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3 **Genetic diversity, demography and connectivity in the marine snail *Thaisella***
4 ***chocolata* (Duclos, 1832): implications for sustainable fisheries management**
5 **along the Peruvian coast**

6

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ABSTRACT

23

24 *Thaisella chocolata* is a marine gastropod (family Muricidae) present from the northern Peru
25 to the central Chile. It is of economic importance in these countries where hundreds of tons
26 are caught every year. In combination with El Niño Southern Oscillation (ENSO) events,
27 fishing activity already led to the collapse of Chilean populations, raising concerns about the
28 state of Peruvian populations. The aim of this study is to assess the demography, genetic
29 diversity and connectivity of *T. chocolata* along the Peruvian coast. This would provide
30 important insights into the resilience of this species to anthropogenic disturbance. In this
31 study, four locations along the coast of Peru were investigated for the first time.
32 Mitochondrial cytochrome oxidase (COI) sequences were obtained from 116 individuals and
33 four microsatellites from 95 individuals. Both COI (combined with 156 publicly available
34 sequences) and microsatellite data revealed very low genetic differentiation, despite a few
35 significant ϕ_{ST} and F_{ST} values between population pairs. The most likely gene flow model
36 (MIGRATE-N) was panmixia between all locations, with gene flow occurring equally
37 northward and southward. This pattern can be related to the surface currents along Peru,
38 combined with the high pelagic larval duration of *T. chocolata*. Hyperdiversity was found for
39 the COI marker ($\pi_{Syn} > 5\%$). Microsatellite loci were also polymorphic, with a mean diversity
40 of 12.69 alleles per locus per population. No recent population bottleneck was observed
41 (microsatellite data) while at least one past demographic expansion was suggested (COI
42 data). Given the high genetic diversity and connectivity, *T. chocolata* is expected to show
43 high evolutionary resilience and can be considered as one management unit in terms of
44 fisheries management. However, further studies are required to confirm this hypothesis,
45 such as the characterisation of the effective population size (using numerous nuclear loci). In

46 addition, precautionary measures in relation to fisheries should be maintained, given the
47 recent collapse of *T. chocolata* stocks in Chile.

48

INTRODUCTION

50 Evolutionary resilience integrates all characteristics influencing species robustness,
51 illustrating how a species is able to cope with abiotic and biotic changes (Sgrò, Lowe &
52 Hoffmann, 2011). Genetic diversity, effective population size and genetic connectivity (gene
53 flow) are important and necessary components to elucidate the evolutionary resilience of a
54 species (Nicholson & Evans, 1997; Sgrò, Lowe & Hoffmann, 2011). For example, a species
55 with high genetic diversity, high connectivity, and a large effective population size would be
56 considered as a robust faunal element (Sgrò, Lowe & Hoffmann, 2011; Jossart, Sands &
57 Sewell, 2019). In the context of conservation and fisheries, management units (Mus) can
58 notably be described considering these three components, and management plans can be
59 implemented to enable sustainable and optimal exploitation of stocks.

60 *Thaisella chocolata* (Duclos, 1832) is a marine gastropod (family Muricidae) present from the
61 northern Peru (5 °S) to the central coast of Chile (33 °S) (Osario, 2002). This carnivorous
62 species (common names: “caracol negro” or “caracol chocolate”) lives on rocky substrates
63 between 5 and 40 metres deep (Cantillanez *et al.*, 2011; Ortiz *et al.*, 2015). *Thaisella*
64 *chocolata* reproduces throughout the year and is a broadcasting species, the pelagic larva
65 staying in the water column for up to four months (Avendaño *et al.*, 1998, Soledad *et al.*,
66 2004). Compared to most marine species, this is a long pelagic larval duration (PLD), which is
67 expected to favour connectivity over long distances when oceanography allows it (Weersing
68 & Toonen, 2009; Jossart *et al.*, 2017). The oceanography of Peru is characterised by the
69 Humboldt Current System (HCS), which flows from south to north, and the Peru Chile Under-
70 current (PCUC), which flows in the opposite direction (Montecino & Lange, 2009). While the
71 PCUC might counteract the HCS under certain conditions, it is generally accepted that the

72 HCS dominates and favours larval dispersal northwards along the coast of Peru, therefore
73 facilitating genetic homogenisation for species with a long PLD such as *T. chocolata*
74 (Cárdenas, Viard & Castilla, 2008).

75 *Thaisella chocolata* is an economically important species in Peru and Chile. It is one of the
76 most fished invertebrate in Peru, being mainly targeted by artisanal fishermen (IMARPE,
77 2023). In total, it was evaluated that hundreds of tons of this species are collected each year
78 in the country. This species is therefore under strong human pressures that can have a
79 significant impact on its populations. In addition to anthropogenic pressure, the natural El
80 Niño-Southern Oscillation (ENSO) periodically changes the environmental conditions, which
81 substantially increases the abundance of *T. chocolata* during each El Niño phase (Díaz &
82 Ortlieb, 1993). Several possible reasons have been proposed to explain such an increase: the
83 capacity to survive in warmer waters, the exploitation of an alternative food source, the
84 higher abundances of usual preys, or the reduction of competition with other species (Arntz
85 & Tarazona, 1990). ENSO also affects the current system in Peru, which in turn impacts larval
86 recruitment of *T. chocolata* (Sarachik & Cane, 2010). Fisheries activity and ENSO are also
87 directly related. In fact, fishermen strongly redirect their activities toward locations where
88 populations increased under the influence of ENSO, which can subsequently lead to
89 overexploitation, as shown for the scallop *Argopecten purpuratus* during the 1983 El Niño
90 event (Arntz & Tarazona, 1990). Numerous fishermen were attracted to the area of
91 Independencia Bay (14°S), where the local scallop population was sixty times larger than
92 usual. By 1986, even with protective measures in place, it was shown that the local
93 population had significantly dropped due to overexploitation. In response to the declining
94 catches of *A. purpuratus*, landings of *T. chocolata* increased dramatically in 1986, before
95 falling off in 1990. More recently, indications of overfishing were found with some local

96 depletions of populations in the northern Peru and an increased proportion (80-98 %) of
97 individuals caught below the minimum landing size (IMARPE, 2017 and unpublished data).

98 A recent study based on mitochondrial markers, cytochrome oxidase I (COI) and 16 rRNA,
99 showed that *T. chocolata* has a high haplotype and nucleotide genetic diversity and lacks
100 significant population differentiation in Peru (Zelada-Mázmela *et al.*, 2022). The authors also
101 showed that the population has undergone two past demographic expansions events from
102 which the current population is likely to have retained its genetic diversity. Additional
103 geographic locations, nuclear markers and gene flow analysis were needed for a better
104 assessment of the evolutionary resilience of *T. chocolata* and provide a strong basis for
105 establishing of sustainable fisheries management.

106 The current study aims to contribute to the assessment of the evolutionary resilience of *T.*
107 *chocolata* along the Peruvian coast, increasing the geographical range previously studied, in
108 order to provide baseline data for a sustainable fisheries management. Two complementary
109 molecular markers, the mitochondrial COI gene and nuclear microsatellite loci, were used to
110 investigate whether: 1) *T. chocolata* shows high genetic diversity and connectivity
111 throughout its distribution area, as expected with the surface currents in Peru and the long
112 PLD of the species; 2) Fisheries, ENSO variations and their interrelationship contribute to a
113 fragmentation of *T. chocolata* populations.

