

RESEARCH ARTICLE

WILEY

Genetic differentiation among Atlantic island populations of the brown spiny lobster *Panulirus echinatus* (Decapoda: Palinuridae)

Juliana Gaeta^{1,2}  | Iván Acevedo³ | Violeta López-Márquez³ | Rui Freitas⁴ | Raúl Cruz^{1,2} | Rodrigo Maggioni¹ | Rogelio Herrera⁵ | Annie Machordom³

¹Instituto de Ciências do Mar (Labomar), Universidade Federal do Ceará, Fortaleza, Brazil

²Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico, Fortaleza, Brazil

³Consejo Superior de Investigaciones Científicas (MNCN-CSIC), Museo Nacional de Ciencias Naturales, Madrid, Spain

⁴Faculdade de Engenharia e Ciências do Mar, Universidade de Cabo Verde, Mindelo, Cabo Verde

⁵Consejería de Política Territorial, Sostenibilidad y Seguridad, Las Palmas de Gran Canarias, Islas, Spain

Correspondence

Gaeta, J. C., Instituto de Ciências do Mar (Labomar), Universidade Federal do Ceará, Avenida da Abolição, 3207, 60165-081, Fortaleza, Ceará, Brazil.
Email: jugaeta@gmail.com

Funding information

Aquawork, S.L., Grant/Award Number: 28-5249 "Genetic analysis of the species *Panulirus echinatus*; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: Process: 88881.132819/2016-01; Division for the Protection of the Sea of the Ministry of Agriculture and Fisheries, Food and Environment, Grant/Award Number: 28-5249; Elittoral, S.L.N.E., Grant/Award Number: "Ejecución de acciones de conservación de la I; Spanish Ministry of Economy and Competitiveness, Grant/Award Number: CTM2014-57949-R

Abstract

1. Declines in *Panulirus echinatus* Smith, 1869 populations along their wide distribution in the Atlantic Ocean have spurred efforts to improve their fisheries management and conservation. In this study, the genetic structure of these populations is reported for the first time.
2. In a survey of 18 species-specific polymorphic microsatellite markers, 152 individuals were genotyped from five Atlantic oceanic islands, covering most of the insular distribution range of the species. The analyses revealed that *P. echinatus* is genetically partitioned into two stocks in the Atlantic Ocean. A highly significant genetic structure was observed between north-east and south-west Atlantic populations based on fixation index, discriminant analysis of principal components, and structure and barrier analysis.
3. We suggest that the Equatorial Circulation System represents a biophysical barrier that effectively limits migration among Atlantic subtropical gyre systems, as has been described for other species. Other physical and ecological barriers, such as the Mid-Atlantic Ridge itself, the distance between the eastern and western sides of the Atlantic (Mid-Atlantic Barrier) and water mass differences, as well as other biological aspects, may also influence larval dispersal and modulate the insular distribution of this species.
4. The results show the existence of two distinct genetic stocks of *P. echinatus* and have implications for fisheries management in the Atlantic Ocean, including their independent management according to their individual status. The Cabo Verde and the Canarian populations (north-east Atlantic) showed the lowest level of genetic variability in comparison with the south-western populations. A combination of factors that have occurred or are occurring in the Canary Islands, such as overfishing and volcanic eruptions, is likely to explain the reduced abundance of this lobster species in the area.

KEYWORDS

connectivity, conservation, equatorial barrier, gene flow, spiny lobster

1 | INTRODUCTION

Marine connectivity occurs due to the exchange of individuals between geographically separated populations and is considered a key process for replenishing populations and for other processes that have relevant implications for the evolution and ecology of species (Becker, Levin, Fodrie, & McMillan, 2007; Cowen, Paris, & Srinivasan, 2006). In the marine environment, islands do not function as closed systems, and adult populations can exhibit habitat discontinuities such that the level of their connectivity, at least for sessile organisms or adults that only migrate short distances, is largely determined by larval dispersal movements (Porobić, Canales-Aguirre, Ernst, Galleguillos, & Hernández, 2013). Therefore, to understand marine population dynamics, knowledge of the extent of larval exchange between populations is fundamental. Although larval transport appears to be simple, the wide range of larval behaviours and physical mechanisms, together with their variability at multiple scales, makes larval transport exceedingly difficult to measure (Butler, Paris, Goldstein, Matsuda, & Cowen, 2011; Pineda, Hare, & Sponaugle, 2007).

Lobsters are the target of one of the largest and most profitable fisheries in the world, due to their high nutritional value and their refined use in the human food sector (Gaeta, Acevedo, & Machordom, 2018). The present study focuses on the brown spiny lobster *Panulirus echinatus* Smith, 1869 for which there is scarce information about population status. Some studies addressing the population biology of the species are only available for specific locations throughout its distribution, such as Rocas Atoll (RA) (Gaeta & Cruz, 2019a, 2019b; Silva, Campos, Targino, & Melo, 2001), St Peter and St Paul archipelago (Pinheiro, Freire, & Lins-Oliveira, 2003; Pinheiro & Lins-Oliveira, 2006), and Canary Islands (CAN) (Moro et al., 2014; Riera, Becerro, Stuart-Smith, Delgado, & Edgar, 2014). This species has been intensively captured in some regions such as off the coast of Brazil (Pinheiro et al., 2003), Cabo Verde (CV) (R. Freitas, personal communication, November 2015), and CAN (Moro et al., 2014; Riera et al., 2014).

Most *Panulirus* spiny lobster species and subspecies are considered panmictic, with clear allopatric distributions and self-recruitment through local current systems; however some of them, such as *P. echinatus*, present a widespread distribution and are morphologically variable (George, 2005a). *Panulirus* spp. have a biphasic life style with a pelagic larval stage and a sedentary benthic adult, and five major life cycle phases: adult, egg, phyllosoma (larval stage), puerulus (post-larval stage), and juvenile (algal and early benthic phases) (Phillips, Cobb, & George, 1980). Eggs remain attached to the females' pleopods until hatching. Phyllosoma larvae have one of the longest known planktonic larval durations (PLD) of any taxa; however, it can vary anywhere from 2 to 24 months, making dispersal patterns in these species difficult to predict (Abrunhosa, Santiago, & Abrunhosa, 2008; Booth & Phillips, 1994; Butler et al., 2011). In addition, widespread dispersion is sometimes prevented by ontogenetic vertical migration (Butler et al., 2011). There is very little information about the distribution, dispersion, and movement of larvae and early benthic forms of *P. echinatus*. Although

P. echinatus is the only *Panulirus* species, among five found in the Atlantic, that has not had its larvae described on a morphological basis (Konishi, Suzuki, & Chow, 2006), phyllosoma larvae within this genus are morphologically very similar (Konishi et al., 2006). According to Cruz et al. (2015), the closely related species *Panulirus argus* (Latreille, 1804) has a PLD ranging from 6 to 8 months in the Brazilian shelf and we hypothesize that the Atlantic *P. echinatus* has a similar PLD.

Larval dispersal has been previously inferred based on PLDs, models of passive particle transport by ocean currents, observations of larval ecological tolerances and analyses of genetic variation (Butler et al., 2009; Cowen & Sponaugle, 2009; Dao, Smith-Keune, Wolanski, Jones, & Jerry, 2015; Iacchei, Gaither, Bowen, & Toonen, 2016; Rudorff, Lorenzetti, Gherardi, & Lins-Oliveira, 2009; Shanks, Grantham, & Carr, 2003). During dispersion over large spatial scales, larvae experience very different environments and suffer extremely high levels of mortality (Marshall, Monro, Bode, Keough, & Swearer, 2010). However, some studies have suggested that there is little to no relationship between PLD and the degree of population structure across a species' range (Bradbury, Laurel, Snelgrove, Bentzen, & Campana, 2008; Cruz et al., 2015; Iacchei, O'Malley, & Toonen, 2014; Riginos, Douglas, Jin, Shanahan, & Tremblay, 2011; Selkoe & Toonen, 2011; Shanks, 2009; Weersing & Toonen, 2009). For instance, despite the possibility of lobster larvae to disperse across thousands of kilometres, connecting distant populations over broad geographic ranges (Shanks et al., 2003; Siegel, Kinlan, Gaylord, & Gaines, 2003), some spiny lobsters have evolved behavioural mechanisms, such as vertical migration and phototactic response, to increase local retention within their restricted ranges (Butler et al., 2009; Jeffs, Montgomery, & Tindle, 2005). Finally, some hydrodynamic and ecological features have been described as dispersal barriers that modulate the capacity to constrain and retain larvae near their spawning sites (Almany, Berumen, Thorrold, Planes, & Jones, 2007; Butler et al., 2011; Paris, Cherubin, & Cowen, 2007; Paris & Cowen, 2004; Pineda et al., 2007; Shanks et al., 2003).

P. echinatus is a widespread Atlantic species that exhibits a habitat preference for shallow (from 0 to 35 m) and clear equatorial oceanic waters around continents or islands (George, 2005a; Holthuis, 1991). The entire distribution range of this lobster consists of the Central Atlantic islands and archipelagos (CAN, CV, São Pedro and São Paulo Archipelago, Fernando de Noronha, RA, Trindade, Ascension and St. Helena), and the Brazilian coast, from Ceará (3°S) to Rio de Janeiro (23°S). There have not been any records of *P. echinatus* from the coast of Africa (Coelho & Ramos-Porto, 1998; Coelho, Almeida, Bezerra, & Souza-Filho, 2007; Faria-Júnior, Gaeta, & Freire, 2013; Gaeta, Silva, Godoy, & Cruz, 2015; Holthuis, 1991; Manning & Chace, 1990; Melo, 1999).

