Shared and distinct patterns of genetic structure in two sympatric large decapods

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RESEARCH ARTICLE

Shared and distinct patterns of genetic structure in two sympatric large decapods

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Abstract

Aim: Comparing genetic structure in species with shared spatial ranges and ecological niches can help identify how dissimilar aspects of biology can shape differences in population connectivity. Similarly, where species are widely distributed across heterogeneous environments and major topographic barriers, knowledge of the structuring of populations can help reveal the impacts of factors which limit dispersal and/or drive divergence, aiding conservation management.

Location: European seas of the northeast Atlantic and Mediterranean.

Taxa: European clawed lobster (*Homarus gammarus*) and European crawfish (*Palinurus elephas*), two sympatric, heavily fished decapods with extensive dispersal potential.

Methods: By RAD-sequencing 214 *H. gammarus* from 32 locations and 349 *P. elephas* from 15 locations, we isolated 6340 and 7681 SNP loci, respectively. Using these data to characterise contemporary population structuring, we investigate potential spatial and environmental drivers of genomic heterogeneity.

Results: We found higher levels of differentiation among clawed lobsters than crawfish, both globally and within basins, and demonstrate where known hydrographic and topographic barriers generate shared patterns of divergence, such as a genetic break between the Atlantic and Mediterranean basins. Genetic structure not common to both species is principally apparent in the Atlantic portions of their range, where clawed lobster exhibits a genetic cline and increased differentiation towards range margins, while crawfish appear effectively panmictic throughout this region.

Main Conclusions: We attribute the comparative lack of crawfish population structuring to their greater dispersal tendencies via a longer pelagic larval duration and sporadic adult movements. In contrast, genetic connectivity in clawed lobster is relatively restricted, with the correlation of site of origin and temperature to geographical heterogeneity at many divergent loci indicative of both neutral and adaptive processes. Our results help inform how contemporary management can account for likely demographic connectivity and marry the conservation of genomic variation with sustainable fisheries in these ecologically and economically important crustaceans.

KEYWORDS
Crustacea, Fisheries, Genetic Structure, Lobster, Marine Connectivity, Phylogeography, RAD-seq, Spiny lobster

1 | INTRODUCTION

Resolving phylogeographical boundaries to define genetic population units is vital to the conservation of marine taxa, particularly where species are targeted by commercial fisheries so that the spatial extent of management units reflect those of biological populations, and recruitment expectations consider connectivity dynamics (Reiss et al., 2009). Assessing demographic connectivity is particularly challenging in marine invertebrates, because most produce pelagic larvae for which obtaining direct observations of movement and behaviour is extremely difficult, and because even closely related species may exhibit extreme heterogeneity in dispersal scales (Kinlan & Gaines, 2003; Levin, 2006; Palumbi, 2003). In the absence of data suitable for directly evaluating intergenerational demographic connectivity, identifying spatial structuring among subpopulations can indicate the extent of genetic connectivity, which provides a longer-term snapshot of multi-generational interdependence between spatial units that can inform management decisions (Levin, 2006; Lowe & Allendorf, 2010; Palumbi, 2003). Moreover, where closely related species cohabit shared geographical ranges, dissimilarities in population structuring can help to elucidate how different demographic and life-history traits shape genetic connectivity (Blakeslee et al., 2021; Haye et al., 2014; Meirmans et al., 2011; Teske et al., 2007; Treml et al., 2012).

The European lobster (*Homarus gammarus*—hereafter commonly termed 'lobster') and the European spiny lobster (*Palinurus elephas*—hereafter commonly termed 'crawfish') are large, long-lived decapod crustaceans that range throughout much of the northeast Atlantic and Mediterranean Sea. Both are highly prized seafood commodities with a long history of exploitation in coastal waters, but are also slow growing and size-specifically fecund, heightening their vulnerability to overfishing and stock collapse (Ellis et al., 2015; Goñi et al., 2003). Both species prefer rocky seabeds and share similar ecological niches in inshore habitats, but some important differences characterise their biology and fisheries. *H. gammarus* is a true clawed lobster (*Nephropidae*), and is most abundant in the Atlantic and at northerly latitudes, with historic evidence of millennial overexploitation in the Mediterranean (Spanier et al., 2015). Modern lobster fisheries mostly utilise baited traps and, since overfishing decimated Scandinavian stocks in the mid-twentieth century, abundance is highest around the British Isles, which account for almost 80% of the ~5000-ton annual catch (FAO, 2021). Adult lobsters are typically solitary with defined foraging ranges and limited migratory movements (Moland et al., 2011; Skerritt et al., 2015), while juveniles are presumed to be restricted to areas of their benthic settlement. Most mature female lobsters extrude biennial clutches of 4000–40,000 eggs, which hatch into ~5–8 mm larvae after 8–10 months incubation, and subsequently undergo a pelagic larval duration (PLD) of 2–5 weeks (Agnalt, 2008; Moland et al., 2010; Schmalenbach & Franke, 2010). Contrastingly, the crawfish, *P. elephas*, is a spiny lobster (*Palinuridae*), which harvest data shows is more abundant in the Mediterranean than Atlantic, but which has been depleted historically in both regions (Jackson, 2021). Most modern crawfish fisheries employ trammel nets, from which post-release survival of returned catch is typically much lower than traps (Amengual-Ramis et al., 2016; Catanese et al., 2018). Recent total crawfish landing volumes are similar to lobster, although data hold greater uncertainty because several major fishing nations pool catch records for *P. elephas* and its deeper-water congener, *P. mauritanicus* (FAO, 2021). Like other spiny lobsters, crawfish are social and can aggregate (Jézéquel et al., 2020) and, compared to clawed lobsters, lay many more eggs which hatch into smaller larvae with longer PLDs. Mature female crawfish typically produce 20,000–200,000 eggs annually, which hatch into ~2–3 mm phyllosoma following around 4–10 months incubation, before a 5–12 month PLD that varies regionally (Goñi et al., 2003; Groeneveld et al., 2013). These differences in fundamental biological traits could drive interspecific variation in their dispersal potential, and thus their genetic connectivity and structuring.

Both species have been the subject of studies investigating their genetic diversity and population structure in recent decades. Early studies of lobster genetic variation, using only a few multi-allelic loci, asserted high gene flow among most Atlantic stocks and marked differentiation between Atlantic and Mediterranean populations (Triantafyllidis et al., 2005). Differentiation of small subpopulations inhabiting semi-enclosed inlets in Norway and the Netherlands, where allelic diversity was low, was attributed to genetic drift following apparent isolation (Jørstad et al., 2004; Triantafyllidis et al., 2005). More recently, studies have used up to 14 microsatellite loci to assert effective panmixia throughout regional seas (the Skagerrak—Huserbråten et al., 2013; the Irish Sea—Watson et al., 2016; the Western Channel and Celtic Sea—Ellis et al., 2017; the Adriatic—Pavičić et al., 2020), as well as evidence of spatial genetic structuring, with restricted connectivity apparent between Scandinavia and continental Atlantic coasts (Ellis et al., 2017), and between the Adriatic, Aegean and Tyrrhenian seas (Pavičić et al., 2020). Most recently, 79 highly differentiated single nucleotide polymorphisms (SNPs) identified a genetic cline of variation across open Atlantic coasts (Jenkins et al., 2019), and detected individuals of Atlantic descent introduced to the Mediterranean (Jenkins et al., 2020). By comparison, crawfish are less well researched. Microsatellites have similarly demonstrated broad-scale differentiation between Atlantic and Mediterranean stocks (Babbucci et al., 2010; Palero et al., 2011), and mitochondrial (mtDNA) analysis has hinted at within-basin substructure (Palero et al., 2008), although regional panmixia has been inferred throughout European coasts of the Western Mediterranean (Benestan et al., 2021; Hamdi et al., 2012). Given their ecological and economic importance, reassessment of range-wide

genetic structuring in both species using more robust techniques is clearly needed, to evaluate whether previous assertions of panmixia reflect genuine genetic homogeneity across vast, heterogeneous environments, or simply the limitations of methodologies which failed to detect subtle population differentiation.