114 MATERIAL AND METHODS

115 *Sampling and DNA extraction*

116 *Thaisella chocolata* tissues were collected between July and August 2018 along the Peruvian
117 coast. Four sampling locations were visited, namely, Isla Grande (11°47'34.98"S,
118 77°12'40.13"W), Isla Chincha Sur (13°38'6.8"S, 76°24'3.1"W), Isla Lobos de Tierra

119 (6°22'55.6"S, 80°51'50.4"W) and Ilo (17°34'52"S, 71°21'31"W) (Fig. 1A). At each location, 30
120 to 32 individuals were sampled, for a total of 122 specimens. The samples from Isla Grande
121 (Ancón) were taken onboard of an artisanal fishing vessel. The samples from the other
122 locations were taken at the landing sites of fishermen by coastal laboratories of the Institute
123 del Mar del Peru (IMARPE). For each individual, a piece of the foot was cut and preserved in
124 96 % ethanol and stored at 4 °C. DNA was extracted following the salting-out method of
125 Sunnucks & Hales (1996).

126 *COI amplification and sequencing*

127 The universal primers LCO1490 (5'- GGTCACAAATCATAAAGATATTGG-3') and HCO2198 (5'-
128 TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al.*, 1994) were used to amplify a 658-bp
129 fragment of the mitochondrial cytochrome oxidase I (COI) gene (610 base pairs were
130 retained after the reading and cleaning of electropherograms). The PCR mix (25 µl)
131 contained 1 µl of DNA template, 0.5 µl of each primer (concentration of 10 µM), 12.5 µl of 2×
132 Taq Master Mix (VWR, Radnor, USA), 3 µl of Bovine Serum Albumin (BSA) and 7.5 µl of
133 purified water.

134 The PCR thermal profile was the following: initial denaturation at 95 °C for 2 minutes,
135 followed by 35 cycles of denaturation at 95 °C for 30 seconds, annealing at 46.5 °C for 30
136 seconds and elongation at 72 °C for 30 seconds, and final elongation phase at 72 °C for 5
137 minutes. The sequencing of the COI PCR products was performed by Macrogen[®] Europe.

138 *Microsatellite amplification and genotyping*

139 A set of four primer pairs initially developed for the closely related species *Concholepas*
140 *concholepas* (Bruguière, 1789) was used (Cárdenas *et al.*, 2011). Additionally, 12 pairs of
141 primers were designed based on nuclear sequences retrieved from GenBank (Accession

142 numbers: HQ700360 to HQ700371, Gallardo-Escarate *et al.*, 2010) using the software Oligo
143 Explorer v.1.2 (GeneLink™). All pairs of primers are recorded in Supplementary Material
144 Table S1.

145 The four loci Cc828, Tchoc1, Tchoc8 and Tchoc11 were kept (Supplementary Material Table
146 S1). The other loci were not kept as no amplification or multiple non-specific amplifications
147 were observed on gels. The PCR thermal profile was the following: initial denaturation at 95
148 °C for 2 minutes, followed by 35 cycles of denaturation at 95 °C for 30 seconds, annealing at
149 a temperature ranging from 48.5 to 60°C depending on the pair of primers for 45 seconds
150 and elongation at 72 °C for 45 seconds, and a final elongation phase at 72 °C for 5 minutes
151 (Supplementary Material Table S1). The PCR mix was the same as the COI mix.

152 PCR products were pooled and diluted with purified water, dilution factors were between
153 1/30 and 1/50. Then, 1 µl of diluted PCR product was added to 8.85 µl formamide and 0.15
154 µl of GENESCAN LIZ-500 size standard (Applied Biosystems). Fragments were analysed using
155 an Applied Biosystems Inc. 3730 48 capillary sequencer with 50 cm capillary length.

156 *COI data analysis*

157 COI sequences were checked and edited with the software Chromas Pro v.2.1.8
158 (Technelysium). In order to detect nuclear pseudogenes, sequences were translated into
159 amino-acid sequences with Mega X (Kumar *et al.*, 2018). Our COI dataset was supplemented
160 with 156 COI sequences available on NCBI (OK087138-OK087293) from the same area
161 between 2018 and 2020 (Zelada-Mázmela *et al.*, 2022). The length of the COI fragments was
162 508 bp after merging our data set to that of Zelada-Mázmela *et al.*, (2022). The identity of
163 each specimen of *T. chocolata* was verified with BLAST/BOLD searches, as well as a
164 Maximum likelihood phylogeny and the Automatic Barcode Gap Discovery (ABGD available

165 at <http://www.wabi.snv.jussieu.fr/public/abgd/abgdweb.html>) using two closely related
166 species (*Thaisella kiosquiformis*: HE584387, *Concholepas concholepas*: EU517122-
167 EU5177458).

168 Given the hyperdiversity observed in the sequence data, a second dataset (Dataset B) was
169 derived from the original one (Dataset A), following the method described by Fourdrilis &
170 Backeljau (2019). This consisted in removing hypervariable nucleotide sites in the COI
171 sequences. To this end, the *.sta* outfile generated with the software Network v.5.0.0
172 (Bandelt *et al.*, 1999) was used, in which the nucleotide sites having a weight > 1 were
173 removed. This method removes hyperdiversity in order to help reveal signal of gene flow by
174 decreasing the amount of polymorphism (S), the number of private haplotypes (N_{Phap}) and
175 hence haplotypic differentiation (D_{EST}), while preserving haplotype diversity (h) and genetic
176 differentiation (F_{ST} and relatives; Fourdrilis & Backeljau, 2019).

177 For Datasets A and B, sequences were collapsed into haplotypes with FaBox v.1.5
178 (<http://users-birc.au.dk/palle/php/fabox/dnacollapser.php#>). TCS haplotype networks were
179 produced using the software PopART (Leigh & Bryant, 2015). Haplotype diversity (Nei, 1987)
180 and nucleotide diversity (Nei & Jin, 1989) were calculated using the program Arlequin
181 v.3.5.2.2 (Excoffier & Lischer, 2010). Correlation between haplotype and nucleotide
182 diversities was assessed using the *Stats* package in R (R Core Team, 2019). The program
183 DnaSP v.6 (Librado & Rozas, 2009) was used to calculate the Jukes-Cantor corrected
184 nucleotide diversity at synonymous (π_{syn}) and non-synonymous (π_{nonsyn}) sites in Dataset A. In
185 coding regions, synonymous sites are characterised by mutations that do not change the
186 amino acid, whereas mutations at non-synonymous sites lead to a different amino acid.
187 Therefore, π_{syn} and π_{nonsyn} were not applicable to Dataset B.

188 Dataset A was used for demographic analysis. DnaSP was used to calculate Tajima's D
189 (Tajima, 1989) and Fu's F_s (Fu, 1997) as neutrality tests. Mismatch distribution (Rogers,
190 1995) was assessed using the sum of square deviation (SDD) (Rogers & Harpending, 1992)
191 and the Harpending's raggedness index (HRI) (Harpending, 1994) in Arlequin. Bayesian
192 Skyline Plot (BSP) analysis was also used to estimate the past demographic trend of the
193 species. It was conducted with the program Bayesian Evolutionary Analysis Sampling Trees
194 v.1.10.1 (BEAST) (Suchard *et al.*, 2018) hosted at CIPRES Science Gateway (Miller *et al.* 2010).
195 Input files were generated using the Bayesian Evolutionary Analysis Utility (BEAUti). The
196 GTR+G+I model (selected with PartitionFinder2, Lanfear *et al.*, 2016) was used with the strict
197 clock model and samples considered as monophyletic. The mutation rate of 7.9×10^{-9}
198 substitution/site/year was based on *Nucella*-specific COI data (McGovern *et al.*, 2010). The
199 generation time was assumed to be a year as reported for other species belonging to
200 Rapaninae (Butler, 1985; Harding, Mann & Kilduff, 2007). MCMC analysis generated 2×10^8
201 chains sampled every 1×10^3 chains. Ten percent burn-in was discarded using the software
202 Tracer v.1.7.1 (Rambaut *et al.*, 2018).