Many studies have suggested counter-intuitive patterns of connectivity that may be resolved by considering the effects of biogeographical barriers (Briggs & Bowen, 2012; Gaines, Gaylord, Gerber, Hastings, & Kinlan, 2007; Grosberg & Cunningham, 2001; Kulbicki et al., 2013; Marshall et al., 2010). Such barriers are:

1. The Equatorial Barrier is a biophysical dispersal barrier for holoplanktonic organisms that may also serve as a dispersal barrier for other lower epipelagic and upper mesopelagic zooplankton species, including lobster larvae (Goetze et al., 2016; Norton, 2013; Norton & Goetze, 2013). The strong topography of the Mid-Atlantic Ridge (MAR) also modulates the circulation 10° north and south of the equator. As a result, this region has its own Equatorial Current System (ECS), which is composed of the North Equatorial Counter Current, the South Equatorial Current, the South Equatorial Counter Current, and the Equatorial Counter Current (Figure 1) (Talley, Pickard, Emery, & Swift, 2011).
2. The Mid-Atlantic Barrier is a physical barrier represented by the width of the Atlantic Ocean. The spread of the MAR due to tectonic movements continuously increase the distance between the western and eastern halves of the Atlantic Ocean (Floeter et al., 2008) and helps to maintain the circulation pattern in this ocean basin. The dense bottom water makes its way north from the Southern Atlantic Ocean. In the east, it runs into the Walvis Ridge, which blocks it from further northward extension and north along the west of the MAR it finds a deep passage in the Romanche Gap and flows eastward and then south to fill the basin north of the Walvis Ridge (Emery, 2003).
3. Barriers due to differences in water masses at different depths. The upper levels are occupied by North Atlantic Central Waters (NACW) and South Atlantic Central Waters (SACW) that feed the nutrient-rich wind-driven upwelling ecosystem. The NACW are formed by surface subduction of winter water in the North Atlantic, while the SACW are formed in the western South Atlantic Ocean. The CV Frontal Zone, located at approximately 15°N, separates the two thermocline waters (Pelegrí & Peña-Izquierdo, 2015). In the North Atlantic, differences between western and eastern upper water masses are evident; however, no such distinction is observed in the South Atlantic. Regardless, the two halves of the North Atlantic are more similar to each other (in terms of temperature and salinity) than they are to the South Atlantic (Emery, 2003).
4. Barriers due to changes in wind circulation patterns, which may cause cyclones, eddies and hurricanes. The superficial circulation of the Atlantic responds strongly to trade wind forcing, which has large seasonal and inter-annual variability (Stramma & Schott, 1999; Talley et al., 2011). Ocean regions such as river outflows and zones where upwelling and eddies predominate enhance larval retention near the continent and islands (Butler et al., 2009; Cruz et al., 2015).

Even considering the existence of biogeographical barriers, it is often difficult to elucidate their precise role and impact on species. The use of molecular tools and genetic analyses can help to assess their influence over distribution and connectivity. Genetic studies provide data on the resilience and sustainability of stocks and can inform species management and conservation plans (Palero, Abelló, Macpherson, Beaumont, & Pascual, 2011). Microsatellites are the

most commonly used genetic markers in population structure and ecological studies due to their ubiquity, high level of polymorphism, co-dominance, and relative facility for isolated sorting (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). Microsatellites analyses have been successfully used for stock identification and management of lobster species (e.g. Dao et al., 2015; Delghandi et al., 2015; Truelove et al., 2015). Recently, a rich panel of microsatellite markers has been developed for *P. echinatus* with the aim to assess diversity and connectivity among its populations (Gaeta et al., 2018; Santos et al., 2018).

Marine species with long PLD typically display a low level of genetic differentiation and a high level of gene flow (Dewood & Avise, 2000). The wide distribution of *P. echinatus* suggests a high dispersal capacity of its larvae (Konishi et al., 2006). However, several connectivity studies have reported population structuring in lobster species, including among those with high dispersal potential (Farhadi et al., 2017; Iacchei et al., 2016). The drastic decline in *P. echinatus* in recent decades has led to it being classified as endangered in certain localities, such as CAN (Moro et al., 2014; Riera et al., 2014). The low abundance of *P. echinatus* in the CV archipelago suggests that this species should be considered endangered in this area as well (Freitas, 2002). This situation is aggravated because existing commercial fisheries of *P. echinatus* lack a management plan to ensure that lobster populations remain at sustainable levels. Fisheries legislation and other policy tools are not established for this lobster species in any of the countries where it is distributed. Updated basic biological information is of paramount importance to help establish whether an impact on the global population is ongoing. Therefore, the main purpose of this study was to assess the patterns of genetic connectivity among *P. echinatus* island populations. To achieve that, genetic differentiation among *P. echinatus* from five Atlantic oceanic islands was assessed through an analysis of 18 species-specific microsatellites, including the 17 described by Gaeta et al. (2018) plus a newly isolated one. Furthermore, we discuss whether the present population structure is influenced by oceanographic and physiological patterns and/or historical factors, as well as the conservation implications derived from the major findings of this study.

2 | METHODS

2.1 | Study area and sample collection

A total of 152 specimens of *Panulirus echinatus* were analysed from five Atlantic oceanic islands/archipelagos. Tissue samples were collected from individuals found in localities with known populations in CAN (El Hierro, La Palma and Tenerife; 28° 02' N; 17° 36' W; 31 samples), the CV archipelago (São Vicente; 16° 45' N; 24° 55' W; 31 samples), and the Brazilian oceanic islands, RA (03° 52' S; 33° 48' W; 30 samples), Fernando de Noronha archipelago (FN; 03° 51' S; 32° 25' W; 30 samples), and Trindade and Martim Vaz archipelago (TRI; 0° 28' S; 29° 21' W; 30 samples; Figure 1). Lobsters were collected by hand while scuba diving without sacrificing specimens, returning them

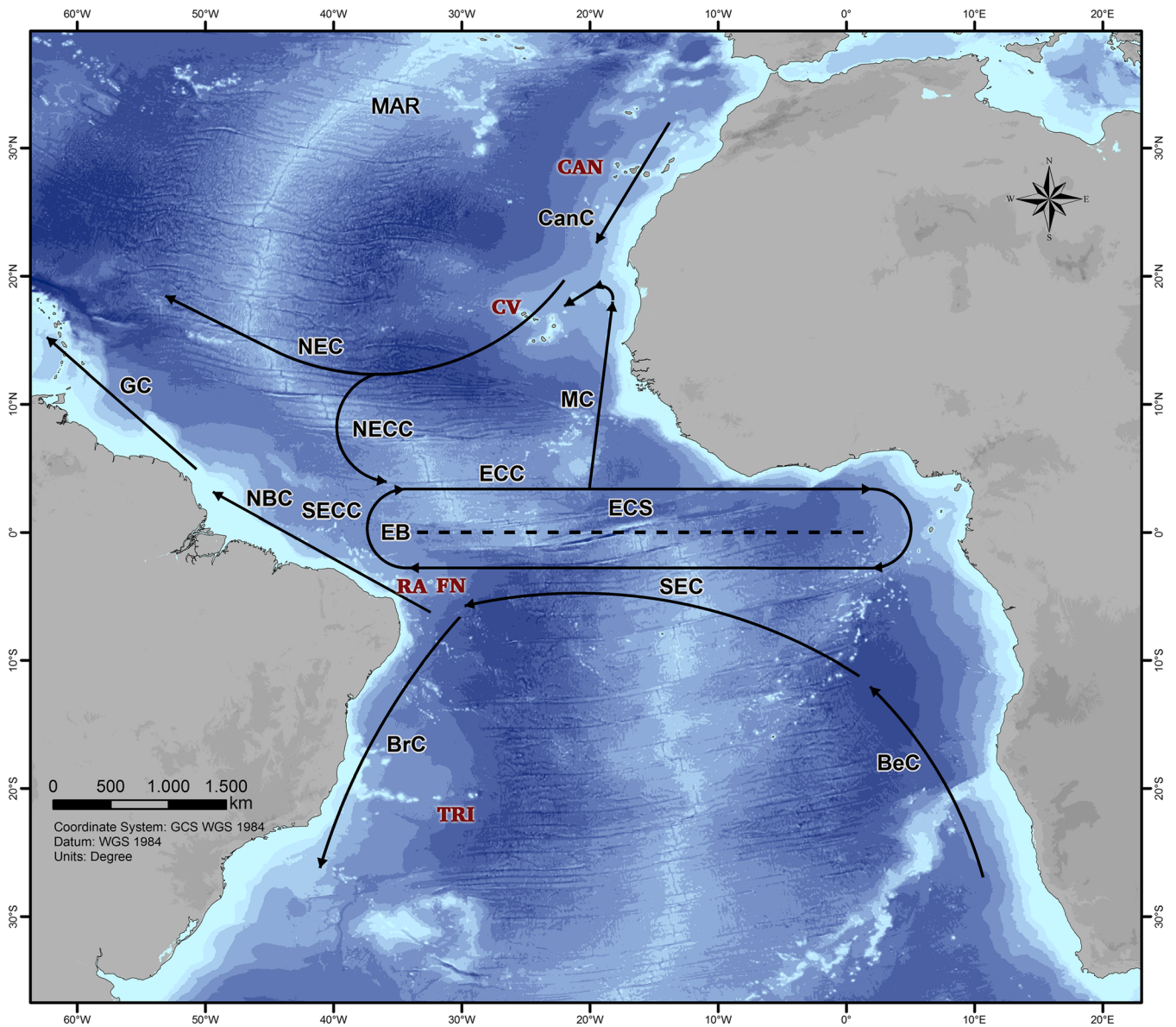


FIGURE 1 Bathymetric map showing the main surface currents and *Panulirus echinatus* Smith, 1869 sampling sites (red) in the Atlantic Ocean (29°N to 22°S, 45°S to 5°S). Locations of *P. echinatus* populations are CAN, Canary Islands; CV, Cabo Verde archipelago; FN, Fernando de Noronha archipelago; RA, Rocas Atoll; TRI, Trindade and Martim Vaz archipelago. Arrows indicate superficial currents; dotted line indicates the geographic location of the Equatorial Barrier (EB). Feature abbreviations (black) BeC, Benguela Current; BrC, Brazil Current; CanC, Canary Current; ECC, Equatorial Counter Current; ECS, Equatorial Circulation System; GC, Guyana Current; MC, Mauritanian Current; NBC, North Brazil Current; NEC, North Equatorial Current; NECC, North Equatorial Counter Current; SEC, South Equatorial Current; SECC, South Equatorial Counter Current; MAR, Mid-Atlantic Ridge. Atlantic circulation pattern based on Stramma (2001) and Aristegui et al. (2009)

back to where they were collected, after muscular tissue was extracted from the last ambulatory leg or pereopod. Tissue samples were preserved in absolute ethanol and stored at 4°C until processed for molecular analyses. Specimens were clearly identified to the species level based on morphological characteristics such as the presence of an antennular plate with a pair of strong thorns, rounded whitish spots covering the body, especially the tail, and yellowish or whitish longitudinal lines along the antennules and legs (which lack bands or spots) (Holthuis, 1991). Morphological identification was confirmed molecularly through 16S rRNA partial sequences. Sequences were

compared using the BLAST algorithm (Altschul et al., 1997). For 16S rRNA amplification and sequencing, the primer pair 16S-ar and 16S-br (Palumbi, 1996) was used (Table S1).

