The antique genetic plight of the Mediterranean monk seal (*Monachus monachus*)

Jordi SALMONA[1*], Julia DAYON[1,2], Emilie LECOMPTE[1], Alexandros A. KARAMANLIDIS[3], Alex AGUILAR[4], Pablo FERNANDEZ DE LARRINOA[5], Rosa PIRES[6], Giulia MO[7], Sabrina AGNESI[7], Asunción BORRELL[4], Erdem DANYER[8,9], Bayram ÖZTÜRK[8,10], Arda M. TONAY[8,10], Luis M. GONZÁLEZ[11], Panagiotis DENDRINOS[3], Philippe GAUBERT[1*]

1. Laboratoire Évolution & Diversité Biologique, CNRS-UPS-IRD, Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse, France
2. CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France
3. MOm/Hellenic Society for the Study and Protection of the Monk seal, Solomou Str. 18, 10682 Athens, Greece
4. Universitat de Barcelona, IRBio and Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, Diagonal 643, 08028 Barcelona, Spain
5. Monk Seal Conservation Program, Fundación CBD-Habitat, Gustavo Fernández Balbuena 2, 28002 Madrid, Spain
6. Instituto das Florestas e Conservação da Natureza IP-RAM, Jardim Botânico da Madeira, Caminho do Meio, Bom Sucesso, 9064-512, Funchal, Madeira, Portugal
7. Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), Via Vitaliano Brancati 48, 00144, Rome, Italy
8. Turkish Marine Research Foundation (TUDAV), PO Box 10, Beykoz, Istanbul, Turkey
9. Veterinary Control Central Research Institute, Ankara, Turkey
10. Istanbul University, Faculty of Aquatic Sciences, Ordu Cad. No: 8 Laleli, Istanbul, Turkey
11. Subdirección General de Biodiversidad Terrestre y Marina, Ministerio para la Transición Ecológica y el Reto Demográfico, Pza. San Juan de la Cruz, 10. E-28071. Madrid, Spain

*Corresponding authors:
Jordi SALMONA: jordi.salmona@gmail.com
Philippe GAUBERT: philippe.gaubert@univ-tlse3.fr

Abstract

Disentangling the impact of Late Quaternary climate change from human activities can have crucial implications on the conservation of endangered species. We investigated the population genetics and demography of the Mediterranean monk seal (*Monachus monachus*), one of the world's most endangered marine mammals, through an unprecedented dataset encompassing historical (extinct) and extant populations from the eastern North Atlantic to the entire Mediterranean Basin. We show that Western-Sahara/Mauritania (Cabo Blanco), Madeira, Western Mediterranean (historical range) and Eastern Mediterranean regions segregate in four populations. This structure is likely the consequence of recent drift, combined with long-term isolation by distance (R^2 = 0.7), resulting from prevailing short-distance (< 500 km) and infrequent long-distance dispersal (< 1,500 km). All populations (Madeira especially), show high levels of inbreeding and low levels of genetic diversity, seemingly declining since historical time, but surprisingly not being impacted by the 1997 massive die-off in Cabo Blanco. Approximate Bayesian Computation analyses support scenarios combining local extinctions and a major effective population size decline in all populations during Antiquity. Our results suggest that the early densification of human populations around the Mediterranean Basin coupled to the development of seafaring techniques were the main drivers of the decline of Mediterranean monk seals.

Keywords

Mediterranean monk seals, Population decline, Demographic history, Marine mammals, Genetic diversity, Isolation by distance.

Background

Because Late Quaternary extinctions were caused by the superimposed effects of climate change and human activities from the Last Glacial Maximum (LGM) onwards (ca. 25–10 ka; [1]), distinguishing between the respective impact of recent climate- and human-driven changes on the biosphere has proven challenging [2]. Differentiating climate- and human-driven impacts is similarly relevant to currently endangered species. Indeed, informed conservation planning relies on a systemic approach including knowledge of species' demographic history [3], which in turn can be used to predict species' ability to adapt to future climate changes [4,5].

Pinnipeds are marine mammals that rely on coastal haul-out areas during their annual life cycle. As such, they have been affected by LGM climate changes and early human activities [6,7], although the impact of the latter (through targeted hunting) may be posterior to the end of the LGM in this case (but see [8]). Despite the fact that the Mediterranean monk seal (MMS; *Monachus monachus*) is arguably the world's most endangered pinniped [9], the factors responsible for its critical conservation status are not well understood. The MMS once ranged across the entire Temperate Northern Atlantic province [10], from the Black Sea and the Mediterranean Basin into North Atlantic eastern waters encompassing the coasts of western Africa, the Macaronesian islands and the northern Iberian Peninsula [11–13]. Nowadays, the species is fragmented into three isolated populations, including the eastern Mediterranean (ca. 187-240 mature individuals [14]) and the eastern North Atlantic, in Cabo Blanco (Western Sahara/Mauritania) (ca. 350 individuals) and the archipelago of Madeira (ca. 20 individuals; [15]) (Fig. 1).

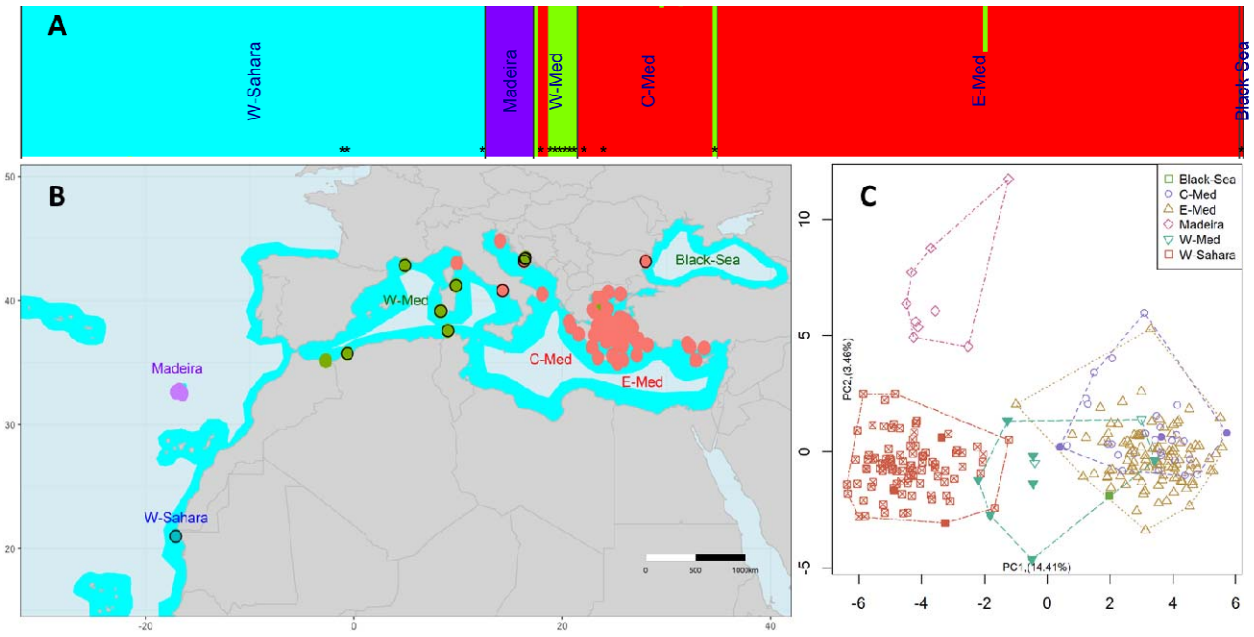

Figure 1. *Monachus monachus* nuclear genetic structure.