203 An analysis of the molecular variance (AMOVA) were performed on both Datasets A and B to
204 quantify genetic differentiation (ϕ_{CT} and ϕ_{ST}) using Arlequin v.3.5.2.2 (Excoffier *et al.*, 1992).
205 Using Pennings' script (2012) implemented in R, Jost's D (D_{EST}) (Jost, 2008) was calculated in
206 order to assess population genetic differentiation in terms of lack of shared haplotypes (as
207 opposed to ϕ_{ST} that measures population genetic differentiation in terms of dissimilarities in
208 the allele frequencies and the degree of fixation of alternative haplotypes). P-values were
209 corrected using the Benjamin-Yekutieli method (Narum, 2006).

210 Gene flow patterns among populations were assessed using MIGRATE-N v.3.6.11 (Beerli,
211 2006). Six migration models were tested, using Dataset B. MIGRATE-N was run on the Core
212 Cluster of the Institut Français de Bioinformatique (IFB) (ANR-11-INBS-0013) under the F84
213 mutational model. Each run was replicated three times and consisted of 200×10^6 generations
214 sampled every 200 iterations (burn-in of 5×10^5). The replicates used four MCMC's with a
215 heating scheme having starting temperatures of 1.0, 1.5, 3.0 and 1,000,000. The program
216 estimates the boundaries of the mutation-scaled population size ($\Theta = 2N_e\mu$) for each
217 sampling site and the mutation-scaled migration rate ($M = m/\mu$), where N_e is the effective
218 population size of females, μ the mutation rate and m the migration rate. Models were
219 ranked using the log Bays factors (LBF) and their probabilities were calculated using the
220 marginal likelihood of each model. The effective number of migrants was calculated
221 following the equation $N_{em} = \Theta_{\text{recipient}} * M$.

222 *Microsatellite data analysis*

223 Chromatograms were analysed using the software PEAK SCANNER v1.0 (Applied
224 Biosystems). The presence of null alleles was assessed using the software MICROCHECKER
225 v.2.2.3 (Van Oosterhout *et al.*, 2004). F_{ST} and corrected F_{ST} were calculated using the
226 software FREENA v.1.2 (Chapuis & Estoup, 2007) to assess the potential effect of null alleles.
227 The number of alleles per locus, allele frequency, allelic richness, the number of private
228 alleles and the observed and expected heterozygosities (Nei, 1973), were estimated for each
229 sampling site using the program GenAEx v.6.5 (Peakall & Smouse, 2012). Linkage
230 disequilibrium (LD) and the inbreeding coefficient within populations (F_{IS}) (Weir &
231 Cockerham, 1984) were assessed with the software FSAT v.2.9.3.2 (Goudet, 2001). The
232 program BOTTLENECK v.1.2.02 (Piry *et al.*, 1999) was used to detect a potential recent

233 bottleneck event. The analysis was conducted with a two-phased mutation model and 10^4
234 iterations, 14 % of variation and the 95 % stepwise mutation model.

235 AMOVA and D_{EST} values were computed using GenAlEx. Pairwise F_{ST} -values were calculated
236 with the program FSTAT v.2.9 (Goudet, 2001). The program STRUCTURE v.2.3.4 (Pritchard *et*
237 *al.*, 2000) was used to determine the most likely number of genetic clusters (K) in the overall
238 dataset. It was run with a burn-in of 10^5 and 10^6 MCMC chains in order to test the
239 probability L (K) for K ranging from one to seven (10 iterations for each K value). The most
240 likely value of K was determined using the original method described in the STRUCTURE
241 manual and the method of Evanno *et al.*(2005) in Structure Harvester v.0.6.94 (Earl &
242 vonHoldt, 2012).

243 RESULTS

244 *COI analysis*

245 The identity of all *Thaisella chocolata* specimens was confirmed based on ABGD analysis and
246 a ML phylogeny that included closely related species. Out of the 272 sequences obtained,
247 210 haplotypes were found in Dataset A. Among those, 188 (89.5 %) were private (Table 1).
248 The most frequent haplotype, found in ten individuals (3.7 %), was present in all the
249 locations excepted Salaverry, Samanco, Chorillos and Ilo. The second most common
250 haplotype, found in eight individuals (2.9 %), was present in Bayovar, Pimentel, Isla Grande
251 and Marcona. At all locations, the number of haplotypes observed was close to the number
252 of individuals sampled. On average, 75 % of the haplotypes observed at one location were
253 private (Table 1). The highest rate of private haplotype was observed in Samanco with 17
254 private haplotypes out of the 18 observed (94.4 %). The lowest rate was observed in Isla
255 Chincha Sur with 19 private haplotypes out of the 28 observed (67.8 %). The haplotype

256 network of Dataset A showed a bush-like pattern (Fig. 1B). A total of 128 ($S = 25\%$)
257 polymorphic sites were found (Table 1). Within each sampling site, there were between 34
258 and 55 polymorphic sites, which represented 7 to 11% of the sequence length.

259 The haplotype diversity was very high (0.99 ± 0.01) in the overall population (Dataset A) and
260 ranged from 0.96 (Pimentel) to 1 (Chao, Pisco and Marcona) within sampling sites. The
261 nucleotide diversity was high and ranged from 1.3% (Chao and Marcona) to 1.6%
262 (Salaverry, Chorrillos and Pisco), while reaching 1.53% (± 0.79) in the overall population
263 (Dataset A). The Jukes-Cantor nucleotide diversity at synonymous sites was 5.8% in the
264 overall population and between 5% and 6.2% within sampling sites. The nucleotide
265 diversity at non-synonymous sites was very low at each sampling site, with less than 1%.

266 Dataset B (without hypervariable nucleotide sites) was composed of COI sequences of 420
267 bp and showed 36 haplotypes. The haplotype network showed a star-like pattern with three
268 dominant haplotypes shared between all populations (Fig. 1C). The overall haplotype
269 diversity dropped to $0.873 (\pm 0.025)$ and the overall nucleotide diversity to $0.3\% (\pm 0.2\%)$.

270 Tajima's D and Fu's F_s were significantly negative in the overall population (Dataset A),
271 rejecting the null hypothesis of neutral evolution and indicating an excess of rare alleles
272 (Supplementary Material Table S2). These results indicated that *T. chocolata* might have had
273 a sudden demographic expansion and/or a selective sweep. Fu's F_s was significantly negative
274 for each sampling site. Tajima's D was negative in all sampling sites but not significantly. The
275 demographic expansion hypothesis was supported by the mismatch distribution analysis for
276 Bayovar, Pimentel, Salaverry, Isla Grande, Marcona and Ilo that showed non-significant tests
277 for SSD and HRI and a unimodal distribution (Supplementary Material Table S2). However,
278 the hypothesis of sudden population expansion was rejected for the population from Pisco,

279 where both indices, SDD (0.014, $p < 0.01$) and HRI (0.041, $p < 0.01$), were significant.
280 Regarding the other locations, SDD was significant but HRI was not. The mismatch
281 distribution analysis for the overall population showed non-significant HRI (0.005, $p = 0.14$)
282 and significant SDD (0.010, $p < 0.01$). However, demographic expansion was sustained by
283 unimodal mismatch distribution (Fig. 2A). The BSP showed a demographic expansion of the
284 overall population in Peru over time (Fig. 2B). The expansion seemed to have happened by
285 two events, around 1.1 and 1.05 Myr before present (BP) and between 0.45 and 0.35 Myr
286 BP.

