

Genetic hypervariability of a Northeastern Atlantic venomous rockfish

Sara M. Francisco¹, Rita Castilho², Cristina S. Lima¹, Frederico Almada¹, Francisca Rodrigues¹, Radek Šanda³, Jasna Vukić⁴, Anna Maria Pappalardo⁵, Venera Ferrito⁵ and Joana I. Robalo¹

¹ MARE—Marine and Environmental Sciences Centre, ISPA Instituto Universitário de Ciências Psicológicas, Sociais e da Vida, Lisbon, Portugal

² Centro de Ciências do Mar (CCMAR), Universidade do Algarve, Faro, Portugal

³ Department of Zoology, National Museum, Prague, Czech Republic

⁴ Faculty of Science, Department of Ecology, Charles University, Prague, Czech Republic

⁵ Department of Biological, Geological and Environmental Sciences, Section of Animal Biology Biology “Marcello La Greca”, University of Catania, Catania, Italy

ABSTRACT

Background: Understanding the interplay between climate and current and historical factors shaping genetic diversity is pivotal to infer changes in marine species range and communities' composition. A phylogeographical break between the Atlantic and the Mediterranean has been documented for several marine organisms, translating into limited dispersal between the two basins.

Methods: In this study, we screened the intraspecific diversity of 150 individuals of the Madeira rockfish (*Scorpaena maderensis*) across its distributional range (seven sampling locations in the Atlantic and Mediterranean basins) using the mitochondrial control region and the nuclear S7 first intron.

Results: The present work is the most comprehensive study done for this species, yielding no genetic structure across sampled locations and no detectable Atlantic-Mediterranean break in connectivity. Our results reveal deep and hyper-diverse bush-like genealogies with large numbers of singletons and very few shared haplotypes. The genetic hyper-diversity found for the Madeira rockfish is relatively uncommon in rocky coastal species, whose dispersal capability is limited by local oceanographic patterns. The effect of climate warming on the distribution of the species is discussed.

Subjects Aquaculture, Fisheries and Fish Science, Biogeography, Evolutionary Studies, Marine Biology, Population Biology

Keywords Population structure, Connectivity, Atlantic-Mediterranean transition, Range expansion, *Scorpaena maderensis*, Scorpaenidae

INTRODUCTION

Understanding the interplay between historical and current climate changes in shaping genetic diversity is pivotal to infer future changes in the distribution of marine species. Climate warming is expected to significantly impact marine organisms with range disturbances anticipated (e.g., *Cheung et al., 2009; Lasram et al., 2010; Hollowed et al., 2013; Poloczanska et al., 2014; Lenoire & Svenning, 2015; García Molinos et al., 2016*). Indeed, climate-induced contractions, expansions, shifts and population extirpations

Submitted 15 January 2021

Accepted 15 June 2021

Published 12 July 2021

Corresponding author

Sara M. Francisco,
sara_francisco@ispa.pt

Academic editor

Tomas Hrbek

Additional Information and
Declarations can be found on
page 12

DOI 10.7717/peerj.11730

© Copyright

2021 Francisco et al.

Distributed under

Creative Commons CC-BY 4.0

OPEN ACCESS

across distribution areas have been amply recorded (e.g., [Nicastrò et al., 2013](#); [Yeruham et al., 2015](#); [Yu & Chen, 2018](#); [Aguilera et al., 2020](#)). In the past three decades, several advances in molecular and analytical tools led to the accumulation of data on the genetic diversity of marine organisms (e.g., [Helyar et al., 2011](#); [Plough, 2016](#); [Allendorf, 2017](#)) and connectivity (for reviews see [Selkoe et al., 2016](#); [Bryan-Brown et al., 2017](#)). Different phylogeographic patterns have been recorded in the North-eastern Atlantic, ranging from panmictic species with homogeneous genetic diversity throughout their distribution range to species with marked population differentiation (e.g., [Francisco et al., 2011](#); [Jenkins, Castilho & Stevens, 2018](#)).

Traditionally, the degree of genetic connectivity has been related to contemporary and historical factors that combined shape the present-day observed patterns (e.g., [Gaggiotti et al., 2009](#); [Woodall, Koldewey & Shaw, 2011](#); [Reis-Santos et al., 2018](#)). Marine species' geographical spread and population differentiation may be influenced by their potential for dispersal and gene flow, depending on passive larval dispersal and active adult migratory movements (e.g., [Selkoe & Toonen, 2011](#); [Pascual et al., 2017](#)). The interaction between life-history traits such as pelagic larval duration (PLD), larval behaviour and swimming abilities, post-settlement processes and oceanographic regimes play a role in the dispersal range of species with low adult dispersal ability (e.g., [Bowen et al., 2006](#); [Galarza et al., 2009](#); [Schunter et al., 2011](#); [Dalongeville et al., 2015](#)) (see [Bryan-Brown et al. \(2017\)](#) for a review). However, there is still an ongoing debate on the reliability of using a species' PLD as a proxy for population connectivity (e.g., [Bradbury et al., 2008](#); [Weersing & Toonen, 2009](#)).

Amongst the historical factors shaping present-day connectivity patterns are climate changes associated with the Pleistocene glacial cycles, geological barriers, salinity gradients, hydrodynamics and paleoecological history (e.g., [Olsen et al., 2004](#); [Bigg et al., 2008](#); [Palero et al., 2008](#)). These very dynamic factors are recurrently invoked to explain the biogeography of marine organisms (e.g., [Jenkins, Castilho & Stevens, 2018](#)). At the peak of the last glacial maximum (LGM), around 21 thousand years ago (kya), the sea level dropped by 110–150 m ([Lambeck & Purcell, 2005](#)). Still, the connection between the Mediterranean and the adjacent Atlantic waters was not interrupted ([Flores et al., 1997](#)), sustaining glacial refugia hypothesised within this basin ([Maggs et al., 2008](#)).

The Atlantic-Mediterranean phylogeographic break is well documented for several marine organisms (e.g., [Magoulas et al., 2006](#); [Taboada & Pérez-Portela, 2016](#)), notwithstanding the reopening of the Gibraltar Strait connection at the end of the Messinian Salinity Crisis (~5.33 Mya) ([Hsü, Ryan & Cita, 1973](#); [Krijgsman et al., 1999](#); [Duggen et al., 2003](#)). For others, often closely related species, the gene flow is unconstrained (e.g., [Stamatis et al., 2004](#); [Castilho et al., 2017](#); [Lourenço et al., 2017](#)) (see [Patarnello, Volckaert & Castilho, 2007](#) and [Kettle et al., 2011](#) for reviews). For the former, the inferred barrier has been associated with hydrological conditions that prevent migration either in recent times or in the Pleistocene, or both. This soft barrier location, however, is not consistent and for some taxa, the observed phylogeographic break is at the Strait of Gibraltar in the entrance of the Mediterranean basin (e.g., [Sala-Bozano, Ketmaier & Mariani, 2009](#); [Fruciano et al., 2011](#); [García-Merchán et al., 2012](#)), whilst for several others

is further East, at the Almeria-Oran front in the Alboran Sea region (e.g., [Zane et al., 2000](#); [Lemaire, Versini & Bonhomme, 2005](#); [Viñas et al., 2014](#)).

One of the evident effects of climate change is the increase in seawater temperature, which translates into a global tropicalization trend (e.g., [Bianchi & Morri, 2003](#); [Wernberg et al., 2016](#)) that also affects the Northeastern Atlantic. Along the southern and western coasts of the Iberian Peninsula, several organisms are expanding their poleward distribution, some with great impact in community composition (e.g., [Lourenço et al., 2012](#); [Nicastró et al., 2013](#); [Bode et al., 2020](#); [Robalo et al., 2020](#)). One of the fish species recently reported off southwestern continental Portugal is the Madeira rockfish, *Scorpaena maderensis* Valenciennes 1833 ([Encarnação et al., 2019](#)), an estimated moderately vulnerable species (36/100) according to the model by [Cheung, Pitcher & Pauly \(2005\)](#). The IUCN Red List highlights the unknown current population trend of this least concerned species ([Nunoo et al., 2015](#)). Its genetic characterization and phylogeography have therefore become imperative.

The Madeira rockfish, *Scorpaena maderensis*, is distributed in the eastern Atlantic, including the islands of Azores, Madeira, Canaries and Cape Verde and in the Mediterranean Sea ([Hureau & Litvinenko, 1986](#); [Eschmeyer et al., 1990](#); [Froese & Pauly, 2019](#)). The species is a benthic sedentary species, mostly occupying shallow coastal areas with rocky bottoms and estuaries (usually underneath boulders or in crevices). Congeneric species, *S. scrofa* and *S. porcus*, have high residency and narrow home ranges ([Özgül et al., 2019](#)). Based on the present-day known distribution, mainly of subtropical nature, the estimated seawater temperature range for the species is 16–25 °C ([Kaschner et al., 2019](#)), but there are no studies on the thermal tolerance of the species. The Madeira rockfish is a generalized and opportunistic feeder of benthic or epibenthic crustaceans and, occasionally, algae, gastropods, polychaetes and small fishes ([La Mesa, La Mesa & Tomassetti, 2007](#)), and shows sexual dimorphism in growth rate, maximum size and longevity, with differences registered between the Mediterranean and Azorean populations ([Morato et al., 2001](#); [La Mesa, La Mesa & Micalizzi, 2005](#)). A specialized mode of oviparity is described for the genus and the eggs are deposited as a whole in a protective gelatinous matrix that facilitates spawning cohesiveness and floatation ([Wourms & Lombardi, 1992](#)). The spawning season takes place from December to February in the Mediterranean ([La Mesa, La Mesa & Micalizzi, 2005](#)) and from March to June in the Azores ([Costa, 2007](#)). However, structural features of its biology are yet to be clarified, particularly the ones related to reproduction and early-life traits.

The present work is the first population study for this species, comprising a wide sampling coverage of its distribution range (seven locations from the Atlantic and the Mediterranean Sea), and two molecular markers (mitochondrial and nuclear) to screen the genetic diversity of *S. maderensis* with the following objectives: (1) evaluate the genetic diversity within and among locations; (2) assess the population genetic structure of the Madeira rockfish; and (3) evaluate the putative existence of a soft barrier between the Atlantic and the Mediterranean populations.

