Genetic composition of queen conch (*Lobatus gigas*) population on Pedro Bank, Jamaica and its use in fisheries management

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ABSTRACT

The queen conch fishery in Jamaica is sustained by Pedro Bank, which is the main harvesting site located approximately 80 km south-west from Kingston. Due to its relative size, Pedro Bank has been subdivided into zones for management purposes by the Fisheries Division and the Veterinary Services Division. Understanding whether these sub-divisions reflect different sub-populations is critical for managing exploitation levels because fisheries management must demonstrate that harvesting does not endanger the future viability of the population as queen conch are on Appendix II of the Convention in Trade in Endangered Species of Wild Fauna and Flora (CITES). This determination is essential for the continued export to international markets such as the European Union. Two hundred and eight samples were collected across the entire Pedro Bank and were genetically characterized using nine polymorphic microsatellite loci. Population structure analysis for *Lobatus gigas* from Pedro Bank yielded low but significant values ($F_{ST} = 0.009$; $p = 0.006$) and suggested a high magnitude of gene flow indicative of a fit and viable population throughout the bank. Analysis of molecular variance (AMOVA) indicated a 100% variation within individual samples with little variation (0.9%) between populations. In contrast pairwise genetic comparisons identified significant differences between populations located to the south eastern and eastern region of the bank to those in the central and western locations. Bayesian clustering analysis also indicated the likelihood of two population subdivisions ($K=2$) on Pedro Bank. The results provided evidence of a weak but significant population structure which has crucial implications for the fishing industry as it suggests the use of ecosystem based management (EBM) in setting quotas to promote sustainable harvesting of *L. gigas* within each monitoring zone on Pedro Bank.

Keywords: Pedro Bank, *Lobatus gigas*, queen conch, microsatellite genetic structure, ecosystem based management

54 1. INTRODUCTION

55 The queen conch *Lobatus gigas*, (Linnaeus 1758), is an edible marine gastropod mollusk of the
56 order Mesogastropod, and one of six species of the family Strombidae found throughout the
57 Caribbean region [1-5]. With the advent of overfishing in coastal waters along with habitat loss
58 due to coastal and marine ecosystem degradation [6], fishers are travelling further away from
59 traditional fishing grounds to sustain their livelihood and fulfill their need for food security [7,8].
60 The main conch grounds in Jamaica are located offshore approximately 80 km south-west of the
61 mainland on Pedro Bank. In 1992, Jamaica became the largest queen conch producer in the
62 Caribbean, and the resources on Pedro Bank began to show signs of overexploitation following a
63 pattern of conch population declines elsewhere in the region [9,10].

64 In response to these events and concerns, the Convention on the International Trade in
65 Endangered Species of Wild Fauna and Flora (CITES), moved queen conch (*L. gigas*) to a listing
66 in Appendix II. This requires that all international trade by signatory countries be accompanied
67 by a valid CITES permit, issued by the authorized National CITES Management Authority and
68 endorsed by the Scientific Authority [2,11,12]. Mahon et al. [9], predicted a collapse in the
69 Jamaican Conch Fishery within three years if adequate management measures were not put in
70 place to reduce or eliminate the harvesting of immature individuals. This led to the drafting of
71 the Conch Management Plan and between 2008 and 2011, conch production decreased from the
72 unsustainable early 1990s harvest figures of close to 3,000 mt to around 400 mt, with a value of
73 approximately 2.6 million US dollars [7,10]. This decrease can be attributed to the
74 implementation of management strategies by the Ministry of Industry, Commerce, Agriculture
75 and Fisheries (MICAFA) to control exploitation of dwindling stocks. Some of the management

regulations currently in place include, licensing of conch fishers and conch fishing vessels, closed season, transferable quota system based on National Total Allowable Catch (NTAC), minimum weight of processed meat, vessel monitoring system (VMS), fishing effort report on each fishing trip along with inspection of catch on landing and a conch export levy which is put into a fisheries management fund for the development of a sustainable fisheries sector in Jamaica [2,13-15].

Pedro Bank (Fig 1A), has an area of 8040 km², a maximum length of 168 km and a maximum width of 83 km in the west [16]. It consists of extensive sand flats interspersed with patches of macroalgae made up of various species, rubble, scattered patch reefs and shoals [10,17,18]. Due to its size, fisheries management zones were assigned across the bank, based on depth and fishing pressure (Fig 1B), by Jamaica's Veterinary Services Division (VSD) which is the competent authority in charge of monitoring conch production areas. These demarcations have allowed for more effective monitoring of the main conch production area as fishing activities can be prohibited based on the health of marine gastropods and prevailing sanitary conditions within a specified zone [19]. Genetic diversity assessments and comparisons between harvesting zones may help assure managers of the integrity of the fishery products if a harvesting zone is closed and allow for specific management measures to be applied to each zone especially where sub-populations are found. The identification of sub-populations could then effect fishing effort control to a specific area and bring management to the sub-population level. In addition, the information on population genetic structure can also be used in the design of stock enhancement programmes by ensuring appropriate genetic diversity in each area [20]. This is especially useful as selection may favor different genotypes from different habitats and geographic locales [21].

Providing more effective monitoring of the Pedro Bank through genetic labelling of conch will also strengthen international trade by meeting stringent requirements set out by the European Commission Decision [19] which outlined special conditions for the import of marine gastropods originating in Jamaica, the U.S. Food and Drug Administration (FDA), Seafood Guidance Documents and Regulatory Information for Shellfish Programs and the *Codex Alimentarius* code of practice for fish and fishery products. The aim of this study was to detect fine-scale population structure and how that could impact long term conservation and sustainable harvest of *L.gigas* stocks on the Pedro Bank along with traceability of product from harvesting site to market.