287 The AMOVA based on Dataset A did not show significant ϕ_{ST} -value ($\phi_{ST} = 0.01232$, $p > 0.01$,
288 Benjamin-Yekutieli corrected) in the overall population. However, a few significant pairwise
289 ϕ_{ST} values were observed: between Marcona and Isla Lobos de Tierra ($\phi_{ST} = 0.069$, $p < 0.01$)
290 between Ilo and Chao ($\phi_{ST} = 0.081$, $p < 0.01$), Ilo and Isla Grande ($\phi_{ST} = 0.057$, $p < 0.01$) and
291 Ilo and Marcona ($\phi_{ST} = 0.101$, $p < 0.01$) (Supplementary Material Table S3). The largest
292 source of molecular variation was observed within sampling site (98.77 %). The AMOVA
293 based on Dataset B also showed a non-significant ϕ_{ST} -value (0.0193, $p > 0.01$) in the overall
294 population. Pairwise ϕ_{ST} -values showed significant genetic differentiation between Ilo and
295 Isla Grande as well as between Ilo and Marcona (respectively $\phi_{ST} = 0.1397$ and $\phi_{ST} = 0.1911$,
296 $p < 0.01$). D_{EST} estimated from Dataset A was significant at the overall population level ($D_{EST} =$
297 0.6078 ± 0.0113). Significant haplotypic differentiation was also found between several
298 sampling sites (Table 2). All D_{EST} values dropped to nearly zero in Dataset B excepted
299 between Isla Grande and Ilo ($D_{EST} = 0.31$, $p < 0.01$) and between Marcona and Ilo ($D_{EST} = 0.29$,
300 $p < 0.01$).

301 MIGRATE-N analysis indicated that the most likely gene flow model was panmixia among all
302 populations ($p = 0.999$) (Table 3). Northward and southward effective number of migrants
303 was equitably balanced. On average, the number of migrants per generation between
304 locations was 355 ($N_{em} = 224$ to 508). The other models (Southward, Northward, N-Islands,
305 Northward SST, Southward SST) all had very low probabilities ($< 10^{-8}$, Table 3).

306 *Microsatellite analysis*

307 Out of the 122 individuals sampled, 95 were retained for further analyses. Samples were
308 removed when the amplification of microsatellites or the fragment analysis failed.
309 MICROCHECKER found null alleles for the loci Tchoc8 and Tchoc11, with an estimated
310 frequency ranging from 0.018 to 0.37. All populations had a heterozygote deficiency that can
311 be linked to the presence of null alleles in these two loci (Table 4, Supplementary Material
312 Table S4). Adjusted F_{ST} values for null alleles were calculated for the software FreeNA
313 (Supplementary Material Table S5). No linkage disequilibrium was found between locus
314 pairs. These four loci were polymorphic with 4 to 33 alleles per locus. The allelic richness per
315 population was high, with an average of 12.69 alleles/locus. The highest allelic richness was
316 observed at Isla Chincha Sur (13.75 alleles/locus) and the lowest at Isla Lobos de Tierra
317 (12.00 alleles/locus) (Table 4). In total, 26 (28 %) private alleles were found and Isla Chincha
318 Sur had the highest number (8). Only four private alleles were found at Isla Grande (Table 4).
319 BOTTLENECK did not find a sign of a recent reduction of the effective population size. The
320 AMOVA indicated a low but significant overall F_{ST} value (0.012, $p < 0.017$). Most of the
321 variation was found within individuals (61 %). The variation among populations represented
322 only 1 % of the variation. No significant pairwise adjusted F_{ST} values was found between
323 population pairs. No significant pairwise D_{EST} -value was found among sampling sites.

324 STRUCTURE showed that the most likely value of K was 1 for the original method and 3
325 according to the Evanno method. The barplot for K = 3 indicated a high admixture of these
326 three clusters for all individuals (regardless of the site, Fig. 1D).

327 DISCUSSION

328 *Presence of mitochondrial hyperdiversity in Thaisella chocolata*

329 Hyperdiversity is observed when a marker shows more than 5 % variability at synonymous
330 sites (Cutter *et al.*, 2013). With 5.8 % for COI, *T. chocolata* can be classified as a species
331 showing hyperdiversity, like several other species characterised in the last decade (e.g.,
332 Cutter *et al.*, 2013; Fourdrilis *et al.*, 2016). This hyperdiversity could be due to different
333 factors: (1) a high mutation rate, (2) a high effective population size, (3) a rapid turnover of
334 generations. *Thaisella chocolata* shows the highest haplotype and nucleotide diversity of all
335 Rapaninae studied so far (Supplementary Material Table S6). Nevertheless, the haplotype
336 diversity seems to be relatively high for most of the species in this subfamily. Hyperdiversity
337 in *Rapana venosa* and in *Thais clavigera* has been attributed to their population expansion
338 and to their large effective population size (Chandler, McDowell & Graves, 2008; Guo *et al.*,
339 2015). Compared to other hyperdiverse molluscs, *T. chocolata* shows the same COI
340 nucleotide diversity levels as *Melarhaphe neritoides*. However, *M. neritoides* shows a higher
341 synonymous nucleotide diversity (7.4 %) than *T. chocolata* (5.8 %). The authors concluded
342 that the hyperdiversity in the species is better explained by a high mutation rate of COI
343 (Fourdrilis *et al.*, 2016). To clarify the origin of the mitochondrial hyperdiversity observed in
344 *T. chocolata* further investigations are required (*i.e.* mutation rate, effective population size,
345 generation time).

346 *Demographic trends in Thaisella chocolata*

347 Both overall Tajima's D and Fu's Fs were significantly negative, suggesting a demographic
348 expansion and/or the effect of selection on the population size. This pattern was not
349 observed in some sampling sites where Tajima's D were not significant in contrast to
350 significant Fu's Fs. This could be due to the sample size and the lower power of Tajima's D
351 compared to Fu's Fs (Ramos-Onsins & Rozas, 2002). A trend of demographic expansion was
352 locally supported in half of the sampled localities according to the mismatch distribution
353 analyses. The BSP showed a first population increase around 1.05 and 1.1 Myr ago and a
354 second one between 370,000 and 400,000 years ago. The most recent strong increase in
355 population size is common in many molluscs in the same geographical area and already
356 pointed out for *T. chocolata* in Peru (Cárdenas, Castilla & Viard, 2009; Marín, Fujimoto &
357 Arai, 2013; Ibáñez & Poulin, 2014; Iba *et al.*, 2018; Zelada-Mázmela *et al.*, 2022). This
358 corresponds to the marine isotope stage 11 (MIS 11), a Pleistocene interglacial stage that
359 was warmer than the other Pleistocene interglacial periods that occurred in the southern
360 hemisphere. This often led to the demographic expansion of marine species distributed from
361 the Panamanian province to Chile (between 6° S and 30° S). The high abundances of *T.*
362 *chocolata* during this period is corroborated by a deposition analysis (fossil shells) in
363 Antofagasta Bay (23° S, Ortlieb *et al.*, 1996). The other population expansion detected
364 around 1.05 and 1.1 Myr ago differs from a previous study made on the same species
365 (Zelada-Mázmela *et al.*, 2022). This period corresponds to the marine isotope stage 31 (MIS
366 31), which occurred during Mid-Pleistocene and is recognised as a very warm interglacial
367 period (Froelich *et al.*, 1991; Beltran *et al.*, 2020). Therefore, a strong population expansion
368 of *T. chocolata* over this period is possible. The discrepancy in period estimation is likely
369 related to the different mutation rates used for BSP analysis in the two studies. Whatever

370 the exact timing of these demographic expansion events, an interesting parallel can be done
371 with the present El Niño events, for which warm waters also lead to the demographic
372 expansion of *T. chocolata* populations.

