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New insight into the genetic structure of an iconic species: the spiny lobster, *Palinurus elephas*

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Summary: The spiny lobster, *Palinurus elephas* (Fabricius 1787) is both a key economic resource and a coastal marine species of conservation concern in the Mediterranean Sea, primarily due to overfishing. To enhance biological understanding and support the integration of fisheries management with conservation efforts, a genetic study was conducted on populations around Corsica (France, Mediterranean Sea). A total of 85 individuals were collected from five sampling sites around the island, in collaboration with local fishermen's associations. These individuals were genotyped at 21 microsatellite loci. An additional 15 specimens from the Atlantic coast (Brittany, France) were included as an outgroup. Genetic analyses revealed low levels of differentiation among Corsican samples, with no evidence of geographic genetic structuring or isolation by distance around the island. Unexpectedly, the Atlantic population showed no pronounced genetic divergence from the Mediterranean populations. However, a significant overall deviation from panmixia was detected. Variation partitioning of redundancy analyses suggest that this pattern is likely driven by irregular annual recruitment events originating from multiple breeding aggregations, resulting in subtle genetic differentiation among locations and year classes.

Keywords: *Palinurus elephas*; Mediterranean; microsatellites; fisheries; genetic; stock management.

Nueva perspectiva sobre la estructura genética de una especie icónica: la langosta roja *Palinurus elephas*

Resumen: La langosta roja (*Palinurus elephas*, Fabricius 1787) es tanto un recurso económico clave como una especie marina costera de interés para la conservación en el mar Mediterráneo, principalmente debido a la sobrepesca. Con el fin de mejorar el conocimiento biológico de esta especie y apoyar la integración de la gestión pesquera con los esfuerzos de conservación, se llevó a cabo un estudio genético en poblaciones localizadas alrededor de la isla de Córcega (Francia, mar Mediterráneo). Se recolectaron un total de 85 individuos en cinco sitios de muestreo, en colaboración con asociaciones locales de pescadores. Estos ejemplares fueron genotipados utilizando 21 loci de microsatélites. Adicionalmente, se incluyeron 15 individuos de la costa atlántica (Bretaña, Francia) como grupo externo. Los análisis genéticos revelaron bajos niveles de diferenciación entre las muestras corsas, sin evidencia de estructuración genética geográfica ni aislamiento por distancia en la isla. De manera inesperada, la población atlántica no mostró una divergencia genética marcada con respecto a las poblaciones mediterráneas. Sin embargo, se detectó una desviación significativa del panmixis en el conjunto de las muestras. El análisis de partición de la variación, mediante análisis de redundancia, sugiere que este patrón probablemente se debe a eventos irregulares de reclutamiento anual, procedentes de múltiples agregaciones reproductivas, lo que genera una diferenciación genética sutil entre ubicaciones y cohortes anuales.

Palabras clave: *Palinurus elephas*; Mediterráneo; microsatélites; pesquerías; genética; gestión de stocks.

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INTRODUCTION

The spiny lobster (*Palinurus elephas*, Fabricius 1787) is a decapod crustacean broadly distributed across the northeastern Atlantic Ocean, from southern Sweden to Mauritania, as well as throughout the Mediterranean Sea. Its complex life cycle encompasses a series of morphological and ecological transformations. Following fertilization, females migrate to deeper waters to release their eggs, which they carry first under their abdomen for approximately one month until hatching occurs.

The first larval stage, termed *phyllosoma* due to its flattened, leaf-like morphology, is planktonic and disperses passively with ocean currents. This is followed by the *puerulus* stage, a more morphologically specialized, nektonic form that actively swims toward coastal habitats. The duration of this larval development spans approximately five to six months in the Mediterranean and up to a year in the Atlantic Ocean, culminating in settlement on rocky benthic substrates (Hunter 1999). This transition is marked by elevated mortality rates, primarily due to predation, physiological stress, and habitat degradation caused by pollution and coastal industrialization (Lecaillon et al. 2011, Ellis et al. 2017, Whomersley et al. 2018).

Post-settlement, individuals enter a benthic juvenile stage lasting four to five years in the Mediterranean, until recruitment into the adult population occurs. *P. elephas* has an estimated lifespan of up to 30 years (Pere 2012). Adult lobsters exhibit strong site homing and typically limited spatial movement, often remaining within a two-kilometre radius of their shelter. These localized movements are generally driven by foraging needs or reproductive activities, or are a response to suboptimal environmental conditions (Follesa et al. 2009). Despite the availability of biological data for *P. elephas* in the Mediterranean (Hunter 1999), knowledge concerning its genetic structure and life history remains incomplete, particularly around Corsica.

As a flagship species for many small-scale Mediterranean fisheries, especially in Corsica, *P. elephas* holds significant ecological and economic value. Historical fisheries data indicate a steep decline in catches: from approximately 1,000 t landed across Europe in 1969, yields had dropped by more than 50% by 2017 (Marengo et al. 2020). Given its vulnerability to overexploitation, the species is currently listed as "vulnerable" on the International Union for Conservation of Nature's Red List (Goñi 2015).

Genetic analyses of harvested marine species offer crucial insights into population structure, connectivity and resilience. Phylogeographic data form the foundation for delineating marine stocks and developing sustainable management strategies. Moreover, population genetic studies can reveal patterns of migration and gene flow, helping to determine whether depleted local populations might be replenished by immigrants (Maltagliati et al. 1998, Elphie et al. 2012, Crochelet 2015). Microsatellites are widely employed in population genetics due to their high polymorphism, codominant inheritance and broad genomic distribution. Their use has enhanced our understanding of genetic diversity, kinship relationships and population connectivity (Silva et al. 2019). More recently, single nucleotide polymorphism (SNP) began to provide new data thanks to the high number of loci (generally more than 1000 and sometimes more than 10000), allowing the detailed study of relationships between migrants (Benestan et al. 2021) and, above all, giving access to the loci carrying adaptation to the environment (Mérot et al. 2023).

In marine systems, often perceived as highly connected and homogeneous (Elphie et al. 2012, Crochelet 2015, Pascual et al. 2017), genetic structure is shaped by a combination of intrinsic factors (larval type, duration of pelagic phase and adult mobility) and extrinsic factors (ocean barriers such as currents, winds, topography, habitat availability, food resources and site fidelity) (Robinson et al. 2001, Palero et al. 2011, Whomersley et al. 2018). Thus, observed genetic patterns reflect a dynamic balance between structuring and homogenizing forces (Pascual et al. 2017). Anthropogenic pressures, particularly overfishing, can disrupt this balance by altering genetic diversity and reducing the effective population size, often through selective removal of large, highly fecund individuals (Fernández et al. 2011, Palero et al. 2011, Kennington et al. 2013). As their number decreases, reproductive success drops and the effective size of the populations decreases even if the census size seems stable (Palero et al. 2011, Kennington et al. 2013).