Our study aimed to assess and compare the extent of genetic structure in lobsters and crawfish across most of their geographical range, using thousands of SNP markers derived from restriction-site-associated DNA (RAD) sequencing. This genotyping-by-sequencing (GBS) approach provides a powerful method for interrogating sufficient genome-wide variation to discern even weakly differentiated sub-groups (Andrews et al., 2016) and has recently improved the identification of population structuring and its evolutionary drivers in other wide-ranging, large decapods (i.e., American lobster, *H. americanus*—Benestan et al., 2015, 2016; Ornate spiny lobster, *Panulirus ornatus*—Farhadi et al., 2022). We hypothesised that GBS of geographically extensive samples could reveal levels of spatial genetic heterogeneity beyond that detected to date, and that correlations with environmental and spatial gradients could identify potential drivers of differentiation. By assessing two closely related species with overlapping spatial ranges, we aimed to identify where common seascape features promote consistent population structuring, and postulate where fundamental differences in life-history strategy may underpin observed dissimilarities in genetic connectivity.

2 | MATERIALS AND METHODS

2.1 | Sample collection, DNA extraction, quality control and RAD sequencing

Tissue samples from live lobsters and crawfish were collected by fishers or collaborating researchers, from 32 and 15 sites, respectively, encompassing much of each species' geographical range (Figure 1). All lobster and crawfish samples comprised small (~1cm^2) sections of pleopod, uropod or antenna tissue excised from mature individuals, except for crawfish from Spanish sites, which were whole early-benthic juveniles. Appendix S1 (S1.1-2) in Supporting Information provides details on sample sizes, capture information, tissue collection and the phylogeographical validity of samples.

Genomic DNA was extracted from all tissues using the salting-out protocol of Jenkins et al. (2018) and underwent quality control (Appendix S1.2). For lobsters ($n = 190$, plus positive and negative controls), Exeter Sequencing Service, UK, undertook RAD library preparation using the restriction enzyme *sbf*I, for sequencing of 150 base pair (bp), paired-end reads. For crawfish ($n = 364$, plus positive, negative and congener species controls), Floragenex Inc., USA, undertook similar *sbf*I RAD library preparations, before sequencing 100 bp, paired-end reads (Appendix S1.3 describes full RAD protocols).

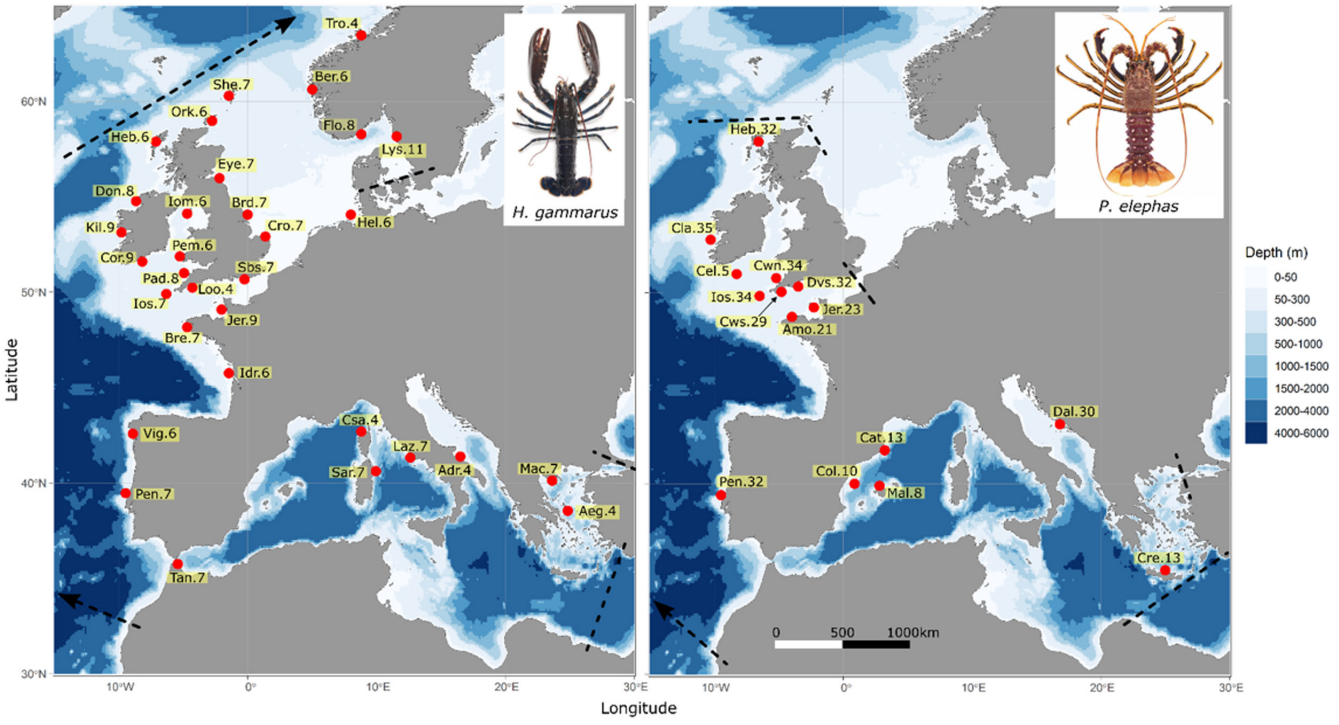

FIGURE 1 Bathymetric maps of western Europe and the Mediterranean showing the locations of sampling sites for lobsters *Homarus gammarus* (left) and crawfish *Palinurus elephas* (right). Labels denote the three-letter location code and number of individuals comprising each geographical sample. Approximate contemporary range margins are denoted with dotted lines, though both species extend beyond the limits of the map westward to inhabit the Azores (~30° W), while lobster also extends northward into Arctic Norway (~68° N). Equal-area projection bathymetric maps created using decimal degree shapefiles in R using the 'ggOceanMaps' package (Vihtakari, 2022).

2.2 | Filtering of reads, RAD loci and SNPs

Preliminary analysis confirmed that all putative crawfish samples were distinct from congener species of similar morphology and overlapping spatial ranges (Appendix S1.4, Figure S2.1). The lobster data were amalgamated with a dataset of 100 bp reads from 47 lobsters previously sequenced using the same RAD protocol (Jenkins et al., 2018), and then both lobster and crawfish datasets underwent identical bioinformatic processing to filter reads and build RAD loci (Appendix S1.5). The *populations* program of 'Stacks' v2.54 (Catchen et al., 2011, 2013; Rochette et al., 2019) was run to isolate and process SNP genotypes from RAD loci, filtering globally for each species to retain only those SNPs which were present (i) in ≥90% of individuals, (ii) at ≤0.6 heterozygosity, (iii) at ≤0.01 minor allele frequency, (iv) in every geographical sample and (v) as the first variant on each RAD-tag (to minimise linkage disequilibrium; Larson et al., 2014). To prevent the potential introduction of artificial structure via alternative protocols, no SNP filtering was conducted based on Hardy–Weinberg equilibrium (Pearman et al., 2022). Finally, using 'R' v4.0.0 (R Core Team, 2020), the *missingno* function of 'poppr' v2.8.5 (Kamvar et al., 2014) was used to remove any individuals missing genotypes for ≥25% of these filtered SNPs, and the *isPoly* function of 'adegenet' v2.1.3 (Jombart, 2008; Jombart & Ahmed, 2011) was used to remove loci subsequently rendered monomorphic.