373 Given the intensive fishing of *T. chocolata* in the recent years, it was important to verify
374 whether a population bottleneck could be detected (based on microsatellite data which
375 reflect shorter time scales). No significant sign of a bottleneck was observed. This could be
376 due to the high fecundity of the species (Soledad *et al.*, 2004), associated with the year-
377 round reproductive period (Avendaño *et al.*, 1998). On the other hand, it could also be due
378 to the low number of microsatellites used in this study, and it would therefore require future
379 investigation.

380 *Is Thaisella chocolata panmictic?*

381 Based on COI data, a bush-like haplotype network was observed, which is characteristic of
382 hyperdiverse genetic markers. This network showed no distinct clade or geographic
383 grouping, even when removing hypervariable sites. This is supported by the overall non-
384 significant ϕ_{ST} value (COI Datasets A and B). A weak pairwise genetic differentiation was
385 observed between few sampling sites (based on ϕ_{ST} and D_{EST} values). The drop of D_{EST} but
386 not ϕ_{ST} values in Dataset B reflected that the apparent lack of shared haplotypes observed in
387 Dataset A was not related to a lack of gene flow or genetic differentiation. This effect has
388 been described in *Melarhappe neritoides* which also showed hyperdiverse COI (Fourdrilis &
389 Backeljau, 2019). Microsatellites showed a shallow genetic differentiation in the overall
390 population ($F_{ST} = 0.012$, $p < 0.017$) while pairwise corrected F_{ST} and D_{EST} showed no
391 difference between sampling sites. In addition, panmixia was suggested by STRUCTURE
392 analysis.

393 Overall, the data showed that despite a weak genetic differentiation between some sites,
394 the overall population of *T. chocolata* in Peru can be considered as panmictic, suggesting
395 high genetic connectivity. Panmixia in *T. chocolata* was confirmed by MIGRATE-N analysis
396 that also suggested balanced rates of migration (northward and southward) along the
397 Peruvian coast. Northward migration is consistent with the main current along the Peruvian
398 coast, the Humboldt Current System (HCS), which flows from south to north (Montecino &
399 Lange, 2009). A balanced southward migration was less expected and is probably related to
400 local and transient currents such as the Peru Chile Undercurrent (PCUC), HCS eddies (Penven
401 *et al.*, 2005) and situations where El Niño reverses the HCS (Smith, 1983). This observation of
402 balanced northward and southward migration confirms the expectations of Zelada-Mázmela
403 *et al.* (2022) inferred from COI and 16S patterns. Interestingly, such a panmixia was also
404 observed in another Rapaninae species, (*Concholepas concholepas*) that is sympatric and
405 occupies the same rocky shore habitats as *T. chocolata* (Osario, 2002; Cárdenas, Castilla &
406 Viard, 2009).

407 *Fisheries management implications*

408 Although some shallow population genetic structure was detected, *T. chocolata* could be
409 considered as one management unit along the Peruvian coast. Additionally, *T. chocolata* has
410 a high genetic diversity (COI and microsatellites) that could be linked to a high mutation rate
411 as it seems to be common in the subfamily Rapaninae (Supplementary Material Table S6).
412 Overall, this could indicate a high evolutionary resilience of *T. chocolata* to abiotic and biotic
413 changes. However, precautions regarding fisheries should be taken, given that *T. chocolata*
414 stocks already collapsed in Chile due to overfishing. The collapse of the Chilean population
415 occurred in the 1990s after the collapse of the more valuable gastropod *C. concholepas* in
416 the 1980s (Leiva & Castilla, 2002). Subsequently, fishing activities were only allowed in some

417 regions of Chile (SERNAPESCA, 2011). Fishing techniques are similar in Chile and Peru
418 (Avendaño *et al.*, 1998a): fishermen take advantage of the species behaviour (*i.e.* that comes
419 closer to the surface to reproduce). Due to these aggregations, fishermen catch large
420 quantities, which can sometimes lead to the depletion of most mature individuals of an area.
421 By collecting these mature individuals, the protection from predation on the egg capsules is
422 also removed, which therefore impacts on the next generation (Cantillanez & Avendaño,
423 2013). In the context of future El Niño events, a high fishing pressure on *T. chocolata* is
424 expected due to the collapse of other valuable molluscs such as *Agropectum purpuratus*. In
425 this context, our study can therefore serve as a baseline for future studies regarding genetic
426 diversity, demography and connectivity. Investigating the effective population size of *T.*
427 *chocolata*, which is a good indicator in fisheries management to estimate sustainable quotas,
428 is a research priority, and requires more nuclear markers. Given the presence of *T. chocolata*
429 until the central coast of Chile (33° S) and that the HCS still flows northward in this region
430 (Osario, 2002), Chilean populations may be a source population. Evaluating the connectivity
431 between Chilean and Peruvian populations is therefore another research priority.

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FIGURES AND TABLES

663 **Table 1.** Genetic diversity statistics in *Thaisella chocolata* from Peru, based on COI sequences
 664 (Dataset A).

Site	N	N _{hap}	N _{Phap}	N _{Shap}	S	Genetic diversity			
						h	π (%)	π _{Syn} (%)	π _{Non-Syn} (%)
Current newly investigated sites									
Isla Lobos de Tierra	30	29	22	7	54	0.997 (+/-0.009)	1.5 (+/- 0.8)	5.6	0.112
Isla Grande	28	26	19	7	55	0.995 (+/- 0.012)	1.4 (+/- 0.8)	5.5	0.053
Isla Chincha Sur	29	28	19	9	53	0.997 (+/-0.009)	1.6 (+/- 0.9)	6.0	0.066
Ilo	29	23	18	5	51	0.978 (+/- 0.017)	1.6 (+/- 0.8)	5.8	0.108
Zelada-Mázmela <i>et al.</i> , 2022 sites									
Bayovar	20	19	13	6	36	0.998 (+/- 0.017)	1.5 (+/- 0.1)	5.9	0.000
Pimentel	20	16	12	4	42	0.963 (+/- 0.033)	1.5 (+/- 0.2)	5.8	0.051
Salaverry	18	15	11	4	39	0.980 (+/- 0.024)	1.6 (+/- 0.2)	6.1	0.086
Chao	20	20	14	6	34	1.000 (+/- 0.016)	1.3 (+/- 0.1)	5.1	0.027
Samanco	19	18	17	1	43	0.994 (+/- 0.019)	1.6 (+/- 0.1)	5.9	0.082
Lima	19	17	13	4	44	0.988 (+/- 0.021)	1.6 (+/- 0.1)	6.2	0.057
Pisco	22	22	15	7	45	1.000 (+/- 0.014)	1.6 (+/- 0.1)	6.1	0.140
Marcona	18	18	15	3	35	1.000 (+/- 0.018)	1.3 (+/- 0.1)	5.0	0.000
Overall population	272	210	188	22	128	0.996 (+/- 0.001)	1.5 (+/- 0.8)	5.8	0.068

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666 Abbreviations: N, number of individuals; N_{hap}, number of haplotypes; N_{Phap}, number of private haplotypes; N_{Shap}, number of shared
 667 haplotypes among sampling sites; S, number of polymorphic sites; h, haplotype diversity (+/- SD); π, nucleotide diversity (+/- SD); π_{Syn},
 668 Jukes-Cantor corrected nucleotide diversity at synonymous sites; π_{Non-Syn}, Jukes-Cantor corrected nucleotide diversity at non-
 669 synonymous sites.

670 **Table 2.** Pairwise mtDNA differentiation (D_{EST}) in *Thaisella chocolata* in Peru (sites from Zelada-
671 Mázmele *et al.*, 2022 are underlined), based on COI sequences. D_{EST} -values for the hypervariable
672 Dataset A are above diagonal, D_{EST} -values for the non-hyperdiverse Dataset B are below the diagonal.
673 Dataset B was derived from the original Dataset A, following the method described by Fourdrilis &
674 Backeljau (2019, see Material & Methods). Bold numbers are significant (Benjamin-Yekutieli
675 correction).

