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BIODIVERSITY RESEARCH

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Isolation by oceanic distance and spatial genetic structure in an overharvested international fishery

Nathan K. Truelove[1] | Stephen J. Box[1] | Karl A. Aiken[2] | Azra Blythe-Mallett[2] | Erik M. Boman[3] | Catherine J. Booker[4] | Tamsen T. Byfield[5] | Courtney E. Cox[1] | Martha H. Davis[4] | Gabriel A. Delgado[6] | Bob A. Glazer[6] | Sarah M. Griffiths[7] | Kimani Kitson-Walters[2] | Andy S. Kough[8] | Ricardo Pérez Enríquez[9] | Richard F. Preziosi[7] | Marcia E. Roy[2] | Iris Segura-García[1] | Mona K. Webber[2] | Allan W. Stoner[4]

[1]Smithsonian National Museum of Natural History, Smithsonian Marine Station, Fort Pierce, FL, USA

[2]University of West Indies, Mona, Jamaica

[3]Wageningen University, Wageningen, The Netherlands

[4]Community Conch, Newport, OR, USA

[5]School for Field Studies, South Caicos, Turks and Caicos Islands

[6]Florida Fish and Wildlife Conservation Commission, Marathon, FL, USA

[7]School of Science and the Environment, Manchester Metropolitan University, Manchester, UK

[8]Shedd Aquarium, Daniel P. Haerther Center for Conservation and Research, Chicago, IL, USA

[9]Centro de Investigaciones Biologicas del Noroeste, La Paz, Baja California Sur, México

Correspondence
Nathan Kobun Truelove, Smithsonian National Museum of Natural History, Smithsonian Marine Station, Fort Pierce, FL, USA.
Email: trueloven@si.edu

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Abstract

Aim: A detailed understanding of spatial genetic structure (SGS) and the factors driving contemporary patterns of gene flow and genetic diversity are fundamental for developing conservation and management plans for marine fisheries. We performed a detailed study of SGS and genetic diversity throughout the overharvested queen conch (*Lobatus gigas*) fishery. Caribbean countries were presented as major populations to examine transboundary patterns of population differentiation.

Location: Nineteen locations in the greater Caribbean from Anguilla, the Bahamas, Belize, Caribbean Netherlands, Honduras, Jamaica, Mexico, Turks and Caicos, and the USA.

Methods: We genotyped 643 individuals with nine microsatellites. Population genetic and multivariate analyses characterized SGS. We tested the alternate hypotheses: (1) SGS is randomly distributed in space or (2) pairwise genetic structure among sites is correlated with oceanic distance (IBOD).

Results: Our study found that *L. gigas* does not form a single panmictic population in the greater Caribbean. Significant levels of genetic differentiation were identified between Caribbean countries (F_{CT} = 0.011; p = .0001), within Caribbean countries (F_{SC} = 0.003; p = .001), and among sites irrespective of geographic location (F_{ST} = 0.013; p = .0001). Gene flow across the greater Caribbean was constrained by oceanic distance (p = .0009; Mantel r = .40), which acted to isolate local populations.

Main conclusions: Gene flow over the spatial scale of the entire Caribbean basin is constrained by oceanic distance, which may impede the natural recovery of overfished *L. gigas* populations. Our results suggest a careful blend of local and international management will be required to ensure long-term sustainability for the species.

KEYWORDS
connectivity, conservation, dispersal, fisheries, genetics, spatial

1 | INTRODUCTION

A detailed understanding of spatial genetic structure (SGS) and the factors driving contemporary patterns of gene flow are fundamental for understanding marine species' responses to fishing pressure, habitat destruction, and climate change (Bay & Palumbi, 2014; D'Aloia, Bogdanowicz, Harrison, & Buston, 2014; D'Aloia et al., 2015; Pinsky & Palumbi, 2014). Likewise, knowledge of SGS is necessary for informing conservation approaches, such as identifying ecologically significant units (Palsbøll, Berube, & Allendorf, 2007), identifying the appropriate spatial scale of marine protected areas (Gaines, White, Carr, & Palumbi, 2010), and fostering international relations to conserve species whose ranges span geopolitical boundaries (Kough, Paris, & Butler, 2013; Truelove et al., 2015). Understanding the ecological and physical drivers of SGS is complicated due to the bipartite life histories of marine species (D'Aloia et al., 2014). For example, the adults of many benthic marine species are primarily sedentary with the majority of dispersal occurring during a pelagic larval phase that is subjected to prevailing ocean currents (Selkoe, Henzler, & Gaines, 2008).

As the resilience of marine species to anthropogenic pressure is strongly linked to the degree of connectivity within metapopulations (Kritzer & Sale, 2004), a great deal of research has focused on developing genetic and biophysical models to quantify larval dispersal and thus understand how it shapes SGS (Selkoe, Gaggiotti, Bowen, & Toonen, 2014). For example, the biophysical modeling studies of the coastal boundary layer (CBL)—a prominent feature in the coastal ocean with reduced velocities due to friction with the shore—suggest that self-retention of larvae is common in the CBL, regardless of the length of a species' pelagic larval duration (PLD; Nickols, White, Largier, & Gaylord, 2015). Therefore, nearshore processes such as those associated with the CBL may have a profound effect on SGS, particularly in benthic marine species that spawn in shallow nearshore habitats.