MATERIALS AND METHODS

Sampling

Specimens of *S. maderensis* were collected from seven locations across its distributional range in the Atlantic and Mediterranean: Cyprus (CYP), Greece (GRE—Euboea), Sicily (SIC—Messina, Riposto and Siracusa; Italy), Azores (AZO—Faial; Portugal), Madeira (MAD—Funchal; Portugal), Selvagens (SEL; Portugal) and Canaries (CAN—Tenerife; Spain) (Fig.1 and Table 1). Specimens were provided by fishers as the species is a frequent by-catch in coastal short-range artisanal fisheries and fins were clipped after assessing the species identification for each individual. Samples were preserved in 96% ethanol and deposited in ISPA-IU/MARE tissue collection.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted with the REDEExtract-N-Amp Kit (Sigma-Aldrich, St. Louis, MO, USA) following the manufacturer's instructions. The mitochondrial control region (CR) and the first intron of the nuclear S7 ribosomal protein gene (S7) were amplified, in a Bio-Rad Mycycler thermal cycler, using primers L-pro1 and H-DL1 (Ostellari et al., 1996), and S7RPEX1F and S7RPEX2R (Chow & Hazama, 1998). The PCR protocol was performed in a 20 µl total reaction volume with 10 µl of REDEExtract-N-amp PCR mix (Sigma-Aldrich, St. Louis, MO, USA), 0.8 µl of each primer (10 µM), 4.4 µl of Sigma water and 4 µl of template DNA using the following PCR conditions: initial denaturation at 94 °C for 7', followed by 35/30 cycles (denaturation at 94 °C for 30/45", annealing at 55 °C for 30/45", and extension at 72 °C for 1'; values CR/S7, respectively) and a final extension at 72 °C for 7'. The forward primers (L-pro1 and S7RPEX1F) were used for the sequencing reaction, and the PCR products were purified and sequenced in STABVIDA (<http://www.stabvida.net/>).

Chromatograms were manually checked, edited with Codon Code Aligner (Codon Code Corporation, <http://www.codoncode.com/index.htm>) and sequences were aligned with Clustal X 2.1 (Larkin et al., 2007). For S7, chromatograms were checked for double peaks (see Fig. S1 in Supplemental Materials) and, whenever possible, both strands of the same specimen were recovered following the approach of Sousa-Santos et al. (2005). All sequences were deposited in GenBank (Accession numbers MN716857–MN717002; and MN717003–MN717124, respectively for CR and S7) (Table S1 in Supplementary Materials).

Molecular data analyses

The genetic diversity and population structure of *S. maderensis* were assessed using several packages developed for R v.4.0.2 (R Core Team, 2020), in RStudio (RStudio Team, 2020). We used haplotypes (Aktas, 2020) and pegas (Paradis, 2010) R-packages to estimate standard descriptive measures of genetic diversity, including number of haplotypes and private haplotypes, haplotype diversity (h , Nei, 1987) and nucleotide diversity (π , Nei, 1987) and respective standard deviations. The software HP-Rare (Kalinowski, 2005) was used to estimate allelic richness (R) and private allelic richness (pR), using rarefaction to correct for sample-size bias associated with the relative abundance or easiness to collect

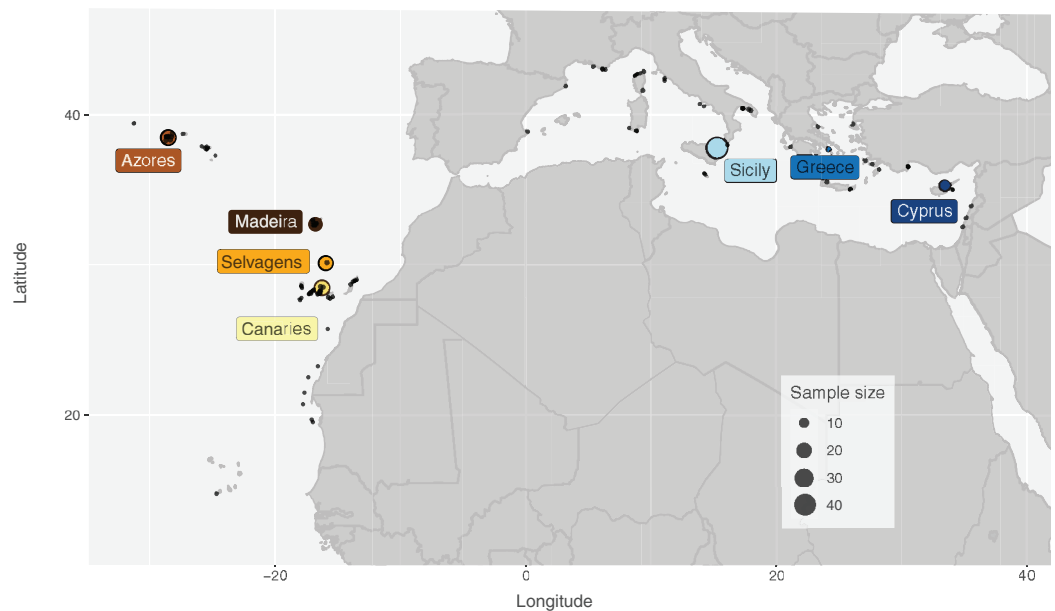


Figure 1 Distribution map and sampling locations for *Scorpaena maderensis*. Distribution map and sampling locations for *Scorpaena maderensis*. Black dots represent GBIF Occurrence Download (GBIF.org, 22 April 2021; <https://doi.org/10.15468/dl.bpf9s8>). Coloured circles represent samples used in this study and are consistent in all figures. Size of circles proportional to sample size.

Full-size [DOI: 10.7717/peerj.11730/fig-1](https://doi.org/10.7717/peerj.11730/fig-1)

Table 1 Sample locations, coordinates, sizes and summary statistics for the mitochondrial control region and the nuclear S7 gene of *Scorpaena maderensis*.

| Location | Code | Long | Lat | Mitochondrial Control Region | | | | | | | | Nuclear S7 | | | | | | | | | |
|---------------|------|--------|---------|------------------------------|-------|-------|-------|-----------|-------|-----------|--------|------------|-----|-------|-------|-------|-----------|-------|-----------|--------|--------|
| | | | | N | n_H | n_P | n_S | $n_{P/H}$ | h | π (%) | R | pR | N | n_H | n_P | n_S | $n_{P/H}$ | h | π (%) | R | pR |
| Cyprus | CYP | 35.091 | 33.344 | 13 | 12 | 9 | 11 | 75.00% | 0.987 | 2.12 | 9.733 | 6.166 | 22 | 22 | 19 | 22 | 86.36% | 1.000 | 3.05 | 19.209 | 9.714 |
| Greece | GRE | 37.740 | 24.059 | 7 | 7 | 7 | 7 | 100.00% | 1.000 | 3.66 | 7.000 | 5.503 | 14 | 12 | 10 | 10 | 83.33% | 0.978 | 3.42 | 12.000 | 5.553 |
| Sicily | SIC> | 37.708 | 15.202 | 42 | 31 | 19 | 22 | 61.29% | 0.984 | 2.50 | 11.741 | 5.780 | 22 | 22 | 20 | 22 | 90.91% | 1.000 | 2.93 | 19.209 | 10.032 |
| Mediterranean | MED | - | - | 62 | 47 | 37 | 36 | 78.72% | 0.989 | 2.58 | 12.445 | 3.872 | 58 | 54 | 50 | 50 | 92.59% | 0.998 | 3.05 | 24.002 | 2.130 |
| Canaries | CAN | 28.47 | -16.255 | 22 | 19 | 11 | 16 | 57.89% | 0.987 | 2.77 | 11.037 | 6.053 | 44 | 40 | 32 | 37 | 80.00% | 0.995 | 3.05 | 22.381 | 15.128 |
| Selvagens | SEL | 30.108 | -15.957 | 20 | 20 | 15 | 20 | 75.00% | 1.000 | 3.02 | 11.667 | 8.097 | 48 | 47 | 39 | 46 | 82.98% | 0.999 | 2.92 | 23.775 | 16.675 |
| Madeira | MAD | 32.694 | -16.775 | 20 | 20 | 17 | 20 | 85.00% | 1.000 | 3.28 | 11.667 | 8.629 | 32 | 27 | 18 | 22 | 66.67% | 0.990 | 3.13 | 19.662 | 10.923 |
| Azores | AZO | 38.522 | -28.716 | 22 | 19 | 12 | 16 | 63.16% | 0.987 | 2.79 | 11.037 | 4.215 | 38 | 32 | 25 | 28 | 78.13% | 0.989 | 3.04 | 20.502 | 12.814 |
| Atlantic | ATL | - | - | 84 | 68 | 58 | 57 | 85.29% | 0.993 | 3.01 | 12.897 | 4.215 | 162 | 127 | 123 | 113 | 96.85% | 0.992 | 2.87 | 24.752 | 8.478 |
| Total | - | - | - | 146 | 105 | - | 81 | - | 0.989 | 2.87 | - | - | 220 | 177 | - | 159 | - | 0.995 | 3.60 | - | - |

Note:

Long, longitude; Lat, latitude; N, number of gene copies; n_H , number of haplotypes; n_P , number of private haplotypes; n_S , singletons; $n_{P/H}$, proportion of private haplotypes; h , haplotype diversity; π , nucleotide diversity; R, allelic richness; pR , private allelic richness.

samples of this species. For the S7 gene fragment the programme ARLEQUIN v3.5 (Excoffier & Lischer, 2010) was used to reconstruct the haplotypes with the ELB algorithm (Excoffier, Laval & Balding, 2003), and to perform the exact probability tests for deviations from the Hardy-Weinberg equilibrium (HWE) (Guo & Thompson, 1992). The same software was used to assess population structure, performing analyses of molecular

variance (AMOVA) (Excoffier, Smouse & Quattro, 1992). The *diveRsity* R-package (Keenan et al., 2013) was used to evaluate the genetic structure, estimating fixation (F_{ST} (Weir & Cockerham, 1984), Nei's G_{ST} (Nei, 1987), Hedrick's G'_{ST} (Hedrick, 2005)) and allelic differentiation (Jost's D (Jost, 2009)) measures. For both fragments, the PopART software (Leigh & Bryant, 2015) was used to build TCS haplotype networks (Clement, Posada & Crandall, 2000) based on the parsimony methodology by Templeton, Crandall & Sing (1992).

RESULTS

For the CR, a fragment of 354 bp was amplified and the 146 sequences obtained defined 105 haplotypes, with a total of 80 polymorphic sites found. Differences among haplotypes corresponded to 80 transitions, 12 transversions and 1 indel. For the S7 the 220 sequences (110 individuals) defined a total of 177 haplotypes. For this marker, the fragment obtained was 517 bp long and the differences among haplotypes corresponded to 206 mutations (70 transitions, 80 transversions and 50 indels). The *S. maderensis* S7 dataset, as a whole, conformed to the HWE ($p = 0.998$), although 36 out of the 171 polymorphic sites were in heterozygote deficit. For both fragments, the genetic diversity indices were generally very high, with little variation among collection sites (Table 1). The proportion of private haplotypes was high for all the locations (Table 1), with only 9.52% and 2.26% being shared between the Atlantic and the Mediterranean, for the CR and the S7, respectively.

