: *p < 0.05.
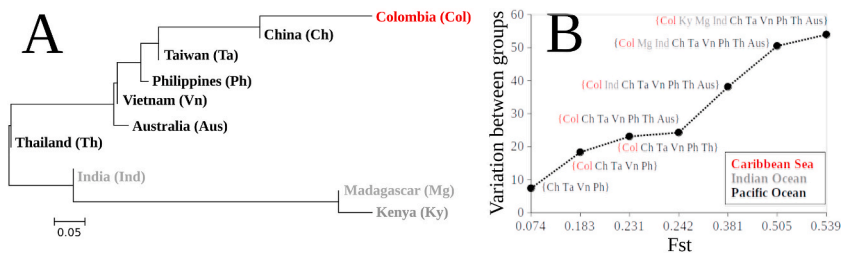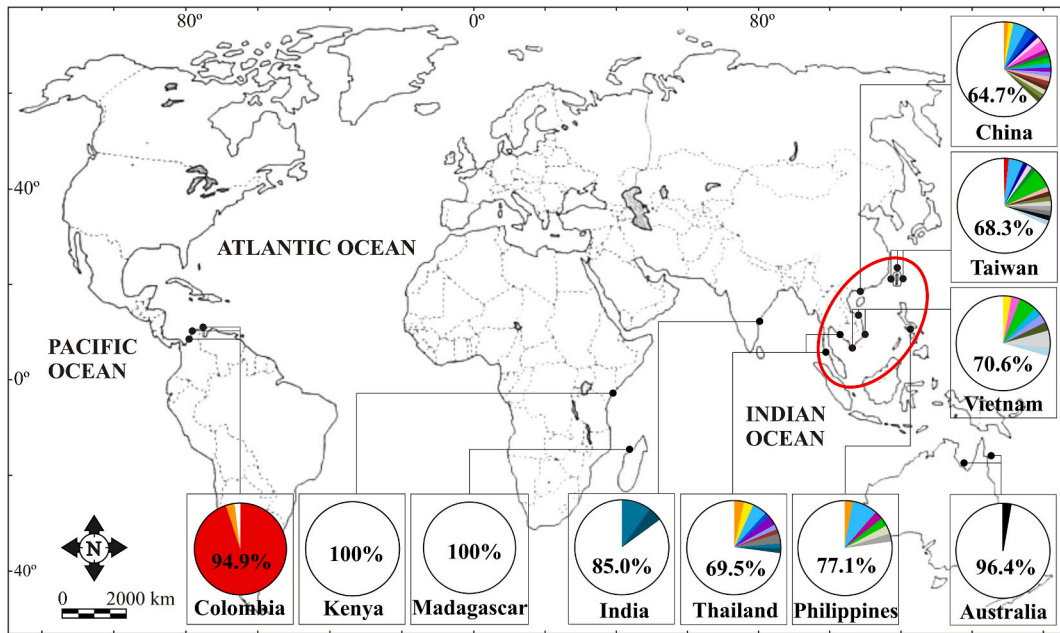
Fig. 3. Genetic relationships

Fig. 4. Haplotypes distribution

Table 4
Indices of genetic diversity from different studies using microsatellite loci and/or mtDNA-CR.