Lobatus gigas is a large benthic marine gastropod (shell length can exceed 30 cm) of high economic and cultural importance that form spawning aggregations in shallow seagrass and sand plain habitats throughout the greater Caribbean (Mueller & Stoner, 2013; Randall, 1964). The species is heavily fished and is the basis of a lucrative export market to the United States and Europe (Acosta, 2006). *Lobatus gigas* is harvested in over 25 Caribbean nations and territories and populations have experienced significant declines throughout its range due to overfishing (Stoner, Davis, & Booker, 2012a). For example, the fishery collapsed in Florida and has yet to recover despite nearly a 30-year ban on fishing and active restoration efforts (Delgado & Glazer, 2007). In addition, *L. gigas* was listed on Appendix II of the Convention on International Trade of Endangered Species of Flora and Fauna (CITES) in 1990 (Acosta, 2006). By 2004, the CITES Authority suspended trade in the Dominican Republic, Haiti, Honduras, Antigua and Barbuda, Barbados, Dominica, and Trinidad and Tobago based on evidence of declining stock or lack of an effective management framework (Acosta, 2006). As such, elucidating the SGS of *L. gigas* in the Caribbean is vital, especially if it can improve management practices (e.g., regional vs. local management efforts).

Early genetic studies of *L. gigas* using electrophoretic methods found a high degree of gene flow among populations dispersed over the species' geographic distribution, with definitive separation observed only between populations in Bermuda and those in the Caribbean basin (Mitton, Berg, & Orr, 1989). At the local level, Perez-Enriquez, Garcia-Rodriguez, Mendoza-Carrion, and Padilla (2011) and Zamora-Bustillos, Rodríguez-Canul, García de León, and Tello-Cetina (2011) found with mitochondrial DNA and microsatellites, respectively, low genetic differentiation among locations in the Mexican Caribbean. In the Florida Keys and Bimini, Campton, Berg, Robinson, and Glazer (1992) also found low genetic differentiation. Although Mitton et al. (1989) found limited evidence of population structure in the Caribbean, the authors hypothesized that the complex ocean currents of the Caribbean may restrict gene flow among Caribbean populations, even though larvae may disperse long distances throughout the Caribbean during their 16–28 days PLD (Davis, Bolton, & Stoner, 1993). Over the last decade, advances in biophysical modeling and seascape genetics suggest that larval behavior of marine species, coupled with the complex hydrodynamics of the marine environment, may limit gene flow leading to fine-scale patterns of SGS (D'Aloia et al., 2015; Iacchei et al., 2013; Selkoe et al., 2010; Thomas et al., 2015). These findings suggest that a more detailed examination of *L. gigas* population connectivity is warranted.

In this study, we used microsatellite markers and a comprehensive sampling strategy to perform a detailed study of SGS of *L. gigas* across the greater Caribbean seascape. First, we conducted basic population genetic analyses to determine if there is evidence for population differentiation among localities within and between Caribbean countries. Second, we used multivariate analysis to visualize SGS. Third, we tested the alternate hypotheses: (1) SGS is randomly distributed in space or (2) pairwise genetic structure among sites is correlated with oceanic distance (IBOD).

2 | METHODS

2.1 | Sample collection

We characterized SGS of *L. gigas* across the greater Caribbean seascape using nine microsatellites and sampling 643 individuals from 19 locations (Figure 1). Small pieces of mantle tissue (<1 cm^2) were excised and preserved in 95% ethanol or placed on filter paper for drying. Genomic DNA was extracted using the Qiagen DNeasy kit. Samples for Alacranes reef were processed as described in Perez-Enriquez et al. (2011).

2.2 | Microsatellite genotyping

Queen conch was genotyped using nine polymorphic microsatellite loci (Truelove, Fai Ho, Preziosi, & Box, 2016; Zamora-Bustillos, Rodríguez-Canul, & De León, 2007). Genotyping was performed using an ABI 3730xl automatic DNA sequencer (Applied Biosystems) at the Smithsonian Institute's Laboratory of Analytical Biology. Microsatellite

alleles were scored manually with GeneMapper® v3.7 software package (Applied Biosystems).

2.3 | Data quality checks

Microsatellite alleles were binned with the R-package MsatAllele version 1.02 (Alberto, 2009). Microsatellite loci were examined with MICROCHECKER 2.2.3 to check for patterns caused by null alleles, allele scoring error due to either large allele dropout or stutter, or other natural processes (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). FREENA was used to assess bias in calculations of F_{ST} caused by null alleles (Chapuis & Estoup, 2007). Linkage disequilibrium was tested using GENEPOP with the values for the dememorization number, number of batches, and number of iterations per batch all set to 10K. (Raymond & Rousset, 1995; Rousset, 2008).