2.2 | DNA extraction, polymerase chain reaction and genotyping

To investigate the population genetics of *P. echinatus* from Atlantic oceanic islands, all samples were extracted, amplified and genotyped

as described by Gaeta et al. (2018) for the 17 previously described polymorphic microsatellites plus a new microsatellite (Pe-L39, Table S1). Briefly, genomic DNA was extracted from muscular tissue of the last pereopod following Qiagen BioSprint 15 DNA Blood Kit (Qiagen Iberia, Madrid, Spain) protocols, including an RNase treatment. DNA quantity and quality were checked using a Nanodrop 1000 and gel electrophoresis (1% agarose gels), respectively. DNA extractions were standardized at 2 ng/ μ L. Polymerase chain reactions (PCRs) were carried out in a total volume of 10 μ L, containing 1 \times PCR Biotools Standard Reaction Buffer, 2 mM MgCl₂, 0.12 μ M forward and 0.8 μ M reverse primers, 0.8 μ M primer PaulAn (Acevedo et al., 2009) fluorescently 5-end labelled with 6-FAM, NED, VIC or PET, 0.2 mM of each dNTP, 0.5 U DNA polymerase (Biotools) and 2 ng of template DNA. A 5-end tag was included in the reverse primers to avoid stutters (Brownstein, 1996). Veriti™ Thermal Cyclers (Applied Biosystems) were used for PCR amplifications with the following conditions: initial denaturation at 94°C for 3 min, followed by 35 cycles at 94°C for 45 s, 56°C for 45 s and 72°C for 30 s, and a final extension at 72°C for 10 min. Fluorescently-labelled PCR products were genotyped by the company Secugen (Madrid, Spain) using an ABI PRISM 3730xl DNA Analyzer (Applied Biosystems) and scored using the GeneScan-500 (LIZ) size standard. GENEMAPPER v4.0 (Applied Biosystems) was used for genotyping analysis.

2.3 | Genetic diversity

Microsatellite quality was first assessed by looking for evidence of stuttering, large allele dropout and null alleles in each population using Micro-Checker v2.2.3 (Van Oosterhout et al., 2004). The genotyping data in GenAlEx format were then transformed for Arlequin, Structure and BayeScan softwares using the file converter Create (Coombs, Letcher, & Nislow, 2008). GenAlEx v6.5 (Peakall & Smouse, 2012) was used to calculate the fixation index (F_{ST}), the number of alleles per locus, polymorphism information content, expected, and observed heterozygosities and number of private alleles. Genepop v4.2 (Raymond & Rousset, 1995; Rousset, 2008) was used to check for deviations from Hardy–Weinberg equilibrium and for evidence of linkage disequilibrium, and to estimate the inbreeding coefficient. Significance levels for multiple comparisons were adjusted using the false discovery rate procedure (Benjamini & Hochberg, 1995) on a Microsoft Excel spreadsheet. To detect loci putatively under selection, two different methodologies were performed: one based on a Bayesian approach in BayeScan v2.1 (Foll & Gaggiotti, 2008), and the other on the island model of migration, with LOSITAN (Antao, Lopes, Lopes, Beja-Pereira, & Luikart, 2008) implemented in the FDist2 program (Beaumont & Nichols, 1996). BayeScan and LOSITAN were run as suggested by Tigano, Shultz, Edwards, Robertson, and Friesen (2017). The StandArich v1.0 package in R program was used to calculate standardized allelic richness (Alberto, 2006). The Wright's fixation indices was calculated using Weir and Cockerham's estimators with GENETIX v4.03 (Belkhir, Borsa, Chikhi, Raufaste, & Bonhomme, 1996). Standardized F_{ST} values were also obtained by recoding the

data matrix, assuming different alleles in each population for each locus, while maintaining their observed allelic frequencies. The standardized F_{ST} was calculated by dividing the original F_{ST} value by the corresponding recoded one as in López-Márquez et al. (2019). This approach was previously used for G_{ST} estimators and indicated that it could be used for F_{ST} indices to correct the bias of F_{ST} dependency on within-population diversity (Jost, 2008; Meirmans & Hedrick, 2011).

2.4 | Genetic divergence

Several methods were used to investigate the genetic divergence of *P. chinatus*. A discriminant analysis of principal components (DAPC) of the global data set was conducted in Adegenet v2.1.1 (Jombart, 2008), in R program. Analyses of molecular variance (AMOVA) were conducted to estimate the distribution of genetic variance at different geographical levels using Arlequin v3.5 (Excoffier, Laval, & Schneider, 2010). A Mantel test on the matrices of pairwise population differentiation in terms of $F_{ST}/(1 - F_{ST})$ and the natural logarithm of geographic distances (in km, water way) was run in GenAlEx to evaluate patterns of isolation-by-distance (IBD) among the sampled populations. Geographic distance between sampling locations, defined as the shortest path over the sea without crossing land, was estimated using Google Earth (<https://earth.google.co.uk/>). Finally, a Bayesian clustering analysis, performed in Structure v2.3.4 (Pritchard, Stephens, & Donnelly, 2000), was used to determine the most likely number of clusters (genetically differentiated populations, K) in the data set. The strategy and parameters used were as described by Evanno, Regnaut, and Goudet (2005): 20 runs per K value, ranging from one to the number of populations plus two, were carried out. For this last analysis, sampling locations were used as prior (model Locprior; Hubisz, Falush, Stephens, & Pritchard, 2009) and admixture was assumed. The model of correlated allele frequencies was also used with a burn-in of 10,000 followed by 100,000 Markov chains Monte Carlo. The most probable number of clusters was determined using the ΔK approach (Evanno et al., 2005) in the online version of Structure Harvester (Earl & VonHoldt, 2012).

To identify the presence of possible barriers without previously defining groups of populations, Monmonier's maximum difference algorithm was implemented in Barrier v2.2 (Manni, Guérard, & Heyer, 2004). This software uses the geographical coordinates and genetic distances to trace the putative dispersal barriers among population pairs (Manni et al., 2004). A significance test was implemented in the software by means of bootstrap matrices analysis. Finally, to assign or exclude individuals from a given population, the Bayesian method described by Rannala and Mountain (1997) was used with a p -value of 0.05 and 100,000 simulated individuals in GeneClass2. Statistical thresholds were estimated by the Monte Carlo resampling algorithm of Rannala and Mountain (1997) with the same simulation algorithm and 100,000 numbers of simulated individuals. To consider immigrants, a probability threshold of $p < 0.05$ (Type I error) was used to assigned individuals to a reference population as suggested by Hamdi, Goñi, Diaz, and Planes (2012).

3 | RESULTS

3.1 | Genetic diversity

Population diversity of *P. echinatus* in the Atlantic Ocean was assessed by analysis of 18 species-specific microsatellites from 152 animals. No significant linkage disequilibrium among loci was found after controlling the false discovery rate using the Benjamini and Hochberg (1995) procedure. The BayeScan analysis indicated that three loci (Pe-L03, Pe-L35 and Pe-L43) were under negative selection, whereas the LOSITAN analysis showed two loci under positive selection (Pe-L10 and Pe-L22; $p < 0.05$). As the two selection analyses were not consistent with each other, none of the loci were excluded from downstream analyses. Null alleles were detected in three (Pe-L03, Pe-L18 and Pe-L35) of the 18 microsatellite loci analysed. To assess their potential bias, results obtained from the analysis of two data sets (one with all 18 loci vs. one with only 15 loci) were compared. No significant differences were detected (except for inbreeding coefficient values). Therefore, all subsequent genetic analyses included all 18 loci. Microsatellite loci were all polymorphic. The number of alleles per locus ranged from two (Pe-L27) to 25 (Pe-L3; Table S2). In total, 130 alleles were detected, with an average of 7.22 alleles across all 18 loci. Measures of genetic diversity and allele size range varied among the 18 loci and across localities (Table S2). The average observed and expected heterozygosities indicated a slight deficit of heterozygotes in most sampled sites (Table 1). The number of alleles and heterozygosity values suggest that CAN and CV have

lower levels of genetic diversity than the other studied populations (Tables 1 and S2). The most frequent private alleles were found in CV (0.081 at locus Pe-L38) and RA (0.05 at locus Pe-L3). Standardized allelic richness over loci for each population ranged from 3.924 for CAN and CV to 5.667 for RA (Table 1). The RA population showed the highest total number of private alleles (Table 1, Figure S1).

3.2 | Genetic structure

The Bayesian clustering (STRUCTURE) and the multivariate (DAPC) analyses partitioned the data set into two groups (Figures 2 and 3, respectively), and a highly significant genetic structure was observed (global $F_{ST} = 0.061$ and standardized global $F_{ST} = 0.131$, $p < 0.001$). The probability of assignment of each individual to one of the two groups ($k = 2$), revealed an overall differentiation between north-east (CAN and CV) and south-west (RA, FN and TRI) Atlantic islands populations (Figure 2). In the DAPC analysis, the first two axes accounted for 87% of the differentiation and clearly differentiated the north-eastern populations from the south-western ones (Figure 3). Comparison of pairwise differences between populations revealed where the main divergences lie within the species. Genetic differentiation based on pairwise F_{ST} values ranged from -0.003 (formally considered as zero) between FN and TRI to 0.109 between CAN and FN (Table 2). Considering the two detected groups (north-east: CAN + CV and south-west: RA + FN + TRI), the AMOVA analysis showed that differences among individuals within populations accounted for

TABLE 1 Estimators of genetic diversity from 152 samples of *Panulirus echinatus* Smith, 1869 genotyped for 18 microsatellite loci. Ho, observed heterozygosity; He, expected heterozygosity; F_{IS} , inbreeding coefficient; PIC, polymorphic information content; A_R , allele richness; A_P , private alleles. Location names: CAN, Canary Islands; CV, Cabo Verde Archipelago; FN, Fernando de Noronha Archipelago; RA, Rocas Atoll; TRI, Trindade and Martin Vaz Archipelago

Location	GPS coordinates	Sample size	Ho	He	F_{IS}	PIC	A_R	A_P number (frequency)
CAN	28° 02' N; 17° 36' W	31	0.486	0.495	0.036	0.944	3.924	1 (0.032)
CV	16° 45' N; 24° 55' W	31	0.486	0.498	0.041	0.889	3.924	2 (0.016); 1 (0.081)
FN	03° 51' S; 32° 25' W	30	0.539	0.541	0.022	1.000	5.444	7 (0.017); 1 (0.033)
RA	03° 52' S; 33° 48' W	30	0.569	0.542	-0.033	1.000	5.667	9 (0.017); 1 (0.033); 1 (0.05)
TRI	20° 28' S; 29° 21' W	30	0.520	0.559	0.085	1.000	5.278	5 (0.017)
		Mean	0.510	0.527	0.030	0.967		