Genetic diversity using microsatellite loci							
#Places	Source	#loci	N (NA)	Ho	He	Fis	Author
3	Colombia	10	84 (13)	0.51	0.90	0.40	This study
5	Australia	3	312 (33)	0.93	0.41	N/A	Brooker et al., 2000
5	Thailand	5	242 (24)	0.78	0.95	N/A	Spungul et al., 2000
5	Philippines	6	352 (20)	0.77	0.81	0.077	Xu et al., 2001
1	Taiwan	23	30 (23)	0.62	0.94	N/A	Pan et al., 2004
2	Australia/Thailand	13	157 (242)	0.69	0.86	0.25	Li et al., 2007
5	Australia	12	437 (9)	0.67	0.75	0.237	Dixon et al., 2008
8	Indo-Pacific	10	355 (29)	0.69	0.94	N/A	You et al., 2008
17	Indo-Pacific	8	682 (13)	0.85	0.83	0.045	Waqairatu et al., 2012
Genetic diversity using mtDNA-RC							
#Places	Source	#pb	N	H(%)	HD	π (%)	Author
3	Colombia	411	98	3 (3)	0.099	0.79	This study
8	India	577	83	69 (83)	0.780	3.4	Kumar et al., 2007
8	Indo-Pacific	531	316	262 (83)	0.992	4.3	You et al., 2008
4	China	497	80	69 (86)	0.996	6.2	Zhou et al., 2009
6	Indonesia	459	115	N/A	N/A	1.8	Walther et al., 2011
17	Indo-Pacific	418	369	247 (67)	0.830	4.0	Waqairatu et al., 2012
3	India	562	81	43 (53)	0.905	14.3	Khedkar et al., 2013

4. Discussion

4.1. Genetic diversity

The genetic diversity of the tiger shrimp in the Colombian Caribbean Sea was shown to be moderate with microsatellite loci and low with mtDNA-CR. In this latter case, they were lower when compared with other studies of populations originating from countries of the Indo-Pacific Ocean (Table 4). This difference in magnitude between the two types of markers is attributable to the rate of evolution of each marker. Mitochondrial markers have a slower rate of evolution and are conserved (they do not recombine), which makes them especially useful for tracing the past history of populations; microsatellites, on the other hand, because they have a faster evolution due to recombination, tend to provide greater detail on recent changes (a fewer number of generations). Additionally, since this is a recent invasion process, with the first introductions dating from the 1970s and 1980s, microsatellites have more power to reveal their adaptive evolution according to the genetic status of the populations distributed in the Caribbean Sea. Consequently, it can be concluded that the values found in the three sites studied (Table 4) were similar to some of the natural populations in the native area.

The above suggests that the tiger shrimp in the Colombian Caribbean Sea has a great adaptive potential that is guaranteeing the success of its invasion process, even managing to minimize the loss of genetic diversity as a consequence of bottlenecks (see Table 2), genetic drift and inbreeding [11,60–63]. Likewise, it has been able to reduce the effect of loss of genetic diversity that normally occurs during the founding event of the invasive population due to the escape of animals from culture systems that, through selective crossbreeding processes in aquaculture, bring with them inbreeding and genetic drift.

Some studies have shown that genetic diversity can be conserved when the invasion process is mediated by the presence of a large number of animals from different areas and with high divergence (e.g. Refs. [64,65]) or when the introduced individuals present a high level of polymorphism [66]. For example, similar or higher values of genetic diversity were reported in invasive populations of the common limpet *Crepidula fornicata*, as a consequence of a combined effect of these two processes [66].

This scenario may be plausible in the tiger shrimp in the Colombian Caribbean Sea if one analyzes the recurrent introductions that have been documented in several coastal countries of the western Atlantic Ocean (e.g., United States, Panama, Venezuela, Brazil, Dominican Republic, Cuba, Colombia [22]). The first sightings in the wild [Brazil in 1987 [26]] and the United States in 1988, the consequence of the loss of 2000 specimens from a station in South Carolina [35]], seem to be chronologically related to these introductions and their subsequent accidental releases in almost all of the Tropical Atlantic (example Fig. 1 and see Ref. [67]). All of the above has influenced the successful establishment of tiger shrimp in the Americas, but without ruling out a colonization process through the dispersal of larvae by means of marine currents [67]. In the case of Colombia, the establishment of tiger shrimp in the Caribbean of Venezuela and Panama may be influencing the dispersal of larvae to Colombia by means of the Caribbean current and the Panama-Colombia countercurrent, respectively [68]. Therefore, this could also explain the values of genetic diversity observed in the three marine sectors.