2.4 | Genetic differentiation

A hierarchical AMOVA was run in GENODIVE (Meirmans, 2012; Meirmans & Van Tienderen, 2004) to identify differences between Caribbean nations/territories (F_{CT}), among sites within Caribbean nations/territories (F_{SC}), and among sites irrespective of political boundaries (F_{ST}). An infinite allele model was used based on Weir and Cockerham's (1984) calculations of F_{ST} (Weir & Cockerham, 1984), and the level of significance was tested using 50,000 permutations. Hedrick's G'_{ST} was calculated in GENODIVE using 50,000 permutations. Hedrick's G'_{ST} can be a more appropriate measure of genetic differentiation when heterozygosity is high, as is the case here, as it corrects for the tendency of F_{ST} to decline as polymorphism increases (Hedrick, 2005). The *p*-values for pairwise comparisons of genetic differentiation were calculated in GENODIVE with the log-likelihood *G*-statistic using 50,000 permutations. The false discovery rate multitest correction was used as a correction against Type I errors for all statistical analyses that included multiple comparisons (Benjamini & Yekutieli, 2001).

2.5 | Isolation-by-oceanic-distance

Euclidean distances may not accurately represent connectivity in the ocean, where islands and currents can impede routes of travel. We developed a simple measure of oceanographic distance between pairs of locations based on current fields from an operational ocean circulation model, Global HYCOM + NCODA assimilated (Chassignet et al., 2007). We calculated the average surface current velocity north and east from 2004 through 2013 during peak conch spawning (June and July; Aldana Aranda et al., 2014) within a rectangle bounded by the latitudes and longitudes of any pair of sites. The average current velocity north and east was then multiplied by a lower estimate of the duration of a conch's planktonic larval phase (14 days; Stoner, 2003) to come up with an oceanographic cost of traveling in each direction. These values were then added to the distance north and distance east, which were calculated using the Pythagorean theorem and the Euclidean distance as the hypotenuse. The Pythagorean theorem was applied again to calculate an oceanographic distance incorporating average decadal circulation through the area separating two points. Thus, a distance was increased if it was against the average current flow and reduced if it went with the current.

We tested for correlations of genetic distance (F_{ST} and G'_{ST}) with oceanic distance, referred to as isolation-by-oceanic-distance (IBOD), in the R-package ADEGENET (Jombart, 2008) using a Mantel test with 10,000 permutations. A separate spatially explicit analysis of genetic variation was conducted using the spatial principal component analysis in the R-package ADEGENET (Jombart, 2008) following the methodology of Truelove et al. (2015). Briefly, we selected the first principal component that contained the highest levels of both spatial autocorrelation and genetic variance. Spatial patterns of genetic variation were visualized by color-coding the lagged score of the first principal component using the RColorBrewer package (http://colorbrewer2.org).

3 | RESULTS

3.1 | Microsatellite analysis

There were 23 significant departures from Hardy–Weinberg Equilibrium HWE out of 171 comparisons across microsatellite loci and populations (Table S1). However, significant deviations from HWE were not consistently observed across loci or populations. All microsatellite loci were polymorphic, with effective number of alleles per population ranging from 5.24 to 7.39 (Tables S2 and S3). No evidence of significant linkage disequilibrium was observed among microsatellite loci. Analyses in MICROCHECKER suggested that deviations from HWE were not due to scoring error or large allele dropout. Although MICROCHECKER did not rule out the possibility of null alleles attributing to deviations from HWE; analysis with FREENA indicated that potential bias on calculations of global F_{ST} caused by null alleles was negligible (Global F_{ST} = 0.0141; Global F_{ST} with correction for null alleles = 0.0142). Therefore, all microsatellite loci were included in analyses of population structure.

3.2 | Population structure

Microsatellite genetics identified significant levels of genetic differentiation between Caribbean countries (F_{CT} = 0.011; p = .0001), within Caribbean countries (F_{SC} = 0.003; p = .001), and among sites irrespective of its geographic location (F_{ST} = 0.013; p = .0001). Pairwise comparisons of F_{ST} ranged from −0.028 to 0.282 with 84 of 171 pairwise comparisons significant after FDR correction (p < .0074; Table 1). Comparisons of the two metrics of population structure, F_{ST} and G'_{ST}, respectively, were highly correlated ($p < 2.2\ e^{-16}$; R^2 = 0.99). Principle coordinate analysis of site-specific levels of pairwise F_{ST} and G'_{ST} were both in agreement indicating that Alacranes Reef (Mexico), Florida Keys (USA), and Saint Eustatius (Caribbean Netherlands) were the most genetically divergent sites (Figure 2).

The spatial principal component analysis using nine microsatellite loci suggested that queen conch in the eastern Caribbean was most differentiated from queen conch from sites in the western Caribbean in terms of positive spatial autocorrelation and genetic variance (Figure 3).