Individual posterior cluster membership coefficients for $K = 4$ presented using vertical barplot (**A**) and geolocated pie-charts (**B**). Sample representation on the first two axes of principal components analysis (**C**) showing a strong West-

East cline of differentiation on the first axis. In **A**, the samples are ordered by regions, sorted from West to East, separated by vertical black lines, and stars denote historical samples. In **B**, black circles denote locations that include historical samples and the cyan area represents the putative ancient MMS distribution. In **C**, full and empty symbols represent historical and modern samples respectively. W-Sahara: Western-Sahara/Mauritania, W-Med: western Mediterranean Sea, C-Med: central Mediterranean Sea, E-Med: eastern Mediterranean Sea.

A combination of extrinsic (human activities) and intrinsic (e.g., low genomic diversity, high susceptibility to diseases) factors has been proposed to explain the local extinctions affecting the species [16,17], and to a larger extent the extinction proneness observed in the entire Monachinae subfamily (which also includes the endangered Hawaiian monk seal *Neomonachus schauinslandii* and the extinct Caribbean monk seal *N. tropicalis* [18]). As an iconic representative of the Mediterranean Basin biodiversity hotspot [19], the MMS could have suffered from targeted hunting since the advent of the early Mediterranean sailors (Bronze Age; [20–22]). From the end of the Middle Age (XVth century), the massive exploitation of the species–notably in the Atlantic Ocean–became documented through the logbooks of European marine explorers [12,23]. Over the last centuries, MMS populations have been further impacted by the expansion of the fishing industry, deliberate killing by fishermen, marine pollution and human coastal encroachment, leading to local extinctions in most of the species' range, notably in the western Mediterranean and the Black Sea [13,24–26].

The decline of the MMS is documented from historical mass killing [11,20,27], local extinctions [28], massive die-off [29], and genetic inferences [30]. However, the respective impacts of Late Quaternary climatic fluctuations and anthropogenic pressures on the demographic history of the species remain poorly understood. Yet, the LGM induced significant changes in the Mediterranean Basin, such as lowering of sea level (down to -120 m; [31]) and sea surface temperatures, and local variations in salinity [32,33]. Moreover, the impacts of human activities on MMS populations may have applied at different periods across the species' range, with early exploitation since the Middle Paleolithic [21,34], followed by a gradual dispersal of seafaring civilizations from the eastern Mediterranean Basin (where habitat loss and overexploitation has been documented since ca. 10,000 yrs) towards the western Mediterranean Basin and North Atlantic Ocean [31,35].

Preliminary genetic studies have revealed the genetic isolation of the three extant populations of MMS, the low levels of genetic diversity (since at least the mid-XIXth century) [36,37], the local extinction of mitochondrial DNA (mtDNA) haplotype in the western Mediterranean Basin [38,39], the demographic bottleneck in the Western Sahara/Mauritania population [30,40], and the signature of past metapopulation dynamics across the species' range [36,41]. In this study, we investigate the genetic patterns and demographic history of the MMS through an unprecedented dataset, including historical individuals collected across the majority of the species' range and the three extant populations. We use microsatellite genotyping and mtDNA sequencing of 375 MMS to assess the historical population structure and dynamics of the MMS across the Mediterranean Basin and Northern Atlantic Ocean. Specifically, we delineate past and present population structure and diversity, and assess whether such patterns are consistent with scenarios of local extinctions together with genetic drift and inbreeding in extant populations. We also confront the different historical drivers (LGM *vs*. human activities) potentially affecting the MMS population dynamics across the Mediterranean Basin and Northern Atlantic Ocean through complementary population genetic

and modeling approaches based on demographic models, incorporating population structure and connectivity among populations through time. Based on our results, we formulate recommendations that might contribute to future evidence-based conservation strategies of the MMS.

Methods

Laboratory procedures and genotyping

We collected 383 samples from recent (1989 – 2020) and historical (N=54; 1833 – 1975) specimens of MMS covering the extant populations' and historical species' range (Figs 1, S1-3). The delineation between recent (from 1989 on) *vs*. historical (prior to 1975) is based on the extinction period of the last resident MMS groups from the western and parts of the central Mediterranean Sea during the 1970s [20], which suggested that after this period the fragmentation of the species' range into North Atlantic and eastern Mediterranean populations, as we know it today, was effective.

Genomic DNA was extracted from fresh tissue and skin samples, hairs, feces, bones and tanned skin using dedicated protocols (Method S1).

We amplified 524 bp of the hypervariable region I of the mitochondrial control region (CR1) following [42] for the modern samples (N = 121), and a reconstructed 484 bp fragment encompassing all the variable sites of CR1 for the historical samples (N = 3) as already described elsewhere [38] and detailed in method S2. We complemented our original dataset with 209 already published CR1 sequences [38,42]. Final CR1 alignment included 299 modern, 25 historical and four historical samples with unknown dating, for a total of 328 sequences (Figs 1, S1-3, Table S1-2).

We genotyped 383 samples at 19 nuclear microsatellites loci (nSSR [37], Method S3) from 329 modern samples and 54 historical samples. In order to mitigate scoring errors, PCRs of DNA extracts from hairs, faeces and museum material were replicated 2-to-5 times ([37], Method S3).

We controlled markers for linkage disequilibrium and departure from Hardy – Weinberg equilibrium (Method S3, Table S3; Fig. S4-7), and applied a two-fold sample selection procedure to optimize the number of individuals genotyped at informative loci. We relied on the minimum number of loci necessary to discriminate among individuals and the region-based DAPC contribution of loci (Method S3, Fig. S8). The final microsatellite data set comprised 253 samples (including 14 historical samples) with 10.18 % missing data (Table S1, Figs 1 & S1-2). In total, 204 samples (including 11 historical) were both sequenced for CR1 and genotyped at 19 loci.

Genetic diversity and structure

To assess the overall, per sampling site and per locus nSSR genetic diversity, we estimated allelic richness (A_R [43]) using minimum sampling sizes of 5, 10 and 25 for rarefaction with the R package *hierfstat* [44], the number of alleles (A), the observed (H_O) and Nei's

unbiased expected heterozygosities (H_E [45]) with the R package *adegenet* [46]. To assess the effect of drift in the small colonies of MMS, we estimated the average individual inbreeding coefficient *F* [46] in *adegenet*, from 100 iterations. We assessed the level of genetic differentiation among localities, populations, and time periods using Nei's F_{ST} [47]. Additionally, we investigated patterns of genetic variance with a principal component analysis (PCA) of allele frequencies, with a discriminant analysis of principal components (DAPC, considering sampling regions as groups), and through the SnapClust clustering approach [48]. To assess how the geographic distance alone explains the genetic diversity [49,50], we investigated individual- and population-based patterns of isolation by distance (IBD) using Mantel tests [51], with the genetic distance metric and the spatial scale that maximizes the amount of variance explained [52,53]. To assess how dispersal is distributed geographically we used Mantel correlograms [54,55].

For CR1, we estimated the number of haplotypes (*Nh*) and polymorphic sites (S), haplotype diversity (*h* [56]), and nucleotide diversity (π [57]) per sampling area using the R package *pegas* [58]. CR1 haplotype relationships were reconstructed with a maximum parsimony network using *pegas*. All above-mentioned methods are detailed in Method S4.