2. METHODS

2.1 Sample collection and processing

A total of 208 *L. gigas* individuals were sampled across the five monitoring zones on Pedro Bank (Fig 1C), with 144 samples collected from the 2015 conch abundance survey (Fig 2) and an additional 64 samples through monitoring by the competent authority of MICAFA, (Table 1). A tissue sample of approximately 4 cm² was removed from the tip of the mantle, rinsed in clean water to remove excess mucus and dirt, then placed on blotting paper for drying before extraction (Fig 3). DNA for each individual sample was extracted and purified using the AutoGenprep 965, a fully automated high throughput system utilizing the solution phase organic extraction method at the Smithsonian Institution's Laboratory for Analytical Biology National Museum of Natural History (LAB-NMNH). The samples were returned as pellets to be re-suspended with 50 ml Elution Buffer before the DNA quality and quantity was assessed using gel electrophoresis and NanoDrop 1000 Spectrophotometer (Thermo Fisher Scientific).

121

122 Figure 1 Map of Pedro Bank: (a.) Highlighting location approximately 80 km SW of
123 mainland Jamaica with major contour lines demarcating Artisanal zone (0-10 m)
124 and Industrial Fishing zone (11-20 m) (Adopted from [11]). (b.) VSD Monitoring
125 zones 1-5 established across the bank for management purposes and straddling
126 the depth zones 0-10 m in yellow (artisanal zone), 11-20 m in blue (industrial
127 zone) and the 21- 30 m zone in red. (c.) Sampling locations within monitoring
128 zones. Three sets of samples were located in zone 1 as differentiated by shades of
129 green triangles. Diamond shapes were representative of samples in zone 3 while
130 zones 2, 4 and 5 were grouped into one sample set (star shapes). Map produced
131 using ArcGIS ver. 10.3.1
132

133

134 Figure 2 Sampling locations on Pedro Bank. (a.) Sites sampled in the 2015 conch
135 abundance survey. (b.) All 80 sites from the 2015 survey with 47 highlighted to
136 show samples taken for genetic studies in keeping with the 1:2:1 ratio associated
137 with fishing pressure across all 3 depth zones while allowing for maximum
138 coverage of Pedro Bank. Map produced using ArcGIS ver. 10.3.1
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141

142

143 Table 1 Samples collected from the five monitoring zones across Pedro Bank.

Sample Locations	Monitoring Zones	Number of Samples
1A	1	46
1B	1	40
1C	1	42
2	2,4,5	34
3	3	46
Total		208

144

145 Figure 3 Individual conch samples: (a.) Showing tip of mantle collected for genetic
 146 analysis. (b.) Air dried on paper with coded sampling location from zones on
 147 Pedro Bank prominently displayed. (Photographs by author)
 148

149 2.2 Microsatellite genotyping

150 All conch individuals were genotyped for nine microsatellite loci: Sgig1, Sgig2 and Sgig6 [22],
 151 and ConchPR11F, ConchF29, ConchF17, ConchPR1F, ConchF21 and ConchF23 [23]. These
 152 loci were successfully grouped into 3 multiplexes (Table 2), and amplified using the Qiagen
 153 Type-it® Microsatellite PCR kit in a 10µL reaction following the standard protocol. The
 154 amplification was performed on a Dyad Thermocycler (Bio-Rad) under the following PCR
 155 conditions: 95°C for 5 minutes denaturation, followed by 28 cycles of 95°C for 30 seconds,
 156 annealing at 62°C for 90 seconds for MP2 and 63°C for MP1 and MP3, 72°C for 30 seconds and
 157 a final extension step at 60°C for 30 minutes. PCR products were separated on an ABI 3730xl
 158 DNA analyzer (Applied Biosystems) with ROX size standard and scored manually using
 159 GeneMapper® Software v 3.7 (Applied Biosystems). All genotyping was conducted at LAB-
 160 NMNH.

161 Table 2 Multiplex grouping for microsatellite markers and primer sequence.

Multiplex	Markers	Forward Sequence	Reverse Sequence
1	Sgig1	TCTTCCTCAGTTGCCTC	ACGAGCGTGTGCGCAAGC
1	ConchPR11F	CACTACGATAGATTGTG	TGTCAGTACAGGTTTGAGTG
2	Sgig2	GGTTAATTCATCAGTG	AAGTCATGGATTGGCGGGGT
2	ConchF29	TCAGTCTGTCTGTTTTG	ATAGAGAATTGGAGACAGTA
2	ConchF17	GAGGGATATGACGATG	TGAGGAACAAGGTCTGGTCG
2	ConchPR1F	GCGAAGCTTGATTCAA	AAAGAGGGTGCTTCTGTGGC
3	ConchF21	CAGGTCTGGCTGGGAA	AAGTTGCCGTCAGTTTTGAGG
3	ConchF23	AACATTTGTCACTGCTG	TGATAGGAGTGGTCAGGATG
3	Sgig6	CCAGCTGGTAGGCTCC	TAACCGTACCAGTTGGCTGG

162

163 Irregularities in the data set such as genotyping errors caused by the presence of null-alleles and
 164 scoring errors due to large allele drop-outs and stuttering were tested for using Micro-Checker
 165 version 2.2.3 [24]. FreeNA was used to estimate genetic distance for each population pair with
 166 and without the ENA (excluding null alleles) correction [25]. Linkage disequilibrium among all
 167 loci and deviations from Hardy-Weinberg Equilibrium (HWE) were calculated at each locus for
 168 all populations sampled using the genetic software Arlequin version 3.5.2.2 [26] and Genepop
 169 version 4.2. [27,28].