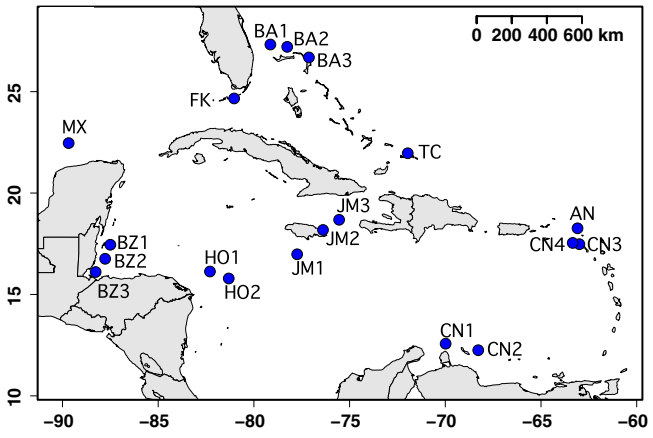

FIGURE 1 Map of the greater Caribbean showing locations of the *Lobatus gigas* sampling sites in blue. Site codes are FK, Delta Shoal, Florida; MX, Alacranes Reef, Mexico; BZ1, Lighthouse Atoll, Belize; BZ2, Glover's Reef, Belize; BZ3, Sapodilla Cayes, Belize; HO1, Banco Gordo, Honduras; HO2, Banco Oneida; JM1, Pedro Bank, Jamaica, JM2, Alligator Head, Jamaica; JM3, Formigas Bank; CN1, Caribbean Netherlands, Aruba; CN2, Caribbean Netherlands, Bonaire; CN3, Caribbean Netherlands, Saint Eustatius; CN4, Caribbean Netherlands, Saba; AN, Anguilla; TC, Turks and Caicos; BA1, Matanilla Shoal, Bahamas; BA2, Double Breasted Cay, Bahamas; and BA3, Whale Cay, Bahamas. [Colour figure can be viewed at wileyonlinelibrary.com]

Isolation-by-oceanic-distance analysis (Figure 4, Table S4) indicated that gene flow across the greater Caribbean was constrained by oceanic distance (p = .0009; Mantel r = .40). For simplicity, we reported F_{ST} and not G'_{ST} as the two metrics of population differentiation were highly correlated.

4 | DISCUSSION

This study advances our understanding of SGS in *L. gigas* throughout the greater Caribbean. The central finding of our study is that gene flow over the spatial scale of the entire Caribbean basin is constrained by oceanic distance. We identified significant genetic IBOD and found evidence of several regionally isolated populations throughout the greater Caribbean. The significant levels of IBOD provide indirect genetic evidence that the dispersal of *L. gigas* larvae is limited in multiple regions throughout the range of the species.

Lobatus gigas does not form a single panmictic population in the Caribbean. Microsatellite genetics identified significant levels of genetic differentiation among Caribbean subregions (e.g., Florida Keys, Mesoamerican Barrier Reef, Lesser Antilles, Honduran/Jamaican Banks, Greater Antilles, and Bahamas) and between the eastern and western Caribbean regions. These findings were supported by the spatial principal component analysis (Jombart, Devillard, Dufour, & Pontier, 2008). Site-specific pairwise comparisons of genetic differentiation found that the Florida Keys (USA), Saint Eustatius (Caribbean Netherlands), and Alacranes Reef (Mexico) were significantly differentiated from nearly all other sites in the Caribbean. These findings provide additional support for hypotheses generated by previous genetic studies of queen conch. Perez-Enriquez et al. (2011) hypothesized that clinal patterns in haplotype frequencies were caused by isolation-by-distance. Likewise, Mitton et al. (1989) hypothesized that Caribbean ocean currents were largely responsible for the lack of panmixia observed in their study. Overall, the findings of our study provide genetic evidence of significant SGS that was explained by IBOD.

Isolation-by-oceanic-distance was a key driver of the limited gene flow we observed among *L. gigas* populations. Likewise, Zhan et al. (2009) found ocean currents to be responsible for genetic differentiation in the Zhikong Scallop (*Clamys farreri*). These findings are corroborated by White et al. (2010), which used an IBOD approach to explain 50% of the genetic variance in the commercially harvested gastropod mollusc *Kelletia kelletii*. Teske, Sandoval-Castillo, van Sebille, Waters, and Beheregaray (2016) used the IBOD approach to reveal high levels of self-recruitment in the limpet *Siphonaria diemenensis* that was driven by low-velocity nearshore currents that acted to retain larvae locally. Biophysical modeling studies of marine species in the Caribbean with a similar PLD to *L. gigas* (e.g., corals and reef fish) suggest that larvae are likely to disperse among localities via the prevailing Caribbean current, which is largely continuous and unidirectional (Galindo, Olson, & Palumbi, 2006; Kool, Paris, Andréfouët, & Cowen, 2010; Purcell, Cowen, Hughes, & Williams, 2009). Persistent gyres and the CBL constitute important oceanographic mechanisms that promote local retention of larvae (Kough et al., 2013; Nickols et al., 2015). The significant levels of IBOD among *L. gigas* populations provides additional support to the growing body of evidence that oceanographic currents help explain SGS in high-gene flow marine species.

The offshore banks of Honduras and Jamaica may play an important role for facilitating connectivity among Caribbean queen conch populations. Pairwise comparison of genetic differentiation and spatial principal component analysis provided evidence of long-distance gene flow (i.e., >1,000 km) between *L. gigas* populations from Pedro Bank (Jamaica) and all sites in the Caribbean Netherlands. Likewise, long-distance gene flow was found among queen conch populations from the Honduran Banks, Bahamas, and Turks and Caicos. These findings suggest that the offshore banks of Honduras and Jamaica may be important stepping stones for facilitating gene flow among queen conch populations on the Caribbean wide scale. Additional evidence of the importance of these offshore banks in facilitating long-distance connectivity comes from genetic research of spiny lobster fishery, which found high levels of gene flow between the Honduran Banks and lobster populations in Panama, Mexico, and Belize (Truelove et al., 2014). The offshore network of banks in Honduras, Nicaragua, and Jamaica remain poorly studied (Chollett, Stoyle, & Box, 2013), and more research is required to understand the role that this remote region of the Caribbean plays in the connectivity of marine species.