Demographic history

We used Approximate Bayesian Computation (ABC; [59]) to compare data simulated under several alternative scenarios to the real data (SSR & CR1), and estimate parameters of interest from the best supported scenario [60–62]. We first tested scenarios assuming a single panmictic population and different histories of population size change (Figs S9-10). Second, we modeled stable-size structured populations with constant migration rates among populations (Figs S9, S11). These models included unsampled ghost populations mimicking extinct populations and a change in connectivity, mimicking the loss of gene flow among extant populations (Figs S9, S11, S12). Third, we combined population size change, structure, ghost populations, and changes in connectivity, to model populations that suffered one or several events of decline and fragmentation (Figs S9, S13). Structured scenarios also compared n-island, stepping-stone and spatially-explicit models of connectivity (Table S4, S5). Further details are described in Method S6.

Results

Genetic diversity and structure

The microsatellite population-structure analyses exhibited at K=2 (Figs 1 & S14-15) a strong East-West pattern of differentiation (F_{ST} > 0.4, Table S6-7) separating the Atlantic and Mediterranean populations. This pattern appeared as a continuous cline of differentiation driving the first component of the PCA (Fig. 1), and was also the first revealed by the DAPC representation (Fig. S16). Second, our analyses showed a clear segregation of Madeira from Western-Saharan/Mauritania individuals, clearly distinguishing the two North-Atlantic populations (Figs 1, S15-16). The Western-Mediterranean population formed a group relatively distinct from the Eastern-Mediterranean, and genetically intermediary between Central-Eastern

Mediterranean and Atlantic populations (Figs 1, S15-16). The only historical sample genotyped from the Black Sea was assigned to the eastern Mediterranean population (Figs 1, S15). Further subdivision of the MMS resulted in erratic clustering results (Figs S14-15, S17).

Overall, all the populations showed relatively low nuclear genetic diversity (H_O = 0.12 - 0.42 & H_E = 0.04 - 0.36) and a wide range of inbreeding levels (Fig. 2). Madeira had the lowest levels of genetic diversity across all estimated indexes and among the highest estimates of inbreeding (Fig. 2, Tables S6-7). The historical Western-Mediterranean population showed a relatively high allelic richness, and the Western-Sahara/Mauritania and Eastern-Mediterranean populations exhibited the highest number of private alleles (Fig. 2). The historical sample from the Black Sea did not harbor private alleles (Fig 2). Similarly, mtDNA (CR1) diversity was low in all populations, with Madeira exhibiting only one haplotype (Table S2, Fig S18).

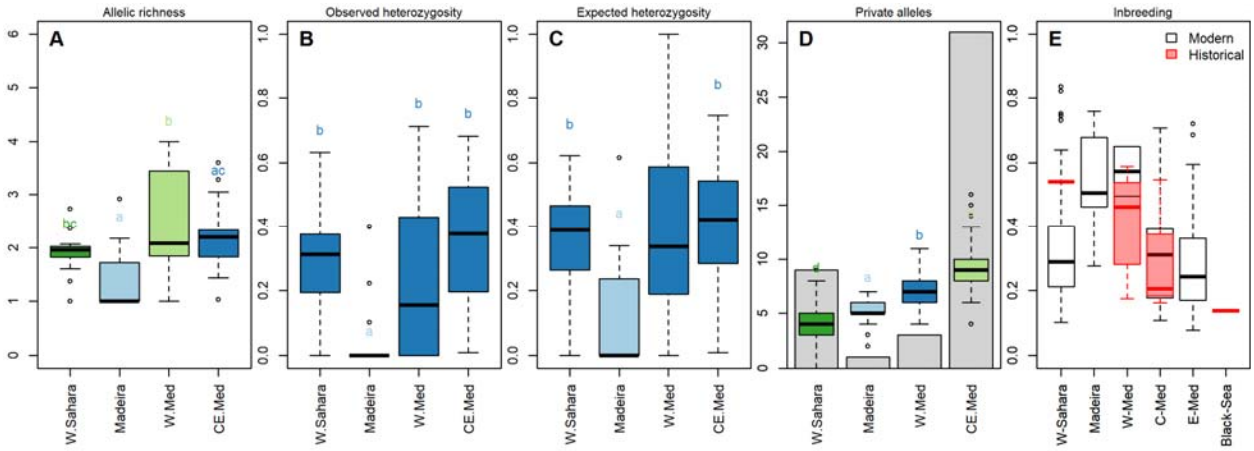

Figure 2. *Monachus monachus* nuclear genetic diversity.

Boxplot of the SSR (**A**) allelic richness (A_R), (**B**) observed (H_O), and (**C**) expected (H_E) heterozygosity, (**D**) mean private alleles (P_A) of 500 resamplings of the smallest sample size across each population, and barplot of the number of private alleles (P_A), and (**E**) boxplot of the average individual inbreeding coefficient (F), per population, expressed for modern (>1979) and historical (<1980) samples. In A-D, historic samples were removed from the analyses for all extant populations apart from the W-Med where no population is clearly identified and for which we almost exclusively have historic samples. Letters and box-colors in A-D illustrate the Tukey post-hoc group assignment. W-Sahara: Western-Sahara/Mauritania, W-Med: Western Mediterranean Sea, CE-Med: Central and Eastern Mediterranean Sea, C-Med: Central Mediterranean Sea, E-Med: Eastern Mediterranean Sea.

The likelihood estimates of individual homozygosity (F) suggested higher levels of inbreeding in modern samples than in historical ones (per population; Fig. 2). In addition, the allelic richness (A_R) and the private allelic richness (P_A) were higher historically than in modern samples (Fig. S19). However, the overall observed (H_O), and expected (H_E) heterozygosity, as well as the overall evolution of inbreeding levels through time (Fig. S19), did not exhibit a pattern of diversity loss across the timespan covered by our dataset (1840-2020). Across modern samples (>1975), and for the two major populations (Western-Sahara/Mauritania and Eastern-Mediterranean), we could not see any clear pattern of diversity loss between 1990 and 2020 (Figs S20-21). At the mtDNA level, one historical CR1 haplotype was not recovered in modern samples (MM07) and, reciprocally, one modern haplotype was not recovered from historical samples (MM06; Figs S18, S22-23).

The investigation of the 1997 massive die-off of the Cabo Blanco (Western Sahara/Mauritania) colony shows that no population and individual-based genetic diversity indexes (A_R, H_O, H_E, F), apart from private alleles (P_A), were consistent with the genetic diversity decrease expected after a bottleneck despite a large sampling before and after the event has taken place (Figs S24-25). Furthermore, we did not record a clear signal of rare allele loss, or decrease in frequency, nor of major allele gain in frequency (Fig. S26-27), that are to be expected after a reduction of the population size [63,64].

In line with the PCA showing an East-West cline of differentiation, we found an isolation by distance (IBD) pattern explaining up to 69.6% of the among-individuals genetic distance variability (Figs 3, S28-29). Such a strong IBD signal was sustained by Mantel correlograms exhibiting high values for the first 500 km classes, progressively declining up to ~1,500 km, above which values were no longer significant or negative (Fig. 3). Females exhibited significant positive values up to higher distance classes (1500 km) than males (700 km), but this signal may have resulted from sample size differences among males and females for each class.