Despite the fact that a long larval stage is a strong genetic homogenizing factor, the panmixia hypothesis is rejected for *P. elephas* at the species scale using seven microsatellite loci (Babbucci et al. 2010). Based on mitochondrial markers—*cytochrome c oxidase subunit I* (*COI*) and *control region* (*CR)*—and nuclear markers (10 microsatellite loci), most studies detected two genetically distinct populations: the Atlantic and the Mediterranean ones (Palero and Pascual 2008, Babbucci et al. 2010). Rare differentiated isolates have also been observed using the *COI* marker in Irish and Tunisian populations (Palero et al. 2008) and with microsatellites in Greece (Palero et al. 2011). Microsatellites have highlighted several exceptions to the simple Atlantic/Mediterranean separation. First, in the

Atlantic Ocean, the Azores, Cape Verde and the south Portuguese populations are genetically closer to the Mediterranean group than to the Atlantic one, according to microsatellites (Babbucci et al. 2010, Faria 2012). Second, the Mediterranean population appears subdivided between east and west subunits on either sides of the Strait of Sicily according to microsatellites and *CR* mtDNA markers (Babbucci et al. 2010, Palero et al. 2011, Elphie et al. 2012). However, these differentiations could be due to simple isolation by distance (Palero et al. 2008).

The present molecular study aims to (i) update nuclear genetic data through the genotyping of *P. elephas* individuals using more than 20 microsatellite markers, focusing on Corsican stocks, with an Atlantic sample serving as an outgroup; (ii) assess the hypothesis of panmixia within the Corsican basin; and (iii) identify potential discrete stocks to inform and improve fisheries management strategies.

MATERIAL AND METHODS

Sampling

The spiny lobsters, captured by trammel net and creels between July 2020 and October 2021, were collected from the Corsican local artisanal fisheries. A total of 85 individuals of *P. elephas* were collected in coastal waters of Corsica (NW Mediterranean Sea), divided in five areas: Cap Corse (n=17), Ajaccio (n=17), Bonifacio (n=17), Balagne (n=17) and Plaine Orientale (n=17) (Fig. 1). Three regions correspond to spatial management areas called fishing *prud'homies* (Journal Officiel de la République Française, 17 January 1993, pp. 922–923). In this study, the original Cap Corse *prud'homie* has been divided in two (Cap Corse and Plaine Orientale) because of their different oceanographic context. In addition, spiny lobsters fished in the Iroise marine park (Brittany, n=15) are also included in this study to compare Atlantic and Mediterranean populations. A fragment of the sixth pleopod of each individual was preserved in 96% ethanol. The carapace length (CL) and gender of each lobster sampled were determined.

Molecular analyses

A small piece of tissue of about 2 mm x 4 mm was taken from ethanol-preserved specimens and dried from alcohol. The DNA extraction was performed according to a Chelex protocol (Estoup et al. 1996): each piece of tissue was dipped into 195 µL of 5% Chelex 100 Resin (Biorad) solution containing 50 mM of Tris-HCL (pH 7) and 500 µg/mL of proteinase K. The mix was placed overnight in an oven at 56°C and then at 95°C for 5 min. Finally, the samples were centrifuged at 3500g for 5 min. The supernatant was then diluted 1:20 with sterile water and frozen at –20°C until required for use.

Table 1. – Characteristics of the 21 chosen microsatellite loci (name, original publication and repeated motifs).

Locus	Reference	Repeated motif
A1	Babucci et al., 2010	(ACC)6
A8	Babucci et al., 2010	(AC)8TA(AC)7
A16	Babucci et al., 2010	(CA)15
A26	Babucci et al., 2010	(GT)6
A28	Babucci et al., 2010	(TG)21
A39	Babucci et al., 2010	(CA)12
A55	Babucci et al., 2010	(AG)20
Pael 1	Palero and Pascual 2008	(CT)26
Pael10	Palero and Pascual 2008	(AAC)6
Pael11	Palero and Pascual 2008	(CAA)7
Pael12	Palero and Pascual 2008	(TAGA)17
Pael14	Palero and Pascual 2008	(AGAT)18
Pael20	Palero and Pascual 2008	(AC)12
Pael21	Palero and Pascual 2008	(ATAG)11
Pael22	Palero and Pascual 2008	(TGT)6
Pael28	Palero and Pascual 2008	(GT)8
Pael31	Palero and Pascual 2008	(ATCT)4ATAT
Pael38	Palero and Pascual 2008	(TG)23. .. (GT)7
Pael44	Palero and Pascual 2008	(GGA)7(GT)28
Pael49	Palero and Pascual 2008	(GTT)8
Pael53	Palero and Pascual 2008	(TA)10

Thirty-two pairs of primer sequences for microsatellite loci amplification were obtained from the literature on the spiny lobster: 15 loci developed by Palero and Pascual (2008) and 17 by Babbucci et al. (2010). Among these, the 21 most efficient ones for genotype scoring were used (Table 1). For each microsatellite, one of the primers was 5'-end-labelled with a fluorescent dye, either 6-FAM, HEX or NED. Polymerase chain reactions (PCR) were performed using the Qiagen multiplex PCR kit (Qiagen, Courtaboeuf, France) in a final volume of 10 µL containing 3 µL of genomic DNA diluted at 10 ng/µL, 5 µL of Qiagen PCR Master Mix, 1 µL of Qiagen Q-solution and 1 µL of primer mix at 2 µM each (Eurofins MWG Operon, Ebersberg, Germany). Amplifications were performed by a GeneAmp PCR System 2700 thermal cycler (Applied Biosystems) according to the supplier's instructions (Qiagen multiplex PCR kit): initial denaturation at 95°C for 15 min; followed by 35 cycles of denaturation at 94°C (30 s), annealing (60° for all loci for 90 s) and extension (72°C, 60 s), with a final extension step at 60°C for 30 min. Amplified PCR fragments were separated on an ABI PRISM 3130xl genetic analyzer (Applied Biosystems) with GeneScan 500 Rox dye size standards. Allele sizes were determined using the GeneMapper v4.1 software system (Applied Biosystems, Life Technologies). The resulting genotypes were used to construct a matrix that served as the basis for all subsequent calculations.

Statistical analyses

Matrix construction. The matrix used for all the calculations was constructed with genotypes constituted by 21 loci genotyped for each individual. Individuals with more than two missing data were removed.

Genetic diversity. In the first step, genetic polymorphism was estimated using unbiased expected heterozygosity (H_{NB}; Nei 1978) and observed heterozygosity, both calculated for each sample (H_O; Nei 1978) using GENETIX software (Belkhir et al. 2004).

F Statistics. At the sample and at the sub-region level, genetic differentiation (F_{ST}) and panmixia (F_{IS}) were estimated (in fact the Θ and f estimators of Weir and Cockerham, 1984, respectively). The significance of the F_{ST} and F_{IS} values was tested by random permutation procedures: 5000 individual permutations between samples for F_{ST} and 5000 allele permutations within each sample for F_{IS}, processed using GENETIX software. The sequential Bonferroni correction was applied for multiple tests (Rice 1989).

Multidimensional analyses. Factorial correspondence analyses (FCA: Benzécri 1973) were run in order to reveal the potential population structure, as implemented in GENETIX.

Bayesian clustering analysis. To detect differentiated subgroups, assignment analyses were performed for the whole sample set using the STRUCTURE 2.3.4 program (Pritchard et al. 2000). Run length was set at 200000 iterations after 100000 burn-in steps, repeated ten times for each K value (K=number of subgroups). The admixture ancestry model and correlated allele frequency options were chosen. Sampling location was not used as prior information. To determine the best K, the KFinder software v. 1.0 was used, applying the Pr[X|K] method (Pritchard et al. 2000), the ΔK method (Evanno et al. 2005) and the parsimony method (Wang 2019).