Biophysical modeling studies have shown coastal boundary features act to retain the bulk of larvae locally while a small, but significant, proportion can be exported vast distances (Butler, Paris, Goldstein, Matsuda, & Cowen, 2011; Nickols et al., 2015). The long-distant migrants at the tail of the dispersal kernel may provide sufficient levels of gene flow to mask SGS when using a small number of neutral nuclear

TABLE 1 Pairwise matrix of above and pairwise F_{ST} below the diagonal. Significant values are displayed in bold after false discovery rate correction ($p < .0074$)

	BA1	BA2	BA3	TC	FK	MX	BZ1	BZ2	BZ3	HO1	HO2	JM1	JM2	JM3	CN1	CN2	CN3	CN4	AN
BA1		−0.028	0.025	−0.005	0.041	**0.214**	0.063	0.045	0.046	−0.017	−0.022	0.004	−0.017	−0.006	−0.007	0.031	−0.007	0.000	0.036
BA2	−0.007		0.008	0.001	0.030	**0.184**	**0.064**	**0.052**	0.040	−0.002	0.012	0.028	−0.001	**0.006**	0.025	**0.079**	**0.048**	0.019	**0.094**
BA3	0.005	0.002		**0.041**	**0.074**	**0.100**	**0.062**	**0.088**	**0.074**	**0.059**	0.052	**0.066**	**0.060**	**0.047**	0.057	**0.124**	**0.111**	**0.089**	**0.124**
TC	−0.001	0.000	**0.009**		0.032	**0.210**	**0.039**	**0.044**	**0.022**	−0.004	0.013	0.017	**0.021**	**0.015**	0.026	**0.079**	**0.062**	0.035	**0.081**
FK	0.009	0.006	**0.015**	0.007		**0.225**	**0.096**	**0.085**	0.060	0.042	**0.078**	0.049	**0.092**	**0.062**	0.058	**0.105**	**0.101**	**0.075**	**0.165**
MX	**0.050**	**0.040**	**0.021**	**0.047**	**0.050**		**0.182**	**0.214**	**0.183**	**0.203**	**0.229**	**0.235**	**0.212**	**0.228**	**0.172**	**0.282**	**0.265**	**0.258**	**0.282**
BZ1	0.013	**0.012**	**0.012**	**0.008**	**0.019**	**0.037**		0.013	−0.008	**0.028**	0.040	**0.054**	**0.060**	**0.050**	**0.064**	**0.118**	**0.076**	**0.109**	**0.135**
BZ2	0.010	**0.011**	**0.018**	**0.009**	**0.019**	**0.048**	0.003		0.005	**0.023**	0.007	0.024	0.050	**0.036**	**0.054**	**0.055**	0.034	0.047	**0.093**
BZ3	0.010	**0.008**	**0.015**	**0.004**	**0.013**	0.039	−0.002	0.001		0.006	0.020	0.047	0.032	**0.046**	0.046	**0.123**	0.075	0.094	**0.128**
HO1	−0.004	−0.001	0.013	−0.001	0.010	0.048	**0.006**	0.005	0.001		−0.014	0.005	−0.012	0.006	0.011	**0.069**	0.040	0.043	**0.085**
HO2	−0.005	0.003	**0.012**	0.003	**0.018**	**0.054**	0.009	0.002	0.004	−0.003		−0.007	−0.014	0.009	0.000	0.025	0.021	0.013	**0.034**
JM1	0.001	0.007	**0.015**	0.004	0.012	**0.058**	**0.012**	0.006	0.011	0.001	−0.002		0.038	0.021	−0.010	−0.007	0.016	0.011	**0.067**
JM2	−0.004	0.000	**0.012**	**0.005**	**0.020**	**0.047**	**0.012**	0.011	0.007	−0.002	−0.003	0.009		0.003	0.024	**0.081**	0.053	0.050	**0.064**
JM3	−0.001	**0.001**	**0.010**	**0.003**	**0.013**	**0.050**	**0.010**	**0.007**	**0.009**	0.001	0.002	0.005	0.001		0.019	**0.060**	**0.049**	0.021	**0.079**
CN1	−0.002	0.005	0.013	0.006	**0.014**	0.041	**0.014**	**0.013**	0.011	0.003	0.000	−0.003	0.006	0.004		0.030	**0.030**	0.018	**0.074**
CN2	0.009	**0.020**	**0.031**	**0.020**	**0.027**	**0.073**	**0.028**	**0.014**	**0.030**	**0.018**	0.007	−0.002	**0.021**	**0.015**	0.009		0.018	0.017	**0.067**
CN3	−0.002	**0.012**	**0.027**	**0.015**	**0.026**	**0.067**	**0.018**	0.009	**0.018**	0.010	0.006	0.004	**0.014**	**0.012**	0.008	0.005		0.023	**0.062**
CN4	0.000	0.004	**0.021**	**0.009**	**0.019**	**0.065**	**0.025**	0.012	**0.022**	0.011	0.004	0.003	0.013	0.005	0.005	0.005	0.006		0.064
CN5	0.010	**0.023**	**0.032**	**0.021**	**0.044**	**0.075**	**0.033**	**0.025**	**0.032**	**0.023**	**0.009**	**0.020**	**0.018**	**0.019**	**0.022**	**0.020**	**0.018**	0.018	