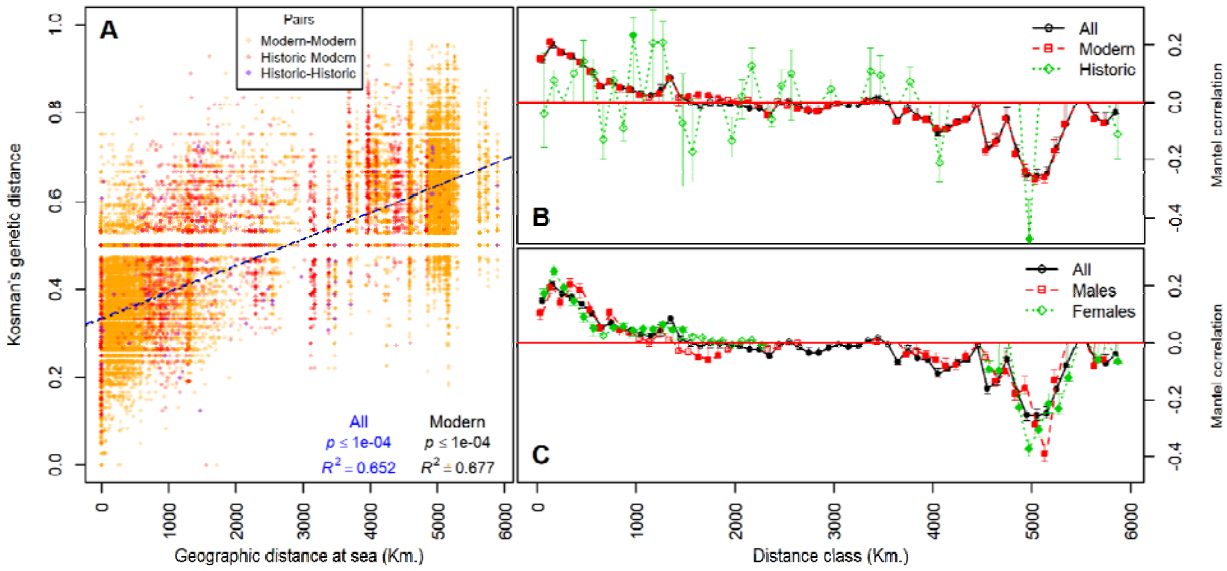

Figure 3. Isolation by distance in *Monachus monachus*.

A: isolation by distance (IBD) relationship between individual based genetic and maritime distances. **B** & **C**: Mantel correlogram of spatial correlation, for 59 classes of 100 Km, in all, modern, and historic samples (**B**), and all, males and females samples (**C**). Significant values, over 1000 permutations, are represented by filled symbols. Complementary analyses using alternative genetic distances are presented in Figs S26-27.

Demographic history

The ABC procedure supported models including population structure, ghost populations (local extinctions) and an effective population size decline (Figs. S9-13). The most supported population structure used a custom stepping stone framework, realistically modeling extant and extinct population connectivity, based on their respective position in space (Table S4, S8-9, & Figs S12-13). Among the models including these features, the most supported ones (M180 & M181) suggest that all sampled populations underwent one to two major declines, most of which

were of at least one order of magnitude (Table S10, Figs 4, S30). Furthermore, it reveals that these declines, and the loss of connectivity among sampled populations, most likely occurred during Antiquity (M181 & M180, Table S10, Figs 4, S30-31), as well as at the onset of the Middle-Age (M180).

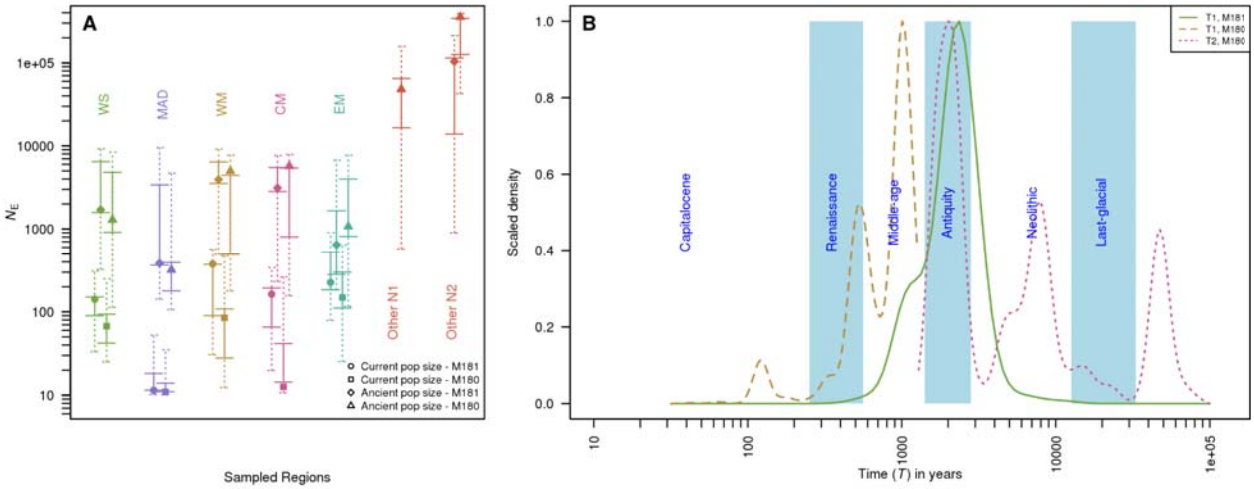

Figure 4. The antique decline of MMS.

ABC-GLM posterior estimates of effective population size (N_e; **A**) and of the time (T_1; **B**) of the major demographic event(s) -Population decline + local extinction + change in connectivity - estimated from the most likely scenarios (M181 & M180), within the ABC framework. **A**: mode (symbol), 50 % (continuous) and 95 % (dotted) quantiles of the effective population size (N_e) under the models 181 and 180, represented after (N_0: current population) and before (N_1: ancient population) the demographic events occurring at T_1 and at T_2. **B**: scaled-density distributions of the time of the demographic event(s) T_1 and at T_2. WS: Western-Sahara/Mauritania, MAD: Madeira, WM: Western-Mediterranean, CM: Central Mediterranean, EM: Eastern-Mediterranean.

Discussion

The genetic structure of Mediterranean monk seals through time and space

Our study is based on an unprecedented genetic sampling, covering the entire distribution range of the Mediterranean monk seal and encompassing historical (extinct) and extant populations. This enabled us to provide the most comprehensive diversity and structure assessment of the species to date in comparison to previous studies limited in their geographic and temporal representation and/or using meager genetic information. Our results illustrate how the inclusion of historical samples helps understanding the dynamics of species' genetic diversity through time and space [65]. The global analysis showed that MMS are composed of four populations, including the previously delineated eastern Mediterranean (reaching the Ligurian Sea as its westernmost location) and two northern Atlantic populations (Madeira and Western Sahara/Mauritania) [36–39,42], and a newly identified, historical population in the Western Mediterranean. The latter ranged from the northern Maghreb to southern France, Sardinia Isl. and the Adriatic Sea, partly overlapping at its eastern fringe with the extant eastern

Mediterranean population (Fig. 1). Because the western Mediterranean population holds both North Atlantic and Mediterranean mitochondrial haplotypes, it could not be clearly delineated in the previous, single-locus studies integrating historical samples [38,39]. The modern sample from northern Morocco (1993) upsurges the long-standing question as to whether the western Mediterranean population still exists today, notably on the western Algerian coast where MMS were present until the recent past [66]. Although sightings of MMS across the western Mediterranean basin have been reported within the last c. 20 yrs [67], their actual relevance is difficult to assess unless proper monitoring of potential breeding sites are systematized.