170

171 Estimates of genetic diversity, including total heterozygosity estimated from observed
 172 heterozygosity (H_o) and expected heterozygosity (H_e), number of alleles per locus, effective
 173 number of alleles along with variance in allele frequency (F_{ST}) based on 1,000 permutations were
 174 computed in Arlequin version 3.5.2.2 [26]. Relatedness was explored by calculating the
 175 inbreeding coefficient within individuals at each locus (F_{IS}) and the inbreeding coefficient

adjusted for bias (G_{IS}) using GenAlEx 6.502 with probability data based on 999 permutations [29,30].

The level of genetic differentiation within and between populations was estimated using the analysis of molecular variance (AMOVA), and the hierarchical AMOVA was effected among populations using Arlequin ver 3.5.2.2. Pairwise population matrices were calculated using the G-statistics option in GenAlex 6.502., with probability based on 999 permutations. To determine the most probable number of populations clusters (K) and assign each individual sampled to these clusters based on their genotype, a Bayesian assignment method was performed as implemented in STRUCTURE version 2.3.4 [31]. A total of 1,000,000 MCMC (Markov Chain Monte Carlo) repetitions were performed with a burn-in period of 10,000 iterations for K ranging from 1- 10 in consideration of the maximum number of expected populations, with 10 independent runs for each putative number of populations. The most likely number of clusters was inferred for population subdivision by the modal value of ΔK , corresponding to the rate of change in the likelihood of K following recommendations by Evanno et al. [32]. DARwin (Dissimilarity Analysis and Representation for Windows) version 6 software [33] was used to visualize the genetic relationship between individuals within and between populations by using the weighted neighbour joining method [34].

3. RESULTS

Linkage disequilibrium was evident in three pairwise comparisons between loci using Fisher's method (Sgig 1 and ConchF23, Sgig 1 and Sgig 6, ConchF23 and Sgig6). After false discovery rate (FDR) correction ($p < 0.001$) only comparisons with Sgig 2 appeared significant. The results

showed two significant deviations from Hardy Weinberg Equilibrium (HWE) from different populations (1C and 3), and at different microsatellite loci (Sgig2 and ConchF23) respectively. Analysis in Micro-Checker [24] suggested that these deviations were caused by the presence of null alleles as there was no consistent evidence of scoring errors due to stuttering or evidence of large allele dropout across all loci. The analysis with FreeNA using the ENA method to correct for bias induced by the presence of null alleles [25], indicated that calculations of Global F_{ST} = 0.0084 and a corrected Global F_{ST} = 0.0083. GenAlEx computations of G-statistics such as F_{ST} adjusted for bias G_{ST} , and standardized G''_{ST} which further corrected for bias when number of population is small (S1 Appendix A), showed values which correlated with calculated F_{ST} , therefore all microsatellite loci were included in further analysis and reported using the fixation index.

All nine microsatellite loci were highly polymorphic across all five sampled locations on Pedro Bank. The average number of alleles per locus ranged from 12.4 to 15.1 with $6.7 (\pm 0.79)$ being the mean effective number of alleles across all sites (Table 3). Zone 1 which constitutes sample locations 1A, 1B and 1C displayed the highest numbers of private alleles and the highest percentages of genetic diversity which was 78% on average across all sampled locations. Average observed homozygosity was slightly higher than expected heterozygosity, 0.81 and 0.77 respectively across Pedro Bank with the inbreeding coefficient F_{IS} detected at low levels and was negative at three of the five locations sampled.

Table 3 Genetic diversity across sampling locations on Pedro Bank. Na: average number of alleles per locus, Ne: number of effective alleles per locus, Np: number of private alleles, He: expected heterozygosity, Ho: observed heterozygosity, Ht: total heterozygosity and Fis: inbreeding coefficient

Sampling Locations	Na	Ne	Np	He	Ho	Ht	Fis
1A	15.111	7.536	1.444	0.779	0.801	0.783	0.003
1B	14.556	7.210	1.556	0.799	0.850	0.804	-0.046
1C	14.222	6.891	1.222	0.792	0.794	0.796	0.040
2	11.444	5.462	0.667	0.777	0.846	0.782	-0.067
3	12.444	6.562	0.778	0.736	0.768	0.736	-0.014
Mean	13.556	6.732	1.133	0.776	0.812	0.780	-0.017
SD	1.546	0.797	0.396	0.024	0.035	0.026	0.042

Analysis of molecular variance (AMOVA) indicated a 0.9% genetic differentiation among sampling locations, while variation within individuals was 100%. The hierarchical AMOVA (Table 4) indicated a low but significant population variation ($F_{ST} = 0.009$; $p = 0.006$). Pairwise F_{ST} comparisons ranged from 0.007 to 0.15, with four significant comparisons observed after FDR correction (Table 5), three of which included sampling location 3. The genetic differentiation between sampling locations was consistent with dendrogram constructed using the DARwin software Neighbour-Joining method (Fig 4) and the principal component analysis (PCA) scatterplot (S2 Appendix B) which showed a high degree of overlap between sampling locations.

Table 4 Global AMOVA results as a weighted average over all nine loci across the five locations sampled.

Source of variation	Sum of squares	Variance components	Percentage variation
Among populations	24.329	0.03165	0.89495
Among individuals within populations	701.480	-0.03931	-1.11134
Within individuals	735.000	3.54458	100.21638
Total	1460.809	3.53693	
Fixation Index	$F_{ST} = 0.00895$, $p = 0.006$		

Table 5 Pairwise comparisons of the five populations sampled across Pedro Bank. F_{ST} values below the diagonal and p values above. Significant values highlighted.