The obtained haplotype networks revealed deep hyper-diverse bush-like genealogies, with a large number of singletons, few shared haplotypes and no evidence for geographic structure (CR: Fig. 2, S7: Fig. 3; see also Table 1, details on haplotype composition are given in Table S1 in Supplemental Materials).

The divergence parameters yielded significant values for the overall CR (Table 2). In both markers, results from the pairwise comparisons were equivocal, with F_{ST} showing non-significant values, Nei's G_{ST} revealing significant values for some of the comparisons, and Hedrick's G'_{ST} and Jost's D yielding all comparisons statistically significant (Table 2), i.e., all pairs of sampling sites usually have distinct haplotypes. In fact, eight (CR and S7) out of 22 pairwise comparisons revealed complete haplotypic differentiation ($D = 1$), including between some of the geographically closest sampling sites (Table 2). This high structuring was supported by the AMOVA results (CR: $F_{ST} = 0.031$, $p = 0.004$; S7: $F_{ST} = 0.016$, $p = 0.005$), which also revealed that variation among sampling sites accounted for only 3.08% (CR) and 1.58% (S7) of the total variation (Table S2 in Supplemental Materials).

DISCUSSION

The present work comprises a wide geographic sampling coverage of *Scorpaena maderensis* with locations from the Atlantic and the Mediterranean Sea and a molecular dataset with two markers. Our results highlight two main features in the population genetics of the Madeira rockfish: (1) deep hyper-diverse bush-like genealogies, characterised by large numbers of singletons and few shared haplotypes; and (2) absence of

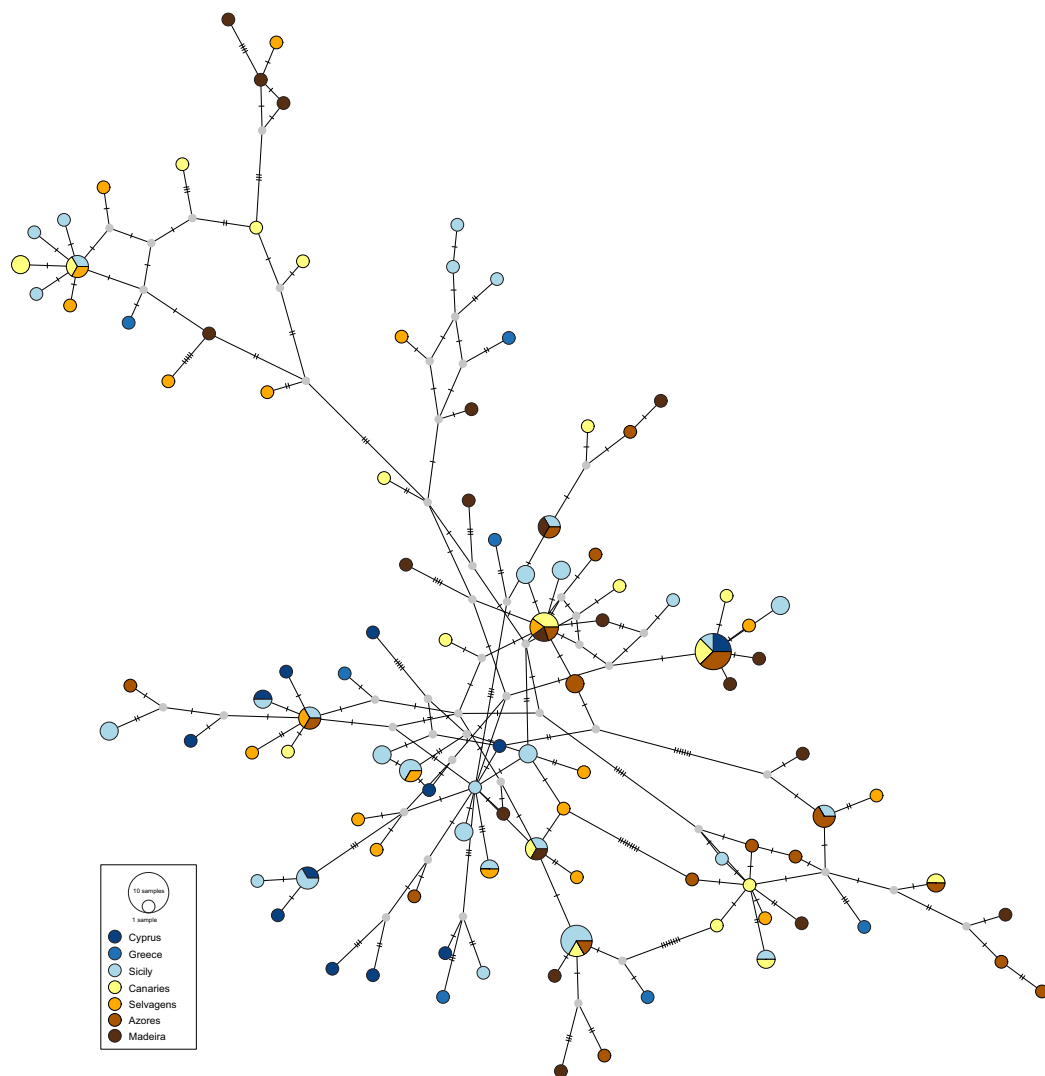


Figure 2 Haplotype network for the mitochondrial control region of *Scorpaena maderensis*. Colours refer to sampling locations (the same as in Fig. 1). The area of the circles is proportional to haplotype frequencies. In the case where haplotypes are shared among sampling locations, the colours represented are proportional to the frequency of the haplotype in each sampling location.

Full-size  DOI: [10.7717/peerj.11730/fig-2](https://doi.org/10.7717/peerj.11730/fig-2)

genetic structure across sampled locations, with no detectable Atlantic-Mediterranean break in connectivity. Before discussing these findings in detail, we address the main caveats concerning this study: the sampling strategy and the molecular markers used. Although most locations are represented by numbers of individuals in line with previous phylogeographic studies in marine species, one can a posteriori posit that the high number of singleton haplotypes found is biased by insufficient sampling. In fact, a recent study published by our team recorded even higher genetic diversity in a coastal fish species, revealing that it would be necessary to sample a total of 700 individuals for the sampling to be representative of the population (Robalo *et al.*, 2020). Additionally, we have no samples from intermediate locations between the Atlantic archipelagos and the

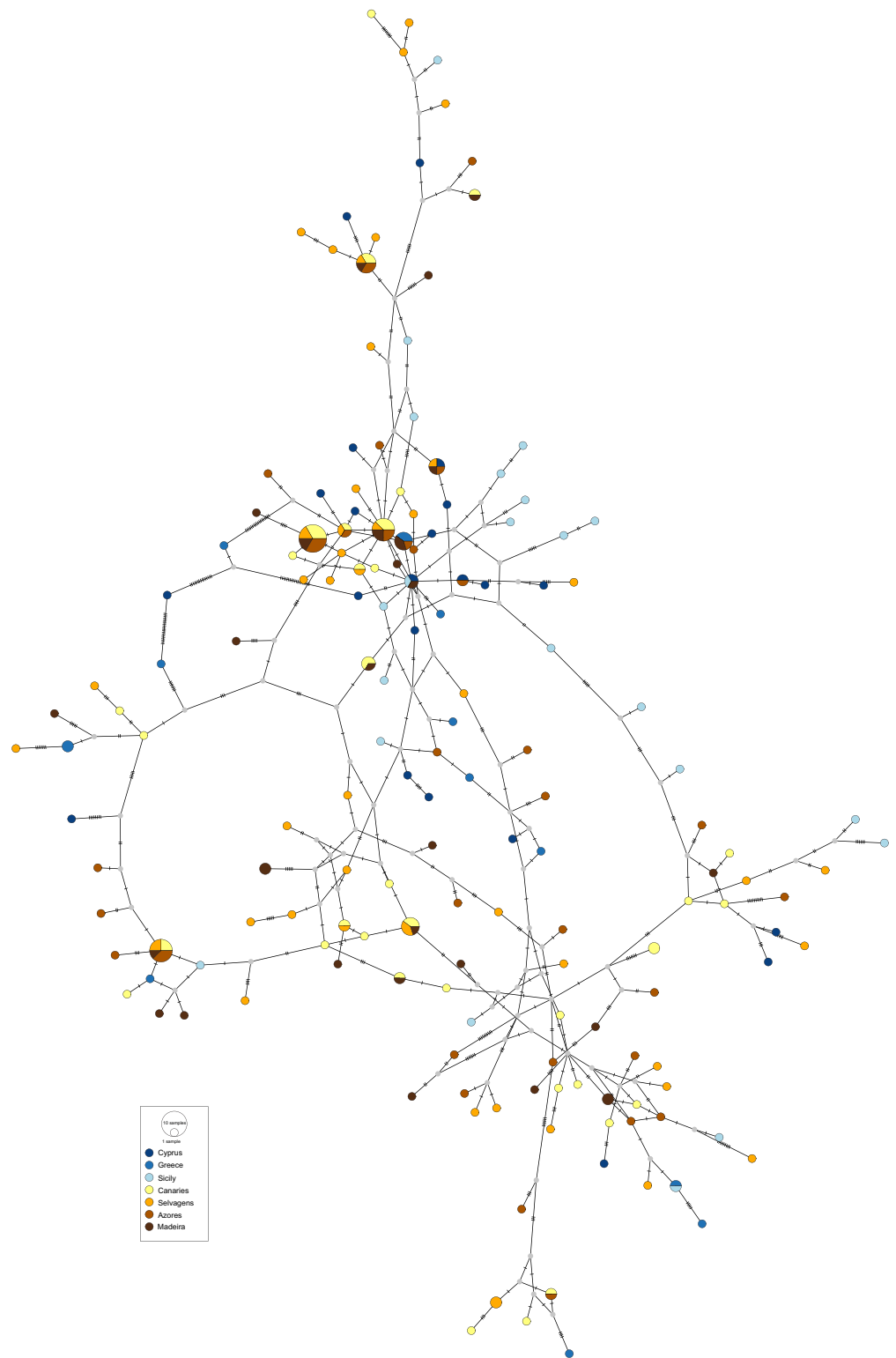


Figure 3 Haplotype network for the nuclear *S7* gene of *Scorpaena maderensis*. Colours refer to sampling locations (the same as in Fig. 1). The area of the circles is proportional to haplotype frequencies. In the case where haplotypes are shared among sampling locations, the colours represented are proportional to the frequency of the haplotype in each sampling location [Full-size !\[\]\(5fd6ef84f97f42d7f8b34275f1b65312_img.jpg\) DOI: 10.7717/peerj.11730/fig-3](https://doi.org/10.7717/peerj.11730/fig-3)