The status of the extinct population in the Black Sea [68] remains unsolved. The sole successfully-genotyped historical sample included in the SSR analyses did however carry information attributing it to the eastern Mediterranean population (Figs 1, S15). Together with the sharing of a unique CR1 haplotype in the Black Sea with individuals from the Aegean Sea, our preliminary results do not support the straits of Çanakkale (Dardanelles) and Istanbul (Bosphorus) as a putative barrier to MMS movements, despite its effect on other species at a wide taxonomic scale, including marine mammals [69,70].

Although substantial differentiation was previously reported between Western Sahara/Mauritania and Madeira [37], Western Sahara/Mauritania and Eastern Mediterranean [36], and Aegean and Ionian seas [41], our results demonstrate that this differentiation is clinal and likely a consequence of isolation by distance (R^2 = 0.7, Figs 1, 3). At the level of the Mediterranean basin, similar continuous differentiation is found in several marine organisms with varying mobility [e.g. dolphins, Sea star [71,72]], suggesting that oceanic distance alone can affect species across a broad taxonomic range. Because the inclusion of historical samples did not disrupt the genetic covariation with geography, the isolation by distance pattern might have been long-standing over the past two centuries. Interestingly, this pattern, previously unveiled at the eastern Mediterranean Sea scale [41], appears driven by prevailing short distance (< 500 km) and infrequent long distance dispersal (< 1,500 km, Fig. 3). MMS may tend to establish in close proximity to their place of birth, eventually dispersing within their local water basin, and, on rare occasions, to further-away places. This is in sharp contrast with the lack of structure of *Neomonachus schauinslandi,* the Hawaiian Monk Seal [73], which shows long distance dispersal across a ~2,700 km linear oceanic distribution likely facilitated by the strong oceanic surface currents active in that region [74]. On the contrary, our results suggest that the weaker and circular Mediterranean Sea currents, together with natal philopatry exacerbated by the rarity of breeding sites, remain likely contributors to the current MMS genetic structure.

A long depauperate and decreasing genetic diversity

Combining data from all extant populations, our genetic survey confirms that MMS harbors the most depauperate genetic diversity (H_E = 0.04-0.36) of all seal species [30]. Furthermore, it reveals Madeira's dramatic levels of genetic diversity (H_E = 0.04, Fig. 2), which echoes its decline to less than 10 individuals in the 1980s [27]. As a matter of comparison, Madeira's diversity is lower than that of the ringed seal population (*Pusa hispida*) landlocked since the LGM in Saimaa Lake, Finland [75].

We uncovered a decrease of allelic richness (A_R) and private allelic richness (P_A) from historical to modern samples, and an increasing trend in inbreeding at the population level (Figs 2, S19). This pattern is consistent with the trend exhibited by CR1 [38] and mitogenome [39]

studies, confirming that MMS genetic diversity has decreased over the past two centuries. In all cases, the decrease in genetic diversity started from remarkably low historical levels, which could explain the relatively stable distribution of heterozygosity that we observed over time (Fig. S19). This contrasts with the sharp drop in diversity caused by commercial exploitation in other seal species [76,77], implying an older exploitation of MMS populations.

Remarkably, the MMS genetic diversity has not been decreasing in the past 30 years (Figs S20-21), at least in the two populations with sufficient temporal sampling (eastern Mediterranean and Cabo Blanco). This encouraging signal can be interpreted as the incipient results of conservation efforts and population recovery over that period [13]. However, this pattern is surprising in the Western Sahara/Mauritania, where we could not trace any substantial genetic diversity or minor allele frequency drop -except private allele loss- following the massive 1997 die-off that decimated more than two thirds of the Cabo-Blanco colony (Figs S24-25 [29]). The originally low diversity and high inbreeding in the population, a higher death rate of most inbred individuals at the time of the die-off, or an insufficient resolution of the studied loci, may have blurred declining pattern signatures. Additionally, individuals from unsurveyed nearby localities (e.g. Guerguerat) at the time of the mass die-off may have participated in maintaining the genetic diversity of the Cabo-Blanco colony (pers. obs. AA).

Human-seal interactions in the Mediterranean basin: a history of overexploitation

The low diversity and high levels of inbreeding in all MMS populations (Fig. 2) are strong signals for the species undergoing a major decline with limited gene flow among populations. Furthermore, the marked IBD pattern (Fig. 3) reveals that MMS populations were connected by gene flow in the recent past. These patterns are confirmed by our demographic modeling analyses, which suggest that populations were organized in a stepping-stone manner, connected by intermediary (extinct) populations. These populations underwent one to two major demographic declines during Antiquity, most of which were at least of one order of magnitude (Figs 4, S30).

Surprisingly, the LGM (~20 ka ago) that dramatically affected the sea level (~120-130 m below current level) and the Mediterranean basin area, did not leave an identifiable signature in the MMS genetic data. The Neolithic transition allowed rapid human population growth and the development of complex civilizations [31,78], mastering increasingly sophisticated seafaring and fishing techniques [79,80]. By the rise of Antiquity, large human populations had spread across the entire Mediterranean basin and its islands [80–82]. Although the extent of hunting pressure on MMS is hard to accurately gauge at this time, historical sources relate hunting, meat consumption, oil use in lamps and skin use [83], conflict with fishermen [84], use in circus shows [85] and use of body parts to produce medicines [83]. In Antiquity, the species was reported to be common, widespread, and of ‘naive’ behavior towards humans, with rookeries of large size, and using open environments such as beaches, outcrops or promontories [83,86,87]. Such descriptions echoes the large ancient effective population sizes (between 100,000 and 356,000 individuals, Table S10) inferred from our demographic reconstructions, and is consistent with the ancestral population size estimates of *Neomonachus tropicalis* [88]. However, it is in sharp

contrast with the current elusive nature of the species, its habits of resting and giving birth in caves and remote islets, all which are probably a result of long lasting persecution [9].

Whether Romans, as previously posited [11], and/or other ancient civilizations played a significant role in the abrupt demographic decline of MMS remains unsolved, given the lack of direct evidence. However, the Romans' Empire large scale wildlife exploitation that lead to local-fish stock depletion and local megafauna extinction [85,89,90], and the emerging evidence of their whaling activities [91] are clues pointing towards their potential role in the demise of MMS. Importantly, humans have been hunting MMS long before Antiquity [21,34,92,93] and have continued afterward [12], together with increasing competition for habitat use and marine resources. Wherefore, the MMS decline was likely a continuous process, with a peak during Antiquity that dramatically sealed the genetic depauperation of the species. Furthermore, sealed animals were undoubtedly processed on the beach, and this explains that only very few bones reached inland sites [93]. Thus, systematic sealing (alike whaling [91]) is unlikely to have produced large archeological accumulations, as is the case for smaller marine resources, like tuna [94]. The resulting paucity of ancient MMS remains [92,93] limit our ability to accurately conclude on a precise period of MMS overexploitation.

Conservation outcomes

The existence of a western Mediterranean MMS population, likely on the verge of extinction, calls for the urgent identification and protection of breeding areas. Prior sightings suggest that several sites potentially hosting individuals belonging to this population should be surveyed, monitored and adequately protected on priority (e.g. from Al Hoceima to Cap des Trois Fourches - Morocco, Balearic Islands - Spain, Corsica -France, Sardinia, Tuscan Archipelago, Sicily - Italy, , La Galite - Tunisia [67,95]).