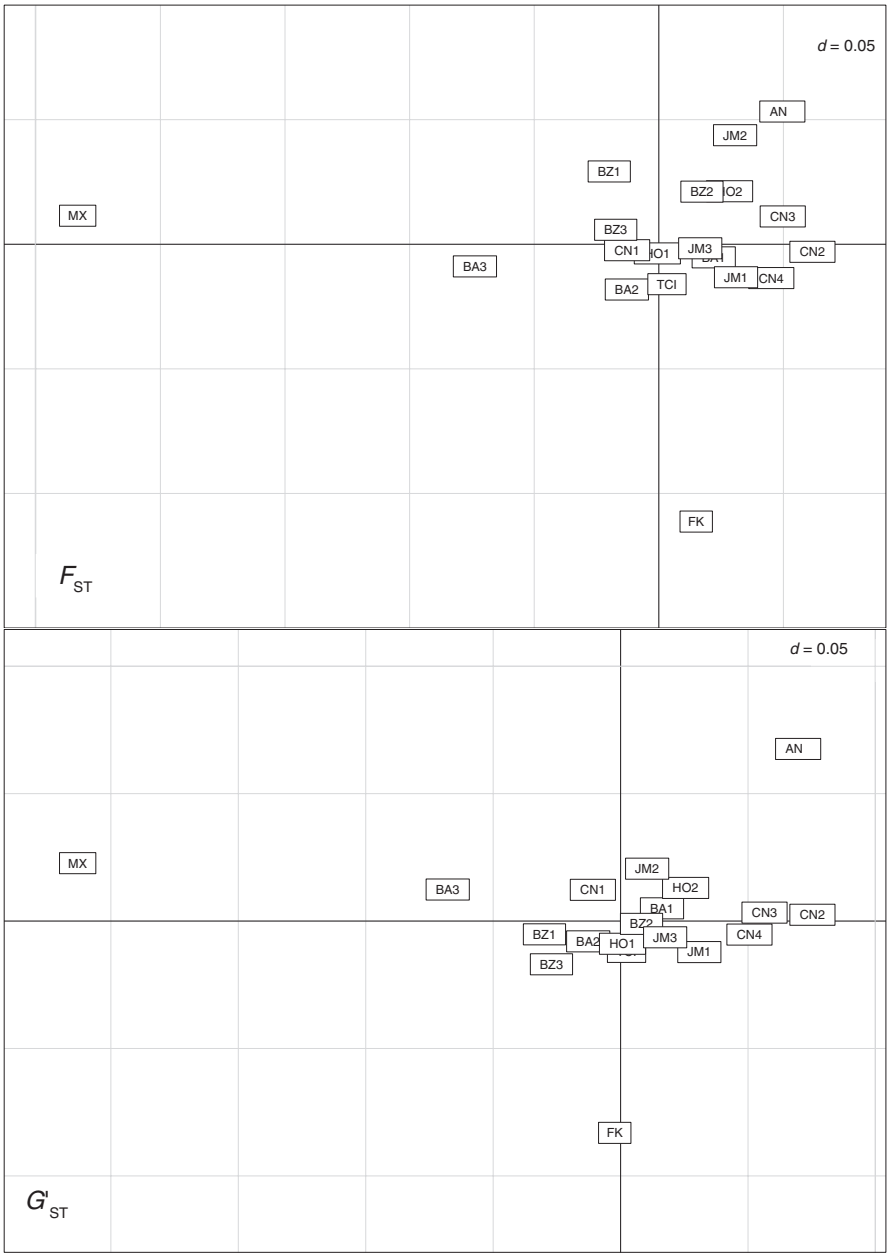

FIGURE 2 Principle coordinates analysis of site-specific pairwise comparisons of genetic differentiation, F_{ST} (top panel) and G'_{ST} (bottom panel). Site codes are FK, Delta Shoal, Florida; MX, Alacranes Reef, Mexico; BZ1, Lighthouse Atoll, Belize; BZ2, Glover's Reef, Belize; BZ3, Sapodilla Cayes, Belize; HO1, Banco Gordo, Honduras; HO2, Banco Oneida; JM1, Pedro Bank, Jamaica, JM2, Alligator Head, Jamaica; JM3, Formigas Bank; CN1, Caribbean Netherlands, Aruba; CN2, Caribbean Netherlands, Bonaire; CN3, Caribbean Netherlands, Saint Eustatius; CN4, Caribbean Netherlands, Saba; AN, Anguilla; TC, Turks and Caicos; BA1, Matanilla Shoal, Bahamas; BA2, Double Breasted Cay, Bahamas; and BA3, Whale Cay, Bahamas

genetic markers (Latch, Dharmarajan, Glaubitz, & Rhodes, 2006). This may explain the lack of significant pairwise comparisons of F_{ST} and G'_{ST} between Honduras and Turks and Caicos.