Table 2 Pairwise differentiation for the mitochondrial CR and nuclear S7 of *Scorpaena maderensis*.

| Pairwise | F_{ST} | 95% CI | G_{ST} | 95% CI | G'_{ST} | 95% CI | D | 95% CI |
|-------------------------------------|----------|---------------|--------------|-------------------|--------------|---------------|--------------|---------------|
| <i>Mitochondrial control region</i> | | | | | | | | |
| CYP-GRE | 0.007 | [0.000–0.098] | 0.033 | [–0.003 to 0.089] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| CYP-SIC> | 0.006 | [0.000–0.098] | 0.016 | [0.000–0.039] | 0.775 | [0.574–0.878] | 0.771 | [0.564–0.879] |
| CYP-CAN | 0.000 | [0.000–0.044] | 0.016 | [–0.002 to 0.040] | 0.688 | [0.390–0.816] | 0.683 | [0.375–0.816] |
| CYP-SEL | 0.006 | [0.000–0.050] | 0.020 | [0.004–0.045] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| CYP-MAD | 0.006 | [0.000–0.049] | 0.020 | [0.004–0.044] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| CYP-AZO | 0.000 | [0.000–0.043] | 0.016 | [–0.002 to 0.040] | 0.688 | [0.385–0.815] | 0.683 | [0.371–0.816] |
| GRE-SIC> | 0.009 | [0.000–0.080] | 0.027 | [–0.001 to 0.076] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| GRE-CAN | 0.007 | [0.000–0.084] | 0.029 | [–0.001 to 0.080] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| GRE-SEL | 0.000 | [0.000–0.050] | 0.026 | [–0.003 to 0.076] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| GRE-MAD | 0.000 | [0.000–0.049] | 0.026 | [–0.004 to 0.076] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| GRE-AZO | 0.007 | [0.000–0.083] | 0.029 | [–0.001 to 0.079] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| SIC-CAN | 0.005 | [0.000–0.030] | 0.011 | [0.001–0.025] | 0.699 | [0.472–0.845] | 0.696 | [0.465–0.846] |
| SIC-SEL | 0.004 | [0.000–0.025] | 0.011 | [0.002–0.023] | 0.825 | [0.671–0.901] | 0.823 | [0.666–0.901] |
| SIC-MAD | 0.007 | [0.000–0.028] | 0.013 | [0.005–0.024] | 0.956 | [0.864–0.975] | 0.956 | [0.861–0.975] |
| SIC-AZO | 0.004 | [0.000–0.029] | 0.011 | [0.001–0.024] | 0.666 | [0.390–0.816] | 0.662 | [0.431–0.815] |
| CAN-SEL | 0.000 | [0.000–0.029] | 0.012 | [0.000–0.028] | 0.781 | [0.558–0.868] | 0.779 | [0.549–0.868] |
| CAN-MAD | 0.000 | [0.000–0.029] | 0.012 | [0.000–0.028] | 0.781 | [0.556–0.869] | 0.779 | [0.548–0.869] |
| CAN-AZO | 0.000 | [0.000–0.028] | 0.010 | [–0.004 to 0.027] | 0.545 | [0.254–0.743] | 0.540 | [0.243–0.744] |
| SEL-MAD | 0.000 | [0.000–0.024] | 0.012 | [0.001–0.026] | 0.904 | [0.749–0.938] | 0.903 | [0.743–0.938] |
| SEL-AZO | 0.002 | [0.000–0.030] | 0.013 | [0.002–0.028] | 0.854 | [0.678–0.913] | 0.852 | [0.671–0.913] |
| MAD-AZO | 0.002 | [0.000–0.030] | 0.013 | [0.002–0.028] | 0.854 | [0.675–0.913] | 0.852 | [0.668–0.913] |
| MED-ATL | 0.003 | [0.000–0.010] | 0.005 | [0.002–0.009] | 0.615 | [0.446–0.747] | 0.613 | [0.443–0.747] |
| <i>Nuclear S7</i> | | | | | | | | |
| CYP-GRE | 0.034 | [0.000–0.052] | 0.021 | [0.006–0.044] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| CYP-SIC> | 0.022 | [0.000–0.020] | 0.011 | [0.002–0.022] | 0.913 | [0.764–0.942] | 0.911 | [0.759–0.942] |
| CYP-CAN | 0.017 | [0.000–0.019] | 0.010 | [0.004–0.019] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| CYP-SEL | 0.014 | [0.000–0.015] | 0.008 | [0.002–0.017] | 0.946 | [0.854–0.964] | 0.945 | [0.852–0.964] |
| CYP-MAD | 0.020 | [0.000–0.022] | 0.011 | [0.003–0.022] | 0.887 | [0.746–0.932] | 0.884 | [0.741–0.932] |
| CYP-AZO | 0.019 | [0.000–0.022] | 0.011 | [0.003–0.021] | 0.902 | [0.777–0.941] | 0.900 | [0.773–0.941] |
| GRE-SIC> | 0.032 | [0.000–0.051] | 0.019 | [0.003–0.043] | 0.923 | [0.764–0.955] | 0.920 | [0.756–0.955] |
| GRE-CAN | 0.022 | [0.000–0.052] | 0.019 | [0.006–0.042] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| GRE-SEL | 0.020 | [0.000–0.049] | 0.018 | [0.004–0.040] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| GRE-MAD | 0.025 | [0.000–0.046] | 0.017 | [0.002–0.039] | 0.794 | [0.560–0.885] | 0.787 | [0.549–0.885] |
| GRE-AZO | 0.026 | [0.000–0.056] | 0.021 | [0.007–0.044] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| SIC-CAN | 0.017 | [0.000–0.200] | 0.010 | [0.004–0.019] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| SIC-SEL | 0.015 | [0.011–0.016] | 0.009 | [0.003–0.017] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| SIC-MAD | 0.021 | [0.000–0.023] | 0.012 | [0.004–0.022] | 0.943 | [0.832–0.966] | 0.942 | [0.828–0.966] |
| SIC-AZO | 0.020 | [0.000–0.024] | 0.012 | [0.005–0.022] | 1.000 | [1.000–1.000] | 1.000 | [1.000–1.000] |
| CAN-SEL | 0.010 | [0.000–0.007] | 0.004 | [0.000–0.009] | 0.599 | [0.403–0.729] | 0.596 | [0.399–0.729] |
| CAN-MAD | 0.013 | [0.000–0.013] | 0.006 | [0.000–0.014] | 0.571 | [0.340–0.727] | 0.565 | [0.335–0.728] |

(Continued)

Table 2 (continued)

| Pairwise | F_{ST} | 95% CI | G_{ST} | 95% CI | G'_{ST} | 95% CI | D | 95% CI |
|----------|----------|---------------|--------------|-------------------|--------------|---------------|--------------|---------------|
| CAN-AZO | 0.011 | [0.000–0.011] | 0.005 | [0.000–0.012] | 0.513 | [0.278–0.686] | 0.507 | [0.273–0.686] |
| SEL-MAD | 0.012 | [0.000–0.013] | 0.006 | [0.001–0.013] | 0.689 | [0.496–0.804] | 0.685 | [0.491–0.804] |
| SEL-AZO | 0.011 | [0.000–0.010] | 0.005 | [0.000–0.011] | 0.547 | [0.335–0.702] | 0.542 | [0.331–0.703] |
| MAD-AZO | 0.013 | [0.000–0.015] | 0.006 | [–0.001 to 0.015] | 0.484 | [0.239–0.668] | 0.477 | [0.234–0.669] |
| MED-ATL | 0.006 | [0.000–0.009] | 0.005 | [0.003–0.008] | 0.904 | [0.829–0.947] | 0.903 | [0.828–0.947] |

Note:

F_{ST} , Nei's G_{ST} , Hedrick's G'_{ST} and Jost's D . Significant values in bold (95% confidence interval not overlapping with zero).

Western Mediterranean. These areas are not in the reported distribution of the species (Froese & Pauly, 2019) and the few reported individuals are occasional appearances (Encarnação et al., 2019). Another caveat is using only one mitochondrial and one nuclear marker in a day and age where next-generation sequencing producing thousands of markers are being increasingly used. This study is in line with previous research in the pursuit for patterns and processes involved in the phylogeography of the species from the North-East Atlantic (e.g., Bargelloni et al., 2005; Debes, Zachos & Hanel, 2008; Francisco et al., 2011; Robalo et al., 2013a). These previous studies used the same set of markers, allowing across species comparisons and multi-species approaches (e.g., Robalo et al., 2012; Robalo et al., 2013b; Francisco et al., 2014; Almada et al., 2017; Castilho et al., 2017) while revealing very distinct patterns.

Genetic hyper-diversity of the Madeira rockfish

All sampling locations show high diversity values, mainly due to a large proportion of singletons. There are two equally possible explanations for this result: (1) if numerous suitable temperature pockets harboured a large enough number of individuals, no demographic bottlenecks would affect the genetic composition and a high genetic variability could be maintained; (2) the species exhibit a patchy distribution near the Macaronesian islands and in scattered locations in the Mediterranean, where self-recruitment may be more dominant than larval drifting to further locations. There are instances where successive self-recruitment generations lead counter-intuitively to the maintenance of high genetic diversity (e.g., Feng, Williams & Place, 2017; Fourdrilis & Backeljau, 2019; Francisco & Robalo, 2020; Robalo et al., 2020). Furthermore, the CR sequence hypervariability may alternatively or concomitantly be explained by the mutation rate of the fragment, the evolutionary-rates hypothesis, or the metabolic rate theory as discussed in Robalo et al. (2020).

Genetic structure of the Madeira rockfish

The present results reveal no evidence for genetic structure, geographically associated or not, and therefore we posit that the Madeira rockfish is not composed of discernible groups within the Atlantic and the Mediterranean, nor these two basins are clearly differentiated. This hypothesis is strongly dependent on the genetic markers used in the study. In studies with other species, the CR region has yielded equivocal results regarding

the detection of genetic structure. We can find in the literature examples of findings of hypervariability and absence of genetic structure (e.g., [Francisco et al., 2011](#); [Mehraban et al., 2020](#); [Song et al., 2020](#)), and studies presenting hypervariability and significant genetic structure (e.g., [Cunha et al., 2014](#); [Castilho et al., 2017](#); [Robalo et al., 2020](#)). North-Eastern Atlantic past recolonization processes and historical and present dispersal movements are influenced by species-specific life-history traits, favourable oceanographic conditions, such as sea surface temperatures, and suitable recruitment habitat (e.g., [Wares & Cunningham, 2001](#); [Pappalardo et al., 2015](#)).