Isolation by distance (IBD). An IBD structure has been suggested in several previous surveys (Babbucci et al. 2010, Palero et al. 2011). Here, the IBD calculation was applied to the Corsican populations of spiny lobster with or without the Atlantic sample. The Nei distance D (Nei 1978) and F_{ST} were both used, and the geographic distances were measured on a map. Most sampling locations were single except the Plaine Orientale location composed of six stations along a linear coast of about 80 km. For this location, the station was considered to be located at the middle of the sampled zone. The Genepop'007 program (Rousset 2008) compared the modified genetic distance D/(1-D) or $F_{ST}/(1-F_{ST})$ and the Naperian logarithm of the geographic distances to produce a one-tailed P-value indicating whether the IBD was significant.

Genetic differentiation of cohorts. Because a localized population depends on the annual arrivals of larvae (recruitment), the possible genetic difference between year cohorts (i.e. between larvae arrivals) was estimated through Corsican specimens. The spiny lobster sizes allow a proxy of the individual age to be estimated. To this end, individual age (t) was estimated using carapace length and the von Bertalanffy (1938) growth function (Equation 1), which describes lobster growth during its benthic phase.

$$CL(t)=CL\infty(1-e^{-K(t-t_0)}) \quad (1)$$

where $CL(t)$ is the carapace length at age t, $CL\infty$ is the asymptotic carapace length, K is the rate at which $CL\infty$ is approached, and t_0 is the theoretical age at zero CL.

The parameters used were estimated by Marin (1987) in Corsican waters (K=0.151 years or K=0.189 years, CL∞=166.025 mm or CL∞=135.916 mm, and t_0=−0.348 or t_0=−0.342 for males and females, respectively). Using this proxy of individual age and their fishing date, an approximate year of settlement was assessed. Then, the whole sample was cut into six approximate different age cohorts of about 15 individuals each when possible, regardless of their geographic origin. The six classes were analysed by both FCA and F_{ST} in two runs each, including the whole sample and the other only the Corsican specimens.

Relative importance of genetic differentiation of localities and cohorts. To confirm via a statistical test the absence of panmixia in Corsica and to assess the relative effects of age and locality on genetic variation, we performed

variation partitioning (using the varpart function) following a distance-based redundancy analyses (db-RDA) with Euclidean distance. The analysis was conducted in R software v3.6 with the vegan and adegenet packages (Oksanen et al. 2008, Jombart et al. 2010). Although RDA uses Euclidean distance by default, explicit calculation was necessary because RDA cannot be performed with missing data, and we aimed to avoid influencing genetic distance through imputation methods. Moreover, Euclidean distance is recommended for multivariate analyses (Legendre and Legendre et al. 2012) and has been successfully applied in various ecological molecular studies (Laporte et al. 2016, Forester et al. 2018, Caron et al. 2022), including those based on microsatellites (Jombart et al. 2010, Berrebi et al. 2022). Variation partitioning is a method that uses the coefficient of determination to partition the variation of a response matrix into four fractions (Borcard et al. 1992). Two of these fractions are the part of the variation exclusively explained by one of the two explanatory variables, one is the proportion shared by the two explanatory variables, and the last one is the part not explained by the model. Thus, the observation of a proportion of genetic variation explained exclusively by a locality effect will support the absence of geographic panmixia, while the observation of a proportion of genetic variation explained exclusively by an age effect will support the absence of panmixia between age cohorts. In a case of panmixia, no genetic variation should be explained by these variables.

RESULTS

Genotyping

Amplifications were generally successful, with few exceptions (4%). Individuals with more than two missing monolocus genotypes (6 individuals) were removed. The 97 remaining individuals were genotyped at all 21 loci (70 individuals) or showed one missing genotype (27).

Genetic diversity and panmixia

Genetic diversity (i.e. heterozygosity) was similar in all samples ($0.65<H_O<0.70$ and $0.77<H_{NB}<0.81$). As expected, the observed diversity (H_o) is surprisingly always lower than H_{NB} (Table 2). Since these two parameters are used in the calculation of the F_{IS} index (or fixation index), the high F_{IS} values corresponding to heterozygote deficits were all highly significant (***), indicating strong deviations from panmictic equilibrium.

Table 2. – Calculation of the genetic diversity (H_O, H_{NB}) and panmixia (F_{IS}) of the five samples analysed.

	H_0	H_{NB}	F_{IS}	Significance
Brittany	0.67	0.80	0.17	***
Ajaccio	0.66	0.79	0.16	***
Balagne	0.69	0.79	0.13	***
Bonifacio	0.65	0.77	0.15	***
Cap Corse	0.69	0.77	0.11	***
Plaine Orientale	0.70	0.81	0.14	***

The panmixia test (F_{IS}) was also applied to the entire set of samples, including the five Mediterranean samples and the single Atlantic one, and then to the Mediterranean samples only. The values obtained were respectively 0.15 and 0.14, both very highly significant ($P<0.0002$ or ***) showing that there is not only one homogeneous population at the level of the species nor at the level of the Mediterranean Sea (see discussion).

Genetic structure

The multidimensional FCA was performed on 97 individuals and 360 alleles, which determined the data matrix size. Two kinds of FCA were performed. (i) When the analysis focused on individuals, it maximized spread the individuals, but no clear structure was visible (Fig. S1). (ii) When the analysis focused on the samples, i.e. localities or populations represented by their centroids, it maximized the dispersion of the centroids, and a structure was visible (Fig. 2): Bonifacio and Ajaccio lobsters were isolated on the left, Balagne lobsters were positioned towards the top, Cap Corse lobsters were located in the background (positive values on axis 3), more clearly visible from an angle emphasizing axis 3 (see inset), and Plaine Orientale and Brittany lobsters were clustered closely together, extending towards the lower right.

The 97 lobsters were assigned to subgroups numbered 1 to 8 by the STRUCTURE software, which infers their population structure. To choose the best partition, the KFinder software suggested that the partition into one to five subgroups, according to the three methods, was the most informative.

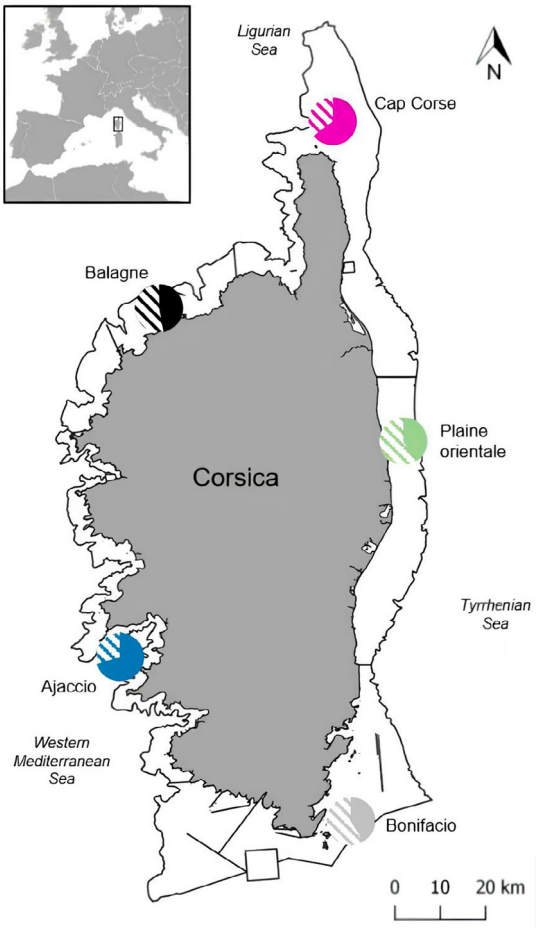

Fig. 1. – Localization of the five sampling areas constituted around Corsica (n=17 each, females are represented with hatched colours and males with plain ones).