2.3 | Exploring genetic diversity and population structure

The R package 'hierfstat' v0.04–22 (Goudet & Jombart, 2015) was used to calculate site-wise expected and observed heterozygosity (H_e/H_o), global and regional *F* statistics and pairwise F_{ST} (θ of Weir & Cockerham, 1984). Confidence intervals (95% CIs) for F_{ST} estimates were calculated via 100 bootstraps across loci in the R package 'diveRsity' v1.9.90 (Keenan et al., 2013). The R package 'marmap' v1.0.4 (Pante & Simon-Bouhet, 2013) was used to calculate pairwise physical (minimum oceanic) distances between sites via the *lc.dist* function, with some minor adjustments of site coordinates undertaken to ensure the integrity of oceanic paths and compatibility of environmental data (Appendix S1.6). Mantel tests between matrices of pairwise genetic and geographical distance (F_{ST} and km, respectively) assessed isolation-by-distance (IBD), using the *mantel.rtest* function of the R package 'ade4' v1.7–15 (Thioulouse et al., 2018).

Genetic clustering and population structure were assessed via discriminant analysis of principal components (DAPC) using the *dapc* function of 'adegenet' (Jombart et al., 2010). The *xvalDapc* function was implemented across 1000 replicates to determine the optimal number of principal component axes (*P*-axes) to retain for DAPC models, with the maximum *P*-axes limited to one fewer than the number of sampling sites in order to prevent overplotting (Thia, 2022). The optimal number of genetic clusters (*K*) and individual membership of these were also explored using adegenet; the *snapclust.choose.k* function enabled comparisons of Akaike information criteria (AICc) across each modelled value of *K*, and the *snapclust* function performed maximum-likelihood estimations of individual assignment probability to each cluster at given values of *K*, both of which are instructive in identifying the likely value of *K* sampled (Beugin et al., 2018).

2.4 | Selection and Genotype–Environment Association

The Bayesian differentiation-based method of 'Bayescan' v2.1 (Foll & Gaggiotti, 2008) was applied to detect SNP outliers potentially under selection. Bayescan was implemented using conservative parameters (Appendix S1.6) with each full dataset and then separately for each basin to detect candidate loci specific to Atlantic or Mediterranean populations. In addition, redundancy analysis (RDA) was used to identify SNPs which were candidates for adaptive selection via genotype–environment association (GEA), and to calculate a distance-based (db) estimation of the extent to which heterogeneous environmental conditions and the spatial distribution of sampling sites explain overall genetic differentiation (dbRDA). Genetic variation was characterised as site-wise mean allele frequencies for all SNPs, calculated in R using the *rraf* function of 'poppr'. Contemporary environmental data (long-term averages, 2000–2014; 5 arcminutes resolution) for ecologically relevant parameters were extracted from Bio-Oracle v2.0 (Assis et al., 2018) for all sampling sites. On the basis of their potential to influence physiology, metabolism and dispersal, five environmental factors were chosen as parameters against which to investigate signals of genetic adaptation: annual mean sea-surface salinity (SSS) and current velocity (SSV), minimum monthly mean benthic dissolved oxygen (SBO), and two measures of temperature: absolute benthic temperature range (SBT) and annual mean sea-surface temperature (SST), which have respectively been linked to population-level variation in female fecundity (Ellis et al., 2015) and to PLD (Quinn et al., 2013) in clawed lobsters (Appendix S6–Figure S6.9a–e). To characterise the spatial distribution of sampling sites, principal coordinates analysis was undertaken on the pairwise geographical distance matrix to compute distance-based Moran's Eigenvector Maps (dbMEMs), via the *dbmem* function of 'adespatial' v0.3–8 (Dray et al., 2020) in R. The package 'psych' v1.9.12.31 (Revelle, 2019) was used to investigate correlations among environmental factors, and adespatial identified significant spatial and environmental variables to include in the dbRDA via 10,000-permutation ANOVA-like tests of forward selection. The package 'vegan' v2.5–6 (Oksanen et al., 2019) was used to run RDAs/dbRDAs, and deliver 10,000-permutation significance tests of their full models, their axes and their individual variable components. SNPs were identified as candidates for local adaptation where they were distributed ≥2.5 standard deviations from the mean (two-tailed $p < 0.012$) on significant RDA/dbRDA axes

(Forester, 2019). Key analyses were visualised in R using 'ggplot2' v3.3.1 (Wickham, 2016).

3 | RESULTS

3.1 | Sequencing depth and SNP discovery

In all, 15 lobsters and 13 crawfish were removed from their respective datasets due to missing data. Using *sbf*I, the mean number of RAD-tags was 36,062 for lobster and 38,004 for crawfish, across which the mean sequencing depth was 44x coverage and 23x coverage, respectively. The final lobster dataset featured 214 individuals genotyped at 6340 SNPs, while the crawfish dataset contained 349 individuals genotyped at 7681 SNPs.

3.2 | Genetic diversity and differentiation

Among lobster samples, H_e was 0.15–0.16 in all but one site (Aeg, H_e=0.14). In all but one site (Jer, H_o=0.15=H_e), H_o<H_e, with Trondheim showing the maximum discrepancy (Tro H_o=0.11 vs H_e=0.15). Globally, F_{ST} was 0.017 (95% CIs 0.015–0.019), F_{IT} was 0.104 and F_{IS} was 0.089. Within-basin variation was markedly higher among Mediterranean sites (F_{ST}=0.030; 95% CIs 0.027–0.033) than Atlantic sites (F_{ST}=0.006; 95% CIs 0.005–0.007), and between these basins F_{ST}=0.031 (Atlantic n=181 vs Med. n=33). Pairwise F_{ST} was greatest when featuring one of the two Greek sites (Aeg and Mac), for which pairwise F_{ST}≥0.05 with all sites except the Adriatic (Figure 2). Mean pairwise F_{ST} between Greek and Atlantic sites was 0.068, reaching a maximum of 0.077 (Heb vs Aeg). Of 496 pairwise F_{ST} estimates, 41 negative values (minimum F_{ST}=−0.006) were converted to zero. IBD was significant across all sites (r^2=0.88, p<0.001) and within both the Atlantic (r^2=0.71, p<0.001) and Mediterranean (r^2=0.62, p<0.05) basins (Figure 3).

Among crawfish samples, H_e was 0.10–0.11 for all sites, and H_o was ≤0.01 H_e at all sites except the Celtic Sea (Cel H_o=0.09 vs H_e=0.11). Globally, F_{ST} was 0.010 (95% CIs 0.008–0.012), F_{IT} was 0.093 and F_{IS} was 0.084. Within-basin variation was very low in both the Atlantic and Mediterranean (Atlantic F_{ST}=0.002, 95% CIs 0.001–0.002; Med. F_{ST}=0.001, 95% CIs 0.000–0.002), while between these basins F_{ST}=0.025 (Atlantic n=276 vs Med. n=73). Pairwise F_{ST} within basins was low (F_{ST}<0.008) and exceeded by all between-basin pairs, reaching a maximum of 0.032 (CwN vs Dal) (Figure 2). From 105 pairwise F_{ST} estimates, five negative values (minimum F_{ST}=−0.002) were converted to zero. IBD was highly significant across all sites (r^2=0.89, p<0.001) and weakly significant within the Mediterranean basin (r^2=0.72, p<0.05), but Atlantic sites showed no correlation between genetic and geographical distance (r^2=−0.06) (Figure 3; Appendix S3–Figure S3.5).