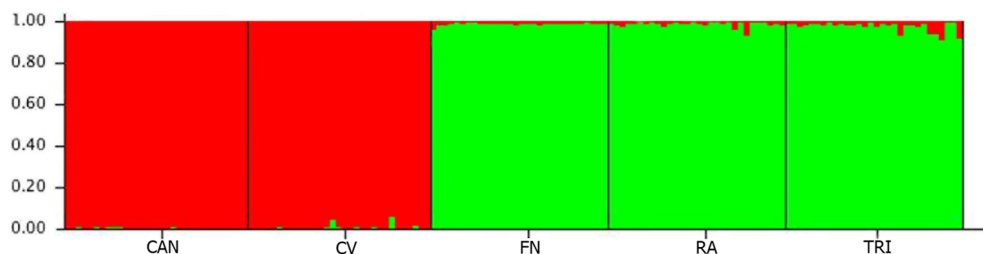


FIGURE 2 Bayesian cluster analysis of *Panulirus echinatus* Smith, 1869 individuals into genetically similar groupings, indicated by different colours. STRUCTURE analysis of microsatellite variation, with optimum $k = 2$. Each bar represents an individual's estimated membership fraction in the two clusters. Population symbol on the x-axis indicates the putative population of sample origin. CAN, Canary Islands; CV, Cabo Verde archipelago; FN, Fernando de Noronha archipelago; RA, Rocas Atoll; TRI, Trindade and Martim Vaz archipelago

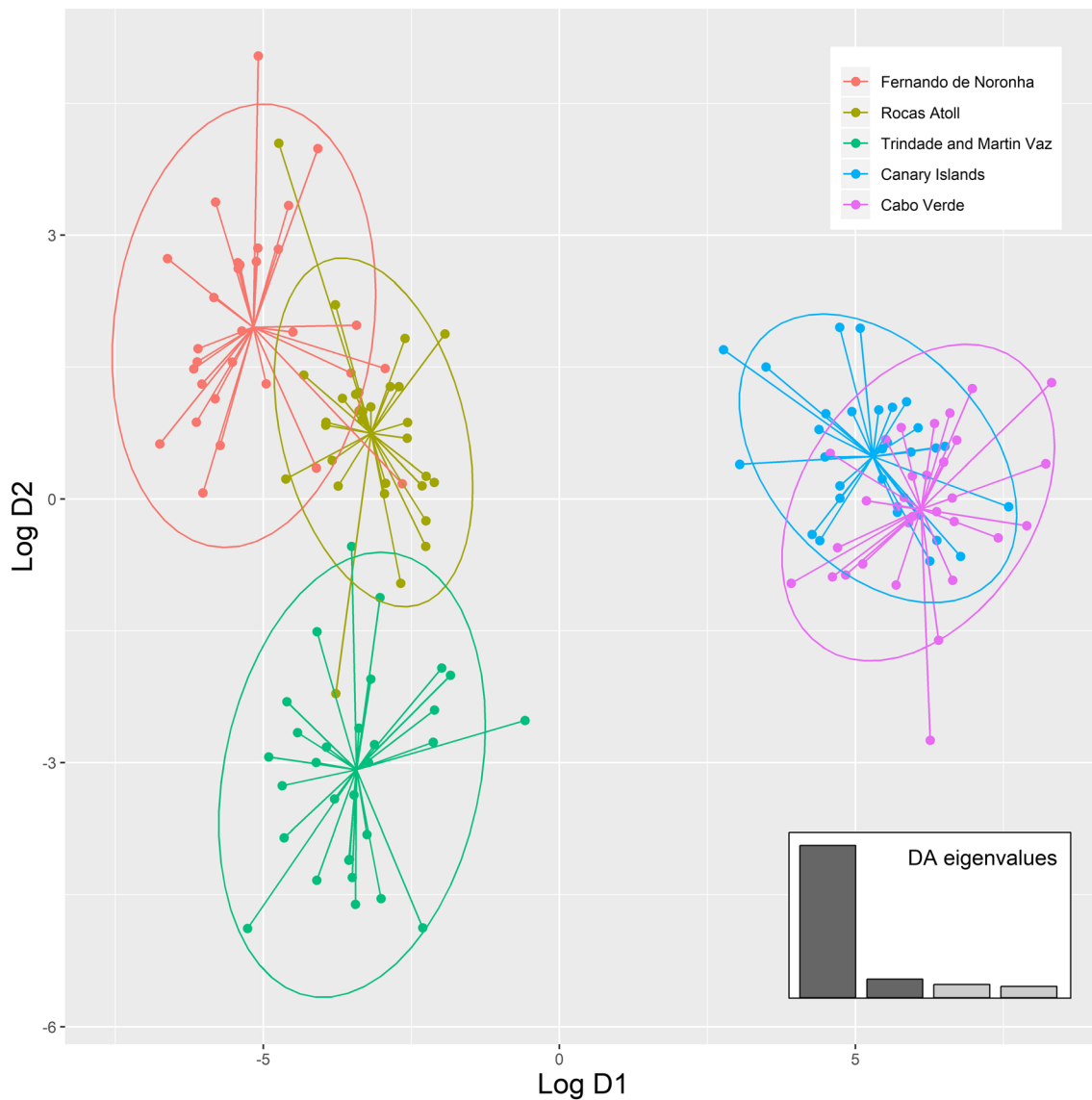


FIGURE 3 Discriminant analysis of principal components based on genotypes of 152 *Panulirus echinatus* Smith, 1869 for 18 microsatellite loci. The two axes presented explain 87% of the total variation. Ellipses indicate 95% confidence intervals of multivariate t -distributions. CAN, Canary Islands; CV, Cabo Verde archipelago; FN, Fernando de Noronha archipelago; RA, Rocas Atoll; TRI, Trindade and Martin Vaz archipelago

TABLE 2 Fixation index values below diagonal (bold for $p < 0.01$) and minimum geographical distance (km) above diagonal. Negative values were considered formally equal to zero. Population name abbreviations as in Table 1

	CAN	CV	FN	RA	TRI
CAN	-	1,460	3,868	3,935	5,517
CV	0.00642	-	2,421	2,428	4,148
FN	0.10978	0.10346	-	156	1,872
RA	0.09349	0.09731	0.00191	-	1,902
TRI	0.08885	0.08555	-0.00319	-0.00310	-

most of the variance (90.43%). However, 9.41% of the variance was explained by differences between the two groups, while differences among populations within each group accounted only for 0.15% of the total variance (Table 3). The Mantel test for IBD showed no significant association between genetic differentiation (F_{ST}) and geographic

distance when using the minimum distance between sample locations ($r_{xy} = 0.653$, $p = 0.07$, $R^2 = 0.426$; Figure S2). The barrier analysis indicated a strong separation between north-east (CV and CAN) and south-west (FN, RA, and TRI) Atlantic. The resulting bootstrap values were 83 from north to south and 71 from the opposite side ($p < 0.01$;

TABLE 3 AMOVA analyses for five populations of *Panulirus echinatus* Smith, 1869 divided in two groups (north-eastern and south-western sides of Atlantic Ocean). Table shows degrees of freedom (d.f.); sum of squares (SS); variance components (Var) and percentage of variation (%Var)

Source of variation	d.f.	SS	Var	%Var
Among groups	1	78.976	0.50163	9.41
Among populations within groups	3	15.935	0.00813	0.15
Within populations	299	1440.744	4.81854	90.43
Total	303	1535.655	5.3283	

Figure S3). The assignment test allocated the majority of individuals (79.61%) to their own population, suggesting that recruitment within the same island group is predominant in *P. echinatus* (Table 4). Assignment to an unknown population, representing individuals that originated from areas not sampled, was low (11.84%). Finally, a small percentage of individuals (8.55%) was assigned to one of the other studied populations, even from the south-west to the north-east Atlantic locations (Table 4; Figure S4).

4 | DISCUSSION

This study represents the first population genetic study reported for *P. echinatus* that evaluates its population structure across the Atlantic Islands. Through an analysis of 18 species-specific microsatellite markers using a variety of approaches (DAPC, AMOVA, Bayesian clustering, barrier analysis, and pairwise F_{ST} comparisons), a strong genetic structure was detected between subtropical gyre populations in the north-east (CAN + CV) and south-west (FN + RA + TRI) Atlantic Ocean. However, the IBD analysis showed no correlation between genetic and geographical distances. George (2005a) has proposed that the ocean current systems affecting the transport of *P. echinatus* larvae in the Atlantic intensified after the Panama Seaway closed, possibly altering the genetic exchange within the North and South Atlantic Basins. These alterations could be involved with the emergence of

morphological variants within *P. echinatus* distribution range (George, 2005a; Vianna, 1986). Previous work has hinted at the limited connectivity among island populations of *P. echinatus*, as revealed by a likely Wahlund effect (Santos et al., 2018).

The north-eastern and south-western populations of *P. echinatus* are exposed to different physical conditions, such as temperature, salinity, density, water masses, and other characteristics of their respective north and south subtropical gyres (Stramma, 2001). These gyres are separated by the ECS, a turbulent flux system composed of the NEC, South Equatorial Current and their associated undercurrents (Weisberg, 2001). The ECS is maintained by a combination of equatorial winds, the topography of the MAR and physical differences between NACW and SACW (Stramma, 2001). As a result, the Equatorial Barrier seems to act as a major biogeographic barrier to plankton dispersal between the north and south regions of the Atlantic Ocean, as has been reported for copepods (Goetze et al., 2016; Norton & Goetze, 2013). By contrast, the Mid-Atlantic Barrier is likely to play a role for the west/east isolation of *P. echinatus* populations. Genetic data from Ascension and Santa Helena Islands, not available in the present work, would help to test this hypothesis.