	<u>By</u>	<u>Ilt</u>	<u>Pm</u>	<u>Sl</u>	<u>Ch</u>	<u>Sm</u>	<u>Ig</u>	<u>Lm</u>	<u>Ics</u>	<u>Ps</u>	<u>Mr</u>	<u>Ilo</u>
<u>By</u>		0.000	0.287	1.000	0.050	0.776	0.000	1.000	0.000	0.000	0.000	0.499
<u>Ilt</u>	0.022		0.743	0.317	0.000	0.567	0.058	1.000	0.000	0.000	0.000	0.906
<u>Pm</u>	0.000	0.000		0.902	0.729	1.000	0.147	1.000	0.558	0.753	0.098	1.000
<u>Sl</u>	0.000	0.029	0.035		1.000	1.000	0.839	1.000	0.825	0.482	1.000	1.000
<u>Ch</u>	0.000	0.009	0.000	0.034		1.000	0.000	0.000	0.000	0.000	0.000	1.000
<u>Sm</u>	0.001	0.000	0.000	0.083	0.000		1.000	1.000	0.998	1.000	1.000	0.871
<u>Ig</u>	0.000	0.154	0.066	0.006	0.026	0.095		0.334	0.047	0.000	0.000	0.641
<u>Lm</u>	0.000	0.002	0.000	0.000	0.000	0.000	0.000		0.745	0.000	1.000	0.573
<u>Ics</u>	0.000	0.008	0.000	0.031	0.000	0.000	0.030	0.000		0.000	0.000	0.614
<u>Ps</u>	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.000	0.000		0.000	0.719
<u>Mr</u>	0.000	0.133	0.042	0.009	0.001	0.064	0.000	0.000	0.005	0.075		1.000
<u>Ilo</u>	0.139	0.000	0.037	0.136	0.111	0.050	0.311	0.141	0.119	0.000	0.295	

676 Abbreviations: By, Bayovar; Ilt, Isla Lobos de la Tierra; Pm, Pimentel; Sl, Salaverry; Ch, Chao; Sm, Samanco; Ig, Isla Grande; Lm, Lima; Ics, Isla
677 Chincha Sur; Ps, Pisco; Mr, Marcona

678 **Table 3.** Ranking of the gene flow models in *Thaisella chocolata* from Peru tested in MIGRATE-N
 679 (Dataset B).

Rank	Model	Log marginal likelihood	LBF	Probability
1	Panmixia	-1109.23	0	9.99×10^{-1}
2	Southward migration	-1127.74	-18.51	9.15×10^{-9}
3	Northward migration	-1129.32	-20.09	1.88×10^{-9}
4	N-Islands	-1149.44	-40.21	3.44×10^{-18}
5	Northward SST model	-1157.56	-48.33	1.02×10^{-21}
6	Southward SST model	-1171.82	-62.59	6.57×10^{-28}

680 Abbreviations: SST, Stepping-Stone; LBF, Log Bayes Factor

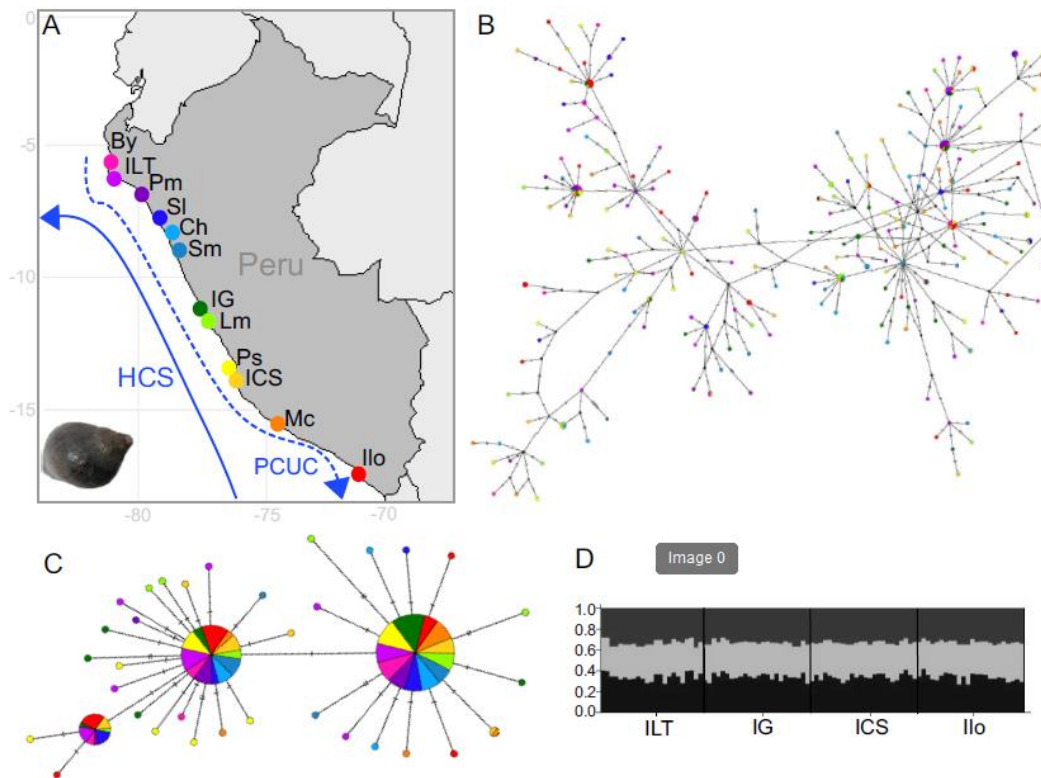
681 **Table 4.** Microsatellite diversity indices of *Thaisella chocolata* from Peru. Numbers in bold are

Site	N	Ar	Nap	Ho	uHe	F _{is}
Isla Lobos de Tierra	2 3	12.00 (+/-3.11)	6	0.496 (+/-0.100)	0.820 (+/- 0.101)	0.401*
Isla Grande	2 4	12.75 (+/- 3.88)	4	0.565 (+/- 0.118)	0.808 (+/- 0.125)	0.306*
Isla Chincha Sur	2 4	13.75 (+/- 4.59)	8	0.519 (+/- 0.150)	0.842 (+/- 0.092)	0.391*
Ilo	2 4	12.25 (+/- 3.01)	6	0.495 (+/- 0.142)	0.805 (+/- 0.103)	0.392*
Overall population	9 5	12.69 (+/- 1.66)	26	0.519 (+/- 0.058)	0.819 (+/- 0.048)	0.372*

682 significant ($0.017 \geq p \geq 0.01$, Benjamin-Yekutieli corrected).

683 Abbreviations: N, Number of individuals; Ar, allelic richness; Nap, number of private alleles; Ho, observed heterozygosity (+/- SD); uHe,
684 unbiased expected heterozygosity (+/- SD); Fis, departure from HWE equilibrium.

685 **Figure 1. A.** Map of sampling sites along the Peruvian coast. Isla Lobos de la Tierra (ILT), Isla Grande
686 (IG), Isla Chincha Sur (ICS), Ilo (Ilo), and from Zelada-Mázmela *et al.* (2022): Bayovar (By), Pimentel
687 (Pm), Salaverry (SI), Chao (Ch), Samanco (Sm), Lima (Lm), Pisco (Ps), Marcona (Mc). The blue arrow
688 represents the Humboldt Current System (HCS) and the blue dashed arrow represents the Peru Chile
689 Under-Current (PCUC). **B.** Haplotype network based on 210 haplotypes from 272 individuals, using
690 the initial COI sequence data composed of 508-bp fragments (Dataset A). **C.** Haplotype network
691 based on 36 haplotypes from 272 individuals, using Dataset B composed of 420-bp long sequences in
692 which highly variable nucleotide sites have been removed. **D.** STRUCTURE bar plot showing the
693 assignment of each individual to the potential genetic clusters (K=3).