	1A	1B	1C	2	3
1A	0.000	0.094	0.172	0.001	0.050
1B	0.007	0.000	0.806	0.023	0.001
1C	0.007	0.005	0.000	0.037	0.003
2	0.015	0.010	0.010	0.000	0.001
3	0.007	0.012	0.010	0.021	0.000

Figure 4 DARwin Neighbour-joining tree showing the admixture of 208 individuals based on estimates of average distances from nine polymorphic microsatellite loci used to characterize the genetic population of *Lobatus gigas* across Pedro Bank. Each location sampled was assigned a colour which magnifies the level of admixture of individuals within and between populations. Below the dendrogram are four defined groups of individuals, while two clades are highlighted above indicating the most likely populations among the samples.

266

267 The optimum number of sub-populations (K) of queen conch on Pedro Bank based on the largest
268 value of ΔK using the Bayesian clustering analyses performed in Structure was K=4 (Fig 5).
269 There was extensive admixture of individuals across the Pedro Bank, hence the clusters as shown
270 in the bar plot were not well defined (Fig 6), and showed a high likelihood of K=2, supported by
271 the dendrogram (Fig 4) which also displayed an admixture of individuals from the different
272 locations sampled. The two clusters identified comprises cluster 1 (sampling locations 1A, 1B,
273 1C and 2), situated to the centre and western end of Pedro Bank and cluster 2 represented by
274 sampling location 3 located on the eastern side of the bank. These results indicating high levels
275 of relatedness was also reflected by the population assignment tests performed in GenAlEx
276 which indicated 68% of individuals being assigned to the population in which it was sampled
277 while 32% indicated a likelihood of being assigned to other populations (S3 Appendix C).

278

279 Figure 5 Determination of homogeneous populations (K) using the modal value of an ad
280 hoc quantity (ΔK) which is based on the second order rate of change in the
281 likelihood function [32].

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283

284 Figure 6 Bayesian clustering analysis of *Lobatus gigas* samples from five sampling sites
285 across Pedro Bank as performed using STRUCTURE. Samples were assigned to
286 four (K=4) population clusters represented by the lines below the bar graph. Lines
287 above the bar plot represents the most reliable populations from the reassignment
288 of individuals as reflected using samples collected from the Queen conch survey
289 only (S4 Appendix D).

290

4 DISCUSSION

This is the first genetic study where all monitoring zones encompassing different depth strata on Pedro Bank were sampled for genetic assessment. Despite the heavy exploitation of queen conch on Pedro Bank, the high genetic diversity values observed within each group of *L. gigas* sampled, is indicative of a vigorous population. This high genetic diversity is likely due to the large area represented by the bank resulting in spatial variability across the Pedro Bank with little population isolation. These results are expected in large populations, which is consistent with the high conch density 374 conch/ha reported by Morris et al. [35] from the Pedro Bank queen conch 2015 abundance survey. Each group exhibited high heterozygosity for all loci with an average of 0.77($\pm$ 0.024), signifying high genetic variability across the bank. Despite the occurrence of high genetic variability maintained by gene flow within the Pedro Bank population, Mitton et al. [36] cautioned against making the assumption that conch is a randomly mating population as they identified gaps in allele frequencies from the populations studied within the Caribbean region. Slatkin [37] also observed that gene flow in natural populations varied widely among species and is dependent on the method of analysis used, one such method being the use of private alleles. Private allelic richness can be used as a simple measure of genetic distinctiveness as it has proven to be informative in conservation genetic studies [38,39]. Slightly elevated frequencies of private alleles were seen in sampling locations 1A, 1B and 1C corresponding to monitoring zone 1 (Fig 1B), which is the most exploited zone. Increased harvesting of species can lead to the depletion of genetic information and later extinction and recolonization of entire populations. Whilst this may prevent differentiation of sub-populations within an area [37,40], an increase in private allele frequency can also be attributed to inbreeding due to the cumulative effect of genetic drift [41]. However, due to the difficulties in collecting data on alleles that are not found

in all subpopulations, F-statistics is a better method by which gene flow can be estimated in natural populations [42].

Our results (Table 3) indicated a slightly higher value for average observed homozygosity (H_o) than expected heterozygosity (H_e). Increased homozygosity is an indication of inbreeding which occurs as a result of mating between two related individuals in a population [43,44,45], or as a result of severe reduction in population size from exploitation [46]. Positive inbreeding coefficient, albeit low values ($F_{IS} = 0.003$ and 0.040) were observed in the most heavily fished areas suggesting some level of relatedness due to removal of alleles from the population. However, the average inbreeding coefficient across Pedro Bank was negligible signifying a population with high genetic variability, which is less related than is expected under the assumption of random mating. Inbreeding can contribute to the failure of a species to recover from exploitation as it increases the frequency of deleterious alleles [44,47]. Despite this detrimental effect, inbreeding has been used for decades to increase favourable selection responses leading to improvements and ensuring uniformity within livestock breeds [35,43] and to promote economically important traits such as fast growth in food fish production [48]. In fact Gjedrem and Robinson [49] noted that although significant strides have been made within the last 40 years to manage genetic diversity and conserve fish populations, genetic improvements from selective breeding in aquatic animals is far behind that achieved for terrestrial animals and plants.

Kenchington and Heino [50], regarded selective fishing as a possible means of not only affecting life history traits such as age and maturation, but as a means to influence the dynamics of fish populations and ultimately sustainable yield of a population. This observation was also made by Stoner et al. [51] when they reported that the selective removal of larger individuals by fishing,

had significant effects on density and biomass as negative growth rates can occur within the population if density was <56 adult conch ha^{-1} [52] or below the recommended 100 conch ha^{-1} [7]. The high conch density calculated for Pedro Bank in the 2015 queen conch abundance survey, especially in the south and south-eastern sections corresponding to monitoring zone 1 of the study area, provided no support for impending local extinction despite heavy exploitation. In fact, the numbers suggest the existence of a substantially large population with high genetic variability [27].