The oceanic scales can act as barriers and separate distant populations (Palumbi, 1994), as observed in the present study. Despite its long PLD, *P. echinatus* shows significant genetic differentiation throughout its distribution. The same differentiation has been observed in other spiny lobster species with widespread distributions including *P. penicillatus*, the sister species of *P. echinatus* (Abdullah, Muththalib, Salama, & Imai, 2014; Chow et al., 2011; Iacchi et al., 2016), *P. argus* (Tourinho, Solé-Cava, & Lazoski, 2012; Truelove et al., 2015) and *Panulirus homarus* Linnaeus, 1758 (Farhadi et al., 2017). Adult *P. echinatus* typically occur in coastal waters at depths from 0 to 25 m, sometimes up to 35 m (Holthuis, 1991). These preferences might explain their distribution specificity on oceanic islands and Brazilian coastal waters. Small eddies that form around these islands may be responsible for the high self-recruitment rates of lobsters in these isolated ecosystems (Cruz et al., 2015; Sangrà et al., 2005). In our analysis, the majority of individuals (79.61%) were assigned to the population from which they were sampled, indicating that self-recruitment is predominant in *P. echinatus*. Arístegui et al. (2009)

TABLE 4 Assignment test of *Panulirus echinatus* in the five Central Atlantic island populations based on 18 microsatellites. Abbreviations as defined in Table 1. For each site, individuals are presented in rows according to their sampling site and classified as individuals assigned to either own population (Self origin), to other sites or to an unknown origin. Total imm. = total number of immigrants detected in each location. The last column list is the total number of individuals that were not assigned to any of the studied populations

Population	Origin centralized						Total imm.	Unknown
	Self	CAN	CV	FN	RA	TRI		
CAN	25	-	2	1	-	-	3	3
CV	28	1	-	-	1	-	2	1
FN	23	-	-	-	2	-	2	5
RA	24	-	-	2	-	1	3	3
TRI	21	-	-	-	3	-	3	6
Total	121 (79.61%)						13 (8.55%)	18 (11.84%)

previously demonstrated the presence of mesoscale eddies near the Canary Islands. We hypothesize that meso- and microscale eddies near these islands enhance self-recruitment, a hypothesis that will be evaluated in a future genetic study of intra-archipelago paternity. Nevertheless, detailed oceanographic studies of all localities, such as those described for the CV archipelago (Medina, 2007) and CAN (Aristegui et al., 2009) are necessary to determine and comprehend the extent to which eddies influence self-recruitment in lobsters. In particular, retention of larvae that exhibit ontogenetic vertical migration is greater than that of passively dispersing larvae (Almany et al., 2007; Paris et al., 2007; Planes, Jones, & Thorrold, 2009). Spiny lobster larval behaviour, such as diel vertical migration and ontogenetic vertical migration, are powerful mechanisms used to bolster self-recruitment especially in larvae with weak swimming abilities, such as phyllosoma (Butler et al., 2009). Although none of these larval behaviours were studied in *P. echinatus*, a high level of self-recruitment in this species is supported by the data presented here, suggesting that it has developed behaviours similar to other lobster species. However, further studies on the larval and post-larval stages of this species are fundamental to have a complete understanding of its connectivity.

Despite the high level of genetic differentiation observed between north-east and south-west Atlantic groups of islands, the assignment test indicated that at least a low level of gene flow occurs between them. Overall, emigration from the southern stock is more prevalent, with the RA population acting as a primary source, as individuals originating from this population were seemingly collected from all the other studied areas, with the exception of CAN. The south-western stock also presented a higher observed heterozygosity compared to the north-eastern one. This finding is consistent with the hypothesis that *P. echinatus* firstly evolved in the Caribbean in the western Atlantic Ocean, spreading from there to more recently formed islands with available habitats (George, 2005b). Subsequently, competition with other lobster species and segregation might have caused *P. echinatus* to become extinct in the Caribbean. The westernmost Atlantic island inhabited by *P. echinatus* is the RA, which might represent one of the first regions to be colonized in the Atlantic (George, 2005a). From the results obtained in the assignment test, RA seems to be acting as a source population. In addition, RA showed the highest frequency and mean number of private alleles. In comparison with the other studied populations, *P. echinatus* at the RA shows high abundance and carapace length distribution in all size classes (Gaeta & Cruz, 2019a, b). The area has been a Marine Protected Area (MPA) since 1971, where fishing activities were prohibited, and that has likely contributed to preserved population stability.

Rudorff et al. (2009), using a simple advection–diffusion model, suggested that Northern Brazilian islands supply lobster larvae to the coastal populations. Larvae emigrating from FN and RA appear to be retained within the ECS, and successful exchange between these islands and the Brazilian continent is highly probable; larvae may be even able to reach the Eastern Atlantic (Rudorff et al., 2009). The Canary Current can carry larvae from CAN to CV. The opposite situation is less likely to occur except when cyclonic and anticyclonic

eddies and African coastal upwelling filaments form and break in this region (e.g. the Cape Blanc giant filament that is closely associated with the CV Frontal Zone), which may allow a few individuals to migrate to CAN (Aristegui et al., 2009; Sangrà, 2015), as suggested in this study.

Previous studies have shown genetic differentiation among Indo-Pacific populations of the widely distributed species *P. penicillatus* (Abdullah et al., 2014; Chow et al., 2011; Iacchei et al., 2016), consistent with a pan-Tethyan progenitor previously suggested by several studies (George, 1997, 2005a; Ptacek, Sarver, Childress, & Herrnkind, 2001). Coalescent analyses date the most recent common ancestor of *P. penicillatus* and *P. echinatus* to approximately 6.98 Ma (Iacchei et al., 2016), which overlaps with the 4.7 Ma proposed by Tourinho et al. (2012). While the microsatellite markers analysed here do not permit a palaeo-historical reconstruction, the clear genetic differences observed among SW and NE Atlantic populations might indicate an incipient speciation process. This genetic differentiation supports the proposal that *P. echinatus* populations could comprise two metapopulations. Thus, genetically distinct *P. echinatus* stocks must be managed according to the characteristics of the region where they occur, as they may differentially affect larval recruitment rates, post-larval settlement, growth, and survival of the stocks.

4.1 | Conservations implications

The existence of genetic differentiation among *P. echinatus* populations has important implications for the management of this lobster species within the central Atlantic Ocean. The Equatorial Barrier, along with other hard and soft barriers, affects larval dispersal, recruitment rates and, consequently, settlement, growth and survival of this lobster. CAN harbours the least abundant population of all studied islands, probably due to human impact, ecological tolerances and physical limitations (Riera et al., 2014). This population is located in the Macaronesia ecoregion, which is undergoing a process of tropicalization with seawater warming whose impact on species was first evidenced in coastal zoanths and fishes (Afonso et al., 2013; Brito, Moreno-Borges, Escánez, Falcón, & Herrera, 2017; González-Delgado, López, Brito, & Clemente, 2018). Currently, this ecoregion is considered a subtropical zone where marine ecosystems are influenced by both high- (temperate) and low-latitude (tropical) waters. Therefore, the Canarian *P. echinatus* population in this subtropical zone is also influenced by the cold and upwelling Canary Current (Riera et al., 2014, see Figure S6). Furthermore, recent projections on the impact of climate changes on the distribution of spiny lobsters have indicated potential high losses in *Panulirus* diversity (including *P. echinatus*) in the Caribbean, Brazil, eastern Africa and the Indo-Pacific (Boavida-Portugal et al., 2018). Therefore, climate change may also be affecting population abundance in the Canary archipelago. This population appears to be poorly adapted to local conditions as specimens are geographically limited to few sites, and at some of these, very few individuals (fewer than three) have been found, indicating their imminent disappearance from these sites

(Riera et al., 2014). Past estimates of population size in the Canary archipelago (e.g. as low as 55 individuals; González-Pérez, 1995) demonstrate the persistent vulnerability of this population to local extinction. Riera et al. (2014) also suggested that volcanic eruptions (that occurred in 2011) affected the abundance of *P. echinatus* in this archipelago. Currently, commercial fishing of this species is prohibited in the area due to its low population size; however, losses due to by-catch on shrimp trawl fishing and captures by recreational scuba divers still represent a major threat. Together with CV, the CAN population showed the lowest level of genetic variability, in terms of both the number of alleles and heterozygosity. This finding may reflect a greater impoverishment of these populations with respect to the Brazilian ones. Low genetic variability is one of the aspects that can lead to inbreeding depression and, finally, to these populations being untenable (Frankham, Ballou, & Briscoe, 2013; Gao & Gao, 2016). This initial survey has provided some insight into the population dynamics of *P. echinatus* at key locations in the Atlantic. However, we acknowledge that a wider sampling, including all sites of occurrence would be of interest, especially considering the ongoing climate change. Wider studies would shed light on the origins of the unknown migrants and on the extent of connectivity to the most distant populations, at Saint Helena, Ascension, and Tristan da Cunha. However, the scarcity of studies on larval and post-larval stages of *P. echinatus* continues to hinder efforts to address questions related to population dynamics, planning, management and recovery of stocks. Therefore, future studies should also aim to investigate larval recruitment (e.g. locations and periods of increased activity) and nesting, vertical migration or the influence of environmental factors on these stages such as temperature, salinity, turbidity and sedimentation by eutrophication, among other aspects. These types of studies are particularly important to evaluate the conservation status of *P. echinatus* local populations across its entire distribution range. In order to propose measures of effective management and protection, we suggest that an evaluation of reproductive aspects is necessary, as well. The reproductive potential (e.g. sex ratio, effective population size, number of eggs), reproductive efficiency and stock recruitment of this species according to location, female reproductive stratification by depth and size class, are essential information in this context.

In conclusion, the geographical division of the distinctive north-east and south-west Atlantic island populations is consistent with the Atlantic circulation pattern. North and South Atlantic subtropical gyres separated by the ECS. The topography of MAR and the distance between continents influence and maintain this circulation pattern. The genetic connectivity of *P. echinatus* island populations is clearly restricted by the ECS, which acts as a barrier to larval dispersal from the North to South Atlantic through this turbulent equatorial region, thus limiting gene flow and favouring the separation of populations into two different stocks. Overall, the findings reported here support the need for governmental intervention in the protection of CN and CV island populations of *P. echinatus*. These populations have low abundances now and face low availability of preferential habitats, poor survival conditions and impacts from fishery activities. In CV, it seems advisable to create a fishing

restriction measure to prevent a local extinction of this species. Another specific conservation measure regarding the north-east Atlantic populations is the designation of MPAs, such as those already existing in the Brazilian oceanic islands that help to protect lobster habitats and helps the recovery and conservation of these populations. To achieve that, it is necessary to study the distribution of *P. echinatus* in the CAN archipelago and CV to designate the most abundant localities as MPAs. Finally, we suggest the maintenance of RA as an MPA in order to safeguard this unique ecosystem to preserve the *P. echinatus* population currently inhabiting it, mostly considering that it likely acts as a source for other populations.