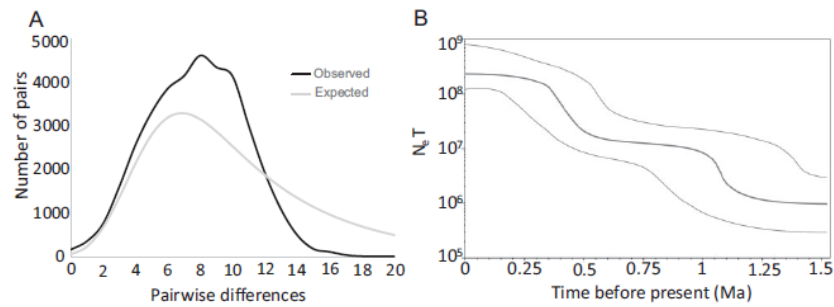


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696 **Figure 2.** Demographic history (based on COI data) of *Thaisella chocolata* along the Peruvian coast.
697 **A.** Mismatch distribution analysis of *T. chocolata* (Dataset A). **B.** Bayesian skyline plot. Demographic
698 reconstructions (N_e = effective population size and T = generation time – 1 year) over time (in million
699 years – Myr) were inferred using BEAST and a mutation rate of 7.9×10^{-9} substitution/site/year. The
700 black line is the median population size, the grey lines are the upper and lower boundary of the 95 %
701 confidence interval.

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SUPPLEMENTARY MATERIAL

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706 **Table S1. A.** List of primer pairs tested. The four first pairs were initially designed for the
 707 closely related species *Concholepas concholepas* and were reported as working with
 708 *Thaisella chocolata* (Cárdenas *et al.*, 2011). The other twelve pairs were designed based on
 709 microsatellites found in GeneBank (Accession numbers: HQ700360 to HQ700371, Gallardo-
 710 Escarate *et al.*, 2010). Primer pairs highlighted in light grey were used in this study.

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Name	Microsatellite GenBank accession number	Repeated motif	Primers	PCR Output
CcSHB	/	(TG)7	F: GCACAACAGAATCCAGCAAA R: AGCAATTGACACAGTTTCTCG	None
CcAZV	/	(AC)6	F: TCCAAGCTAAGCGACCTGGGGA R: AGCGCCAGACCACAACTCA	Multiple bands
Cc201	/	(CTGG)5N38 (TGG)5(AT)4	F: CACTCCAAGCGGCCAGGG R: CACAGGAACGAGGGGCAGGC	Multiple bands
Cc828	/	(TTTG)2	F: CAGCCTGCCGCTGTCCAACA R: CACAGCTGGGCAGCAATGAACA	~150 bp
Tchoc1	HQ700371	(TGA)20	F: TCTTCCATCTCGTCATCATCGT R: ACATAGCGTTTCCATCTTCGT	~500 bp
Tchoc 2	HQ700370	(CCAT)9	F: GTGGGCAAAACAGTCGCATA R: CTACCAGTTCACCGATTCAT	Multiple bands
Tchoc 3	HQ700368	(TG)26	F: ATCCAAGATAGGCTCAGAAAAG R: GGGCGAAAAGGGGGGAAT	None
Tchoc 4	HQ700361	(ATCC)30	F: AAGCGATTGACAAGATGGAG R: ATAGAGTAGGGTTTTTTTTTGT	Multiple bands
Tchoc 5	HQ700366	(ATAG)15	F: GGGGCCGATGAAATCTTACA R: ACCGGGCCAGTTGAATT	None
Tchoc 6	HQ700369	(AGAT)11	F: ACCAGTAGCAGAGGACAAAC R: CGACTGTCAGCCTCTCACT	Multiple bands
Tchoc 7	HQ700363	(AC)31	F: GTAATAAACTCACTGCCAATG R: ATCAAAGTAGAAGGCAAGCAA	None
Tchoc 8	HQ700367	(CA)32	F: TTAATTGTTGACTGATCTGACTTGT R: AATCTGTTATAAGCTCTTGTC	~600 bp
Tchoc 9	HQ700365	(TCA)45	F: AGCCTGTTGAAGAGACTGTTGA R: TCTGCAGGGACACTTGAG	~500 bp (not working for all)
Tchoc 10	HQ700360	(CAT)20	F: AATGACCGTGGAGAGACA R: GACTCACTCATCCCACCT	Multiple bands
Tchoc 11	HQ700364	(ATCC)15	F: CTTCTCTGTCTGTGTTTCTTACTG R: GCCAACGATAACCACTACAG	~500 bp
Tchoc 12	HQ700362	(ATCC)22	F: GCTGGGAATCGAACCCAGAA R: CCCGGGTCAGCAGATCAC	None

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716 **B.** Characteristics of microsatellite primer pairs used in *Thaisella chocolata*.

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Name	Primer	Fluorochrome	Annealing temperature
Cc828	F: CAGCCTGCCGCTGTCCAACA R: CACAGCTGGGCAGCAATGAACA	6-FAM	60 °C
Tchoc1	F: TCTTCATCTCGTCATCATCGT R: ACATAGCGTTTCCATCTTCGT	6-FAM	60 °C
Tchoc8	F: TTAATTGTTGACTGATCTGACTTGT R: AATCTGTTATAAGCTCTTGTC	6-FAM	48.5 °C
Tchoc11	F: CTTCTCTGTCTGTGTTTCTTACTG R: GCCAACGATAACCACTACAG	HEX	50 °C

718 **Table S2.** Neutrality tests and mismatch distribution statistics in *Thaisella chocolata* from
 719 Peru, based on COI sequences (Dataset A).

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Site	Neutrality tests		Mismatch distribution	
	Tajima's D	Fu's Fs	SSD	HRI
This study sites				
Isla Lobos de Tierra	-1.68*	-25.09*	0.015*	0.008
Isla Grande	-1.86*	-19.60*	0.008*	0.014
Isla Chincha Sur	-1.54	-23.01*	0.012*	0.008
Ilo	-1.51	-10.65*	0.009	0.014
Zelada-Mázmela <i>et al.</i> (2022) sites				
Bayovar	-1.00	-11.70*	0.003	0.013
Pimentel	-1.41	-5.42*	0.001	0.008
Salaverry	-1.22	-4.94*	0.010	0.023
Chao	-1.33	-16.16*	0.019*	0.020
Samanco	-1.42	-10.14*	0.019*	0.014
Lima	-1.39	-7.55*	0.017	0.024
Pisco	-1.28	-16.54*	0.014*	0.041*
Marcona	-1.62*	-13.89*	0.014	0.030
Overall population	-2.04*	-40.09*	0.010*	0.005

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Abbreviations: HRI, Harpending's raggedness index. Stars indicate significant values. Bold numbers indicate the support of demographic expansion.

736 **Table S3.** Pairwise mtDNA differentiation (ϕ_{ST}) in *Thaisella chocolata* in Peru (sites from
737 Zelada-Mázquez *et al.* 2022 are underlined), based on COI sequences. ϕ_{ST} values above the
738 diagonal are computed from Dataset A, and values below the diagonal are computed from
739 Dataset B. Bold numbers are significant. The alpha value was Benjamin-Yekutieli corrected to
740 0.0105 (Narum, 2006).