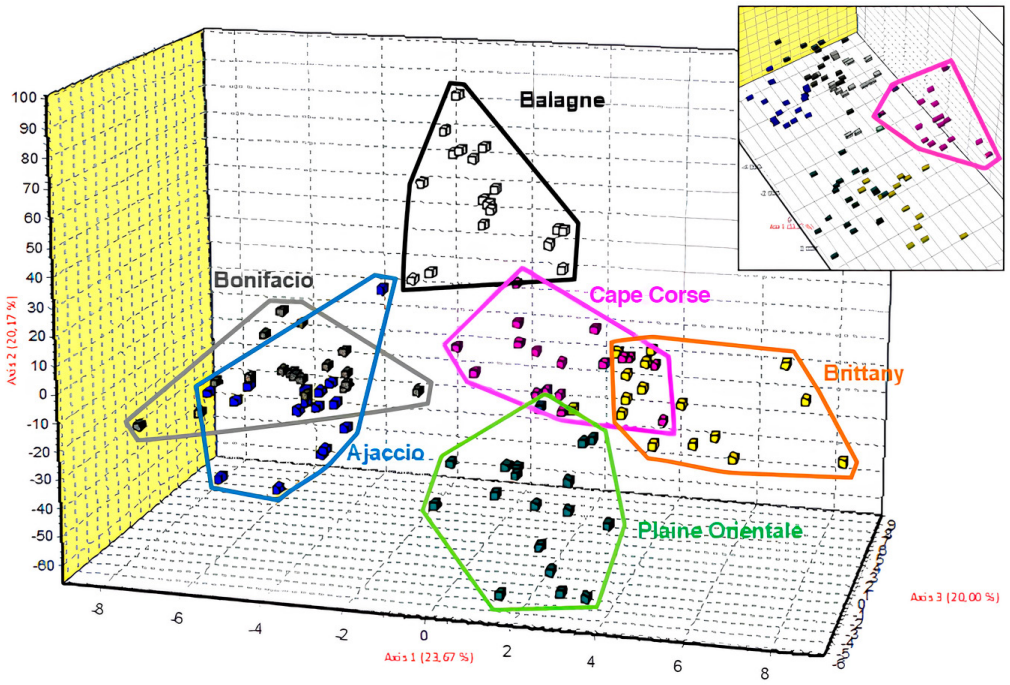

Fig. 2. – Factorial correspondence analysis of the centroids (or centres of gravity, not represented) of the six samples. The distinction of Cap Corse can be seen from another angle of the 3D diagram (inset top right).

The partition K=3 is presented in the Supplementary Figure S2 but is not of great interest, at least visually. It seems that if three genetic entities exist, they distribute themselves slightly differently from sample to sample, causing little differentiation. In fact, the partitioning seems to occur primarily within individuals rather than between individuals, suggesting weak geographical structuring.

Genetic differentiation between localities and isolation by distance

To measure the amount of genetic difference between samples, pairwise F_{ST} values were estimated (Table 3A). The values obtained were extremely low, indicating that the differentiation—if present—was minimal and not statistically significant. The Breton samples also did not differ statistically from the Corsican ones.

Around Corsica, the IBD calculation gave non-significant values of P=0.436 using Nei distance and P=0.426 using F_{ST}, under null hypothesis. The calculation is also not significant when the whole sampling (Mediterranean and Atlantic) is used. There is no correlation between genetic and geographic distances.

Table 3. – Estimation of F_{ST} among samples (A) and among age cohorts (B). Negative values are equivalent to zero. Most positive values are extremely small and not significant. Among localities, only the Ajaccio/Plaine Orientale comparison is at the limit of significance (in italics) with P=0.0542 (conventional significance below 0.05). Among age cohorts, the younger one is frequently differentiated (highly significant in bold and just below 0.05 in italics.

A	Brittany	Ajaccio	Balagne	Bonifacio	Cap Corse	Plaine Orientale
Brittany	0	0.00070	-0.00108	0.00741	0.00304	-0.00286
Ajaccio		0	-0.00515	-0.00188	0.00158	*-0.00685*
Balagne			0	0.00080	-0.00028	-0.00439
Bonifacio				0	0.00281	0.00380
Cap Corse					0	-0.00176
Plaine Orientale						0

B	More than 7 years	7 years	6 years	5 years	4 years	Less than 4 years
more than 7 years	0	-0.00232	0.00248	0.00464	-0.00584	0.00664
7 years		0	0.00496	0.00247	-0.00508	*0.01186*
6 years			0	0.00354	-0.00548	**0.01571****
5 years				0	-0.00508	**0.01618*****
4 years					0	*0.01056*
less than 4 years						0

Individual ageing as structuring parameter

Each sample set captured was composed of several age cohorts, each of them corresponding to distinct recruitments of larvae potentially coming from distant and different breeding areas. The same 97 lobsters analysed according to locations were now distributed according to 6 age cohorts. It was noticeable that each population was composed of a different age cohort assemblage (Table 4). The FCA results showed no significant differences between age classes when the Corsican lobsters were analysed at the individual level (similar to Fig. S1), but a clear structure of the sampling according to the age cohorts was observed when the analysis considered cohort centroids (Fig. 3).

When neutral genetic inter-cohort differentiation was measured (F_{ST}, Table 3B), a significant deviation from zero was observed twice, between the less-than-4-year cohort and the 5-year and 6-year cohorts.

Table 4. – Matrix giving the number of individuals of each age cohort in each population around Corsica.

	2–3 years	4 years	5 years	6 years	7 years	8-17 years	Total
Ajaccio	4	5	4	2	0	0	15
Balagne	0	3	4	7	2	1	17
Bonifacio	0	0	0	3	9	5	17
Cap Corse	4	3	7	2	0	0	16
Plaine Orientale	3	3	3	1	3	4	17

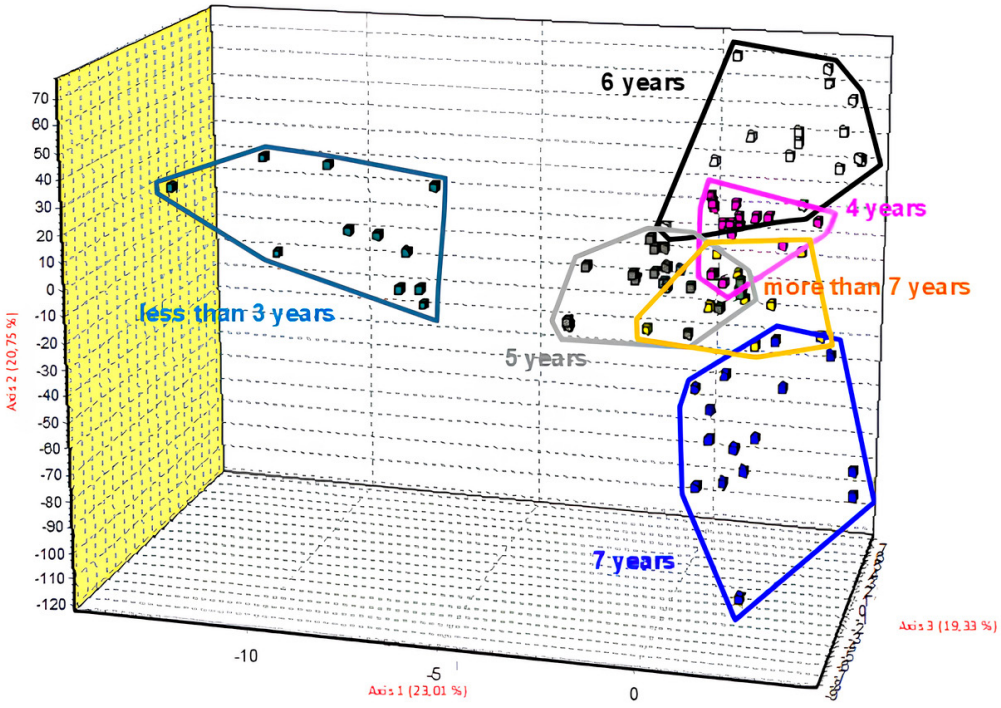

Fig. 3. – Genetic differentiation of cohorts using factorial correspondence analysis performed on the age centroids.