The clinal pattern of genetic diversity across the entire species distribution supports the absence of locally manageable conservation units. It therefore calls for an ambitious integrative conservation plan that comprehensively includes all countries (30) of the MMS past distribution range. Such concerted actions should be strengthened by governmental and intergovernmental agencies efforts and policies [96].

The low genetic diversity of extant populations calls for the development of an ambitious program that includes (i) increasing the size of colonies and populations and (ii) restoring genetic diversity and connectivity among extant populations. Ensuring population growth should be at the core of the MMS conservation program, as it will directly improve the resilience of populations to stochastic events [29]. Ways of re-establishing dispersion among populations should be considered, through, for example, the conservation of historical breeding sites (see [67]).

However, the dramatic levels of genetic diversity reported from our study indicate that rescuing the genetic diversity of MMS through the translocation of individuals among extant populations [97,98] is a scientifically-backed option to promote the long-term recovery of the species and should not be disregarded. Translocation should balance the benefits of counteracting the present limited gene flow among populations with any potential detrimental effects, such as the introduction into the receiving MMS community of parasites or disease to which it had not been previously exposed.

Furthermore, our results demonstrate that all extant MMS populations were connected until recently, and that their differentiation is explained by their frequent short distance and rare long distance dispersal (< 1,500 km). Theory predicts that gene flow reduces local adaptation [99], and small populations governed by strong genetic drift (e.g. Madeira) are less likely to have fine-scale local adaptations [100]. Therefore, translocation among inbred nearby populations presents limited risks of outbreeding depression [101,102]. The success of such genetic rescue is however conditioned by long-term conservation of extant populations, their habitat and resources, and actions to re-establishing natural dispersion among populations [102].

Finally, our broad scale genetic survey provides a new turnkey cost-efficient tool to accurately trace the origin of vagrant MMS individuals and monitor the genetic diversity of MMS populations and colonies. The combination of the 19 MMS microsatellites markers with the CR1 mitochondrial sequence may indeed serve not only to select the MMS individuals for potential translocation, but also to assess translocation success over time [98].

Data accessibility

Microsatellite data is available in table S1. All additional data, scripts and materials are available to readers at 10.5281/zenodo.5796262.

Acknowledgments

We thank all the collectors and museums listed in Table S1 for providing access to genetic samples. We are grateful to Sophie Courjal and the staff of the “Plateau technique - Biologie moléculaire et microbiologie” at EDB for their assistance during lab work. This work was funded by the Fondation Prince Albert II de Monaco (project “Génétique de la conservation du phoque moine de Méditerranée”). The Genotoul bioinformatics (Bioinfo Genotoul) platforms provided computing resources, and the LABEX TULIP (ANR-10-LABX-0041) contributed to JS’ salary.

Conflict of interest disclosure

The authors of this article declare that they have no financial conflict of interest with the content of this article.

Authors’ contribution

PG, EL and JS designed the study. AA, AAK, PFL, RP, GM, SA, AB, ED, BO, AMT, LMG and PD collected the genetic samples and supplied curated databases. JD and PG did the lab work. JS conducted data analyses. JS and PG drafted a first version of the manuscript. All co-authors participated in the writing of the manuscript and agreed with its last version.

References

1. Lister AM, Stuart AJ. 2008 The impact of climate change on large mammal distribution and extinction: evidence from the last glacial/interglacial transition. *Comptes Rendus Géoscience* **340**, 615–620.
2. Koch PL, Barnosky AD. 2006 Late Quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.* , 215–250.
3. Shafer AB *et al.* 2015 Genomics and the challenging translation into conservation practice. *Trends Ecol. Evol.* **30**, 78–87. (doi:10.1016/j.tree.2014.11.009)
4. Fordham DA, Brook BW, Moritz C, Nogués-Bravo D. 2014 Better forecasts of range dynamics using genetic data. *Trends Ecol. Evol.* **29**, 436–443.
5. Fenderson LE, Kovach AI, Llamas B. 2020 Spatiotemporal landscape genetics: Investigating ecology and evolution through space and time. *Mol. Ecol.* **29**, 218–246.
6. Bicho N, Haws J. 2008 At the land's end: marine resources and the importance of fluctuations in the coastline in the prehistoric hunter–gatherer economy of Portugal. *Quat. Sci. Rev.* **27**, 2166–2175.
7. Davidson AD, Boyer AG, Kim H, Pompa-Mansilla S, Hamilton MJ, Costa DP, Ceballos G, Brown JH. 2012 Drivers and hotspots of extinction risk in marine mammals. *Proc. Natl. Acad. Sci.* **109**, 3395–3400.
8. Hofman CA, Rick TC, Erlandson JM, Reeder-Myers L, Welch AJ, Buckley M. 2018 Collagen fingerprinting and the earliest marine mammal hunting in North America. *Sci. Rep.* **8**, 1–6.
9. Karamanlidis AA, Dendrinos P. 2015 *Monachus monachus*. The IUCN Red List of Threatened Species: e.T13653A117647375.
10. Spalding MD *et al.* 2007 Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* **57**, 573–583.
11. Johnson WM, Lavigne DM. 1999 Monk seals in antiquity. *Mediterr. Monk Seal* , 1–101.
12. González LM. 2015 Prehistoric and historic distributions of the critically endangered Mediterranean monk seal (*Monachus monachus*) in the eastern Atlantic. *Mar. Mammal Sci.* **31**, 1168–1192.
13. Karamanlidis AA, Dendrinos P, De Larrinoa PF, Gücü AC, Johnson WM, Kiraç CO, Pires R. 2016 The Mediterranean monk seal *Monachus monachus*: status, biology, threats, and conservation priorities. *Mammal Rev.* **46**, 92–105.
14. Karamanlidis AA, Adamantopoulou S, Tounta E, Dendrinos D. 2019 *Monachus monachus* Eastern Mediterranean subpopulation. *IUCN Red List Threat. Species 2019* , e.T120868935A120869697. (doi:https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T120868935A120869697.)
15. Pires R, Aparicio Garcia F, Pereira S, Cedenilla M, Fernandez De Larrinoa P. 2019 Conservation status of the Mediterranean monk seal *Monachus monachus* population at Madeira archipelago. Barcelona, Catalonia, Spain.
16. Hernández M *et al.* 1998 Did algal toxins cause monk seal mortality? *Nature* **393**, 28–29.
17. Osterhaus A *et al.* 1998 Monk seal mortality: virus or toxin? *Vaccine* **16**, 979–981.
18. Scheel D-M, Slater GJ, Kolokotronis S-O, Potter CW, Rotstein DS, Tsangaras K, Greenwood AD, Helgen KM. 2014 Biogeography and taxonomy of extinct and endangered monk seals illuminated by ancient DNA and skull morphology. *ZooKeys* , 1–33.
19. CEPF. 2010 Mediterranean basin biodiversity hotspot.
20. Johnson WM. 2004 Monk seals in post-classical history: The role of the Mediterranean monk seal (*Monachus monachus*) in European history and culture, from the fall of Rome to the 20th century. *Mededelingen* **39**, 1–91.
21. Stringer CB *et al.* 2008 Neanderthal exploitation of marine mammals in Gibraltar. *Proc.*