ACKNOWLEDGEMENTS

This study forms part of the doctoral thesis of the first author JCG, who was supported by a grant from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES - process no. 88881.132819/2016-01), Brazil. This work was also supported by Aquawork, S.L., Elittoral, S.L.N.E., the Division for the Protection of the Sea of the Ministry of Agriculture and Fisheries, Food and Environment for the service contract "Genetic analysis of the species *Panulirus echinatus*" (grant reference: 28-5249) and "Ejecución de acciones de conservación de la langosta herreña (*Panulirus echinatus*) y redacción del plan de recuperación", and partially by a project of the Spanish Ministry of Economy and Competitiveness (CTM2014-57949-R). All necessary permits for sampling and observational field studies were obtained in accordance with current regulations (ICMBio Brazilian permission: 36207-6 and 43398-7). A special thanks to the governments of the Canary Islands, Cabo Verde and Brazil for financial support of this research. Our gratitude to all sample collectors (Anildo Silva, Bianca del Bianco, Edson Faria-Júnior, Kyllderes Lima, Leopoldo Moro, Manuel Coronel, Rafael Herrero and Renan Saes). Thanks to Victoria González Cascón and Jonathan Pereira Miller (MNCN-CSIC) for helping in map development and we are also thankful to Melinda Modrell for the English revision. The authors declare that they have no conflict of interest.

DATA ACCESSIBILITY

Panulirus echinatus contig sequences containing new microsatellites locus and 16S were deposited into GenBank (Accession number: Pe-L39 - MK830038 and 16S - MK836100 to MK836104).

ORCID

Juliana Gaeta  <https://orcid.org/0000-0002-4796-5948>

REFERENCES

- Abdullah, M. F., Muththalib, M., Salama, A. J., & Imai, H. (2014). Genetic isolation among the northwestern, southwestern and central-eastern Indian Ocean populations of the pronghorn spiny lobster *Panulirus penicillatus*. *International Journal of Molecular Sciences*, *15*, 9242–9254. <https://doi.org/10.3390/ijms15069242>
- Abrunhosa, F. A., Santiago, A. P., & Abrunhosa, J. P. (2008). The early phyllosoma stages of spiny lobster *Panulirus echinatus* Smith, 1869

- (Decapoda: Palinuridae). *Brazilian Journal of Biology*, 68, 179–186. <https://doi.org/10.1590/S1519-69842008000100026>
- Acevedo, I., Bloor, P., Cabezas, P., Toledo, C., Calvo, M., & Machordom, A. (2009). Development of tetranucleotide microsatellite markers for the cushion star, *Asterina gibbosa*, and cross-species amplification. *Molecular Ecology Resources*, 9, 274–277. <https://doi.org/10.1111/j.1755-0998.2008.02267.x>
- Afonso, P., Porteiro, F. M., Fontes, J., Tempera, F., Morato, T., Cardigos, F., & Santos, R. S. (2013). New and rare coastal fishes in the Azores islands: Occasional events or tropicalization process? *Journal of Fish Biology*, 83, 272–294. <https://doi.org/10.1111/jfb.12162>
- Alberto, F. (2006). StandArich v1.0: An R package to estimate population allelic richness using standardized sample size. <http://www.webcitation.org/6FvpviTep> [05 September 2017].
- Almany, G. R., Berumen, M. L., Thorrold, S. R., Planes, S., & Jones, G. P. (2007). Local replenishment of coral reef fish populations in a marine reserve. *Science*, 316, 742–747. <https://doi.org/10.1126/science.1140597>
- Altschul, S. F., Madden, T. L., Schäffer, A. A., Zhang, J., Zhang, Z., Miller, W., & Lipman, D. J. (1997). Gapped BLAST and PSI-BLAST: A new generation of protein database search programs. *Nucleic Acids Research*, 25, 3389–3402. <https://doi.org/10.1093/nar/25.17.3389>
- Antao, T., Lopes, A., Lopes, R. J., Beja-Pereira, A., & Luikart, G. (2008). LOSITAN: A workbench to detect molecular adaptation based on a F_{ST} -outlier method. *BMC Bioinformatics*, 9, 1–5. <https://doi.org/10.1186/1471-2105-9-323>
- Aristegui, J., Barton, E. D., Álvarez-Salgado, X. A., Santos, A. M. P., Figueiras, F. G., Kifani, S., ... Demarcq, H. (2009). Sub-regional ecosystem variability in the Canary Current upwelling. *Progress in Oceanography*, 53, 33–48. <https://doi.org/10.1016/j.pocean.2009.07.031>
- Beaumont, M. A., & Nichols, R. A. (1996). Evaluating loci for use in the genetic analysis of population structure. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 263, 1619–1626. <https://doi.org/10.1098/rspb.1996.0237>
- Becker, B. J., Levin, L. A., Fodrie, F. J., & McMillan, P. A. (2007). Complex larval connectivity patterns among marine invertebrate populations. *Proceedings of the National Academy of Science of the United States of America*, 104, 3267–3272. <https://doi.org/10.1073/pnas.0611651104>
- Belkhir K., Borsa P., Chikhi L., Raufaste N., & Bonhomme F. (1996-2004). GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier, France.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B (Methodological)*, 57, 289–300. <https://www.jstor.org/stable/2346101>
- Boavida-Portugal, J., Rosa, R., Calado, R., Pinto, M., Boavida-Potugal, I., Araújo, M. B., & Guilhaumon, F. (2018). Climate change impacts on the distribution of coastal lobsters. *Marine Biology*, 165–186. <https://doi.org/10.1007/s00227-018-3441-9>
- Booth, J. D., & Phillips, B. F. (1994). Early life history of spiny lobster. *Crustaceana*, 66, 271–294. <https://www.jstor.org/stable/20104952>
- Bradbury, I. R., Laurel, B., Snelgrove, P. V. R., Bentzen, P., & Campana, S. E. (2008). Global patterns in marine dispersal estimates: The influence of geography, taxonomic category and life history. *Proceedings of the Royal Society Series B: Biological Sciences*, 275, 1803–1809. <https://doi.org/10.1098/rspb.2008.0216>
- Briggs, J. C., & Bowen, B. W. (2012). A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography*, 39, 12–30. <https://doi.org/10.1111/j.1365-2699.2011.02613.x>
- Brito, A., Moreno-Borges, S., Escáñez, A., Falcón, J. M., & Herrera, R. (2017). New records of Actinopterygian fishes from the Canary Islands: Tropicalization as the most important driving force increasing fish diversity. *Revista de la Academia Canaria de Ciencias*, 29, 31–44.
- Brownstein, M. J. (1996). Modulation of non-templated nucleotide addition by Taq DNA polymerase: Primer modifications that facilitate genotyping. *BioTechniques*, 20, 1004–1010.
- Butler, M. J., Mojica, A. M., Sosa-Cordero, E., Millet, M., Sanchez-Navarro, P., Maldonado, M. A., ... Cowen, R. (2009). Patterns of spiny lobster (*Panulirus argus*) postlarval recruitment in the Caribbean: A CRTR Project. *Proceedings of the 62nd Gulf and Caribbean Fisheries Institute*, 62, 360–369.
- Butler, M. J., Paris, C. B., Goldstein, J. S., Matsuda, H., & Cowen, R. K. (2011). Behavior constrains the dispersal of long-lived spiny lobster larvae. *Marine Ecology Progress Series*, 422, 223–237. <https://doi.org/10.3354/meps08878>
- Chow, S., Jeffs, A., Miyake, Y., Konishi, K., Okazaki, M., Suzuki, N., ... Sakai, M. (2011). Genetic isolation between the Western and Eastern Pacific populations of pronghorn spiny lobster *Panulirus penicillatus*. *PLoS ONE*, 6, e29280. <https://doi.org/10.1371/journal.pone.0029280>
- Coelho, P. A., Almeida, A. O., Bezerra, L. E. A., & Souza-Filho, J. F. (2007). An updated checklist of decapod crustaceans (infraorders Astacidea, Thalassinidea, Polychelida, Palinura, and Anomura) from the northern and northeastern Brazilian coast. *Zootaxa*, 1519, 1–16. <https://doi.org/10.11646/zootaxa.1519.1.1>
- Coelho, P. A., & Ramos-Porto, M. (1998). Malacostraca - Eucarida - Palinuridea. In P. S. Young (Ed.), *Catalogue of crustacea of Brazil. Série Livros 6*. (pp. 387–391). Rio de Janeiro: Museu Nacional/UF RJ.
- Coombs, J. A., Letcher, B. H., & Nislow, K. H. (2008). CREATE: A software to create input files from diploid genotypic data for 52 genetic software programs. *Molecular Ecology Resources*, 8, 578–580. <https://doi.org/10.1111/j.1471-8286.2007.02036.x>
- Cowen, R. K., Paris, C. B., & Srinivasan, A. (2006). Scaling of connectivity in marine populations. *Science*, 311, 522–527. <https://doi.org/10.1126/science.1122039>
- Cowen, R. K., & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 1, 443–466. <https://doi.org/10.1146/annurev.marine.010908.163757>
- Cruz, R., Teixeira, C. E. P., Menezes, M. O. B., Santana, J. V. M., Neto, T. M., Gaeta, J. C., ... Cintra, I. H. A. (2015). Large-scale oceanic circulation and larval recruitment of the spiny lobster *Panulirus argus* (Latreille, 1804). *Crustaceana*, 88, 298–323. <https://doi.org/10.1163/15685403-00003411>
- Dao, H. T., Smith-Keune, C., Wolanski, E., Jones, C. M., & Jerry, D. R. (2015). Oceanographic Currents and Local Ecological Knowledge Indicate, and Genetics Does Not Refute, a Contemporary Pattern of Larval Dispersal for The Ornate Spiny Lobster, *Panulirus ornatus* in the South-East Asian Archipelago. *PLoS ONE*, 10, e0124568. <https://doi.org/10.1371/journal.pone.0124568>
- Delghandi, M., Goddard, S., Jerry, D. R., Dao, H. T., Al-Hinai, M. S. N., Al-Amry, W., & Al-Marzouqi, A. (2015). Novel genomic microsatellite markers for genetic population and diversity studies of tropical scalloped spiny lobster (*Panulirus homarus*) and their potential application in related *Panulirus* species. *Genetics and Molecular Research*, 15, 1–5 (gmr.15027846). <https://doi.org/10.4238/gmr.15027846>
- Dewood, J. A., & Avise, J. C. (2000). Microsatellite variation in marine, freshwater and anadromous fishes compared with other animals. *Journal of Fish Biology*, 56, 461–473. <https://doi.org/10.1111/j.1095-8649.2000.tb00748.x>
- Earl, D. A., & VonHoldt, B. M. (2012). Structure Harvester: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetic Resources*, 4, 359–361. <https://doi.org/10.1007/s12686-011-9548-7>
- Emery, W. J. (2003). Water types and water masses. In J. R. Holton, J. A. Curry, & J. A. Pyle (Eds.), *Encyclopedia of atmospheric sciences* (pp. 1556–1567). Boulder, USA: Elsevier.

- Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, 14, 2611–2620. <https://doi.org/10.1111/j.1365-294X.2005.02553.x>
- Excoffier, L., Laval, G., & Schneider, S. (2010). Arlequin version 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, 10, 564–567. <https://doi.org/10.1111/j.1755-0998.2010.02847.x>
- Farhadi, A., Jeffs, A. G., Farahmand, H., Rejiniemon, T. S., Smith, G., & Lavery, S. D. (2017). Mechanisms of peripheral phylogeographic divergence in the Indo-Pacific: Lessons from the spiny lobster *Panulirus homarus*. *BMC Evolutionary Biology*, 17, 1–14. <https://doi.org/10.1186/s12862-017-1050-8>
- Faria-Júnior, E., Gaeta, J. C., & Freire, A. S. (2013). An update on the lobster species (*Panulirus* White, 1847) from the Abrolhos Marine National Park, Northern Brazil. *Revista de Investigações Marinhas*, 33, 37–42.
- Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J. C., Smith-Vaniz, W. F., Wirtz, P., ... Bernardi, G. (2008). Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, 35, 22–47. <https://doi.org/10.1111/j.1365-2699.2007.01790.x>
- Foll, M., & Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: A Bayesian perspective. *Genetic Society of America*, 180, 977–993. <https://doi.org/10.534/genetics.108.092221>
- Frankham, R., Ballou, J. D., & Briscoe, D. A. (2013). Introduction to Conservation Genetics. In *Chapter 13: Inbreeding depression*. Cambridge University Press.
- Freitas, R. (2002). Contribuição para o conhecimento da biologia da lagosta verde *Panulirus regius* (De Brito Capello, 1864) de Cabo Verde. Relatório de estágio do curso de bacharelado em biologia marinha e pescas, Mindelo, DPTRA. Instituto Superior de Engenharia e Ciências do Mar, 35, 62pp.
- Gaeta, J., Acevedo, I., & Machordom, A. (2018). Characterization of 17 novel microsatellite loci for the brown spiny lobster *Panulirus echinatus* Smith, 1869 using MiSeq. *Crustaceana*, 91, 413–424. <https://doi.org/10.1163/15685403-00003774>
- Gaeta, J., & Cruz, R. (2019a). *Panulirus echinatus* population in the Brazilian oceanic ecosystem Rocas Atoll. *Crustaceana*, 92, 221–232. <https://doi.org/10.1163/15685403-00003859>
- Gaeta, J., & Cruz, R. (2019b). Distribution and density of lobsters in the Brazilian oceanic ecosystem Rocas Atoll. *Crustaceana*, 92, 335–351. <https://doi.org/10.1163/15685403-00003876>
- Gaeta, J., Silva, M. B., Godoy, T., & Cruz, R. (2015). Update on the lobster species from Rocas Atoll Marine Reserve, Brazil. *Check List*, 11, 1–7. <https://doi.org/10.15560/11.4.1705>
- Gaines, S. D., Gaylord, B., Gerber, L. R., Hastings, A., & Kinlan, B. P. (2007). Connecting places: The ecological consequences of dispersal in the sea. *Oceanography*, 20, 90–99. <https://doi.org/10.5670/oceanog.2007.32>
- Gao, L.-Z., & Gao, C.-W. (2016). Lowered Diversity and Increased Inbreeding Depression within Peripheral Populations of Wild Rice *Oryza rufipogon*. *PLoS ONE*, 11, e0150468. <https://doi.org/10.1371/journal.pone.0150468>
- George, R. W. (1997). Tectonic plate movements and the evolution of *Jasus* and *Panulirus* spiny lobsters (Palinuridae). *Marine and Freshwater Research*, 48, 1121–1130.
- George, R. W. (2005a). Tethys sea fragment and speciation of *Panulirus* species. *Crustaceana*, 78, 1281–1309. <https://doi.org/10.1163/156854005776759780>
- George, R. W. (2005b). Evolution of life cycles, including migration, in spiny lobsters (Palinuridae). *New Zealand Journal of Marine and Freshwater Research*, 39, 503–514. <https://doi.org/10.1080/00288330.2005.9517329>
- Goetze, E., Hüdelpohl, P. T., Chang, C., Van Woudenberg, L., Iacchei, M., & Peijnenburg, K. T. C. A. (2016). Ecological dispersal barrier across the equatorial Atlantic in a migratory planktonic copepod. *Progress in Oceanography*, 158, 203–212. <https://doi.org/10.1016/j.pocean.2016.07.001>
- González-Delgado, S., López, C., Brito, A., & Clemente, S. (2018). Marine community effects of two colonial zoanths in intertidal habitats of the Canary Islands. *Regional Studies in Marine Science*, 23, 23–31. <https://doi.org/10.1016/j.rsma.2018.03.006>
- González-Pérez, J. A. (1995). Catálogo de los crustáceos decápodos de las Islas Canarias. Gambas. Langostas. Cangrejos. Publicaciones Turquesa, Santa Cruz de Tenerife.
- Grosberg, R., & Cunningham, C. W. (2001). Genetic structure in the sea, from populations to communities. In M. Bertness, S. Gaines, & M. Hay (Eds.), *Marine community ecology* (pp. 61–84). Sunderland, Massachusetts: Sinauer Associates.
- Hamdi, E., Goñi, R., Diaz, D., & Planes, S. (2012). Detecting immigrants in a highly genetically homogeneous spiny lobster population (*Panulirus elephas*) in the northwest Mediterranean Sea. *Ecology and Evolution*, 2, 2387–2396. <https://doi.org/10.1002/ece3.349>
- Holthuis, L. B. (1991). Marine lobsters of the world: An annotated and illustrated catalogue of species of interest to fisheries known to date. In *FAO species catalogue*. FAO fisheries synopsis 125. Rome: FAO. 292 pp
- Hubisz, M. J., Falush, D., Stephens, M., & Pritchard, J. K. (2009). Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources*, 9, 1322–1332. <https://doi.org/10.1111/j.1755-0998.2009.02591.x>
- Iacchei, M., Gaitner, M. R., Bowen, B. W., & Toonen, R. J. (2016). Testing dispersal limits in the sea: Range-wide phylogeography of the pronghorn spiny lobster *Panulirus penicillatus*. *Journal of Biogeography*, 43, 1032–1044. <https://doi.org/10.1111/jbi.12689>
- Iacchei, M., O'Malley, J. M., & Toonen, R. J. (2014). After the gold rush: Population structure of spiny lobsters in Hawaii following a fishery closure and the implications for contemporary spatial management. *Bulletin of Marine Science*, 90, 331–357. <https://doi.org/10.5343/bms.2013.1042>
- Jeffs, A. G., Montgomery, J. C., & Tindle, C. T. (2005). How do spiny lobster post-larvae find the coast? *New Zealand Journal of Marine and Freshwater Research*, 39, 605–617. <https://doi.org/10.1080/00288330.2005.9517339>
- Jombart, T. (2008). adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24, 1403–1405. <https://doi.org/10.1093/bioinformatics/btn129>
- Jost, L. (2008). G_{ST} and its relatives do not measure differentiation. *Molecular Ecology*, 17, 4015–4026. <https://doi.org/10.1111/j.1365-294X.2008.03887.x>
- Konishi, K., Suzuki, N., & Chow, S. (2006). A late stage phyllosoma larva of the spiny lobster *Panulirus echinatus* Smith, 1869 (Crustacea: Palinuridae) identified by DNA analysis. *Journal of Plankton Research*, 28, 841–845. <https://doi.org/10.1093/plankt/fbl019>
- Kulbicki, M., Parravicini, V., Bellwood, D. R., Arias-González, E., Chabanet, P., Floeter, S. R., ... Mouillot, D. (2013). Global biogeography of reef fishes: A hierarchical quantitative delineation of regions. *PLoS ONE*, 8, e81847. <https://doi.org/10.1371/journal.pone.0081847>
- López-Márquez, V., Templado, J., Buckley, D., Marino, I., Boscarì, E., Micu, D., ... Machordom, A. (2019). Connectivity among populations of the top shell *Gibbula divaricata* in the Adriatic Sea. *Frontiers in Genetics*, 10, 1–13. <https://doi.org/10.3389/fgene.2019.00177>
- Manni, F., Guérard, E., & Heyer, E. (2004). Geographic patterns of (genetic, morphologic, linguistic) variation: How barriers can be detected by “Monmonier's algorithm”. *Human Biology*, 76, 173–190. <https://www.jstor.org/stable/41466226>