4.2. Genetic relationships with native populations of the Indo-Pacific Ocean (mtDNA-CR)

Structure analyses detected three populations of tiger shrimp in the Colombian Caribbean Sea, each relatively discrete at each site (Fig. 2). This result supports the hypothesis of an invasion driven by multiple origins of the founder animals in each sector and by the possible arrival of larvae via marine currents to GUA from Venezuela and to GM from Panama. In addition, its tolerance capacity to adapt to contrasting environmental conditions [41,42], as in the case of the Colombian Caribbean, has allowed it to develop the level of genetic substructuring observed. For example, CGSM is a coastal lagoon with an estuarine condition [69]; GUA is characterized by a greater continental shelf coverage, less warm waters (<28 °C) due to a permanent upwelling [70] and higher salinities (>35 UPS) than those present in the GM sector [71,72]. This could explain the genotypic proportions of each population determined by Bayesian analysis, where the green population dominates in CGSM, the blue in GUA and the red in GM (Fig. 2). A similar genetic substructuring is also present in the pink shrimp *Penaeus notialis*, which is distributed in the Atlantic Ocean, including Colombia, where Atencia et al. [68] identified three populations defined by oceanographic and environmental conditions.

Regarding the origin of the tiger shrimp in Colombia, the analysis of the mtDNA-CR sequences revealed that two (H1 and H2) of the three haplotypes found are closely related and come from several countries in the Pacific Ocean (Taiwan: H1; Thailand, Philippines and China: H2; Fig. 4; Supplement 4). In the information consigned in Supplement 3 and reported by Aguirre-Guzman and Lopez-Acevedo [67], this finding is evident when there is concordance with the introductions made by several countries for cultivation purposes or intent. For example, Hawaii imported it in 1980 from the Philippines, Tahiti and Taiwan [73,74]; subsequently, the United States imported it in 1988 from Hawaii [75]. Brazil imported in 1977 from the Philippines [39,40] and in 1984 from Taiwan [39,76], Colombia imported in 1987 from Brazil [77]. Mexico and the Dominican Republic also imported from Taiwan in 1976 and 1985 [73, 74,78], respectively, while Panama imported from the United States in 1976 ([78]; Supplement 3). Without mentioning other introductions made to countries on the continent of Africa, Europe and the Arabian Peninsula, the above demonstrates the aquaculture success that awakened an interest in cultivating this species throughout the world.

Another important aspect to consider is the high divergence between native populations in the Indo-Pacific Ocean [21,79] and the frequent exchange of broodstock between aquaculture farms in different countries in order to meet the need to maintain optimal levels of genetic diversity [79]. This situation could significantly affect the shrimp establishment process because multiple introductions with different origins in their native area ensure high levels of polymorphism in the Colombian Caribbean, which could be maximizing the high divergence among the three populations and maintaining it by the arrival of larvae through the currents.

4.3. Perspective of invasion processes mediated by farming systems

The current scenario in the invasion process of the tiger shrimp in the Colombian Caribbean Sea is similar to that of other species that have been successful in marine invasions (e.g. *Pterois volitans* in the Western Atlantic, *Cyclope neritea* in the Mediterranean Sea and *Crassostrea gigas* in northeastern Europe and the east coast of Brazil). Some common aspects include movement outside their native range by humans; high capacity to tolerate variable environmental conditions; the ability to distribute and colonize diverse environments, great reproductive potential, and generalist habits. This life history added to the above description, gave the tiger shrimp an articulated scenario of favorable conditions to guarantee its success as an invasive species in the western [22,67] and eastern [24], coasts of the Atlantic Ocean, and recently in its colonization process of the Mediterranean Sea [33,75]. Evidence of this are the abundances reported in recent years in different areas of the western Atlantic, the capture of specimens of different sizes (juveniles and adults) and even ovigerous females [25,31,32,34,80].