Low estimates of population structure are typically found in benthic marine invertebrates such as *L. gigas* with an extended planktonic larval stage, which may last up to 8 weeks and hence have a high dispersal potential [4,53,54]. Our estimates of population structure indicated a weak but significant population variation ($F_{ST} = 0.009$; $p = 0.006$), across Pedro Bank, suggesting genetic homogeneity which can be maintained by the exchange of genetic material between a few individuals per generation [36,37,55]. Significant genetic differences were seen among groups and within individuals but not among individuals within each group sampled. This pattern of genetic variation over small spatial scales was described by Campton et al. [54] as genetic patchiness which can be attributed to post-settlement natural selection where variation among groups is greater than variation within each group. Similar patterns of genetic structure was observed in previous studies of *L. gigas* within the Caribbean region by Mitton et al. [36] and Kitson-Walters et al. [56], and for *Stegastes partitus* (damselfish) by Villegas-Sanchez et al. [57]. The latter attributed the small-scale genetic variation to a temporally unstable genetic structure, a phenomenon known as ‘sweepstake-chance effect’ where most recruits to the fishery are from a few individuals due to random assortment and matching of reproductive activity with

oceanographic conditions conducive to spawning, fertilization, larvae development and recruitment.

While many of these processes may contribute to the fine-scale and large-scale spatial variation within the population on Pedro Bank, the results from the pairwise comparisons which indicated that the easternmost group (sampling location 3) was the most significantly different from the other groups in the central and western end, supports the mechanism of genetic variation caused by oceanographic conditions. Surface currents in the Caribbean generally flow towards the west [50,58,59], and Jamaica is supplied from large upstream reef areas and as such may be less susceptible to overfishing and species loss [53,58]. Kitson-Walters et al. [56] also suggested that Pedro Bank receives recruitment from outside the Jamaican exclusive economic zone (EEZ) corroborating the hypothesis that queen conch recruitment would be greatest on the eastern end of the bank, which also has the highest conch density [27]. The substrate cover in that area is predominantly sand sediment, seagrass, coral reefs and small areas of macroalgae [18,60]. Previous studies conducted on Pedro Bank indicate a direct relationship between substrate type, depth and *L. gigas* density [2,11,18, 27,61]. Tewfik and Appeldoorn [61] and Morris [18], found that substrate type and depth were influential in the distribution of queen conch across Pedro Bank, while Stoner et al. [62] reported habitat limitation as the most plausible explanation for low abundances in the conch population west of Cat Island in the Bahamas.

The neighbour joining (NJ) tree is in congruence with the pattern of genetic structure found (Fig 4), where Group 3 was significantly different from the other groups except for Group 1A which is closest geographically and consistent with the genetic structure pattern of queen conch in Yucatan, Mexico [20]. Contrastingly, Campton et al. [54] described queen conch as displaying

spatial and temporal genetic variation as geographical distance did not correlate with relatedness of individuals, instead he attributed this genetic patchiness to pre-settlement events due to stochastic variations in the marine environment, temporal variations in recruit source for each locality and/or genetic drift. The distribution of queen conch on Pedro Bank was also described as patchy by Appeldoorn [11] due to densities found throughout the bank from sporadic larval settlement which may also lead to distinct genetic populations being formed [14]. A combination of barriers to dispersal and ocean circulation could also be used to explain variation between groups of marine species [63].

The Bayesian clustering analysis indicated four clusters ($K=4$) with an admixture of individuals assigned to all clusters indicative of mixed ancestry with a richer and more complex representation than is traditionally assumed by clustering models where each individual belongs to a unique cluster [64]. This analysis also indicated a high likelihood at ($K=2$), which corresponded to results obtained using samples collected only from the 2015 queen conch abundance survey (S4 Appendix D) which had less individuals to assign. Kalinowski [65] concluded from his simulation exercise that clusters produced by the software STRUCTURE can be strongly influenced by differences in sample size but the same data set can produce realistic results when using traditional methods such as pairwise comparisons. The most probable number of populations identified on Pedro Bank was two which corresponds to the pairwise comparisons where spatial variation was evident between sample location 3 and the rest of the bank.

Sample location 3 situated on the eastern side of Pedro Bank (zone 3) has a predominant depth of 11-20 m and considered to be a nursery area due to the substrate type. Here larvae transported by the Caribbean current could settle and metamorphose into juveniles [27,35,66]. In their study on

coral reef connectivity throughout the Caribbean, Schill et al. [58] stated that coral reefs rely heavily on ocean currents in order to maintain genetic vigour as currents are a valid source of new recruits which influences biomass, population persistence, resilience and species diversity. Sample location 3, based on its position, is directly impacted by westerly flowing currents and incidentally displayed the lowest average for total heterozygosity (0.736). This corroborates the indication that exploitation, genetic drift and potential larval retention may promote genetic differentiation among groups [67]. Additionally, Stoner et al. [62] cautioned that increased recruitment from upstream areas does not guarantee high queen conch production as mortality rates in newly settled invertebrates can be high. The highest juvenile densities are found on the southeastern edge of the bank [35,61], however the presence of small juveniles with limited capacity for migration and dispersal across Pedro Bank indicates that significant larval recruitment and settlement are occurring throughout the bank. It also suggests that replenishment of queen conch is not solely dependent upon recruitment from traditional nursery areas [11], that is, Pedro Bank may be self-recruiting [56] but still receives larvae from upstream areas which have greatest influence at the eastern end of the bank.