Relative importance of age and localities on genetic structure

Variation partitioning revealed that the full model significantly explained 1.0% of the genetic variation (P=0.030; Fig. 4). Age alone accounted for a significant 1.0% of the genetic variation (P=0.033), with 0.6% being exclusively attributed to this variable (Fig. 4). Locality was associated with 0.4% of the genetic variation, although this effect was not statistically significant (P=0.065), and no genetic variation was explained exclusively by this variable (Fig. 4). Altogether, this indicates that all the genetic variation explained (not significantly) by the variable locality is included inside the genetic variation explained by the variable age.

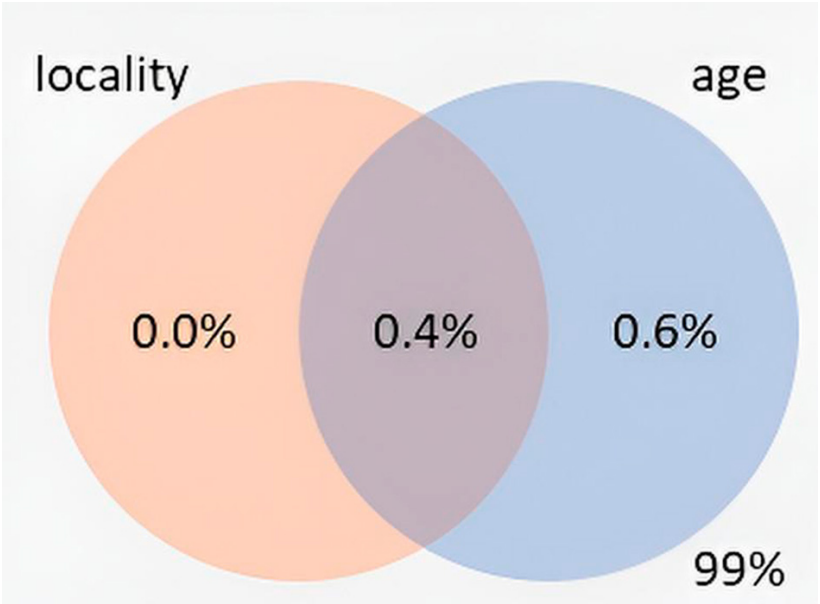

Fig. 4. – Venn diagram showing variation partitioning results in which genetic variation was calculated on 21 microsatellites surrogated by Euclidean distance and was significantly explained by age but not locality of individuals. All genetic variations explained by the model were significant (P<0.05).

DISCUSSION

Main results

This study represents the first comprehensive assessment of the genetic structure of the spiny lobster (*Palinurus elephas*) around the island of Corsica. Though we used the most extensive nuclear dataset assembled to date for this species, comprising 21 microsatellite markers across six sampling sites, the results did not reveal any pronounced geographic genetic structuring either among Corsican localities or between Mediterranean and Atlantic localities. Clear patterns of differentiation were only observed through multidimensional analyses focused on sample centroids, representing the average genetic profiles of groups rather than individual-level variation. The centroid-based analyses of localities and age groups, which prioritize group separation over individual clustering, did reveal structured patterns (Figs 2B and 5), which were statistically supported by inter-cohort F_{ST} values (Table 3B) and by variation partitioning analysis (Fig. 4). Conversely, other analytical approaches aimed at detecting fine-scale structure were largely inconclusive: (i) individual-based FCA (Fig. S1) yielded a diffuse and incoherent distribution of points with no discernible pattern; (ii) Bayesian clustering (Fig. S2) failed to detect coherent population units, instead arbitrarily partitioning individuals without reflecting geographic or ecological separation; finally (iii) pairwise F_{ST} estimates between sampling stations (Table 3A) produced non-significant values, indicating an absence of genetic differentiation (i.e. values indistinguishable from zero).

This apparent lack of fine-scale genetic structuring around Corsica is consistent with findings from other regions of the species' range: the Azores Archipelago (Faria 2012) and the northwestern Mediterranean Sea (Elphie et al. 2012), where similarly weak or absent population differentiation has been reported.

A weak differentiation

This study provides valuable insights into the mechanisms underpinning the weak genetic differentiation observed among age cohorts of *Palinurus elephas* around Corsica. The slight but consistent genetic divergence between cohorts may reflect transient, temporally driven differentiation processes rather than stable population structure. Several biological and ecological phenomena can explain such patterns, including stochastic reproductive dynamics across the Mediterranean, commonly referred to as "sweepstakes chance-matching" (Hogan, et al. 2010), as well as interannual variability in larval dispersal, recruitment and survival (Hedgecock 1994, Hogan et al. 2010, Gibson-Hall et al. 2018). These processes can result in "chaotic genetic patchiness", where spatial genetic structure arises intermittently due to differences in the genetic composition of successfully recruiting larvae.

The genetic homogeneity observed across broad spatial scales, including between Corsica and the Atlantic site, is consistent with high connectivity among populations, primarily via larval dispersal. Partial geographic isolation is insufficient to generate or maintain substantial genetic divergence due to the homogenizing effect of gene flow across generations (Jackson et al. 2017). Two key life-history traits likely contribute to this weak structure: (i) the prolonged pelagic larval duration of five to six months in the Mediterranean, and (ii) the species' widespread distribution across the region. These features promote extensive mixing, reducing the likelihood of persistent geographic structure. Rather than representing discrete, reproductively isolated populations, the Atlantic and Mediterranean groups identified in earlier studies (e.g. Babbucci et al. 2010) appear to be admixed assemblages arising from temporally and spatially variable reproductive and dispersal events (Calderón et al. 2012, Hogan et al. 2010). Moreover, larval behaviour, such as vertical migration, likely enhances dispersal efficiency by enabling larvae to exploit favourable currents throughout the water column (Faria et al. 2013).

Crucially, the weak differentiation observed in this study appears to be temporally unstable and subject to rapid turnover. Because larval recruitment is heavily influenced by local oceanographic conditions, the genetic makeup of a population can shift annually. Theoretically, even a single migrant per generation may be sufficient to counteract the effects of genetic drift across large distances (Slatkin 1995, Muths et al. 2008). However, empirical observations suggest that population recovery following anthropogenic declines can be exceedingly slow, as illustrated by the case of *P. elephas* in southwest Britain, where recolonization took over 40 years (Gibson-Hall et al. 2018).

The fact that age cohorts account for 1.0% of total genetic variance—including the 0.4% attributed to inter-locality differentiation (Fig. 4)—suggests that its primary source lies in the irregular geographic origins of recruited juveniles. This aligns with Elphie et al.'s (2012) hypothesis, which attributed weak spatial genetic structure in Spanish populations to the random settlement of genetically distinct larvae. Similar patterns of interannual variation in genetic diversity have been documented in another Mediterranean species, sea urchins, whose larval cohorts differ significantly in genetic composition from year to year (Calderón and Turon 2010). Earlier studies (Babbucci et al. 2010, Palero et al. 2011) also reported limited or absent genetic differentiation among Mediterranean *P. elephas* populations.