Our findings of limited larval dispersal resulting from indirect genetic methods should be interpreted with caution (*sensu* Christie, Johnson, Stallings, & Hixon, 2010). The indirect genetic methods we use to assess the connectivity of *L. gigas*, such as F_{ST} based analyses, rely upon theoretical assumptions (e.g., Hardy–Weinberg equilibrium and drift-mutation equilibrium) that are often limited by a lack of statistical power for detecting ecologically relevant patterns of connectivity when faced with moderate to high levels of gene flow (Hellberg, 2009). Multivariate analyses such as the spatial principal component analysis should be more robust to these limitations as it requires no theoretical genetic assumptions (Jombart, 2008). While our study found significant levels of population differentiation and IBOD, there may have been ecologically relevant levels of SGS that went undetected.

Our findings have direct implications for informing local and regional management practices for *L. gigas*. The limited dispersal potential of *L. gigas* larvae, as suggested by significant IBOD, may impede the natural recovery of overfished *L. gigas* populations. For example, this could be a key factor for explaining why the Florida Keys fishery has yet to rebound after 30 years of closure to fishing (Delgado et al., 2008). Previous research has posited that there are hydrodynamic processes that act as retentive mechanisms for locally produced queen conch larvae in the Florida Keys and that there are few larvae coming from upstream sources (Delgado et al., 2008). Further evidence to support our hypothesis of IBOD-limited recovery comes from population declines in the Exuma Cays Marine Protected Area (MPA) in the Bahamas, despite decades of protection and high levels of MPA compliance (Stoner et al., 2012a). It has been suggested that queen conch conservation efforts focus on local management (Delgado et al., 2008; Paris, Aldana-Aranda, Pérez-Pérez, & Kool, 2008), and our results corroborate this assertion

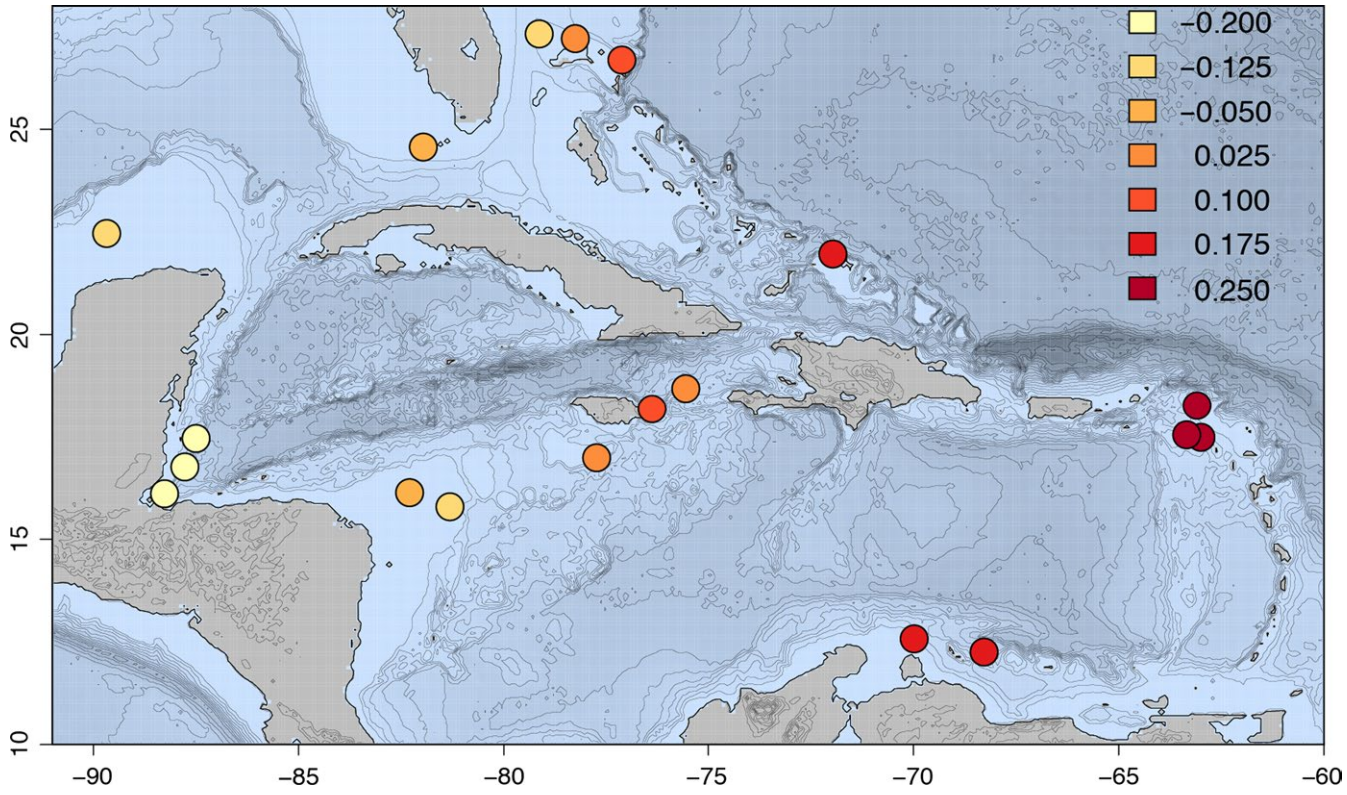

FIGURE 3 Map of large-scale spatial genetic structure of *Lobatus gigas* in the greater Caribbean. Principle component analysis of spatial genetic structure detected by ADEGENET with colors corresponding to the lagged score of the first principal component. [Colour figure can be viewed at wileyonlinelibrary.com]