4.3 Management Implications

Over the years the impacts of commercial fishing and overexploitation of *L. gigas* on Pedro Bank have received considerable attention from a wide variety of stakeholders ranging from within Jamaica and the wider Caribbean, to international trading partners concerned with conservation of the species [3,7,68-70]. Solutions to these impacts have been sought through biological surveys and assessments [11,18,35,61] marine spatial planning [60] and genetic assessment [56].

425 However, management plans thus far have only utilized biological surveys to guide the queen
426 conch fishery in Jamaica which is primarily based on Pedro Bank. The results from this study
427 revealed a weak but significant population structure which may be habitat dependent and would
428 benefit from EBM as suggested by Morris [18].

429 Genetic diversity of queen conch on Pedro Bank embodies that of a fit population in all
430 monitoring zones sampled under prevailing environmental conditions, however the central to
431 eastern and southeastern end of the bank comprising monitoring zones 1 and 3 are heavily fished
432 and incidentally comprise dense patches of seagrass beds which potentially act as nursery areas
433 for recruitment to the fishery. These zones are predominantly < 20 m in depth hence the
434 increased exploitation as it is more economical and safer for commercial fishers to fill their
435 quotas in these areas [35]. The deeper areas in open water locations are also more exposed to
436 high waves [71] and ocean currents which are variable in strength [56]. The constant removal of
437 species from one area can be detrimental as entire cohorts may be removed over successive
438 fishing seasons causing the fishery to eventually collapse by the removal of reproductive
439 individuals before they make a contribution to the fishery. This type of serial dilution was
440 observed in the Bahamian queen conch fishery by Stoner et al. [71], to cause low densities of
441 adult conch incapable of successful mating and reproduction hence a fishery on the verge of
442 collapse if strong management measures are not instituted. Even though the total allowable catch
443 for queen conch in Jamaica is relatively low per fishing season, commercial fishing should be
444 encouraged across the entire Pedro Bank perhaps with incentives to offset economic losses such
445 as an increased quota to fish in particular areas, thus safeguarding the genetic diversity across the
446 bank. Instituting the marine spatial planning (MSP) for Pedro Bank as suggested by Baldwin et
447 al. [60], would also allow for important nursery areas to be protected and permit the Fisheries

448 Division to meet one objective of the conch management plan for rehabilitation of overexploited
449 stocks.

450 A closed season to protect the reproductive period is a common management strategy in
451 fisheries. This is particularly important for queen conch because they are susceptible to
452 overexploitation when they aggregate in particular areas to spawn [2,52,72]. Reproduction in
453 queen conch occurs year round in some areas [59,73], although reproduction seems to be
454 triggered by temperature [18,21], so spawning tends to occur in the warmer months of the year
455 [69,74]. The closed season for queen conch in Jamaica is set by the Fisheries Division through
456 the Minister with responsibility of MICAF and currently varies from year to year. With the event
457 of climate change and other environmental factors that may impact spawning, there needs to be a
458 concerted effort to investigate temporal variability of the life history stages of *L. gigas* and as
459 such institute appropriate periods for fishing restrictions suitable to the biology of the species.
460 An alternate management measure to closed seasons may be closed areas as monitoring zones
461 can be closed for specific periods to achieve the objectives of a closed season.

462 Without proper enforcement, management strategies are mere suggestions for good practices.
463 Aiken et al. [13] has lamented the fact that enforcement has historically been a weak point for the
464 fishing industry in Jamaica. Cochrane and Garcia [72] made the realistic observation that if
465 enforcement is to take place in remote areas which cover a large expanse such as Pedro Bank the
466 practicalities and cost of enforcement can be prohibitive. Although enforcement in Jamaica has
467 been a challenge, exceptions to this are highlighted to some degree for the conch fishery because
468 it is a commercial fishery and production is primarily export oriented. Whilst landings geared
469 towards export are captured in the queen conch production for Jamaica, landings by artisanal

fishermen for local consumption by restaurants and hotels may go unnoticed and hence not captured in the total estimated figure for queen conch production. In addition to contributing to serial dilution of stocks, this may affect the NTAC set by fisheries managers and hence calls for increased monitoring of harvesting areas and local landings by artisanal fishermen.

The identification of two possible subpopulations on Pedro Bank will assist fisheries managers in regulating harvesting areas and strengthen the certification scheme implemented to facilitate trade with the EU as entire sections of the bank may be closed off to fishing if necessary, and traceability of the individuals landed will be possible. The genetic information elucidated from the study will also strengthen the non-detrimental findings (NDF) required by CITES as traceability of the products can be substantiated along with the data provided for export.

Knowing the genetic composition of the stocks on Pedro Bank and being able to trace the final product to the source stock will also serve as a deterrent to IUU fishing [75], which can only be substantially decreased with enforcement.

5. CONCLUSION

The results from this study revealed a weak but significant population structure for *L. gigas* on Pedro Bank as was seen in previous studies done elsewhere in the Caribbean [21,23,36,54, 67]. Queen conch displayed a patchy distribution across the monitoring zones sampled with significant but weak genetic variation found in zone 3 which is located on the heavily exploited eastern end of the bank. This genetic differentiation may be attributed to two main factors, namely the serial dilution of species and the complex oceanic current patterns associated with the eastern end of the bank. Pedro Bank is directly impacted by the westward flow of the Caribbean

current and could serve as the primary recruitment area of queen conch larvae from upstream locations. The geographical and ecological conditions on the eastern end of the bank are also conducive to post larval settlement, however the high densities of juvenile conch found throughout the bank coupled with high gene flow across the bank suggests that self-recruitment is taking place and is possible due to the different depth strata presently unexploited within the monitoring zones. These recruitment options available to the *L. gigas* stocks on Pedro Bank should ensure a viable population continues to exist with the use of proper management tools incorporating all available data into ecosystem management and continued monitoring of the stocks.