The results also do not reveal any phylogeographic break between the Atlantic and the Mediterranean locations for *S. maderensis* ([Fig. 2](#), [Table 2](#)), similarly to what has been previously recorded in other species (e.g., *Trachurus trachurus* ([Comesaña, Martínez-Areal & Sanjuan, 2008](#)), *Diplodus sargus* ([Stefanni et al., 2015](#)) and *Dentex dentex* ([Viret et al., 2018](#))). Although many factors can explain this outcome, there are two biological characteristics that may play a relevant role: large mean pelagic larval duration and high adult dispersal capability, features common to all these species. The observed discrepancy across statistics can be attributed to their different nature ([Bird et al., 2011](#)). In cases where the geographic distribution of haplotypes is uncorrelated with the relationship among alleles, which is *S. maderensis* case ([Figs. 2 and 3](#)), the fixation indices will not accurately depict the structure, and the differences found among the different measures can often be uninformative to the underlying biology of population structuring.

The mean pelagic larval duration (PLD) influences on a certain degree a species dispersal potential before reaching the juvenile stages. Although it is recognized the PLD is not a universal driver of range size and therefore a promoter of connectivity in many fish (e.g., [Weersing & Toonen, 2009](#); [Selkoe & Toonen, 2011](#)), in certain situations it seems to have some influence ([Lester & Ruttenberg, 2005](#)). To our knowledge there is no data on the PLD of *S. maderensis*, but congeners are known to spend 29 (*S. porcus* in [Macpherson & Raventos \(2006\)](#)) and 30 days (*S. guttata* in [Carr & Reed \(1993\)](#)) in the plankton, which is not a short duration. The hydrographic regime in this stretch of the North-East Atlantic is dominated by the Azores Current and its south-eastward branch, the Canary Current, a complex system of eddies ([Stramma, 1984](#); [Hernández-Guerra et al., 2001](#)). At the Atlantic-Mediterranean transition, the eastward flowing Atlantic water describes a quasi-permanent anticyclonic gyre ([Millot, 1999](#)). The PLD and the circulation regime of the area would thus contribute to the unconstrained gene flow between the two basins and among the Macaronesian archipelagos.

Adult rockfish of the genus *Scorpaena* display a low active dispersal capacity ([Özgül et al., 2019](#)). Nevertheless, adults of the Madeira rockfish may perform short-distance movements. Short dispersal movements following suitable habitat may have happened, in the past decade, with individuals of this species being recorded for the first time in the Gorringe seamount ([Abecasis et al., 2009](#)) and in South Portugal ([Encarnação et al., 2019](#)), near the entrance of the Gibraltar Strait. Although a certain degree of connectivity is expected from the results of this study it would be interesting to investigate the origin of these newcomers, mainly because adult dispersal is one of the essential life-history

patterns influencing connectivity and population structure (e.g., [Francisco, Pereira & Robalo, 2019](#)).

In conclusion, although no specific information is available regarding *S. maderensis*, its putative life-history patterns (i.e., dispersal mostly through the larval stage given the more sedentary nature of adults) is conducive to the lack of genetic structure. This lack in structure is shared by other fish groups in the same geographical areas, like gobids. A recent work on *Gobius cruentatus* ([Čekovská et al., 2020](#), for additional species see references within), a species with a similar life-history pattern, has also revealed high genetic variability and no geographic structure with an estimated migration route following the main currents of the distribution area.

A meta-analysis to tackle whether or not climate change influences marine ecological phenomena found that over 80% of all observations were coherent with the expected impacts of climate change. Moreover, the rates of geographic distribution shifts were, on average, consistent with those needed to track ocean surface temperature changes ([Poloczanska et al., 2013](#)). It is expected that *S. maderensis* will similarly follow a trajectory compatible with its optimal physiological temperature, and therefore it may extend its geographic distribution towards north. *S. maderensis* is a species with both a commercial and a biotechnological interest, it would be of importance to conduct fishery census to detect the arrival of this species to new locations.

ACKNOWLEDGEMENTS

The authors are thankful to Sergio Moreno-Borges for supplying samples from Tenerife (Canaries, Spain) and Stamatis Zogaris for help to obtain samples from Greece and Cyprus. We thank the IT Services of the University of Algarve for hosting and maintaining the R2C2 computational cluster facility.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This study was funded by Fundação para a Ciência e Tecnologia (FCT) Portugal, through the strategic projects MARE/UIDB/MAR/04292/2020 and MARE/UIDP/MAR/04292/2020 granted to MARE (MARE-ISPA), and UID/Multi/04326/2019 and UIDB/04326/2020 granted to CCMAR. This study was also supported by the University of Catania through the “PIA.CE.RI.” grant 2020. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:

MARE (MARE-ISPA): MARE/UIDB/MAR/04292/2020 and MARE/UIDP/MAR/04292/2020.

CCMAR: UID/Multi/04326/2019 and UIDB/04326/2020.

PIA.CE.RI: grant 2020.

Competing Interests

Rita Castilho is an Academic Editor for PeerJ.

Author Contributions

- Sara M. Francisco conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Rita Castilho conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Cristina S. Lima performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Frederico Almada conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Francisca Rodrigues performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Radek Šanda performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Jasna Vukić performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Anna Maria Pappalardo performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Venera Ferrito performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Joana I. Robalo conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

DNA Deposition

The following information was supplied regarding the deposition of DNA sequences:

All sequences are available at GenBank: [MN716857](#) - [MN717002](#) and [MN717003](#) - [MN717124](#).

Data Availability

The following information was supplied regarding data availability:

The FASTA files with the alignments for CR and S7 markers are available as [Supplemental Files](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.11730#supplemental-information>.

REFERENCES

- Abecasis D, Cardigos F, Almada F, Gonçalves JMS. 2009.** New records on the ichthyofauna of the Gorringer seamount (Northeastern Atlantic). *Marine Biology Research* **5(6)**:605–611
DOI [10.1080/17451000902729696](https://doi.org/10.1080/17451000902729696).

- Aguilera MA, Valdivia N, Broitman B, Jenkins SR, Navarrete S. 2020.** Novel co-occurrence of functionally redundant consumers induced by range expansion alters community structure. *Ecology* **101**(11):e03150 DOI [10.1002/ecy.3150](https://doi.org/10.1002/ecy.3150).
- Aktas C. 2020.** Haplotypes: manipulating DNA sequences and estimating unambiguous haplotype network with statistical parsimony. R package version 1.1.2. Available at <https://CRAN.R-project.org/package=haplotypes>.
- Allendorf FW. 2017.** Genetics and the conservation of natural populations: allozymes to genomes. *Molecular Ecology* **26**(2):420–430 DOI [10.1111/mec.13948](https://doi.org/10.1111/mec.13948).
- Almada F, Francisco SM, Lima CS, FitzGerald R, Mirimin L, Villegas-Ríos D, Saborido-Rey F, Afonso P, Morato T, Bexiga S, Robalo JI. 2017.** Historical gene flow constraints in a northeastern Atlantic fish: phylogeography of the ballan wrasse *Labrus bergylta* across its distribution range. *Royal Society Open Science* **4**:160773 DOI [10.1098/rsos.16077](https://doi.org/10.1098/rsos.16077).
- Bargelloni L, Alarcon JA, Alvarez MC, Penzo E, Magoulas A, Palma J, Patarnello T. 2005.** The Atlantic-Mediterranean transition: discordant genetic patterns in two seabream species, *Diplodus puntazzo* (Cetti) and *Diplodus sargus* (L.). *Molecular Phylogenetics and Evolution* **36**(3):523–535 DOI [10.1016/j.ympev.2005.04.017](https://doi.org/10.1016/j.ympev.2005.04.017).
- Bianchi CN, Morri C. 2003.** Global sea warming and tropicalization of the Mediterranean Sea: biogeographic and ecological aspects. *Biogeographia* **24**:319–327 DOI [10.21426/B6110129](https://doi.org/10.21426/B6110129).
- Bigg GR, Cunningham CW, Ottersen G, Pogson GH, Wadley MR, Williamson P. 2008.** Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. *Proceedings of the Royal Society B* **275**(1631):163–172 DOI [10.1098/rspb.2007.1153](https://doi.org/10.1098/rspb.2007.1153).
- Bird CE, Karl SA, Smouse PE, Toonen RJ. 2011.** Detecting and measuring genetic differentiation. In: Held C, Koenemann S, Schubart CD, eds. *Phylogeography and Population Genetics in Crustacea*. Boca Raton: CRC Press, 31–39.
- Bode A, Álvarez M, García LMG, Louro MÁ, Nieto-Cid M, Ruíz-Villarreal M, Varela MM. 2020.** Climate and local hydrography underlie recent regime shifts in plankton communities off Galicia (NW Spain). *Oceans* **1**(4):181–197 DOI [10.3390/oceans1040014](https://doi.org/10.3390/oceans1040014).
- Bowen BW, Bass AL, Muss A, Carlin J, Robertson DR. 2006.** Phylogeography of two Atlantic squirrelfishes (Family Holocentridae): exploring links between pelagic larval duration and population connectivity. *Marine Biology* **149**(4):899–913 DOI [10.1007/s00227-006-0252-1](https://doi.org/10.1007/s00227-006-0252-1).
- Bradbury I, Laurel B, Snelgrove P, Bentzen P, Campana S. 2008.** Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proceedings of the Royal Society B: Biological Sciences* **275**(1644):1803–1809 DOI [10.1098/rspb.2008.0216](https://doi.org/10.1098/rspb.2008.0216).
- Bryan-Brown DN, Brown CJ, Hughes JM, Connolly RM. 2017.** Patterns and trends in marine population connectivity research. *Marine Ecology Progress Series* **585**:243–256 DOI [10.3354/meps12418](https://doi.org/10.3354/meps12418).
- Carr MH, Reed DC. 1993.** Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **50**(9):2019–2028 DOI [10.1139/f93-226](https://doi.org/10.1139/f93-226).
- Castilho R, Cunha RL, Faria C, Velasco EM, Robalo JI. 2017.** Asymmetrical dispersal and putative isolation-by-distance of an intertidal blenniid across the Atlantic-Mediterranean divide. *PeerJ* **5**:e3195 DOI [10.7717/peerj.3195](https://doi.org/10.7717/peerj.3195).
- Čekovská K, Šanda R, Eliášová K, Kovačič M, Zogaris S, Pappalardo AM, Soukupová T, Vukić J. 2020.** Population genetic diversity of two marine gobies (Gobiiformes: Gobiidae) from the North-Eastern Atlantic and the Mediterranean Sea. *Journal of Marine Science and Engineering* **8**(10):792 DOI [10.3390/jmse8100792](https://doi.org/10.3390/jmse8100792).