The current study adds further nuance by juxtaposing several key observations: (i) the full dataset can be subdivided into six age cohorts, each represented in varying proportions across local samples (Table 4); (ii) while individual cohorts appear genetically homogeneous, they are distinguishable from one another (Fig. 3, Table 3B); and (iii) geographic structuring is nearly absent (Figs 2, 3 and 4). Taken together, these results support a model in which annual larval recruitment is driven by stochastic oceanographic processes, leading to the formation of larval "clouds" that vary in origin and composition each year. These clouds settle differentially across sites, introducing genetically

distinct cohorts and generating Hardy-Weinberg disequilibria due to fluctuating recruitment intensity and genotype composition. However, because all cohorts are drawn from the broader Mediterranean meta-population, the resulting geographic and temporal divergences remain relatively minor.

Lourenço et al. (2017) proposed a similar model to explain the absence of genetic structure in *Perna perna*, an intertidal mussel with a long pelagic larval phase and broad distribution. In their case, connectivity was facilitated by habitat continuity and stepping-stone dispersal. Likewise, in *P. elephas*, the oceanographic currents surrounding Corsica likely enhance larval mixing, contributing to genetic homogenization across the region. Even when these currents are not strong promoters of connectivity, their seasonal or weak nature means that they may not act as significant barriers to gene flow (Buranelli et al. 2019).

The findings of this study stand in partial contrast to previous work by Babbucci et al. (2010) and Palero et al. (2008, 2011), which reported slight but statistically significant differentiation between Atlantic and Mediterranean populations. Palero et al. (2008), using mitochondrial COI sequences, attributed this differentiation to a gene flow barrier at the Strait of Gibraltar, although southern Portugal was classified within the Mediterranean group. The prevalence of a dominant haplotype (Haplotype I) across both basins (~63% average frequency) led the authors to hypothesize that genetic homogeneity reflects a post-glacial demographic expansion from a reduced ancestral population. Similarly, Babbucci et al. (2010) sequenced the mitochondrial control region and identified a shared dominant haplotype in both basins, again suggesting weak spatial structure. However, their microsatellite analyses revealed Hardy-Weinberg disequilibrium in all Mediterranean populations, contrasting with the equilibrium observed at two Atlantic sites from the Bay of Biscay. Interestingly, the Azores population clustered genetically with the Mediterranean one, a finding also supported by Palero et al. (2011), who identified two overlapping Atlantic and Mediterranean clusters. While all three studies (Palero et al. 2008, 2011, Babbucci et al. 2010) detected subtle Atlantic-Mediterranean divergence and a pattern of IBD, the present study did not corroborate these findings. One possible explanation is the mismatch between geographical and genetic structures: for example, the Azores and southern Portugal may be geographically Atlantic but genetically Mediterranean. A similar phenomenon might explain the placement of the Breton sample, potentially obscuring a clear Atlantic-Mediterranean division. Moreover, given the subtlety of the observed differentiation, the ability to detect IBD likely depends on the specific microsatellite loci employed, which may vary in resolution and informativeness across studies.

Stock management

Enhancing our understanding of genetic patterns and population structure is a fundamental prerequisite for the development of effective and sustainable stock management strategies for exploited marine species (Palero et al. 2011). In the case of *Palinurus elephas*, this necessitates a shift in management perspective from localized or regional frameworks to a broader, Mediterranean-wide scale. The high connectivity among populations, driven by extensive larval dispersal and the temporally variable origin of recruits, renders the identification of larval provenance infeasible. This is compounded by the low levels of genetic differentiation observed across vast geographic distances, a well-documented phenomenon in marine species with long pelagic larval durations (Hedgecock 1994). Given the scale and complexity of gene flow across the species' range, a paradigm shift toward multinational, cooperative management approaches appears essential. Although the implementation of such international strategies poses logistical and political challenges, it offers the most promising path to ensuring both the long-term conservation of *P. elephas* and the sustainability of its exploitation.

Fishing pressure, particularly when unregulated, can profoundly affect the demographic and genetic structure of target species. Fisheries often exert selective pressures based on size, age, sex or reproductive status (Rodhouse et al. 1998). These selective forces can lead to a suite of unintended evolutionary and ecological consequences, including shifts in size or age at maturity, altered growth rates, disruptions to mating systems, changes in interspecific interactions (e.g. predation or competition), and ultimately, reductions in genetic diversity and connectivity (Rodhouse et al. 1998, Marcias 2012, Kennington et al. 2013). Empirical evidence from Sardinia supports these concerns. A study examining connectivity among *P. elephas* populations at three sites revealed that the most heavily exploited area exhibited the lowest levels of genetic diversity and allelic richness (Cannas et al. 2006). In contrast, Marcias (2012) demonstrated that the establishment of marine protected areas (MPAs) around Sicily contributed to population recovery, as evidenced by increases in individual abundance and body size. MPAs also exerted positive spillover effects, contributing to the replenishment of adjacent, non-protected fishing grounds.

One of the most effective tools in the sustainable management of marine resources is the implementation of harvest regulations, particularly through quota systems designed to maintain population densities and genetic variability above critical thresholds. Natural mechanisms can compensate for high mortality with a faster larval growth rate and higher survival, leading to density-dependent effects. This may be the reason why some strongly exploited species tend to maintain their genetic diversity. Nonetheless, reliance on these compensatory processes is no substitute for proactive management. Maintaining genetic diversity is essential not only for short-term resilience but also for the long-term adaptive potential of species facing changing environmental conditions. In the case of *P. elephas*, integrative management strategies that combine genetic monitoring, habitat protection, regulated harvesting and international collaboration offer the most promising route to ensuring the viability of both the species and the fisheries it supports.

CONCLUSION

Our findings indicate that *Palinurus elephas* populations exhibit a high degree of genetic homogeneity across their range, though they do not conform to a strictly panmictic model. The subtle genetic differences observed appear to be driven more by temporal variability in larval cohort composition, both in intensity and geographic origin, than by spatial separation. These results highlight the dominant role of stochastic larval recruitment events in shaping genetic structure over geographic distance. To gain a more nuanced understanding of larval dispersal and population connectivity, particularly around Corsica and within the broader Mediterranean basin, there is a need for improved knowledge of mesoscale oceanographic processes. The dynamic interactions between currents, larval behaviour and habitat distribution likely play a central role in shaping recruitment patterns and, consequently, the genetic makeup of local populations.

In order to assess more precisely the genetic structure of *P. elephas*, finer genetic analyses could be developed. Classic genetic tools (allozymes, mitochondrial markers and microsatellite loci) generally show weak genome coverage and low power. An alternative to these tools could be single nucleotide polymorphism, which reduces these limitations, or other structural variants, such as insertion, deletion and inversion, which are recognized to be ubiquitous and allow a better understanding of population structure shaping and local adaptation (Dorant et al. 2020, Benestan et al. 2021, Mérot et al. 2023).

SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article:

Figure S1. Factorial correspondence analysis of the 97 lobsters analysed. No structure is apparent when the elementary information is the individual.

Figure S2. Assignment of the 97 lobsters to 3 clusters. The samples are 1=Brittany; 2=Ajaccio; 3=Balagne; 4=Bonifacio; 5=Cap Corse; 6=Plaine Orientale. No structure is noticeable.