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Conceptualization: AB, MKW, KAA

Formal Analysis: AB, NT, IS

515 Funding Acquisition: KAA, SB, MKW
516 Investigation: AB
517 Methodology: NT, IS, AB
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519 Resources: AB, IS, NT
520 Supervision: KAA, MKW, MER
521 Validation: IS, NT, AB
522 Writing – Original Draft: AB
523 Writing – Review & Editing: AB, KAA, MKW, IS, MER, SB

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525 7. REFERENCES

- 526 1. Brownell WN, Stevely JM. The biology, fisheries and management of the queen conch
527 *Strombus gigas*. Mar Fish Rev. 1981; 43: 1-12.
- 528 2. Tewfik A. An assessment of the biological characteristics, abundance, and potential yield
529 of the queen conch (*Strombus gigas* L.) Fishery on the Pedro Bank off Jamaica. M.Sc.
530 thesis, Acadia University, Canada. 1996.
- 531 3. Theile S. Queen conch fisheries and their management in the Caribbean. TRAFFIC,
532 Europe. Technical Report to the CITES Secretariat. 2001.
533 www.trafficj.org/publication/02_Queen_Conch.pdf
- 534 4. Davis M. Species Profile Queen Conch, *Strombus gigas*. Mississippi State University:
535 Southern Regional Aquaculture Center (SRCA) Publication No. 7203. 2005.

https://agrifecdn.tamu.edu/fisheries/files/2013/09/SRAC-Publication-No.-7203-Species-Profile-Queen-Conch-Strombus-gigas.pdf.

5. NOAA. Queen Conch (*Strombus gigas*). 2015.

<http://www.nmfs.noaa.gov/pr/species/invertebrates/queen-conch.html>

6. Smithen N. Ecosystem-Based Management Principles in the Caribbean. Caribbean Law Institute, University of the West Indies, Cave Hill Campus, Barbados, CERMES Technical Report 47. 2011.

7. FAO/WECAFC/COPACO/CFMC. FAO Report of the First Meeting of the CFMC/OSPESCA/WECAFC/CRFM Working Group on Queen Conch, Panama City, Panama, 23-25 October 2012. FAO Fisheries and Aquaculture Report No. 1029. 2012.

8. Albert S, Aswani S, Fisher PL, Albert J. Keeping Food on the Table: Human Responses and Changing Coastal Fisheries in Solomon Islands. PLoS ONE. 2015; 10(7): e0130800. doi:10.1371/journal.pone.0130800.

9. Mahon R, Kong GA, Aiken KA. A preliminary assessment of the conch fishery on the shelf and banks off the south coast of Jamaica. CARICOM Fisheries Research Document No. 8. 1992.

10. Aiken KA, Kong GA, Smikle S, Mahon R, Appeldoorn R. The queen conch fishery on Pedro Bank, Jamaica: discovery, development, management. Ocean & Coastal Management. 1999; 42(12): 1069-1081.

11. Appeldoorn RS. Stock abundance and potential yield of queen conch on Pedro Bank. University of Puerto Rico/ Fisheries Division Jamaica. 1995.

12. Grant S, Blythe A. The conch fishery in Jamaica. CFMC/CFRAMP International Conch Assessment Workshop, Belize. 1999.

13. Aiken KA, Kong A, Smikle S, Appeldoorn R, Warner G. Managing Jamaica's queen conch resources. *Ocean & Coastal Management*. 2006; 49(5-6): 332-341.
14. Prada M, Castro E, Taylor E, Puentes V, Appeldoorn R, Daves N. Non-detrimental findings for the queen conch (*Strombus gigas*) in Colombia. NDF Workshop Case Studies WG 9 – Aquatic Invertebrates, Case Study 3. 2008.
15. Murray A, Smikle S, Cooke-Panton K, Squire J, Hansel F. Assessment of the 2012 catch and effort data for the Pedro Bank queen conch fishery. Fisheries Division, Ministry of Agriculture and Fisheries. 2012.
16. Munro JL, Thompson R. Areas investigated, objectives, and methodology. In: Munro JL editor. Caribbean Coral Reef Fishery Resources. ICLARM Studies and Reviews 7. 1973. pp. 15-19.
17. Bruckner A. Global Reef Expedition: Pedro Bank, Jamaica. MD, USA: Khaled bin Sultan Living Oceans Foundation Publication No. 8. 2012.
18. Morris RA. Distribution of queen conch (*Strombus gigas*) on the Pedro Bank, Jamaica: Descriptive and predictive distribution models. Master's thesis, University of Iceland. 2016.
19. Commission Decision No. 2001/37/EEC. Laying down special conditions for the import of marine gastropods originating in Jamaica. *Official Journal of the European Union L*. 2000; 10: 64-65.
20. Pérez-Enriquez R, Garcia-Rodriguez FJ, Mendoza-Carrion G, Padilla C. Geographical variation in the genetic diversity and composition of the endangered queen conch *Strombus gigas* (Mesogastropoda: Strombidae) from Yucatan, Mexico. *Rev Biol Trop*. (Int J Trop Biol ISSN-0034-7744) 2011; 59(3): 1115-1126.