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	<u>By</u>	<u>Ilt</u>	<u>Pm</u>	<u>Sl</u>	<u>Ch</u>	<u>Sm</u>	<u>Ig</u>	<u>Lm</u>	<u>Ics</u>	<u>Ps</u>	<u>Mr</u>	<u>Ilo</u>
<u>By</u>		0.011	-0.006	-0.015	0.000	0.013	-0.012	-0.015	-0.014	-0.000	0.000	0.024
<u>Ilt</u>	-0.004		-0.019	0.012	0.057	0.006	0.033	0.030	0.000	-0.012	0.069	-0.011
<u>Pm</u>	-0.028	-0.022		-0.002	0.041	-0.003	0.013	0.016	-0.007	-0.023	0.045	-0.002
<u>Sl</u>	-0.030	0.002	0.003		0.015	0.017	-0.004	-0.002	-0.010	-0.003	0.016	0.023
<u>Ch</u>	-0.023	0.039	-0.004	0.019		0.031	-0.004	-0.018	0.009	0.034	-0.018	0.081
<u>Sm</u>	-0.020	-0.002	-0.035	0.020	-0.014		0.002	0.019	0.001	-0.007	0.044	0.027
<u>Ig</u>	-0.012	0.064	0.025	0.015	-0.022	0.016		-0.008	-0.001	0.016	-0.007	0.057
<u>Lm</u>	-0.030	0.017	-0.014	-0.010	-0.026	-0.015	-0.014		-0.009	0.020	-0.003	0.051
<u>Ics</u>	-0.020	-0.006	-0.032	0.010	-0.007	-0.026	0.021	-0.009		-0.006	0.022	0.017
<u>Ps</u>	-0.014	-0.029	-0.028	-0.010	0.030	-0.009	0.053	0.005	-0.013		0.045	-0.012
<u>Mr</u>	0.018	0.105	0.070	0.049	-0.008	0.048	-0.020	-0.003	0.049	0.091		0.101
<u>Ilo</u>	0.051	-0.007	0.029	0.030	0.119	0.059	0.140	0.074	0.044	-0.009	0.191	

742 Abbreviations: By, Bayovar; Ilt, Isla Lobos de la Tierra; Pm, Pimentel; Sl, Salaverry; Ch, Chao; Sm, Samanco; Ig, Isla Grande; Lm, Lima; Ics, Isla
743 Chincha Sur; Ps, Pisco; Mr, Marcona

744 **Table S4.** Microsatellite diversity indices in *Thaisella chocolata* per locus at four sampling
745 sites, along the Peruvian coast. Four microsatellites were tested using between 14 and 24
746 individuals per cluster. Abbreviations: N, Number of individuals; Na, Number of alleles; Nap,
747 Number of private alleles; H_o, observed heterozygosity (+/- SD); uH_e, Unbiased expected
748 heterozygosity (+/- SD); F_{IS}, Departure from HWE equilibrium; HWE: significant HWE
749 equilibrium departure.

Site	Locus	N	Na	Nap	H _o	uH _e	F _{IS}	HWE
Isla	Cc828	23	3	0	0.478	0.517	0.076	ns
Lobos de	Tchoc 1	23	17	1	0.783	0.937	0.168	**
Tierra	Tchoc 8	21	15	3	0.333	0.920	0.643	***
	Tchoc 11	23	13	2	0.391	0.907	0.574	***
Isla	Cc828	24	3	0	0.542	0.434	-0.256	ns
Grande	Tchoc 1	24	22	2	0.875	0.957	0.087	ns
	Tchoc 8	20	13	1	0.300	0.929	0.683	***
	Tchoc 11	24	13	1	0.542	0.910	0.410	**
Isla	Cc828	24	4	0	0.542	0.568	0.048	ns
Chincha	Tchoc 1	24	26	6	0.917	0.964	0.050	ns
Sur	Tchoc 8	15	14	2	0.200	0.943	0.794	***
	Tchoc 11	24	11	0	0.417	0.894	0.539	***
Ilo	Cc828	24	4	0	0.292	0.499	0.421	ns
	Tchoc 1	24	18	2	0.792	0.916	0.138	ns
	Tchoc 8	14	12	3	0.214	0.934	0.777	***
	Tchoc 11	22	15	1	0.682	0.870	0.220	ns

750 Significance levels: *: 0.05 ≥ p ≥ 0.01; **: 0.01 > p ≥ 0.001; ***: p < 0.001

751 **Table S5.** Pairwise nuclear differentiation (F_{ST} and corrected F_{ST}) in *Thaisella chocolata*
 752 among four sampling sites along the Peruvian coast, based on four microsatellites. Above
 753 the diagonal, F_{ST} are calculated according to Weir (1996), and below the diagonal, ENA
 754 corrected F_{ST} as described in Chapuis and Estoup (2007).

	Isla Lobos de Tierra	Isla Grande	Isla Chincha Sur	Ilo
Isla Lobos de Tierra		0.004	0.018**	0.032**
Isla Grande	0.006		0.002	0.020**
Isla Chincha Sur	0.009	-0.003		0.000
Ilo	0.019	0.014	0.000	

755 Significance levels : *: $0.017 \geq p \geq 0.01$; **: $0.01 > p \geq 0.001$; ***: $p < 0.001$

756 **Table S6.** Diversity indices and Pelagic Larval Duration (PLD) of species of Rapaninae and
 757 other genetically hyperdiverse molluscs.

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Species	N	N_{hap}	Distribution	Marker	h	π (%)	π_{syn} (%)	Source
<i>Thaisella chocolata</i> (Duclos, 1832)	272	210	SE Pacific	COI	0.996	1.5	5.8	This study
<i>Thais clavigera</i> (Küster, 1860)	602	298	NW Pacific	COI	0.982	0.81	n.a.	(Guo <i>et al.</i> , 2015)
<i>Rapana venosa</i> (Valenciennes, 1846)	284	51	E and W Atlantic, W Pacific	COI + ND2	0.981	n.a.	All result in synonymous changes	(Chandler <i>et al.</i> , 2008)
<i>Stramonita haemastoma</i> (Linnaeus, 1767)	496	197	NE Atlantic	COI	0.976	1.6	n.a.	(El Ayari <i>et al.</i> , 2017)
<i>Concholepas concholepas</i> (Bruguière, 1789)	337	179	SE Pacific	COI	0.88	0.4	n.a.	(Cárdenas <i>et al.</i> , 2009)
<i>Melarhaphe neritoides</i> (Linnaeus, 1758)	185	156	NE Atlantic	COI	0.996	1.38	7.4	(Fourdrilis <i>et al.</i> , 2016)
<i>Brachidontes pharaonis</i> (Fischer, 1870)	34	25	Mediterranean-Red Sea	COI	0.973	3.9	n.a.	(Terranova <i>et al.</i> , 2007)
<i>Bembicium nanum</i> (Lamarck, 1822)	50	25	Australia	COI	0.920	0.6	n.a.	(Ayre <i>et al.</i> , 2009)
<i>Neritina canalis</i> (Sowerby, 1825)	202	117	W Pacific	COI	0.912	0.6	n.a.	(Crandall <i>et al.</i> , 2010)
<i>Neripteron dilatatum</i> (Broderip, 1833)	115	85	W Pacific	COI	0.871	1.0	n.a.	(Crandall <i>et al.</i> , 2010)
<i>Bursa fijiensis</i> (R.B. Watson, 1881)	59	n.a.	SW Pacific	COI	0.848	0.3	n.a.	(Castelin <i>et al.</i> , 2012)

759 Abbreviations: n, number of individuals; N_{hap}, number of haplotypes; h, haplotype diversity; π, nucleotide diversity; π_{syn}, Jukes-Cantor
 760 corrected nucleotide diversity at synonymous sites, n.a. not available.