Natl. Acad. Sci. U. S. A. **105**, 14319–14324.
22. Trantalidou K. 2011 From Mesolithic fishermen and bird hunters to Neolithic goat herders: the transformation of an island economy in the Aegean. *Cave Cyclops Mesolith. Neolit. Netw. North. Aegean Greece* **2**, 53–150.
23. Brito C. 2012 Portuguese sealing and whaling activities as contributions to understand early northeast Atlantic environmental history of marine mammals. *New Approaches Study Mar. Mamm.* , 207–222.
24. Panou A, Jacobs J, Panos D. 1993 The endangered Mediterranean monk seal *Monachus monachus* in the Ionian Sea, Greece. *Biol. Conserv.* **64**, 129–140.
25. Borrell A, Cantos G, Aguilar A, Androukaki E, Dendrinos P. 2007 Concentrations and patterns of organochlorine pesticides and PCBs in Mediterranean monk seals (Monachus monachus) from Western Sahara and Greece. *Sci. Total Environ.* **381**, 316–325.
26. Kovacs KM *et al.* 2012 Global threats to pinnipeds. *Mar. Mammal Sci.* **28**, 414–436.
27. Pires R, Neves HC, Karamanlidis AA. 2008 The critically endangered Mediterranean monk seal *Monachus monachus* in the archipelago of Madeira: Priorities for conservation. *Oryx* **42**, 278–285.
28. Silva MA, Brito C, Santos SV, Barreiros JP. 2009 Historic and recent occurrences of pinnipeds in the Archipelago of the Azores. *Mammalia* **73**, 60–62.
29. Forcada J, Hammond PS, Aguilar A. 1999 Status of the Mediterranean monk seal *Monachus monachus* in the western Sahara and the implications of a mass mortality event. *Mar. Ecol. Prog. Ser.* **188**, 249–261.
30. Stoffel MA *et al.* 2018 Demographic histories and genetic diversity across pinnipeds are shaped by human exploitation, ecology and life-history. *Nat. Commun.* **9**, 1–12.
31. Benjamin J *et al.* 2017 Late Quaternary sea-level changes and early human societies in the central and eastern Mediterranean Basin: An interdisciplinary review. *Quat. Int.* **449**, 29–57.
32. Thunell RC. 1979 Eastern Mediterranean Sea during the last glacial maximum; an 18,000-years BP reconstruction. *Quat. Res.* **11**, 353–372.
33. Mikolajewicz U. 2011 Modeling Mediterranean ocean climate of the last glacial maximum. *Clim. Past* **7**, 161–180.
34. Colonese AC, Mannino MA, Mayer DB-Y, Fa DA, Finlayson JC, Lubell D, Stiner MC. 2011 Marine mollusc exploitation in Mediterranean prehistory: an overview. *Quat. Int.* **239**, 86–103.
35. Cunliffe B. 2017 *On the Ocean: The Mediterranean and the Atlantic from prehistory to AD 1500*. Oxford University Press.
36. Pastor T, Garza JC, Aguilar A, Tounta E, Androukaki E. 2007 Genetic diversity and differentiation between the two remaining populations of the critically endangered Mediterranean monk seal. *Anim. Conserv.* **10**, 461–469.
37. Dayon J, Lecompte E, Aguilar A, de Larrinoa PF, Pires R, Gaubert P. 2020 Development and characterization of nineteen microsatellite loci for the endangered Mediterranean monk seal *Monachus monachus*. *Mar. Biodivers.* **50**, 1–7.
38. Gaubert P *et al.* 2019 Insights from 180 years of mitochondrial variability in the endangered Mediterranean monk seal (*Monachus monachus*). *Mar. Mammal Sci.* **35**, 1489–1511.
39. Rey-Iglesia A *et al.* 2021 Mitogenomics of the endangered Mediterranean monk seal (*Monachus monachus*) reveals dramatic loss of diversity and supports historical gene-flow between Atlantic and eastern Mediterranean populations. *Zool. J. Linn. Soc.* **191**, 1147–1159.
40. Pastor T, Garza JC, Allen P, Amos W, Aguilar A. 2004 Low genetic variability in the highly endangered Mediterranean monk seal. *J. Hered.* **95**, 291–300.
41. Karamanlidis AA, Skrbinšek T, Amato G, Dendrinos P, Gaughran S, Kasapidis P, Kopatz

A, Stronen AV. 2021 Genetic and demographic history define a conservation strategy for earth's most endangered pinniped, the Mediterranean monk seal *Monachus monachus*. *Sci. Rep.* **11**, 1–10.
42. Karamanlidis AA, Gaughran S, Aguilar A, Dendrinos P, Huber D, Pires R, Schultz J, Skrbinšek T, Amato G. 2016 Shaping species conservation strategies using mtDNA analysis: the case of the elusive Mediterranean monk seal (*Monachus monachus*). *Biol. Conserv.* **193**, 71–79.
43. Hurlbert SH. 1971 The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**, 577–586.
44. Goudet J. 2005 Hierfstat, a package for R to compute and test hierarchical F-statistics. *Mol. Ecol. Notes* **5**, 184–186.
45. Nei M. 1978 Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* **89**, 583–590.
46. Jombart T. 2008 adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* **24**, 1403–1405.
47. Nei M. 1973 Analysis of gene diversity in subdivided populations. *Proc. Natl. Acad. Sci. U. S. A.* **70**, 3321–3323.
48. Tonkin-Hill G, Lees JA, Bentley SD, Frost SD, Corander J. 2019 Fast hierarchical Bayesian analysis of population structure. *Nucleic Acids Res.* **47**, 5539–5549.
49. Wright S. 1943 Isolation by distance. *Genetics* **28**, 114–138.
50. Slatkin M. 1993 Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* **47**, 264–279.
51. Mantel N. 1967 The detection of disease clustering and a generalized regression approach. *Cancer Res.* **27**, 209–220.
52. Cayuela H, Boualit L, Laporte M, Prunier JG, Preiss F, Laurent A, Foletti F, Clobert J, Jacob G. 2019 Kin-dependent dispersal influences relatedness and genetic structuring in a lek system. *Oecologia* **191**, 97–112.
53. Salmona J *et al.* 2021 How ancient forest fragmentation and riparian connectivity generate high levels of genetic diversity in a micro-endemic Malagasy tree. *BioRxiv 20201125394544 Ver 4 Peer-Rev. Recomm. Peer Community Evol. Biol.* (doi:https://doi.org/10.1101/2020.11.25.394544)
54. Oden NL, Sokal RR. 1986 Directional autocorrelation: an extension of spatial correlograms to two dimensions. *Syst. Zool.* **35**, 608–617.
55. Sokal RR. 1986 Spatial data analysis and historical processes. *Data Anal. Inform. IV* , 29–43.
56. Nei M, Tajima F. 1981 DNA polymorphism detectable by restriction endonucleases. *Genetics* **97**, 145–163.
57. Nei M. 1987 *Molecular Evolutionary Genetics*. Columbia University Press.
58. Paradis E. 2010 pegas: an R package for population genetics with an integrated–modular approach. *Bioinformatics* **26**, 419–420.
59. Beaumont MA. 2019 Approximate Bayesian computation. *Annu. Rev. Stat. Its Appl.* **6**, 379–403.
60. Wegmann D, Leuenberger C, Neuenschwander S, Excoffier L. 2010 ABCtoolbox: a versatile toolkit for approximate Bayesian computations. *BMC Bioinformatics* **11**, 1–7.
61. Csilléry K, François O, Blum MG. 2012 abc: an R package for approximate Bayesian computation (ABC). *Methods Ecol. Evol.* **3**, 475–479.
62. Nunes MA, Prangle D. 2015 abctools: an R package for tuning approximate Bayesian computation analyses. *R J.* **7**, 189–205.
63. Cornuet JM, Luikart G. 1996 Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics* **144**, 2001–2014.
64. Garza JC, Williamson EG. 2001 Detection of reduction in population size using data from