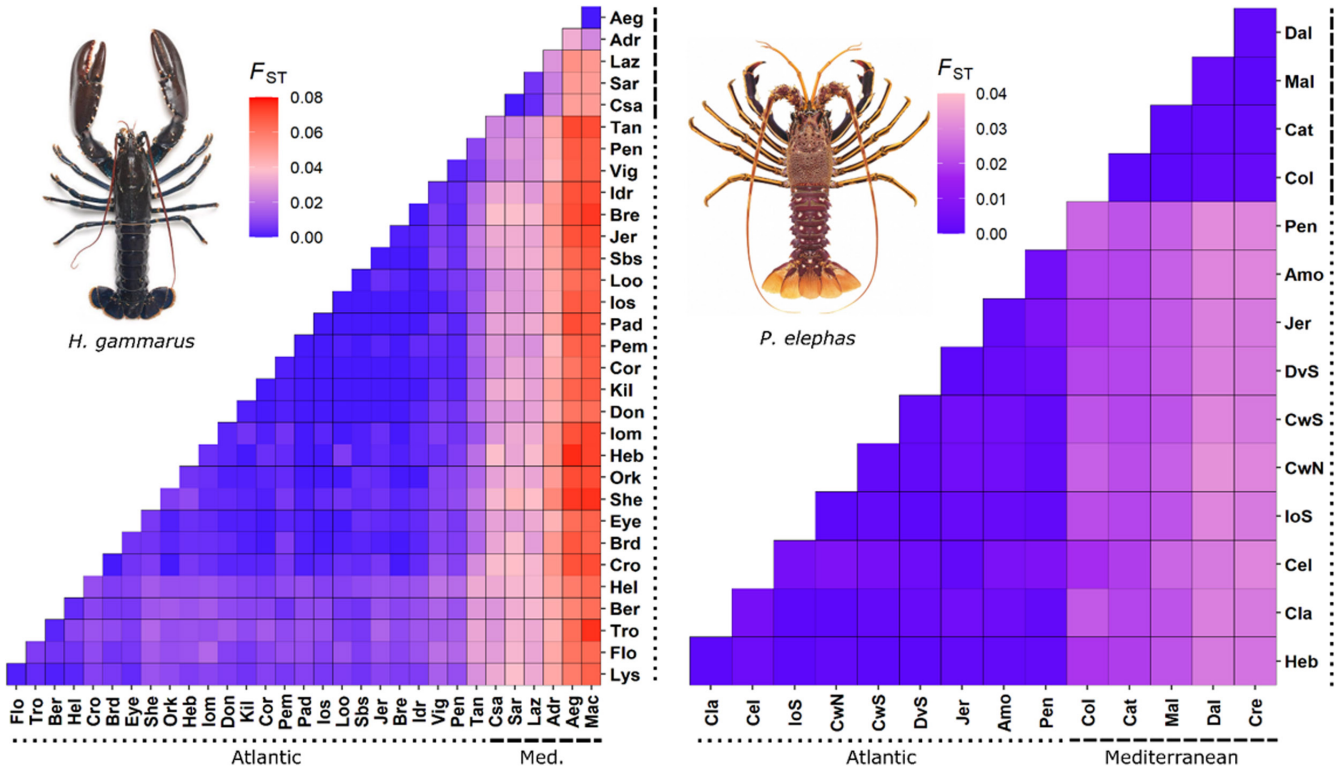

FIGURE 2 Heatmap matrices of pairwise F_{ST} (Weir & Cockerham's θ, 1984) between geographical samples for lobsters *Homarus gammarus* (left) and crawfish *Palinurus elephas* (right), calculated across all SNP loci. Atlantic sites are indicated with a dotted line, and Mediterranean sites with dashed line. Sample sites are broadly arranged via relative position within the extremes of the spatial range (with most northerly Atlantic furthest left/bottom, and most easterly Mediterranean furthest right/top).

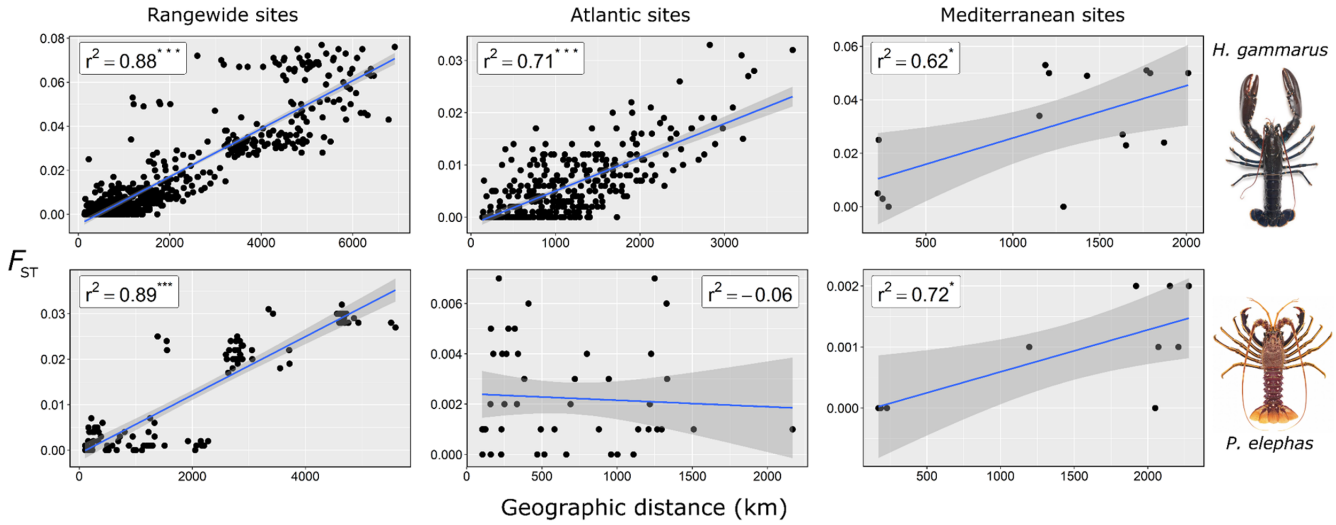

FIGURE 3 Unscaled plots of isolation-by-distance (IBD) for lobsters *Homarus gammarus* (upper) and crawfish *Palinurus elephas* (lower), with measures of pairwise genetic (F_{ST}—Weir & Cockerham's θ, 1984) and geographical (kilometres—minimum oceanic paths) distance regressed between geographical sites for all samples (left) and only those from the Atlantic (middle) and Mediterranean (right) basins. Correlation coefficients (r^2) and associated *p*-values are calculated from Mantel testing (significance denoted as $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$). Blue lines depict linear regression model fits, with corresponding 95% confidence intervals shaded in darker grey. To enable best depiction of IBD for each species, axes are not standardised at each spatial scale; for a direct comparison between species at each spatial scale, see Appendix S3 (Figure S3.5).