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DECLARATION OF COMPETING INTERESTS

The authors of this article declare that they have no financial, professional or personal conflicts of interest that could have inappropriately influenced this work.

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Nine Doutreloux: Formal analysis, Investigation, Methodology, Project administration, Writing – original draft, Writing – review and editing. **Michel Marengo:** Conceptualization, Formal analysis, Funding acquisition, Project administration, Writing – review and editing. **Dimitri Theuerkauff:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – review and editing. **Martial Laurans:** Formal analysis, Investigation, Methodology, Writing – review and editing. Michela Patrissi: Investigation, Methodology, Writing – review and editing. **Pierre Lejeune:** Conceptualization, Funding acquisition, Project administration, Writing – review and editing. **Martin Laporte:** Formal analysis, Methodology, Writing – review and editing. **Patrick Berrebi:** Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review and editing.

REFERENCES

Babbucci M., Buccoli S., Cau A., et al. 2010. Population structure, demographic history, and selective processes: Contrasting evidences from mitochondrial and nuclear markers in the European spiny lobster *Palinurus elephas* (Fabricius, 1787). Mol. Phylogenet. Evol. 56: 1040–1050. https://doi.org/10.1016/j.ympev.2010.05.014

Belkhir L.C., Raufaste N., Bonhomme F. 2004. GENETIX 4.05, Logiciel Sous Windows TM Pour la Génétique des Populations. In: Laboratoire Génome P, Interactions, CNRS UMR 5171. Université de Montpellier II, Montpellier.

Benestan L., Fietz K., Loiseau N. et al. 2021. Restricted dispersal in a sea of gene flow. Proc. R. Soc. B 288: 20210458. https://doi.org/10.1098/rspb.2021.0458

Berrebi P., Jesenšek D., Laporte M., et al. 2022. Restoring marble trout genes in the Soča River (Slovenia). Conserv. Genet. 23: 481-494. https://doi.org/10.1007/s10592-022-01430-0

Borcard D., Legendre P., Drapeau P. 1992. Partialling out the Spatial Component of Ecological. Ecology. 73: 1045–1055. https://doi.org/10.2307/1940179

Buranelli R.C., Felder D.L., Mantelatto F.L. 2019. Genetic diversity among populations of the Western Atlantic mangrove crab *Ucides cordatus* (Linnaeus, 1763) (Decapoda: Brachyura: Ocypodidae): Evidence for panmixia and useful data for future management and conservation. J. Crustac. Biol. 39 : 386–395. https://doi.org/10.1093/jcbiol/ruz036

Calderón I., Pita L., Brusciotti S., et al. 2012. Time and space: Genetic structure of the cohorts of the common sea urchin *Paracentrotus lividus* in Western Mediterranean. Mar. Biol. 159: 187–197. https://doi.org/10.1007/s00227-011-1799-z

Calderón I., Turon X. 2010. Temporal genetic variability in the Mediterranean common sea urchin *Paracentrotus lividus*. Mar. Ecol. Prog. Ser. 408: 149–159. https://doi.org/10.3354/meps08576

Cannas R., Cau A., Deiana A.M., et al. 2006. Discrimination between the Mediterranean spiny lobsters *Palinurus elephas* and *P. mauritanicus* (Crustacea: Decapoda) by mitochondrial sequence analysis. Hydrobiologia. 557: 1–4. https://doi.org/10.1007/s10750-005-9301-x

Caron F., Laporte M., Bernatchez L. 2022. Inventaire ichtyologique du bassin versant de la zone du Chêne et de la forêt de la Seigneurie de Lotbinière au moyen de l'ADN environnemental. Nat Can. 146 (2): 3-18. https://doi.org/10.7202/1091884ar

Crochelet E. 2015. Modélisation de la connectivité larvaire et implications en terme de gestion de l'environnement. Biodiversité et Ecologie. PhD thesis, Université de la Réunion, 168 pp. https://theses.hal.science/tel-01269631/document

Dorant Y., Cayuela H., Wellband K., et al. 2020. Copy number variants outperform SNPs to reveal genotype–temperature association in a marine species. Mol. Ecol. 29: 4765– 4782. https://doi.org/10.1111/mec.15565

Ellis C.D., Hodgson D.J., Daniels C.L., et al. 2017. Population genetic structure in European lobsters: Implications for connectivity, diversity and hatchery stocking. Mar. Ecol. Prog. Ser. 563: 123–137. https://doi.org/10.3354/meps11957

Elphie H., Goñi R., Díaz D., et al. 2012. Detecting immigrants in a highly genetically homogeneous spiny lobster population (*Palinurus elephas*) in the northwest Mediterranean Sea. Ecol. Evol. 2: 2387–2396. https://doi.org/10.1002/ece3.349

Estoup A., Largiadèr C.R., Perrot E., et al. 1996. Rapid one-tube DNA extraction for reliable PCR detection of fish polymorphic markers and transgenes. Mol. Mar. Biol. Biotechnol. 5: 295–298.

Evanno G., Regnaut S., Goudet J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Mol. Ecol. 14: 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Faria J. 2012. Population structure and genetic diversity of three marine lobsters from the NE Atlantic and Mediterranean. PhD thesis, Universidade de Porto, 113 pp.

Faria J., Froufe E., Tuya F., et al. 2013. Panmixia in the endangered slipper lobster *Scyllarides latus* from the Northeastern Atlantic and Western Mediterranean. J. Crustac. Biol. 33: 557–566. https://doi.org/10.1163/1937240X-00002158

Fernández M.V. Heras S., Maltagliati F., et al. 2011. Genetic structure in the blue and red shrimp *Aristeus antennatus* and the role played by hydrographical and oceanographical barriers. Mar. Ecol. Prog. Ser. 421: 163–171. https://doi.org/10.3354/meps08881

Follesa M.C., Cuccu D., Cannas R., et al. 2009. Movement patterns of the spiny lobster *Palinurus elephas* (Fabricius, 1787) from a central western Mediterranean protected area. Sci. Mar. 73: 499–506. https://doi.org/10.3989/scimar.2009.73n3499

Forester B.R., Lasky J.R., Wagner H.H., et al. 2018. Comparing methods for detecting multilocus adaptation with multivariate genotype–environment associations. Mol. Ecol. 27 (9): 2215–2233. https://doi.org/10.1111/mec.14584

Gibson-Hall E., Jackson A., Marshall C. 2018. European spiny lobster (*Palinurus elephas*). MarLIN – Mar. Life Inf. Netw. 29.

Goñi R. 2015. *Palinurus elephas*, Common spiny lobster, The IUCN Red List of Threatened Species 2014: e.T169975A1281221. https://doi.org/10.2305/IUCN.UK.2014-1.RLTS.T169975A1281221.en

Hedgecock D.1994. Temporal and spatial genetic structure of marine animal populations in the California Current. Calif. Coop. Ocean. Fish. Investig. Reports 35: 73–81.