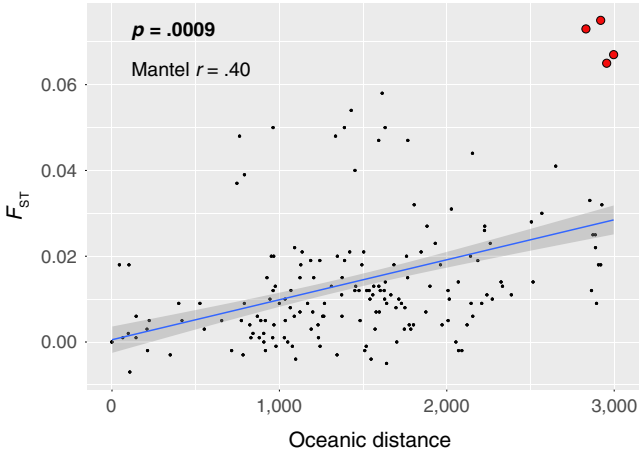

FIGURE 4 Scatter plot showing positive isolation-by-oceanic-distance between pairwise genetic differentiation (linearized F_{ST}) and oceanic distance (km) among *Lobatus gigas* sampling sites. Confidence intervals are visualized as the shaded areas above and below the blue trend line. The red dots indicate pairwise comparisons between Mexico and Anguilla, St. Eustatius, Saba, and Bonaire (starting at the red dot with the highest F_{ST} and moving clockwise. [Colour figure can be viewed at wileyonlinelibrary.com]

to a certain degree. We recommend that management of *L. gigas* be tailored toward localized stock structure in regions with the highest levels of genetic divergence such as in the Caribbean Netherlands, Mexico, and Florida. In contrast, the remote offshore network of banks in the Nicaraguan rise—which includes the territorial seas of Honduras, Nicaragua, Colombia, and Jamaica—is likely to be an important region for maintaining population connectivity over larger spatial scales that span international boundaries. Analyses of genetic diversity among sites identified a high variation in the effective number of alleles among sites. Anguilla and Mexico had the lowest effective number of alleles. These two sites had the highest levels of IBOD suggesting that oceanic isolation may have reduced levels of genetic diversity at these sites. Overall, the results of our study suggest that a careful blend of local and international management will be required to ensure long-term sustainability for the species throughout its range in the Caribbean.

Future studies will be required to more accurately delineate stock boundaries, ESUs, and thoroughly investigate mechanisms responsible for the high variation in genetic diversity observed among *L. gigas* populations. For example, Pinsky and Palumbi (2014) found that overexploitation in highly abundant marine fishes lowered allelic richness on average of 12% compared to closely related species that are not overharvested. Future genetic research should apply this approach to understand how overharvest may impact the evolutionary potential of *L. gigas*. In addition, we expect that the next generation of higher resolution genomic techniques will be capable of identifying queen conch subpopulations harboring unique genes adapted to local environmental conditions (*sensu* Hemmer-Hansen et al., 2013) as well as improving our understanding of genetic changes caused by fishery-induced evolution. For example, fishers selectively harvesting the largest queen conch individuals have been hypothesized to be responsible for a smaller

morphotype of *L. gigas* in the Bahamas, known locally as samba conch (Stoner, Davis, & Booker, 2012b). To conclude, our finding of significant isolation-by-oceanic-distance suggests that queen conch fisheries cannot rely solely on outside sources of larvae to rebuilt overfished stocks.

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SUPPORTING INFORMATION

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BIOSKETCH

Nathan Truelove is a post-doctoral fellow at the Smithsonian Marine Conservation Program. He is broadly interested in using molecular techniques to help develop conservation and management strategies for ecologically and commercially important marine species. His current work focuses on the genetics of queen conch and Caribbean spiny lobster.

Author contributions: S.J.B. was the principal supervisor of the entire study; K.A.A., M.E.R., and M.K.W. supervised the Jamaican portion of the study; A.W.S., M.H.D., C.J.B., and A.S.K. supervised the Bahamas portion of the study; E.M.B. supervised the Caribbean Netherlands and Anguilla portions of the study; G.A.D. and B.A.G. supervised the Florida Keys Portion of the study; M.H.D. and A.W.S. supervised the Belize portion of the study; T.T.S. supervised the Turks and Caicos portion of the study; I.S.G. and R.P.E. supervised the Mexico portion of the study; S.J.B., N.K.T., A.W.S., M.H.D., A.S.K., K.A.A., G.A.D., and B.A.G. designed the study; N.K.T., A.B.M., E.M.B., C.J.B., M.H.D., G.A.D., K.K.W., A.S.K., T.T.B., C.E.C., and R.P.E. assisted with sample collection; N.K.T., A.B.M., K.K.W., S.M.G., and I.S.G. completed the laboratory work; N.K.T., A.S.K., R.F.P., C.E.C., and S.M.G. analyzed the data; N.K.T. and A.S.K. drafted the manuscript; all co-authors contributed to editing the manuscript and approved the final draft.