3.3 | Genetic structure

The range-wide DAPC with the full lobster dataset clearly differentiated Atlantic individuals from those originating from the Western Mediterranean, Adriatic, and Aegean seas, which were separated, with increasing distance respectively, along linear discriminant axis 1 (LD1), which explained 72.5% of between-site variation. LD2 (10.0%) was more powerful but less informative than LD3 (8.8%), which separated the means of Scandinavian sites from other Atlantic samples, rather than further differentiating existing clusters (Figure 4a). This sub-structuring was confirmed when Atlantic lobsters ($n = 181$) were analysed separately, with LD1 (43.2%) distinguishing Scandinavian and other Atlantic sample means, while LD2 (15.8%) differentiated more southerly samples, with Moroccan individuals (Tan) typically the most disparate, and tentative segregation of western Iberian samples (Vig, Pen) (Appendix S3–Figure S3.6a). Separate analysis of only Mediterranean individuals ($n = 33$) confirmed regional clustering, with samples from the Western Mediterranean (Csa, Sar, Laz), Adriatic Sea (Adr), and Aegean Sea (Aeg, Mac) all clearly segregated along LD1, which explained >99% of between-site variance (Appendix S3–Figure S3.6b). *Snapclust* suggested hierarchical population structure at a range-wide level, with $K = 2$ having the sharpest drop in AICc (reflective of the Atlantic-Mediterranean break) but individual assignment supported clustering up to $K = 5$ (at which primary membership reflected regions of East Med., West Med., Morocco, Atlantic Europe and Scandinavia) (Appendix S4–Figure S4.7a). When $K > 5$, new clusters featured only a few individuals from single sample sites, usually towards range edges. Primary cluster membership supported greater genetic connectivity in the Atlantic than the Mediterranean. Within both basins, *snapclust* supported $K = 2$ via AICc weightings, and $K = 3$ via individual assignment. Notably, the Atlantic partition analogous to the Scandinavian cluster at a range-wide level was better described as a North Sea cluster at this finer resolution, since assignment included most individuals from north-eastern UK (Brd, Eye) (Appendix S4–Figure S4.7b). Cluster membership followed regional origin for all Mediterranean lobsters except one Aegean-assigning individual from the Adriatic sample, whose capture location was discrete from the rest of the cohort, towards the Ionian Sea boundary (Appendix S4–Figure S4.7c).

The range-wide DAPC with the full crawfish dataset was informative only in distinguishing Atlantic and Mediterranean individuals, which partitioned along LD1 (98.7%) (Figure 4d). Separate analysis of Atlantic crawfish ($n = 276$) revealed a single cluster (Appendix S3–Figure S3.6c), even when using basin-specific outlier SNPs (Appendix S2–Figure S2.2). This was also the case with only Mediterranean crawfish ($n = 73$), although there was tentative evidence of a geographical cline via sample means aligning to LD1 (65.0%) (Appendix S3–Figure S3.6d). Via AICc weightings, *snapclust* supported range-wide clustering up to $K = 3$, but individual assignment only supported $K = 2$ and the genetic break between basins (Appendix S4–Figure S4.7d). At $K = 2$, primary assignment was to the basin of sampling origin for all individuals except three from Western Mediterranean sites (2x Cat, 1x Col) assigned Atlantic ancestry. When run range-wide with $K \geq 3$, cluster membership was incompatible with differentiation attributable to sampling location, and no value of *K* produced clusters with spatial links when running Atlantic and Mediterranean samples separately.

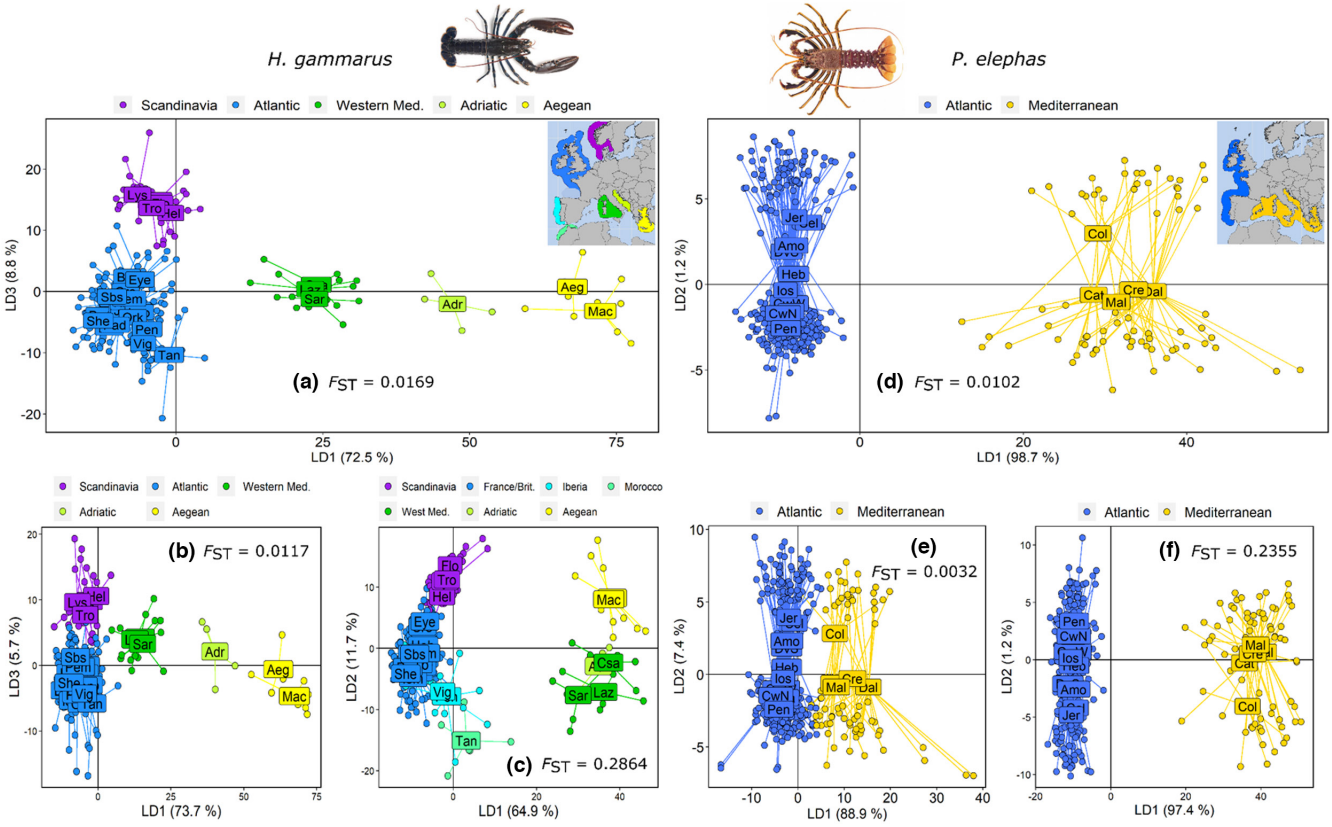

FIGURE 4 Range-wide plots of discriminant analysis of principal components (DAPC), in which points represent individuals and labels represent the mean position of all individuals comprising each geographical sampling site, with colours set according to discrete regional genetic clusters [denoted above each plot and linked to geography in the inset maps of (a) for lobster and (d) for crawfish]. For all 214 lobsters, plots depict clustering across (a) all 6340 loci, retaining 15 *P*-axes, (b) only 6289 putatively neutral loci, retaining 15 *P*-axes, and (c) only 51 putative outlier loci, retaining 25 *P*-axes. For all 349 crawfish, plots depict clustering across (d) all 7681 loci, retaining 3 *P*-axes, (e) only 7590 putatively neutral loci, retaining 5 *P*-axes, and (f) only 91 putative outlier loci, retaining 11 *P*-axes. Associated range-wide F_{ST} of these SNP datasets are displayed on each plot. Plots c-f depict LD1 vs LD2, whereas plots (a) and (b) depict LD1 vs LD3, which was more informative. Explanatory power of LD axes (%) are displayed on plots.