Hogan J.D., Thiessen R.J., Heath D.D. 2010. Variability in connectivity indicated by chaotic genetic patchiness within and among populations of a marine fish. Mar. Ecol.Prog. Ser. 417: 263–275. https://doi.org/10.3354/meps08793

Hunter 1999. Biology of the European spiny lobster, *Palinurus elephas* (Fabricius, 1787) (Decapoda, Palinuridae). Crustaceana 72: 545–565. https://doi.org/10.1163/156854099503609

Jackson N.D., Carstens B.C., Morales A.E., et al. 2017. Species delimitation with gene flow. Syst. Biol. 66: 799–812. https://doi.org/10.1093/sysbio/syw117

Jombart T., Devillard S., Balloux F. 2010. Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. BMC Genet. 11: 15. https://doi.org/10.1186/1471-2156-11-94

Kennington W.J., Cadee S.A., Berry O., et al. 2013. Maintenance of genetic variation and panmixia in the commercially exploited western rock lobster (*Panulirus cygnus*). Conserv. Genet. 14: 115–124. https://doi.org/10.1007/s10592-012-0433-z

Laporte M., Pavey S.A., Rougeux C., et al. 2016. RAD sequencing reveals within-generation polygenic selection in response to anthropogenic organic and metal contamination in North Atlantic Eels. Mol. Ecol. 25: 219-237. https://doi.org/10.1111/mec.13466

Lecaillon G., Blin E., Lenfant P., et al. 2011. Des solutions opérationnelles et innovantes de restauration des populations de poissons marins côtiers associés à des aménagements littoraux. Coastal and Maritime Mediterranean Conference, Tanger, 6 pp. https://doi.org/10.5150/cmcm.2011.014

Legendre P., Legendre L. 2012. Numerical Ecology. Elsevier, Amsterdam, 1006 pp.

Lourenço C.R., Nicastro K.R., McQuaid C.D., et al. 2017. Evidence for range wide panmixia despite multiple barriers to dispersal in a marine mussel. Sci. Rep. 7: 1–16. https://doi.org/10.1038/s41598-017-10753-9

Maltagliati F., Camilli L., Biagi F., et al. 1998. Genetic structure of Norway lobster, *Nephrops norvegicus* (L.) (Crustacea: Nephropidae), from the Mediterranean Sea. Sci. Mar. 62: 91–99. https://doi.org/10.3989/scimar.1998.62s191

Marcias S. 2012. Misura della connettività e della dispersione dell'aragosta rossa *Palinurus elephas* (Fabricius, 1787) in Sardegna con l'uso di marcatori genetici STRs e mitocondriali. Ph.D. thesis, Università degli Studi di Cagliari, 138 pp. https://hdl.handle.net/11584/266092

Marengo M., Theuerkauff D., Patrissi M., et al. 2020. A Typical Mediterranean Fishery and an Iconic Species: focus on the common Spiny Lobster (*Palinurus elephas*, Fabricius, 1787) in Corsica. Oceanogr. Fish. Open access J. 12: 10–13. https://doi.org/10.19080/OFOAJ.2020.12.555827
Marin J. 1987. Exploitation, biologie et dymanique du stock de langouste rouge de corse *Palinurus elephas* Fabricus 327p. PhD thesis, Université d'Aix-Marseille II, 348 pp. https://archimer.ifremer.fr/doc/00000/1036/687.pdf
Mérot C., Stenløkk K.S.R., Venney C., et al. 2023. Genome assembly, structural variants, and genetic differentiation between Lake Whitefish young species pairs (*Coregonus* sp.) with long and short reads Contributors. Mol. Ecol. 32: 1458–1477. https://doi.org/10.1111/mec.16468
Muths D., Tessier E., Bourjea J. 2008. Contribution de la génétique des populations à l'étude de la connectivité régionale de certaines espèces de poissons commerciaux présents dans la Réserve Naturelle Marine de La Réunion : étude de faisabilité. Parc Marin, Le Port, 25 pp. https://ocean-indien.ifremer.fr/content/download/24587/file/Etufaisabilit%C3%A9_nov08.pdf
Nei M. 1978. Estimation of Average Heterozygosity and genetic distance from a small number of individuals. Genetics. 89: 583–590. https://doi.org/10.1093/genetics/89.3.583
Oksanen J., Kindt R., Legendre P., et al. 2008. The vegan package. Community Ecol. Packag. 190 pp.
Palero F., Abelló P., Macpherson E., et al. 2008. Phylogeography of the European spiny lobster (*Palinurus elephas*): Influence of current oceanographical features and historical processes. Mol. Phylogenet. Evol. 48: 708–717. https://doi.org/10.1016/j.ympev.2008.04.022
Palero F., Abelló P., Macpherson E., et al. 2011. Effect of oceanographic barriers and overfishing on the population genetic structure of the European spiny lobster (*Palinurus elephas*). Biol. J. Linn. Soc. 104: 407–418. https://doi.org/10.1111/j.1095-8312.2011.01728.x
Palero F., Pascual M. 2008. Isolation and characterization of microsatellite loci in *Palinurus elephas*. Mol. Ecol. Resour. 8: 1477–1479. https://doi.org/10.1111/j.1755-0998.2008.02230.x
Pascual M., Rives B., Schunter C., et al. 2017. Impact of life history traits on gene flow: A multispecies systematic review across oceanographic barriers in the Mediterranean Sea. PLoS One. 12 : 1–20. https://doi.org/10.1371/journal.pone.0176419
Pere A. 2012. Déclin des populations de langouste rouge et baisse de la ressource halieutique en Corse - Causes et perspectives. PhD thesis, Corte, France. https://theses.fr/2012CORT0004
Pritchard J.K., Stephens M., Donnelly P. 2000. Inference of population structure using multilocus genotype data. Genetics. 155: 945–959. https://doi.org/10.1093/genetics/155.2.945
Rice W.R. 1989. Analyzing tables of statistical tests. Evolution. 43: 223–225. https://doi.org/10.1111/j.1558-5646.1989.tb04220.x
Robinson A.R., Leslie W.G., Theocharis A., et al. 2001. Mediterranean Sea Circulation. In: Steele J.H. (eds), Encycl. Ocean Sci. Academic press, pp. 1689–1705. https://doi.org/10.1006/rwos.2001.0376
Rodhouse P.G., Murphy E.J., Coelho M.L. 1998. Impact of fishing on life histories. In: Rodhouse, P.G.; Dawe, E.G.; O'Dor, R.K., (eds) Squid recruitment dynamics. The genus Illex as a model. The commercial Illex species. Influences on variability. FAO Fisheries Technical Paper. pp. 255-268.
Rousset F. 2008. GENEPOP'007: A complete re-implementation of the GENEPOP software for Windows and Linux. Mol. Ecol. Resour. 8: 103–106. https://doi.org/10.1111/j.1471-8286.2007.01931.x
Silva C.N.S., Villacorta-Rath C., Woodings L.N., et al. 2019. Advancing our understanding of the connectivity, evolution and management of marine lobsters through genetics. Rev. Fish Biol. Fish. 29: 669–687. https://doi.org/10.1007/s11160-019-09573-z
Slatkin M. 1995. A Measure of population subdivision based on microsatellite allele frequencies. Genet. 139: 457–462. https://doi.org/10.1093/genetics/139.1.457
Von Bertalanffy L. 1938. A quantitative theory of organic growth (inquiries in growth laws. II). Hum. Biol. 10(2): 181-213.
Wang J. 2019. A parsimony estimator of the number of populations from a STRUCTURE-like analysis. Mol. Ecol. Resour. 19(4): 970-981. https://doi.org/10.1111/1755-0998.13000
Whomersley P., Van der Molen J., Holt D., et al. 2018. Modelling the dispersal of spiny lobster (*Palinurus elephas*) larvae: Implications for future fisheries management and conservation measures. Front. Mar. Sci. 5: 1–16. https://doi.org/10.3389/fmars.2018.00058