- Cheung WWL, Pitcher TJ, Pauly D. 2005.** A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* **124**(1):97–111 DOI [10.1016/j.biocon.2005.01.017](https://doi.org/10.1016/j.biocon.2005.01.017).
- Cheung WW, Lam VW, Sarmiento JL, Kearney K, Watson R, Pauly D. 2009.** Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**(3):235–251 DOI [10.1111/j.1467-2979.2008.00315.x](https://doi.org/10.1111/j.1467-2979.2008.00315.x).
- Chow S, Hazama K. 1998.** Universal PCR primers for S7 ribosomal protein gene introns in fish. *Molecular Ecology* **7**:1247–1263.
- Comesaña AS, Martínez-Areal MA, Sanjuan A. 2008.** Genetic variation in the mitochondrial DNA control region among horse mackerel (*Trachurus trachurus*) from the Atlantic and Mediterranean areas. *Fisheries Research* **89**(2):122–131 DOI [10.1016/j.fishres.2007.09.014](https://doi.org/10.1016/j.fishres.2007.09.014).
- Clement M, Posada D, Crandall KA. 2000.** TCS: a computer program to estimate gene genealogies. *Molecular Ecology* **9**(10):1657–1659 DOI [10.1046/j.1365-294x.2000.01020.x](https://doi.org/10.1046/j.1365-294x.2000.01020.x).
- Costa ARSG. 2007.** Reproduction, age and growth of four coastal fish species in the NE Atlantic. MSc dissertation in Marine and Coastal Studies, University of Algarve, 70.
- Cunha IMC, Souza AS, Dias EA, Amorim KDJ, Soares RX, Costa GWWFC, García-Machado E, Galetti PM. 2014.** Genetic multipartitions based on D-Loop sequences and chromosomal patterns in Brown Chromis, *Chromis multilineata* (Pomacentridae), in the Western Atlantic. *BioMed Research International* **2014**:254698 DOI [10.1155/2014/254698](https://doi.org/10.1155/2014/254698) 2014.
- Dalongeville A, Andreello M, Mouillot D, Albouy C, Manel S. 2015.** Ecological traits shape genetic diversity patterns across the Mediterranean Sea: a quantitative review on fishes. *Journal of Biogeography* **43**(4):845–857 DOI [10.1111/jbi.12669](https://doi.org/10.1111/jbi.12669).
- Debes PV, Zachos FE, Hanel R. 2008.** Mitochondrial phylogeography of the European sprat (*Sprattus sprattus* L., Clupeidae) reveals isolated climatically vulnerable populations in the Mediterranean Sea and range expansion in the northeast Atlantic. *Molecular Ecology* **17**(17):3873–3888 DOI [10.1111/j.1365-294X.2008.03872.x](https://doi.org/10.1111/j.1365-294X.2008.03872.x).
- Duggen S, Hoernle K, van den Bogaard P, Rüpke L, Morgan JP. 2003.** Deep roots of the Messinian salinity crisis. *Nature* **422**(6932):602–606 DOI [10.1038/nature01553](https://doi.org/10.1038/nature01553).
- Encarnação J, Morais P, Baptista V, Cruz J, Teodósio MA. 2019.** New evidence of marine fauna tropicalization off the Southwestern Iberian Peninsula (Southwest Europe). *Diversity* **11**(4):48 DOI [10.3390/d11040048](https://doi.org/10.3390/d11040048).
- Eschmeyer WN, Dempster LJ, Quero JC, Hureau JC, Karrer C, Post A, Saldanha L. 1990.** *Scorpaenidae, Check-list of the fishes of the eastern tropical Atlantic (CLOFETA)*. Vol. 2. Lisbon; SEI, Paris, Paris: JNICT, UNESCO, 665–679.
- Excoffier L, Laval G, Balding D. 2003.** Gametic phase estimation over large genomic regions using an adaptive window approach. *Human Genomics* **1**(1):7 DOI [10.1186/1479-7364-1-1-7](https://doi.org/10.1186/1479-7364-1-1-7).
- Excoffier L, Lischer HEL. 2010.** Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* **10**(3):564–567 DOI [10.1111/j.1755-0998.2010.02847.x](https://doi.org/10.1111/j.1755-0998.2010.02847.x).
- Excoffier L, Smouse PE, Quattro JM. 1992.** Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetic* **131**:479–491.
- Feng X, Williams EP, Place AR. 2017.** High genetic diversity and implications for determining population structure in the blue crab *Callinectes sapidus*. *Journal of Shellfish Research* **36**(1):231–243 DOI [10.2983/035.036.0126](https://doi.org/10.2983/035.036.0126).

- Flores JA, Sierro FJ, Frances G, Vazquez A, Zamarreno I. 1997. The last 100,000 years in the western Mediterranean: sea surface water and frontal dynamics as revealed by coccolithophores. *Marine Micropaleontology* 29(3–4):351–366 DOI 10.1016/S0377-8398(96)00029-1.
- Fourdrilis S, Backeljau T. 2019. Highly polymorphic mitochondrial DNA and deceiving haplotypic differentiation: implications for assessing population genetic differentiation and connectivity. *BMC Evolutionary Biology* 19(1):92 DOI 10.1186/s12862-019-1414-3.
- Francisco SM, Almada VC, Faria C, Velasco EM, Robalo JI. 2014. Phylogeographic pattern and glacial refugia of a rocky shore species with limited dispersal capability: the case of Montagu's blenny (*Coryphoblennius galerita*, Blenniidae). *Marine Biology* 161(11):2509–2520 DOI 10.1007/s00227-014-2523-6.
- Francisco SM, Faria C, Lengkeek W, Vieira MN, Velasco EM, Almada VC. 2011. Phylogeography of the shanny *Lipophrys pholis* (Pisces: Blenniidae) in the NE Atlantic records signs of major expansion event older than the last glaciation. *Journal of Experimental Marine Biology and Ecology* 403(1–2):14–20 DOI 10.1016/j.jembe.2011.03.020.
- Francisco SM, Pereira AM, Robalo JI. 2019. Disentangling biological variables affecting population structure and genetic connectivity. In: *Frontiers in Marine Science, Conference Abstract: IMMR'18 | International Meeting on Marine Research 2018*.
- Francisco SM, Robalo JI. 2020. Time matters: genetic composition and evaluation of effective population size in temperate coastal fish species. *PeerJ* 8:e9098 DOI 10.7717/peerj.9098.
- Froese R, Pauly D. 2019. FishBase. World Wide Web electronic publication. Available at www.fishbase.org.
- Fruciano C, Hanel R, Debes PV, Concetta T, Ferrito V. 2011. Atlantic-Mediterranean and within-Mediterranean molecular variation in *Coris julis* (L. 1758) (Teleostei, Labridae). *Marine Biology* 158(6):1271–1286 DOI 10.1007/s00227-011-1647-1.
- Gaggiotti OE, Bekkevold D, Jørgensen HBH, Foll M, Carvalho GR, Andre C, Ruzzante DE. 2009. Disentangling the effects of evolutionary, demographic, and environmental factors influencing genetic structure of natural populations: atlantic herring as a case study. *Evolution* 63(11):2939–2951 DOI 10.1111/j.1558-5646.2009.00779.x.
- Galarza JA, Carreras-Carbonell J, Macpherson E, Pascual M, Roques S, Turner GF, Rico C. 2009. The influence of oceanographic fronts and early-life-history traits on connectivity among littoral fish species. *Proceedings of the National Academy of Sciences USA* 106(5):1473–1478 DOI 10.1073/pnas.0806804106.
- García Molinos J, Halpern B, Schoeman D, Brown CJ, Kiessling W, Moore PJ, Pandolfi JM, Poloczanska ES, Richardson AJ, Burrows MT. 2016. Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change* 6(1):83–88 DOI 10.1038/nclimate2769.
- García-Merchán VH, Robainas-Barcia A, Abelló P, Macpherson E, Palero F, García-Rodríguez M, Gil de Sola L, Pascual M. 2012. Phylogeographic patterns of decapod crustaceans at the Atlantic-Mediterranean transition. *Molecular Phylogenetics and Evolution* 62(2):664–672 DOI 10.1016/j.ympev.2011.11.009.
- Guo SW, Thompson EA. 1992. Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics* 48(2):361–372 DOI 10.2307/2532296.
- Hedrick PW. 2005. A standardized genetic differentiation measure. *Evolution* 59(8):1633–1638 DOI 10.1111/j.0014-3820.2005.tb01814.x.
- Helyar SJ, Hemmer-Hansen J, Bekkevold D, Taylor MI, Ogden R, Limborg MT, Cariani A, Maes GE, Diopere E, Carvalho GR, Nielsen EE. 2011. Application of SNPs for population