3.4 | Candidates for selection and local adaptation

From range-wide analyses, Bayescan identified 50 lobster SNPs and 80 crawfish SNPs as outlier candidates for adaptive divergence. For both species, the most divergent locus reached F_{ST}>0.4 (Appendix S5). When run separately within basins, Bayescan detected 21 outliers from Atlantic lobsters, all but one of which was already flagged via the full dataset, and detected 15 outliers from Atlantic crawfish, 11 of which were in addition to those from the full dataset. Using only Mediterranean samples, Bayescan detected no outliers for either species. Via DAPC, these subsets of highly divergent loci depicted similar patterns of population structure to that from all SNPs. Unlike the full complement of loci, the 51 lobster outlier SNPs (F_{ST}=0.286, 95% CIs 0.246–0.334) provided sufficient resolution to depict the Atlantic's genetic cline along LD2 (11.7%), even where Mediterranean samples were also included (Figure 4c). Outliers also depicted a more distinct genetic break between basins compared with putatively neutral loci (6289 SNPs—the full dataset minus the 51 outliers; F_{ST}=0.012, 95% CIs 0.011–0.013), although the latter better maintained Mediterranean substructuring (Figure 4b). Intra-Mediterranean regional differentiation was preserved by outliers via LD3 (4.7%) (Appendix S2–Figure S2.3). For crawfish, the 91 outlier loci (F_{ST}=0.236, 95% CIs 0.191–0.359) separated Atlantic and Mediterranean individuals along LD1 (97.4%), though samples within basins remained unstructured (Figure 4f). Via the remaining 7590 neutral SNPs (F_{ST}=0.003, 95% CIs 0.003–0.004), the inter-basinal clusters were still apparent but lost clear separation via LD1 (88.9%) (Figure 4e).

None of the environmental data were correlated across lobster sample sites (Appendix S6–Figure S6.10). As such, these same five variables were retained for crawfish sites despite close correlation of SST and SSS variation (r^2=0.93) (Appendix S6–Figure S6.11). For lobster, the RDA of environmental factors (GEA-RDA) was significant (p=0.012, adjusted r^2=0.024), with RDA1 the only significant axis (p=0.001) (Figure 5a). For this axis, 87 loci were outlying, 85 of which had a principal GEA to SST, including all 30 which shared detection by Bayescan (Appendix S7.1); these subsets both depicted population clustering similarly to the full dataset and Bayescan outliers, with the exception of discriminating Scandinavian samples (Appendix S2–Figure S2.4). SST (p<0.0001) and three dbMEM factors (MEM1 p<0.0001; MEM2 p=0.0014; MEM3 p=0.043) were identified by

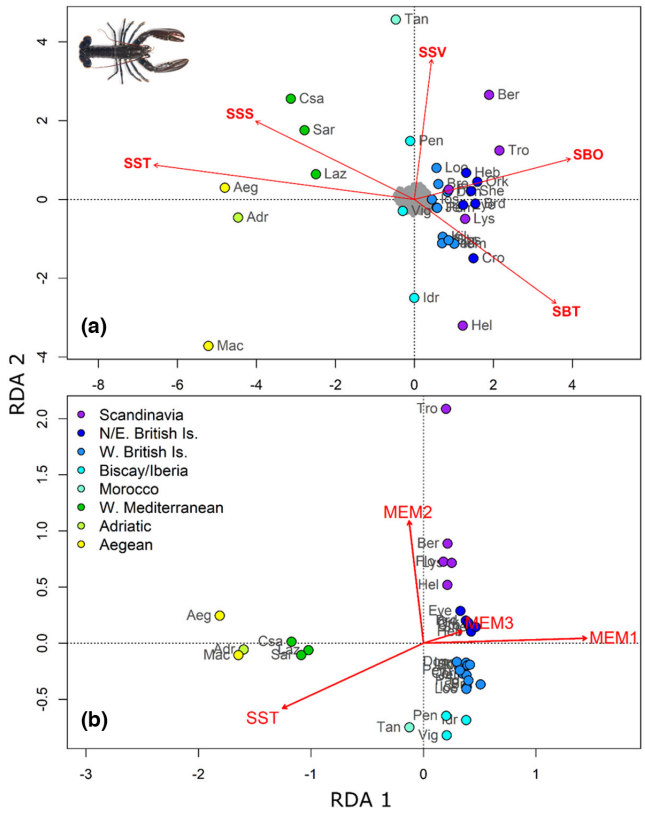

FIGURE 5 Plots for the lobster, *Homarus gammarus*, of (a) the partial genotype–environment association redundancy analysis (GEA-RDA), with all environmental factors (adjusted $r^2 = 0.024$), and (b) the full spatio-environmental distance-based redundancy analysis (db-RDA), with only significant spatial and environmental factors (bottom, adjusted $r^2 = 0.049$). Sample means are coloured according to their regional population structure, as per the legend in (b). The Scandinavian sample outlying on RDA2 in (b) is Trondheim (Tro).

forward selection as significant variables to include in the dbRDA model, although SST and MEM1 had high variance inflation factors, indicative of non-independence. The adjusted coefficient for this dbRDA, $r^2 = 0.116$, suggested these parameters explain only about 12% of the spatial variation in lobster allele frequencies (Legendre et al., 2010) (Figure 5b), and no axis was significant. Run with significant variables, dbRDA flagged only one candidate SNP, but this locus did not share detection via either Bayescan or GEA-RDA, so was not added to the outlier subset (Appendix S7.1). In contrast, for crawfish neither the GEA-RDA model nor any individual environmental variables were significant (all $p > 0.86$), and no environmental or spatial factors were significant for the dbRDA. Even when run with the most impactful environmental (SBO; $p = 0.078$) and spatial factors (MEM1; $p = 0.383$), the dbRDA model failed to explain any site-wise variation in crawfish allele frequencies (adjusted $r^2 = -0.004$).

4 | DISCUSSION

This SNP-based study represents the most powerful and accurate assessment to date of contemporary population structuring in the two most valuable commercially fished large lobster species of the northeast Atlantic and Mediterranean Sea. Undertaking near range-wide sampling and a consistent analytical approach enabled us to directly infer important commonalities and differences in the genetic connectivity of the two species. A phylogeographical break between the Atlantic and Mediterranean basins and strong range-wide IBD were common to both species as the primary features of spatial heterogeneity, while both showed relatively greater sub-structuring in the Mediterranean. Similarly, samples of both species from widely separated Atlantic locations displayed very limited differentiation in the absence of obvious physical barriers to dispersal (i.e., pairwise $F_{ST} \leq 0.001$ between northwest France and northwest Scotland, ≥1100 km apart, and $F_{ST} \leq 0.002$ between western Portugal and western Ireland, ≥1500 km apart). Of the two species, we detected greater spatial assortment of genetic variation in lobsters. For crawfish, despite using a genomic approach, we discovered no widespread population structure that previous studies had failed to detect. Our results suggest that, in the Atlantic at least, the species is genetically panmictic.