microsatellite loci. *Mol. Ecol.* **10**, 305–318.
65. Slatkin M, Racimo F. 2016 Ancient DNA and human history. *Proc. Natl. Acad. Sci. U. S. A.* **113**, 6380–6387.
66. Boutiba Z, Squabria B, Robineau D. 1988 Etat actuel de la population du phoque-moine (Monachus monachus) sur le littoral ouest algérien (région d'Oran). *Mammalia* **52**, 549–556.
67. Bundone L, Panou A, Molinaroli E. 2019 On sightings of (vagrant?) monk seals, *Monachus monachus*, in the Mediterranean Basin and their importance for the conservation of the species. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **29**, 554–563.
68. Kiraç C, Savaş Y. 1996 Status of the monk seal (*Monachus monachus*) in the neighbourhood of Ereğli, Black Sea coast of Turkey. *Zool. Middle East* **12**, 5–12.
69. Kalkan E, Karhan SÜ, Bilgin R, Hemond EM. 2016 The Turkish straits system as a phylogeographic boundary–a literature review. *Sea Marmara* , 550–69.
70. Tonay AM *et al.* 2017 Is there a distinct harbor porpoise subpopulation in the Marmara Sea? *Mitochondrial DNA Part A* **28**, 558–564.
71. Zulliger DE, Tanner S, Ruch M, Ribi G. 2009 Genetic structure of the high dispersal Atlanto-Mediterranean sea star Astropecten aranciacus revealed by mitochondrial DNA sequences and microsatellite loci. *Mar. Biol.* **156**, 597–610.
72. Gaspari S, Scheinin A, Holcer D, Fortuna C, Natali C, Genov T, Frantzis A, Chelazzi G, Moura AE. 2015 Drivers of population structure of the bottlenose dolphin (*Tursiops truncatus*) in the Eastern Mediterranean Sea. *Evol. Biol.* **42**, 177–190.
73. Schultz JK, Baker JD, Toonen RJ, Harting AL, Bowen BW. 2011 Range-wide genetic connectivity of the Hawaiian monk seal and implications for translocation. *Conserv. Biol.* **25**, 124–132.
74. Toonen RJ *et al.* 2011 Defining boundaries for ecosystem-based management: a multispecies case study of marine connectivity across the Hawaiian Archipelago. *J. Mar. Biol.* **2011**, 460173.
75. Valtonen M, Palo JU, Aspi J, Ruokonen M, Kunnasranta M, Nyman T. 2014 Causes and consequences of fine-scale population structure in a critically endangered freshwater seal. *BMC Ecol.* **14**, 1–15.
76. Weber D, Stewart BS, Garza JC, Lehman N. 2000 An empirical genetic assessment of the severity of the northern elephant seal population bottleneck. *Curr. Biol.* **10**, 1287–1290.
77. Cammen KM *et al.* 2018 Genetic diversity from pre-bottleneck to recovery in two sympatric pinniped species in the Northwest Atlantic. *Conserv. Genet.* **19**, 555–569.
78. Bocquet-Appel J-P. 2008 Explaining the Neolithic demographic transition. In *The Neolithic demographic transition and its consequences*, pp. 35–55. Springer.
79. Zilhão J. 2014 Early prehistoric navigation in the Western Mediterranean: Implications for the Neolithic transition in Iberia and the Maghreb. *Eurasian Prehistory Isl. Archaeol. Orig. Seafar. East. Mediterr.* **11**, 185–200.
80. Simmons AH. 2016 *Stone Age sailors: Paleolithic seafaring in the Mediterranean*. Routledge.
81. Zeder MA. 2008 Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 11597–11604.
82. Phoca-Cosmetatou N. 2011 *The first Mediterranean islanders: initial occupation and survival strategies*. University of Oxford School of Archaeology.
83. Plinius Secundus G. 77 AD*Naturalis Historiae*. 1940th-The Loeb Classical Library edn. Cambridge, Massachusetts,: Harvard University Press.
84. Oppianus Corycius. 169 AD*Halieutica*. Harvard University Press.
85. Scullard HH. 2010 *From the Gracchi to Nero: a history of Rome 133 BC to AD 68*. Routledge.
86. Όμηρος αποσαφήνιση. BC750 *Οδύσσεια (Odyssey)*.

87. Αριστοτέλης. BC340 *Τ□ν περ□ τ□ ζ□α □στορι□ν (Historia animalium)*.
88. McClenachan L, Cooper AB. 2008 Extinction rate, historical population structure and ecological role of the Caribbean monk seal. *Proc. R. Soc. B Biol. Sci.* **275**, 1351–1358.
89. Trakadas A. 2006 'Exhausted by Fishermen's Nets' Roman Sea Fisheries and their Management. *J. Mediterr. Stud.* **16**, 259–272.
90. Kidd E. 2012 "Beast-Hunts" in Roman Amphitheaters: The Impact of the Venationes on Animal Populations in the Ancient Roman World. *Eagle Feather* **9**.
91. Bernal-Casasola D. 2018 Whale Hunting in the Strait of Gibraltar during the Roman Period? *SAA Archaeol. Rec.*
92. Steele TE, Álvarez-Fernández E. 2011 Initial investigations into the exploitation of coastal resources in North Africa during the Late Pleistocene at Grotte des Contrebandiers, Morocco. In *Trekking the Shore*, pp. 383–403. Springer.
93. Morales-Pérez JV, Ripoll MP, Pardo JJ, Álvarez-Fernández E, González AM, Tortosa JA. 2019 Mediterranean monk seal hunting in the regional Epipalaeolithic of Southern Iberia. A study of the Nerja Cave site (Málaga, Spain). *Quat. Int.* **515**, 80–91.
94. Bernal-Casasola D, Expósito JA, Díaz JJ. 2018 The Baelo Claudia Paradigm: The Exploitation of Marine Resources in Roman Cetariae. *J. Marit. Archaeol.* **13**, 329–351.
95. Mo G, Bazairi H, Bayed A, Agnesi S. 2011 Survey on Mediterranean Monk Seal (Monachus monachus) Sightings in Mediterranean Morocco. *Aquat. Mamm.* **37**.
96. Reilly SB. 2005 Report of the scientific research program under the International Dolphin Conservation Program Act.
97. Batson WG, Gordon IJ, Fletcher DB, Manning AD. 2015 Translocation tactics: a framework to support the IUCN Guidelines for wildlife translocations and improve the quality of applied methods. *J. Appl. Ecol.* **52**, 1598–1607.
98. Pacioni C, Wayne AF, Page M. 2019 Guidelines for genetic management in mammal translocation programs. *Biol. Conserv.* **237**, 105–113.
99. Lenormand T. 2002 Gene flow and the limits to natural selection. *Trends Ecol. Evol.* **17**, 183–189.
100. Leimu R, Fischer M. 2008 A meta-analysis of local adaptation in plants. *PloS One* **3**, e4010.
101. Edmands S. 2007 Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Mol. Ecol.* **16**, 463–475.
102. Bell DA, Robinson ZL, Funk WC, Fitzpatrick SW, Allendorf FW, Tallmon DA, Whiteley AR. 2019 The exciting potential and remaining uncertainties of genetic rescue. *Trends Ecol. Evol.* **34**, 1070–1079.