- genetics of nonmodel organisms: new opportunities and challenges. *Molecular Ecology Resources* **11**(Suppl 1):123–136 DOI [10.1111/j.1755-0998.2010.02943.x](https://doi.org/10.1111/j.1755-0998.2010.02943.x).
- Hernández-Guerra A, López-Laatzén F, Machín F, Armas D, Pelegrí JL. 2001.** Water masses, circulation and transport in the eastern boundary current of the North Atlantic subtropical gyre. *Scientia Marina* **65**(S1):177–186 DOI [10.3989/scimar.2001.65s1177](https://doi.org/10.3989/scimar.2001.65s1177).
- Hollowed AB, Barange M, Beamish R, Brander K, Cochrane K, Drinkwater K, Foreman M, Hare J, Holt J, Ito S-I, Kim S, King J, Loeng H, MacKenzie B, Mueter F, Okey T, Peck MA, Radchenko V, Rice J, Schirripa M, Yatsu A, Yamanaka Y. 2013.** Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science* **70**(5):1023–1037 DOI [10.1093/icesjms/fst081](https://doi.org/10.1093/icesjms/fst081).
- Hsü K, Ryan W, Cita M. 1973.** Late Miocene desiccation of the Mediterranean. *Nature* **242**(5395):240–244 DOI [10.1038/242240a0](https://doi.org/10.1038/242240a0).
- Hureau JC, Litvinenko NI. 1986.** Scorpaenidae. In: Whitehead PJP, Bauchot ML, Hureau JC, Nielsen J, Tortonese E, eds. *Fishes of the North-eastern Atlantic and the Mediterranean*. Vol. 3. Paris: UNESCO, 1211–1229.
- Jenkins TL, Castilho R, Stevens JR. 2018.** Meta-analysis of northeast Atlantic marine taxa shows contrasting phylogeographic patterns following post-LGM expansions. *PeerJ* **6**(5):e5684 DOI [10.7717/peerj.5684](https://doi.org/10.7717/peerj.5684).
- Jost L. 2009.** *D* vs. *GST*: response to Heller and Siegmund, 2009 and Ryman and Leimar (2009). *Molecular Ecology* **18**(10):2088–2091 DOI [10.1111/j.1365-294X.2009.04186.x](https://doi.org/10.1111/j.1365-294X.2009.04186.x).
- Kalinowski ST. 2005.** hp-rare 1.0: a computer program for performing rarefaction on measures of allelic richness. *Molecular Ecology Notes* **5**(1):187–189 DOI [10.1111/j.1471-8286.2004.00845.x](https://doi.org/10.1111/j.1471-8286.2004.00845.x).
- Kaschner K, Kesner-Reyes K, Garilao C, Segschneider J, Rius-Barile J, Rees T, Froese R. 2019.** AquaMaps: predicted range maps for aquatic species. Version 10/2019. Available at www.aquamaps.org.
- Keenan K, McGinnity P, Cross TF, Crozier WW, Prodöhl PA. 2013.** diveRsity: an R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods in Ecology and Evolution* **4**(8):782–788 DOI [10.1111/2041-210X.12067](https://doi.org/10.1111/2041-210X.12067).
- Kettle AJ, Morales-Muñiz A, Roselló-Izquierdo E, Heinrich D, Vøllestad LA. 2011.** Refugia of marine fish in the northeast Atlantic during the last glacial maximum: concordant assessment from archaeozoology and palaeotemperature reconstructions. *Climate of the Past* **7**(1):181–201 DOI [10.5194/cp-7-181-2011](https://doi.org/10.5194/cp-7-181-2011).
- Krijgsman W, Hilgen FJ, Raffi I, Sierro FJ, Wilson DS. 1999.** Chronology, causes and progression of the Messinian salinity crisis. *Nature* **400**:652–655.
- Lambeck K, Purcell A. 2005.** Sea-level change in the Mediterranean Sea since the LGM: model predictions for tectonically stable areas. *Quaternary Science Reviews* **24**(18–19):1969–1988 DOI [10.1016/j.quascirev.2004.06.025](https://doi.org/10.1016/j.quascirev.2004.06.025).
- La Mesa G, La Mesa M, Tomassetti P. 2007.** Feeding habits of the Madeira rockfish *Scorpaena maderensis* from central Mediterranean Sea. *Marine Biology* **150**(6):1313–1320 DOI [10.1007/s00227-006-0414-1](https://doi.org/10.1007/s00227-006-0414-1).
- La Mesa M, La Mesa G, Micalizzi M. 2005.** Age and growth of madeira scorpionfish, *Scorpaena maderensis* Valenciennes, 1833, in the central Mediterranean. *Fisheries Research* **74**(1–3):265–272 DOI [10.1016/j.fishres.2005.01.018](https://doi.org/10.1016/j.fishres.2005.01.018).
- Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG. 2007.** Clustal W and Clustal X version 2.0. *Bioinformatics* **23**(21):2947–2948 DOI [10.1093/bioinformatics/btm404](https://doi.org/10.1093/bioinformatics/btm404).

- Lasram FBR, Guilhaumon F, Albouy C, Somot S, Thuiller W, Mouillot D. 2010.** The Mediterranean Sea as a ‘cul-de-sac’ for endemic fishes facing climate change. *Global Change Biology* **16**(12):3233–3245 DOI [10.1111/j.1365-2486.2010.02224.x](https://doi.org/10.1111/j.1365-2486.2010.02224.x).
- Leigh JW, Bryant D. 2015.** PopART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution* **6**(9):1110–1116 DOI [10.1111/2041-210X.12410](https://doi.org/10.1111/2041-210X.12410).
- Lemaire C, Versini J-J, Bonhomme F. 2005.** Maintenance of genetic differentiation across a transition zone in the sea: discordance between nuclear and cytoplasmic markers. *Journal of Evolutionary Biology* **18**(1):70–80 DOI [10.1111/j.1420-9101.2004.00828.x](https://doi.org/10.1111/j.1420-9101.2004.00828.x).
- Lenoire J, Svenning J-C. 2015.** Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography* **38**(1):15–28 DOI [10.1111/ecog.00967](https://doi.org/10.1111/ecog.00967).
- Lester SE, Ruttenberg BI. 2005.** The relationship between pelagic larval duration and range size in tropical reef fishes: a synthetic analysis. *Proceedings of the Royal Society B* **272**(1563):585–591 DOI [10.1098/rspb.2004.2985](https://doi.org/10.1098/rspb.2004.2985).
- Lourenço CR, Nicastro KR, Serrão EA, Zardi GI. 2012.** First record of the brown mussel (*Perna perna*) from the European Atlantic coast. *Marine Biodiversity Records* **5**:e39 DOI [10.1017/s1755267212000280](https://doi.org/10.1017/s1755267212000280).
- Lourenço CR, Nicastro KR, McQuaid CD, Chefaoui RM, Assis J, Taleb MZ, Zardi GI. 2017.** Evidence for rangewide panmixia despite multiple barriers to dispersal in a marine mussel. *Scientific Reports* **7**(1):10279 DOI [10.1038/s41598-017-10753-9](https://doi.org/10.1038/s41598-017-10753-9).
- Macpherson E, Raventos N. 2006.** Relationship between pelagic larval duration and geographic distribution of Mediterranean littoral fishes. *Marine Ecology Progress Series* **327**:257–265 DOI [10.3354/meps327257](https://doi.org/10.3354/meps327257).
- Maggs CA, Castilho R, Foltz D, Henzler C, Jolly MT, Kelly J, Olsen J, Perez KE, Stam W, Väinölä R, Viard F, Wares J. 2008.** Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. *Ecology* **89**(Suppl):S108–S122 DOI [10.1890/08-0257.1](https://doi.org/10.1890/08-0257.1).
- Magoulas A, Castilho R, Caetano S, Marcato S, Patarnello T. 2006.** Mitochondrial DNA reveals a mosaic pattern of phylogeographical structure in Atlantic and Mediterranean populations of anchovy (*Engraulis encrasicolus*). *Molecular Phylogenetics and Evolution* **3**(3):734–746 DOI [10.1016/j.ympev.2006.01.016](https://doi.org/10.1016/j.ympev.2006.01.016).
- Mehraban H, Esmaeili HR, Zarei F, Ebrahimi M, Gholamhosseini A. 2020.** Genetic diversification, population structure, and geophylogeny of the Scarface rockskipper *Istiblennius pox* (Teleostei: Blenniidae) in the Persian Gulf and Oman Sea. *Marine Biodiversity* **50**(2):20 DOI [10.1007/s12526-020-01045-z](https://doi.org/10.1007/s12526-020-01045-z).
- Millot C. 1999.** Circulation in the Western Mediterranean sea. *Journal of Marine Systems* **20**(1–4):423–442 DOI [10.1016/S0924-7963\(98\)00078-5](https://doi.org/10.1016/S0924-7963(98)00078-5).
- Morato T, Afonso P, Lourinho P, Barreiros JP, Santos RS, Nash RDM. 2001.** Length-weight relationships for 21 coastal fish species of the Azores, northeastern atlantic. *Fisheries Research* **50**(3):297–302 DOI [10.1016/S0165-7836\(00\)00215-0](https://doi.org/10.1016/S0165-7836(00)00215-0).
- Nei M. 1987.** *Molecular evolutionary genetics*. New York: Columbia University Press, 512.
- Nicastro KR, Zardi GI, Teixeira S, Neiva J, Serrão EA, Pearson GA. 2013.** Shift happens: trailing edge contraction associated with recent warming trends threatens a distinct genetic lineage in the marine macroalga *Fucus vesiculosus*. *BMC Biology* **11**:6 DOI [10.1186/1741-7007-11-6](https://doi.org/10.1186/1741-7007-11-6).
- Nunoo F, Russell B, Bannermann P, Poss S. 2015.** *Scorpaena maderensis*. *The IUCN Red List of Threatened Species* **2015**:e.T198745A15591548 DOI [10.2305/IUCN.UK.2015-4.RLTS.T198745A15591548.en](https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T198745A15591548.en).

- Özgül A, Lök A, Tanrikul TT, Alós J. 2019. Home range and residency of *Scorpaena porcus* and *Scorpaena scrofa* in artificial reefs revealed by fine-scale acoustic tracking. *Fisheries Research* 210(2):22–30 DOI 10.1016/j.fishres.2018.10.008.
- Olsen JL, Stam WT, Coyer JA, Reusch TBH, Billingham M, Boström C, Calvert E, Christie H, Granger S, Lumière RL, Milchakova N, Oudot-Le Secq M-P, Procaccini G, Sanjabi B, Serrão E, Veldsink J, Widdicombe S, Wyllie-Echeverria S. 2004. North Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina* L. *Molecular Ecology* 13(7):1923–1941 DOI 10.1111/j.1365-294X.2004.02205.x.
- Ostellari L, Bargelloni L, Penzo E, Patarnello P, Patarnello T. 1996. Optimization of single-strand conformation polymorphism and sequence analysis of the mitochondrial control region in *Pagellus bogaraveo* (Sparidae, Teleostei): rationalized tools in fish population biology. *Animal Genetics* 27(6):423–427 DOI 10.1111/j.1365-2052.1996.tb00510.x.
- Palero F, Abelló P, Macpherson E, Gristina M, Pascual M. 2008. Phylogeography of the European spiny lobster (*Palinurus elephas*): Influence of current oceanographical features and historical processes. *Molecular Phylogenetics and Evolution* 48(2):708–717 DOI 10.1016/j.ympev.2008.04.022.
- Pappalardo P, Pringle JM, Wares JP, Byers JE. 2015. The location, strength, and mechanisms behind marine biogeographic boundaries of the east coast of North America. *Ecography* 38(7):722–731 DOI 10.1111/ecog.01135.
- Paradis E. 2010. pegas: an R package for population genetics with an integrated-modular approach. *Bioinformatics* 26(3):419–420 DOI 10.1093/bioinformatics/btp696.
- Pascual M, Rives B, Schunter C, Macpherson E. 2017. Impact of life history traits on gene flow: a multispecies systematic review across oceanographic barriers in the Mediterranean Sea. *PLOS ONE* 12(5):e0176419 DOI 10.1371/journal.pone.0176419.
- Patarnello T, Volckaert FAMJ, Castilho R. 2007. Pillars of Hercules: is the Atlantic-Mediterranean transition a phylogeographical break? *Molecular Ecology* 16(21):4426–4444 DOI 10.1111/j.1365-294X.2007.03477.x.
- Plough LV. 2016. Genetic load in marine animals: a review. *Current Zoology* 62(6):567–579 DOI 10.1093/cz/zow096.
- Poloczanska E, Brown C, Sydeman W, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Hapern BS, Holding J, Kappel CV, O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ. 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3(10):919–925 DOI 10.1038/nclimate1958.
- Poloczanska ES, Hoegh-Guldberg O, Cheung W, Pörtner H-O, Burrows M. 2014. Cross-chapter box on Observed global responses of marine biogeography, abundance, and phenology to climate change. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AS, MacCracken S, Mastrandrea PR, White LL, eds. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press, 123–127.
- R Core Team. 2020. *R: a language and environment for statistical computing*. Vienna, Austria: The R Foundation for Statistical Computing. Available at <https://www.R-project.org/>.
- Reis-Santos P, Tanner SE, Aboim MA, Vasconcelos RP, Laroche J, Charrier G, Pérez M, Presa P, Gillanders BM, Cabral HN. 2018. Reconciling differences in natural tags to infer