Variation in population structure is apparent in two key areas of our results: between basins, and between species. Regarding intra-basin variation, both species showed greater genetic structuring within the Mediterranean than the Atlantic, as previously observed for a number of marine species (e.g., mackerel—Rodríguez-Ezpeleta et al., 2016; dolphinfish—Maggio et al., 2019; sea bass—Souche et al., 2015). This is typically attributed to basinal differences in temperature and the spatial definition of water masses, and both are likely to be important factors in limiting genetic connectivity in Mediterranean populations. Habitat complexity typically impacts IBD more than dispersal factors (Meirmans et al., 2011; Selkoe et al., 2014), and the Mediterranean supports greater localised topographical and hydrographic heterogeneity than the Atlantic, including strong gyres and frontal systems, which may serve to limit emigration of adults and/or larvae (Pascual et al., 2017). Similarly, water temperatures are generally higher in the Mediterranean, which acts to shorten PLD and thus restrict larval dispersal potential (Raventos et al., 2021). Lobster PLD is doubled at 14°C compared to 22°C (Schmalenbach & Franke, 2010), while occasional observations of larval and post-larval crawfish support Atlantic PLD estimates (10–12 months) as being double those of the Mediterranean (5–6 months) (Gõni & Latrouite, 2005).

Regarding interspecific differences, lobster exhibits far more genetic divergence, with some relatively adjacent lobster samples from the same basin being as genetically differentiated as some crawfish samples from discrete oceanic basins (i.e. Tro–She lobsters, ~750 km, and Col–Cel crawfish, ~2600 km; both = F_{ST} 0.017). Our results confirm previous findings for lobster of range-wide and within-basin IBD (Ellis et al., 2017; Jenkins et al., 2019), heterogeneity between Scandinavian and open Atlantic stocks (Ellis et al., 2017), a genetic cline across the species' Atlantic range (Jenkins et al., 2019) and more pronounced differentiation towards range extremes (Triantafyllidis et al., 2005). Lobsters from Tangier in Morocco were weakly

differentiated from other Atlantic locations, indicating regional substructuring along the continental Atlantic coast. The capture locations of Moroccan individuals were imprecise compared to other samples, yet their Atlantic ancestry was expected; whether originating from west or east of the Straits of Gibraltar, the major hydrographic barrier between Atlantic and Mediterranean surface waters is the Almeria-Oran Front, beyond Morocco's eastern border with Algeria (Patarnello et al., 2007). Range-wide differentiation in lobster (F_{ST}=0.0169) was higher than GBS-based estimates for its closest relative, *H. americanus* (F_{ST}=0.0019—Benestan et al., 2015), although that may reflect differences in sample sizes between studies.

In contrast, we found only limited evidence for structuring among Mediterranean crawfish, and none at all for Atlantic crawfish. There was no positive association between genetic and geographical distance across the Atlantic, in which the most remote samples showed minimal divergence (Heb vs Pen, ~2200 km = F_{ST} 0.001). This conflicts some previous results. Using seven microsatellites, Babbucci et al. (2010) found Azorean crawfish to be differentiated from other Atlantic samples, and more similar to Mediterranean populations. Without Macaronesian crawfish among our Atlantic samples, we cannot assess differentiation between offshore archipelagos and continental coasts, but a lack of any Mediterranean assignment among our Portuguese (PEN) samples effectively dispels the prospect that Mediterranean populations act as a source of recruitment to crawfish stocks in their southerly Atlantic range. Meanwhile, based on mtDNA haplotypes, Palero et al. (2008) asserted differentiation between crawfish from Western Ireland and Scotland and those further south. However, estimates of differentiation via mtDNA often far exceed those of nuclear markers (Selkoe & Toonen, 2011), and more powerful studies have since detected no genetic heterogeneity between these regions (this study; Palero et al., 2011). For Mediterranean crawfish, marginally positive IBD and a tentative geographical cline across sample means indicate very weak genetic structuring. However, this was not consistently depicted by all analytical approaches, and was in spite of within-basin differentiation (F_{ST}=0.0010) being even lower than that of the entirely unstructured Atlantic (F_{ST}=0.0015). Benestan et al. (2021) recently detected no IBD or other indications of reduced genetic connectivity when using GBS methods to assess population structuring among Western Mediterranean crawfish. However, their results are not incompatible with our tentative signals of within-basin differentiation between Mediterranean crawfish, given our analysis also includes coverage of Eastern Mediterranean populations via Croatian and Greek samples. Notably, the levels of differentiation we detected for crawfish were lower both range-wide (F_{ST}=0.010) and between basins (Atlantic vs Mediterranean F_{ST}=0.025) than comparable GBS-based estimates between Australian and New Zealand populations of another temperate spiny lobster, *Jasus edwardsii* (pairwise F_{ST}=0.052–0.070), despite the latter species' longer PLD (Ilyushkina, 2018).

We detected greater overall differentiation in lobsters than crawfish, which most likely stems from differing aspects of species biology. Dispersal potential is generally the most significant factor shaping population genetic structure (Meirmans et al., 2011; Selkoe & Toonen, 2011), so this likely drives much of the interspecific variation we evidenced. Greater differentiation among lobsters implies reduced gene flow and connectivity between stocks, and therefore lower levels of dispersal than crawfish exhibit. While not a direct proxy of larval dispersal distance, PLD is generally a good predictor of seascape-scale genetic connectivity, with shorter PLDs restricting gene flow and increasing structure (Selkoe & Toonen, 2011; Treml et al., 2012). For both species, PLD estimates are subject to much uncertainty, but are typically in the order of weeks for lobster and months for crawfish, giving crawfish a greater likelihood of distant emigration before settlement. Indeed, both biophysical modelling across the southwestern British Isles (Whomersley et al., 2018) and uniform variation in juvenile settlement across the Western Mediterranean (Muñoz et al., 2021) support the prospect that crawfish phyllosoma may disperse hundreds of kilometres and become admixed at a regional level. Local retention of larvae may be extremely rare in some locations (Whomersley et al., 2018) and recruitment is influenced by mesoscale oceanic dynamics (Muñoz et al., 2021), both of which indicate high levels of demographic connectivity via larval dispersal. Yet, it is not contradictory that the Atlantic-Mediterranean phylogeographical break appears equally conspicuous in both crawfish and lobsters; marine species with longer PLDs are more likely to be genetically differentiated where separated by marked hydrographic stratification than those with shorter PLDs (Pascual et al., 2017). Other tenets of larval biology are also likely to promote greater genetic connectivity in crawfish than lobsters. First, crawfish spawn larger clutch sizes than lobsters so, at similar abundance and demographic balance, they have greater fecundity, a trait typically associated with enhanced connectivity (Treml et al., 2012). Likewise, crawfish larvae are initially smaller and more passive in the water column, so may be more readily dispersed beyond their local environment by currents. Lobster larvae are capable of swimming against weak horizontal flows and undertaking vertical migrations (Schmalenbach & Buchholz, 2010), and may seek retentive currents to inhibit extensive dispersal (Øresland & Ulmestrand, 2013), which would increase self-recruitment (Shanks, 2009; Teske et al., 2007).