For example, early work on the invasion of the lionfish *Pterois volitans* in the Atlantic Ocean suggested that the source was an escape from commercial ornamental fish farms in Florida in 1985 and from there, it had spread through currents along the coasts of the entire Atlantic Ocean through Central and South America, reaching the Greater and Lesser Antilles [17]; However, Hunter et al. [81] using microsatellites and mtDNA proposed that the invasion process was actually triggered by several introductions in different areas, given that the H05–H09 haplotypes found in the Bahamas, North Carolina and Bermuda are not present in Florida, where the origin of the invasion was initially proposed. Likewise, Dimitriou et al. [82] provided evidence suggesting that the invasion of *P. miles* in the Mediterranean Sea is the product of multiple introductions for ornamental purposes, by dispersal and colonization through the Suez Canal, and by transport in ballast water.

Other examples of successful invasions originating from multiple introductions include the green crab *Carcinus maenas*, black carp *Mylopharyngodon piceus*, shrimp *Palaemon macrodactylus*, and marsh grass *Sporobolus alterniflorus* [82–85].

In terms of invasions associated with farming systems, Simon-Bouhet et al. [64] found that the rapid spread of the gastropod *Cyclope neritea* along the coasts of France was associated with recurrent introductions from several areas in the Mediterranean Sea, including important farming centers in Spain, France, and Italy, thus increasing genetic diversity in the invasive populations as a consequence of mixing of divergent lineages. Other precedents include the intentional introduction of the kelp *Undaria pinnatifida* for farming in the Northeast Atlantic and of the oyster *Crassostrea gigas* in several countries in northeastern Europe and the east coast of Brazil, ending in accidental escapes that resulted in naturalized and self-sustaining populations due to their high genetic potential [86–88].

These and many other examples, as ballast water, suggest greater attention to the movement and introduction of live organisms for aquatic culture purposes. This implies the need to inform companies involved in the culture of aquatic organisms and the general public about the risk of introducing potentially invasive organisms. It also makes clear the need for commitment to new local regulations and international conventions to control the transport and introduction of aquatic species for farming purposes (e.g. European Community no. 708/2007 (June 11, 2007), regarding the use of alien and locally absent species in aquaculture, or the -European Union Biodiversity Strategy 2020 regarding the protection of biodiversity and introduced species; in Rius et al. [89]), thus allowing to prevent or minimize possible invasions of new species.

In the case of the invasion of the tiger shrimp in the Colombian Caribbean Sea, it is evident that its success is now a fact and that the main protection mechanisms, such as regulation or strict control of its introduction or avoiding its release into the natural environment through prevention and mitigation mechanisms, were ignored. The next step needed is to understand in detail the current state of their invasion in terms of magnitude and to try to quantify their effect in relation to the impact on local biodiversity and ecosystems. Therefore, we suggest carrying out studies to evaluate the ecology of its colonization and expansion process (e.g., local densities, spatial distribution and habitat use, etc.), trophic ecology and reproductive biology, as well as carrying out periodic monitoring to better understand the progress of its invasion process. It would also be beneficial to promote its fishery as a mechanism to regulate abundance and minimize the risks that it may be causing to biodiversity. Finally, we suggest conducting genetic studies involving the entire area of current distribution in the western Atlantic Ocean with mitochondrial and microsatellite markers to understand if the scenario evidenced in this study follows the same pattern of diversity and genetic structure.

5. Conclusions

The results reported in this study indicate that the invasive tiger shrimp in the Caribbean Sea of Colombia have similar genetic diversity to native populations from the Indo-Pacific Ocean (with microsatellites). The presence of three populations (microsatellites) and three haplotypes (mtDNA-CR) in the study area suggest multiple introductions from the Pacific Ocean (Thailand, Philippines, Taiwan and China) with culture purpose. It is discussed how the oceanographic conditions and the culture systems facilitated and promoted the success in the process of invasion of the tiger shrimp in the marine ecosystems of the Colombian Caribbean.

Author contribution statement

Aguirre-Pabón JC, Muñoz E: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Chasqui L: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Narváez-Barandica JC: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

Data availability statement

Data included in article/supplementary material/referenced in article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2023.e17727.

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