- demographic and genetic connectivity in marine fish populations. *Scientific Reports* **8**(1):10343 DOI [10.1038/s41598-018-28701-6](https://doi.org/10.1038/s41598-018-28701-6).
- Robalo JI, Castilho R, Francisco SM, Almada F, Knutsen H, Jorde PE, Pereira AM, Almada VC. 2012.** Northern refugia and recent expansion in the North Sea: the case of the wrasse *Symphodus melops* (Linnaeus, 1758). *Ecology and Evolution* **2**(1):153–164 DOI [10.1002/ece3.77](https://doi.org/10.1002/ece3.77).
- Robalo JI, Crespo AM, Castilho R, Francisco SM, Amorim MCP, Almada VC. 2013b.** Are local extinctions and recolonizations continuing at the colder limits of marine fish distributions? *Halobatrachus didactylus* (Bloch & Schneider, 1801), a possible candidate. *Marine Biology* **160**(9):2461–2467 DOI [10.1007/s00227-013-2241-5](https://doi.org/10.1007/s00227-013-2241-5).
- Robalo JI, Francisco SM, Vendrell C, Lima CS, Pereira A, Brunner BP, Dia M, Gordo L, Castilho R. 2020.** Against all odds: a tale on fish tropicalization with maintenance of extremely high genetic diversity. *Scientific Reports* **10**(1):12707 DOI [10.1038/s41598-020-69374-4](https://doi.org/10.1038/s41598-020-69374-4).
- Robalo JI, Lima CS, Francisco SM, Almada F, Bañon R, Villegas-Rios D, Almada VC. 2013a.** Monitoring climate change impact on the genetic population structure: the case of the fivebeard rockling (*Ciliata mustela*, Linnaeus, 1758) in its Southern limit of distribution. *Journal of Phylogenetics and Evolutionary Biology* **1**:123 DOI [10.4172/2329-9002.1000123](https://doi.org/10.4172/2329-9002.1000123).
- RStudio Team. 2020.** RStudio: integrated development for R. RStudio, PBC, Boston, MA. Available at <http://www.rstudio.com/>.
- Sala-Bozano M, Ketmaier V, Mariani S. 2009.** Contrasting signals from multiple markers illuminate population connectivity in a marine fish. *Molecular Ecology* **18**(23):4811–4826 DOI [10.1111/j.1365-294X.2009.04404.x](https://doi.org/10.1111/j.1365-294X.2009.04404.x).
- Schunter C, Carreras-Carbonell J, MacPherson E, Tintoré J, Vidal-Vijande E, Pascual A, Guidetti P, Mascual P. 2011.** Matching genetics with oceanography: directional gene flow in a Mediterranean fish species. *Molecular Ecology* **20**(24):5167–5181 DOI [10.1111/j.1365-294X.2011.05355.x](https://doi.org/10.1111/j.1365-294X.2011.05355.x).
- Selkoe KA, Toonen RJ. 2011.** Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. *Marine Ecology Progress Series* **436**:291–305 DOI [10.3354/meps09238](https://doi.org/10.3354/meps09238).
- Selkoe A, D'Aloia CC, Crandall ED, Iacchei M, Liggin L, Puritz JB, von der Heyden S, Toonen RJ. 2016.** A decade of seascape genetics: contributions to basic and applied marine connectivity. *Marine Ecology Progress Series* **554**:1–19 DOI [10.3354/meps11792](https://doi.org/10.3354/meps11792).
- Song CY, Sun ZC, Gao TX, Song N. 2020.** Structure analysis of mitochondrial DNA control region sequences and its applications for the study of population genetic diversity of *Acanthogobius ommaturus*. *Russian Journal of Marine Biology* **46**(4):292–301 DOI [10.1134/S1063074020040082](https://doi.org/10.1134/S1063074020040082).
- Sousa-Santos C, Robalo JI, Collares-Pereira MJ, Almada VC. 2005.** Heterozygous indels as useful tools in the reconstruction of DNA sequences and in the assessment of ploidy level and genomic constitution of hybrid organisms. *DNA Sequence* **16**(6):462–467 DOI [10.1080/10425170500356065](https://doi.org/10.1080/10425170500356065).
- Stamatis C, Triantafylidis A, Moutou KA, Mamuris Z. 2004.** Mitochondrial DNA variation in Northeast Atlantic and Mediterranean populations of Norway lobster, *Nephrops norvegicus*. *Molecular Ecology* **13**(6):1377–1390 DOI [10.1111/j.1365-294X.2004.02165.x](https://doi.org/10.1111/j.1365-294X.2004.02165.x).
- Stefanni S, Castilho R, Sala-Bozano M, Robalo JI, Francisco SM, Santos RS, Marques N, Brito A, Almada VC, Mariani S. 2015.** Establishment of a coastal fish in the Azores: recent colonisation or sudden expansion of an ancient relict population? *Heredity* **115**(6):527–537 DOI [10.1038/hdy.2015.55](https://doi.org/10.1038/hdy.2015.55).

- Stramma L. 1984.** Geostrophic transport in the Warm Water Sphere of the eastern subtropical North Atlantic. *Journal of Marine Research* **42**(3):537–558 DOI [10.1357/002224084788506022](https://doi.org/10.1357/002224084788506022).
- Taboada S, Pérez-Portela R. 2016.** Contrasted phylogeographic patterns on mitochondrial DNA of shallow and deep brittle stars across the Atlantic-Mediterranean area. *Scientific Reports* **6**(1):32425 DOI [10.1038/srep32425](https://doi.org/10.1038/srep32425).
- Templeton AR, Crandall KA, Sing F. 1992.** Cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. 111. Cladogram estimation. *Genetics* **132**:619–633.
- Viñas J, Sanz N, Peñarrubia L, Araguas RM, García-Marín JL, Roldán MI, Pla C. 2014.** Genetic population structure of European anchovy in the Mediterranean Sea and the Northeast Atlantic Ocean using sequence analysis of the mitochondrial DNA control region. *ICES Journal of Marine Science* **71**(2):391–397 DOI [10.1093/icesjms/fst132](https://doi.org/10.1093/icesjms/fst132).
- Viret A, Tsaparis D, Tsigenopoulos CS, Berrebi P, Sabatini A, Arculeo M, Fassatoui C, Magoulas A, Marengo M, Morales-Nin B, Caill-Milly N, Durieux EDH. 2018.** Absence of spatial genetic structure in common dentex (*Dentex dentex* Linnaeus, 1758) in the Mediterranean Sea as evidenced by nuclear and mitochondrial molecular markers. *PLOS ONE* **13**(9):e0203866 DOI [10.1371/journal.pone.0203866](https://doi.org/10.1371/journal.pone.0203866).
- Wares JP, Cunningham CW. 2001.** Phylogeography and historical ecology of the North Atlantic intertidal. *Evolution* **55**(12):2455–2469 DOI [10.1111/j.0014-3820.2001.tb00760.x](https://doi.org/10.1111/j.0014-3820.2001.tb00760.x).
- Weersing K, Toonen RJ. 2009.** Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology Progress Series* **393**:1–12 DOI [10.3354/meps08287](https://doi.org/10.3354/meps08287).
- Weir BS, Cockerham CC. 1984.** Estimating F-statistics for the analysis of population structure. *Evolution* **38**(6):1358–1370 DOI [10.1111/j.1558-5646.1984.tb05657.x](https://doi.org/10.1111/j.1558-5646.1984.tb05657.x).
- Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA, Wilson S. 2016.** Climate driven regime shift of a temperate marine ecosystem. *Science* **353**:169–172 DOI [10.1126/science.aad8745](https://doi.org/10.1126/science.aad8745).
- Woodall LC, Koldewey HJ, Shaw PJ. 2011.** Historical and contemporary population genetic connectivity of the European short-snouted seahorse *Hippocampus hippocampus* and implications for management. *Journal of Fish Biology* **78**(6):1738–1756 DOI [10.1111/j.1095-8649.2011.02974.x](https://doi.org/10.1111/j.1095-8649.2011.02974.x).
- Wourms JP, Lombardi J. 1992.** Reflections on the evolution of piscine viviparity. *American Zoologist* **32**:276–293.
- Yeruham E, Rilov G, Shpigel M, Abelson A. 2015.** Collapse of the echinoid *Paracentrotus lividus* populations in the Eastern Mediterranean—result of climate change? *Scientific Reports* **5**(1):13479 DOI [10.1038/srep13479](https://doi.org/10.1038/srep13479).
- Yu W, Chen X. 2018.** Ocean warming-induced range-shifting of potential habitat for jumbo flying squid *Dosidicus gigas* in the Southeast Pacific Ocean off Peru. *Fisheries Research* **204**(1):137–146 DOI [10.1016/j.fishres.2018.02.016](https://doi.org/10.1016/j.fishres.2018.02.016).
- Zane L, Ostellari L, Maccatrozzo L, Bargelloni L, Cuzin-Roudy J, Buchholz F, Patarnello T. 2000.** Genetic differentiation in a pelagic crustacean *Meganycitiphanes norvegica*: euphausiacea from the North East Atlantic and the Mediterranean Sea. *Marine Biology* **136**(2):191–199 DOI [10.1007/s002270050676](https://doi.org/10.1007/s002270050676).