Another potential mechanism of demographic connectivity is dispersal via adult movements; key differences in this important behavioural factor could contribute to the interspecific variation in gene flow we observed. Whereas lobsters are typically solitary, territorial and show high site fidelity (i.e., <600 m movement per ≤1 year—Moland et al., 2011; 1.1 km^2 mean home range—Skerritt et al., 2015), crawfish may undertake mass seasonal movements associated with storms or breeding seasons (Gõni & Latrouite, 2005). Around the Scilly Isles off southwest Britain, 14% of tagged lobsters were recaptured within 24 months, compared to only 1% of crawfish (Holt & Kelly-Fletcher, 2016), and only ~2% of crawfish around Columbretes, Spain, were inter-annual recaptures during a decadal study (Goñi et al., 2010). Although most tagged crawfish are typically recorded as travelling only modest distances (i.e., 3.2 km—Goñi et al., 2003; 2.5 km/year—Follesa et al., 2009), distantly dispersing individuals are under-represented in mark–recapture studies (Koenig

et al., 1996), and some crawfish exhibit highly transient behaviour (e.g. 50 km—Follesa et al., 2011; 500–800 km over 3–4 years—Tully & Pedraza, 2020). Demographic connectivity in both species could also be human mediated. Adult lobsters and crawfish are prized as seafood and typically traded live, such that escape or release following anthropogenic transit could generate genetic homogenisation, which could be misinterpreted as natural gene flow between otherwise differentiated populations (Einfeldt et al., 2020). During the 1800s, crawfish were routinely transported from northern Spain to markets in France and Britain, although given that lobsters were similarly widely traded (Spanier et al., 2015), inherent ecological factors remain the most likely cause of interspecific differences in genetic structure. Indeed, our clustering assignments support larval drift as the principal mechanism of genetic connectivity in both species; of individuals sampled from the Western Mediterranean, four lobsters (of 18) and three crawfish (of 31) were assigned Atlantic descent (Appendix S4–Figure S4.7a,d), an eastward direction of dispersal which matches net surface water exchange between the basins (Patarnello et al., 2007). In contrast, no Atlantic-sampled individuals of either species were assigned Mediterranean ancestry, as might be anticipated if human-mediated transport or widespread adult emigration were major contributors to gene flow.

Extrapolating our results for genetic structuring into inferences of the demographic interdependence of regional lobster and crawfish populations is not straightforward. Clearly, our analyses indicate greater exchange of individuals among crawfish than lobsters at similar spatial scales. We did not calculate pairwise migration rates, since gene flow-based measures lack sufficient accuracy to estimate larval exchange, and functional dispersal is often greatly overestimated via such approaches (Palumbi, 2003; Shanks, 2009). However, while our results evidence no definitive genetic breaks in either species beyond the Atlantic-Mediterranean divide, this does not mean that many individuals are routinely exchanged between regions; only a handful of immigrants per generation are required to provide sufficient gene flow to prevent the divergence of otherwise disconnected populations (Shanks, 2009). Indeed, even among apparently panmictic Atlantic crawfish populations, self-recruitment may be locally significant; crawfish in southwestern Britain suffered stock collapses from which it has taken decades to generate any semblance of recovery (Jackson, 2021), despite adjacent regions (i.e., Ireland, northwest France) maintaining sufficient crawfish biomass to support commercial fisheries. Similarly, given the extent to which many important oceanographic variables covary spatially across the two species' shared range (longitudinally in the Mediterranean, and latitudinally in the northeast Atlantic), it is difficult to ascertain the evolutionary foundations of the differentiation our data depict. Outlier analyses identified highly differentiated SNPs, fewer than a hundred of which adequately depict range-wide structure in each species. RDA failed to detect strong correlations to important abiotic factors for any crawfish loci, but site-wise mean allele frequencies for 85 lobster loci were found to be correlated with SST via GEA. Adaptive evolution to temperature has previously been linked to spatial variation in the American lobster, *H. americanus*, with PLD reduced among larvae reared at temperatures matching their local environments (Quinn et al., 2013), and SNPs driving population divergence being located in genes associated with thermal adaptation (Benestan et al., 2016). However, although genetic variation and SST are correlated at many of the most divergent lobster loci, we cannot confirm this evidences adaptive selection, since no GEA candidate SNPs remained significantly associated with SST once spatial components were controlled. Indeed, as indicated by model flags of potential non-independence for SST and the primary spatial driver (MEM1), ranking sites by both mean SST and geographical origin produces a near-linear regression ($r^2 = 0.96$; Appendix S7.3).

To conclude, our results present the most comprehensive depiction of contemporary population structuring for the two most ecologically and economically important large lobsters of the northeast Atlantic and Mediterranean Sea. Applying a consistent methodological approach, we have identified notable consistencies in the genetic structuring of these sympatric species, such as the Atlantic-Mediterranean break and heightened intra-basinal divergence in the Mediterranean, which are explicable in the context of known oceanographic barriers and hydrographic conditions. We were also able to highlight important dissimilarities in genetic structuring, particularly in the Atlantic, where lobsters exhibit a genetic cline, weak regional divergence and a pattern of IBD, but throughout which crawfish appear panmictic. We postulate that these interspecific differences arise from contrasting aspects of ecology, with greater dispersal—especially of larvae following a longer PLD—serving to prevent genetic drift and/or the accumulation of adaptive variation from arising in crawfish as extensively as observed in lobster. Our finding of intra-basinal genetic homogeneity in crawfish suggests that fragmented and inconsistent conservation legislation threatens the widespread overexploitation of fisheries, for which cooperative and transnational management may be required to ensure regionally sustainable yields. Meanwhile, our finding of more spatial structuring in lobsters indicates that they may be more acutely susceptible to localised overfishing, and that management measures which maintain spawning stock biomass may be particularly important in creating sufficient self-recruitment to sustain productive harvests. Finally, the structuring we evidence suggests that biological parameters that are key to sustainable fisheries management (growth rates, maturation size, fecundity, etc) should not be universally inferred where data have been collected from genetically differentiated populations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw genetic data underpinning this work are available via the NCBI Sequence Read Archive (SRA) database; BioProject Accession ID: PRJNA954007, https://www.ncbi.nlm.nih.gov/bioproject/PRJNA954007. All analytical resources relevant to this study and its reproducibility are available via the Dryad Digital Repository; Ellis (2023), Data from Shared and distinct patterns of genetic structure in two sympatric large decapods, Dryad, Dataset, https://doi.org/10.5061/dryad.zgmsbccdz.

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BIOSKETCH

Charlie Ellis researches the biogeography, molecular ecology and population genetics of marine species, with a particular focus on decapod crustaceans of the Atlantic Ocean. This work represents a component of his postdoctoral research into European clawed and spiny lobster population genomics at the University of Exeter, where he and the institute's other authors collaborate in studies of molecular ecology and evolution (see MEEG lab, https://projects.exeter.ac.uk/meeg). The authors from other institutes all research lobsters, so provided valuable expertise to this study.

Author contributions: Charlie D. Ellis, Tom L. Jenkins and Jamie R. Stevens conceived the ideas; Charlie D. Ellis, Tom L. Jenkins, Lénia D. Rato, Youenn Jézéquel, Mišo Pavičić, David Díaz and Jamie R. Stevens conducted the fieldwork and collected the tissue samples; Charlie D. Ellis, Kirsty L. MacLeod and Tom L. Jenkins conducted the laboratory work; Charlie D. Ellis analysed the data with additional code from Kirsty L. MacLeod and Tom L. Jenkins; and Charlie D. Ellis led the writing with assistance from Kirsty L. MacLeod, Tom L. Jenkins, Lénia D. Rato, Youenn Jézéquel, Mišo Pavičić, David Díaz and Jamie R. Stevens.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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