- Manning, R. B., & Chace, F. A. (1990). Decapod and Stomatopod Crustacea from Ascension Island, South Atlantic Ocean. *Smithsonian Contribution to Zoology*, 503, 1–91. http://www.sil.si.edu/smithsoniancontributions/zoology/pdf_hi/sctz-0503.pdf
- Marshall, D. J., Monro, K., Bode, M., Keough, M. J., & Swearer, S. (2010). Phenotype-environment mismatches reduce connectivity in the sea. *Ecology Letters*, 13, 128–140. <https://doi.org/10.1111/j.1461-0248.2009.01408.x>
- Medina, A. D. (2007). Structure et dynamique spatio-temporelle des populations démersales dans un système d'archipel océanique tropical. Le cas de l'archipel du Cap Vert (océan Atlantique Est) (PhD thesis). Université du Québec, Rimouski, Canada.
- Meirmans, P. G., & Hedrick, P. W. (2011). Assessing population structure: F_{ST} and related measures. *Molecular Ecology Resources*, 11, 5–18. <https://doi.org/10.1111/j.1755-0998.2010.02927.x>
- Melo, G. A. S. (1999). *Manual de identificação dos Crustacea Decapoda do Litoral Brasileiro: Anomura, Thalassinidea, Palinuridea, Astacidea*. São Paulo: Ed. Plêiade/FAPESP, Brazil.
- Moro, L., Herrera, R., Ortea, J., Riera, R., Bacallado, J. J., & Martín, J. (2014). Aportaciones al conocimiento y distribución de los decápodos y estomatópodos (Crustacea: Malacostraca) de las Islas Canarias. *Revista de la Academia Canaria de Ciencias (= Folia Canariensis Academiae Scientiarum)*, 26, 33–82.
- Norton, E. L. (2013). Empirical and biophysical Modeling studies of dispersal barriers for marine plankton (MSc thesis). University of Hawaii at Manoa, Honolulu, Hawaii.
- Norton, E. L., & Goetze, E. (2013). Equatorial dispersal barriers and limited population connectivity among oceans in a planktonic copepod. *Limnology and Oceanography*, 58, 1581–1596. <https://doi.org/10.4319/lo.2013.58.5.1581>
- Palero, F., Abelló, P., Macpherson, E., Beaumont, M., & Pascual, M. (2011). Effect of oceanographic barriers and overfishing on the population genetic structure of the European spiny lobster (*Palinurus elephas*). *Biological Journal of Linnean Society*, 104, 407–418. <https://doi.org/10.1111/j.1095-8312.2011.01728.x>
- Palumbi, S. R. (1994). Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics*, 25, 547–572. <https://doi.org/10.1146/annurev.es.25.110194.002555>
- Palumbi, S. R. (1996). Chapter 7: Nucleic Acids II: The Polymerase Chain Reaction. In D. Hillis, & C. Moritz (Eds.), *Molecular systematic* (pp. 205–247). Sunderland, USA: Sinauer Associates.
- Paris, C. B., Cherubin, L. M., & Cowen, R. K. (2007). Surfing, diving or spinning: Effects on population connectivity. *Marine Ecology Progress Series*, 347, 285–300. <https://doi.org/10.3354/meps06985>
- Paris, C. B., & Cowen, R. K. (2004). Direct evidence of a biophysical retention mechanism for coral reef fish larva. *Limnology and Oceanography*, 49, 1064–1079. <https://doi.org/10.4319/lo.2004.49.6.1064>
- Peakall, R., & Smouse, P. E. (2012). GenAEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research - an update. *Bioinformatics*, 28, 2537–2539. <https://doi.org/10.1093/bioinformatics/bts460>
- Pelegrí, J. L., & Peña-Izquierdo, J. (2015). Eastern boundary currents off North-West Africa. In L. Valdés, & I. Déniz-González (Eds.), *Oceanographic and biological features in the canary current large marine ecosystem* (pp. 115–383). Paris, FRA: IOC-UNESCO Technical Series.
- Phillips, B. F., Cobb, J. S., & George, R. W. (1980). General biology. In J. S. Cobb, & B. F. Phillips (Eds.), *The biology and management of lobsters* (pp. 1–82). New York, USA: Academic Press.
- Pineda, J., Hare, J. A., & Sponaugle, S. (2007). Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography*, 20, 22–39. <https://doi.org/10.5670/oceanog.2007.27>
- Pinheiro, A. P., Freire, F. A. M., & Lins-Oliveira, J. E. (2003). Population biology of *Panulirus echinatus* Smith, 1869 (Decapoda: Palinuridae) from São Pedro and São Paulo Archipelago, northeastern Brazil. *Nauplius*, 11, 27–35.
- Pinheiro, A. P., & Lins-Oliveira, J. E. (2006). Reproductive biology of *Panulirus echinatus* (Crustacea: Palinuridae) from São Pedro and São Paulo Archipelago, Brazil. *Nauplius*, 14, 89–97.
- Planes, S., Jones, G. P., & Thorrold, S. R. (2009). Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Science in the United States of America*, 106, 5693–5697. <https://doi.org/10.1073/pnas.0808007106>
- Porobić, J., Canales-Aguirre, C. B., Ernst, B., Galleguillos, R., & Hernández, C. E. (2013). Biogeography and historical demography of the Juan Fernández rock lobster, *Jasus frontalis* (Milne Edwards, 1837). *Journal of Heredity*, 104, 223–233. <https://doi.org/10.1093/jhered/ess141>
- Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155, 945–959.
- Ptacek, M. B., Sarver, S. K., Childress, M. J., & Herrnkind, W. F. (2001). Molecular phylogeny of the spiny lobster genus *Panulirus* (Decapoda: Palinuridae). *Marine and Freshwater Research*, 52, 1037–1048. <https://doi.org/10.1071/MF01070>
- Rannala, B., & Mountain, J. L. (1997). Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Science in the United States of America*, 94, 9197–9201. <https://doi.org/10.1073/pnas.94.17.9197>
- Raymond, M., & Rousset, F. (1995). Genepop (version 1.2) population genetics software for exact tests and ecumenicism. *Journal of Heredity*, 86, 248–249. <https://doi.org/10.1093/oxfordjournals.jhered.a111573>
- Riera, R., Becerro, M. A., Stuart-Smith, R. D., Delgado, J. D., & Edgar, G. J. (2014). Out of sight, out of mind: Threats to the marine biodiversity of the Canary Islands (NE Atlantic Ocean). *Marine Pollution Bulletin*, 86, 9–18. <https://doi.org/10.1016/j.marpolbul.2014.07.014>
- Riginos, C., Douglas, K. E., Jin, Y., Shanahan, D. F., & Tremblay, E. A. (2011). Effects of geography and life history traits on genetic differentiation in benthic marine fishes. *Ecography*, 34, 566–575. <https://doi.org/10.1111/j.1600-0587.2010.06511.x>
- Rousset, F. (2008). Genepop'007: A complete re-implementation of the Genepop software for Windows and Linux. *Molecular Ecology Resources*, 8, 103–106. <https://doi.org/10.1111/j.1471-8286.2007.01931.x>
- Rudorff, C. A. G., Lorenzetti, J. A., Gherardi, D. F. M., & Lins-Oliveira, J. E. (2009). Modeling spiny lobster larval dispersion in the Tropical Atlantic. *Fisheries Research*, 96, 206–215. <https://doi.org/10.1016/j.fishres.2008.11.005>
- Sangrà, P. (2015). Canary Islands eddies and coastal upwelling filaments off North-west Africa. In L. Valdés, & Déniz-González, I. (Eds.), *Oceanographic and biological features in the canary current large marine ecosystem*. IOC-UNESCO technical series. (pp. 105–114). Paris: FRA. URL: <http://hdl.handle.net/1834/9181>
- Sangrà, P., Pelegrí, J. L., Hernández-Guerra, A., Arregui, I., Martín, J. M., Marrero-Díaz, A., ... Rodríguez-Santana, A. (2005). Life History of an anticyclonic eddy. *Journal of Geophysical Research*, 110, 1–19. <https://doi.org/10.1029/2004JC002526>
- Santos, M. F., Souza, I. G. B., Gomes, S. O., Silva, G. R., Bentzen, P., & Diniz, F. M. (2018). Isolation and characterization of microsatellite markers in the spiny lobster, *Panulirus echinatus* Smith, 1869 (Decapoda: Palinuridae) by Illumina MiSeq sequencing. *Journal of Genetics*, 97, e25–e30. <https://doi.org/10.1007/s12041-018-0895-y>
- Selkoe, K. A., & Toonen, R. J. (2011). Marine connectivity: A new look at pelagic larval duration and genetic metrics of dispersal. *Marine Ecology Progress Series*, 436, 291–305. <https://doi.org/10.3354/meps09238>
- Shanks, A. L. (2009). Pelagic larval duration and dispersal distance revisited. *The Biological Bulletin*, 216, 373–385. <https://doi.org/10.1086/BBLv216n3p373>
- Shanks, A. L., Grantham, B. A., & Carr, M. H. (2003). Propagule dispersal distance and the size and spacing of marine reserves. *Ecological*

- Applications*, 13, S159–S169. [https://doi.org/10.1890/1051-0761\(2003\)013\[0159:PDDATS\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0159:PDDATS]2.0.CO;2)
- Siegel, D. A., Kinlan, B. P., Gaylord, B., & Gaines, S. D. (2003). Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series*, 260, 83–96. <https://doi.org/10.3354/meps260083>
- Silva, M. B., Campos, C. E. C., Targino, S. G., & Melo, E. D. C. A. (2001). Aspectos populacionais da lagosta *Panulirus echinatus* Smith, 1869 na Reserva Biológica do Atol das Rocas - Brasil. *Holos Environment*, 1, 187–198.
- Stramma, L. (2001). Current systems in the Atlantic Ocean. In J. Steele, S. Thorpe, & K. Turekian (Eds.), *Encyclopedia of ocean sciences* (pp. 589–598). London, UK: Academic Press.
- Stramma, L., & Schott, F. (1999). The mean flow field of the tropical Atlantic Ocean. *Deep Sea Research II: Topical Studies in Oceanography*, 46, 279–303. [https://doi.org/10.1016/S0967-0645\(98\)00109-X](https://doi.org/10.1016/S0967-0645(98)00109-X)
- Talley, L. D., Pickard, G. L., Emery, W. J., & Swift, J. H. (2011). *Descriptive physical oceanography: An introduction* (6th ed.). Boston, USA: Elsevier.
- Tigano, A., Shultz, A. J., Edwards, S. V., Robertson, G. J., & Friesen, V. L. (2017). Outlier analyses to test for local adaptation to breeding grounds in a migratory arctic seabird. *Ecology and Evolution*, 7, 2370–2381. <https://doi.org/10.1002/ece3.2819>
- Tourinho, J. L., Solé-Cava, A. M., & Lazoski, C. (2012). Cryptic species within the commercially most important lobster in the tropical Atlantic, the spiny lobster *Panulirus argus*. *Marine Biology*, 159, 1897–1906. <https://doi.org/10.1007/s00227-012-1977-7>
- Truelove, N. K., Ley-Cooper, K., Segura-García, I., Briones-Fourzán, P., Lozano-Álvarez, E., Phillips, B. F., ... Preziosi, R. F. (2015). Genetic analysis reveals temporal population structure in Caribbean spiny lobster (*Panulirus argus*) within marine protected areas in Mexico. *Fisheries Research*, 172, 44–49. <https://doi.org/10.1016/j.fishres.2015.05.029>
- Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., & Shipley, P. (2004). MICROCHECKER: Software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, 4, 535–538. <https://doi.org/10.1111/j.1471-8286.2004.00684.x>
- Vianna, M. L. (1986). On the ecology and intraspecific variation in the spiny lobster *Panulirus echinatus* Smith, 1869 (Decapoda, Palinuridae) from Brazil. *Crustaceana*, 51, 25–37. <https://www.jstor.org/stable/20104161>
- Weersing, K., & Toonen, R. J. (2009). Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology Progress Series*, 393, 1–12. <https://doi.org/10.3354/meps08287>
- Weisberg, R. H. (2001). An observer's view of equatorial Ocean Currents. *Oceanography*, 14, 27–33.

SUPPORTING INFORMATION

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

How to cite this article: Gaeta J, Acevedo I, López-Márquez V, et al. Genetic differentiation among Atlantic island populations of the brown spiny lobster *Panulirus echinatus* (Decapoda: Palinuridae). *Aquatic Conserv: Mar Freshw Ecosyst*. 2020;30: 868–881. <https://doi.org/10.1002/aqc.3297>