21. Morales F. Metapopulation structure of the queen conch, *Strombus gigas* (Linne, 1758) throughout the intra-Americas sea. PhD thesis, College of Engineering: Florida Institute of Technology. 2004.
22. Zamora-Bustillos R, Rodriguez-Canul R, Garcia de Leon FJ. Isolation and characterization of eight microsatellite markers from pink conch (*Strombus gigas*). Molecular Ecology Notes. 2007; 7: 597-599.
23. Truelove N, Box S, Aiken K, Blythe-Mallett A, Boman E, Booker C, Davis M, Delgado G, Glazer R, Kitson-Walters K, Kough A, Perez-Enriquez R, Roye M, Segura-Garcia I, Webber M, Stoner A. Isolation by distance and spatial genetic structure in an overharvested international fishery. Diversity and Distributions. 2016; 23(11):1292-1300.
24. Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P. Micro-checker: Software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes. 2004; 4(3): 535-538. <https://doi.org/10.1111/j.1471-8286.2004.00684.x>
25. Chapuis MP, Estoup A. Microsatellite null alleles and estimation of population differentiation. Mol Biol Evol. 2007; 24(3): 621-631.
26. Excoffier L, Lischer HEL. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 2010; 10: 564-567.
27. Raymond M, Rousset F. GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. J. Heredity 1995; 86: 248-249.
28. Rousset F. Genepop'007: A complete reimplementation of the Genepop software for Windows and Linux. Mol. Ecol. Res. 2008; 8: 103-106.

29. Peakall R, Smouse PE. GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 2006; 6: 288-295.
30. Peakall R, Smouse PE. GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research – an update. *Bioinformatics*. 2012; 28: 2537-2539.
31. Pritchard JK, Stephens M, Donnelly P. Inference of population structure using multilocus genotype data. *Genetics*. 2000; 155: 945-959.
32. Evanno G, Regnaut S, Goudet J. Detecting the number of clusters of individuals using the software structure: A simulation study. *Molecular Ecology*. 2005; 14: 2611-2620.
33. Perrier X, Jacquemoud-Collet JP. DARwin software. 2006. <http://darwin.cirad.fr/darwin>
34. Perrier X, Flori A, Bonnot F. Data analysis methods. In: Hamon P, Seguin M, Perrier X, Glaszmann JC. Editors. Genetic diversity of cultivated tropical plants. Montpellier: Enfield Science Publishers. 2003. pp. 43-76.
35. Morris RA, Smikle S, Murray A. Pedro Bank Jamaica queen conch (*Strombus gigas*) abundance survey report 2015. Fisheries Division, Ministry of Industry, Commerce, Agriculture and Fisheries. 2016.
36. Mitton JB, Berg CJ, Orr KS. Population structure, larval dispersal, and gene flow in the queen conch, *Strombus gigas*, of the Caribbean. *The Biological Bulletin*. 1989; 177(3): 356-362.
37. Slatkin M. Gene flow in natural populations. *Ann Rev Ecol Syst*. 1985; 16: 393-430.
38. Kalinowski ST. Counting alleles with rarefaction: Private alleles and hierarchical sampling designs. *Conservation Genetics*. 2004; 5: 539-543.
39. Szpiech AA, Rosenberg NA. On the size distribution of private microsatellite alleles. *Theoretical Population Biology*. 2011; 80: 100-113. doi: 10.1016/j.tpb.2011.03.006.

40. Dalvit C, Marchi MD, Zanetti E, Cassandro M. Genetic variation and population structure of Italian native sheep breeds and undergoing in situ conservation. *Journal of Animal Science*. 2009; 87: 3837-3844. doi:10.2527/jas.2008-1682.
41. Hedrick PW, Kalinowski ST. Inbreeding depression in conservation biology. *Ann Rev Ecol Syst*. 2000; 31(1): 139- 162. <https://doi.org/10.1146/annurev.ecolsys.31.1.139>.
42. Waples RS Separating the wheat from the chaff: Patterns of genetic differentiation in high gene flow species. *Journal of Heredity*. 1998; 89(5): 438-450. doi:10.1093/jhered/89.5.438
43. Curik I, Ferencakovic M, Sölkner J. Inbreeding and runs of homozygosity: A possible solution to an old problem. *Livestock Science*. 2014; 166(1):4-9. doi: 10.1016/j.livsci.2014.05.034
44. Kenney J, Allendorf WF, McDougal C, Smith JLD. How much gene flow is needed to avoid inbreeding depression in wild tiger populations? *Proc R Soc B. Biological Sciences*. 2014; 281:20133337.
45. Kim E-S, Sonstegard TS, Van Tassell CP, Wiggans G, Rothschild MF. The relationship between runs of homozygosity and inbreeding in Jersey cattle under selection. *PLoS ONE*. 2015; 10(7): e0129967. doi:10.1371/journal.pone.0129967.
46. Sampson JF, Hankinson M, McArthur S, Tapper S, Langley M, Gibson N, Yates C, Byrne M. Long-term 'islands' in the landscape: Low gene flow, effective population size and genetic divergence in the shrub *Hakea oldfieldii* (Proteaceae). *Botanical Journal of the Linnean Society*. 2015; 179: 319-334; <https://academic.oup.com/botlinnean/article-abstract/179/2/319/2416506>.

47. O’Leary SJ, Hice LA, Feldheim KA, Frisk MG, McElroy AE, Fast MD, Chapman DD. Severe inbreeding and small effective number of breeders in a formerly abundant marine fish. *PloS ONE*. 2013; 8(6): e66126. doi:10.1371/journal.pone.0066126.
48. Causey DR, Kim J, Stead DA, Martin SA, Devlin RH, Macqueen DJ. Proteomic comparison of selective breeding and growth hormone transgenesis in fish: Unique pathways to enhanced growth. *Journal of Proteomics*. 2019; 192: 114-124. doi:10.1016/j.jprot.2018.08.013.
49. Gjerdem T, Robinson N. Advances by selective breeding for aquatic species: A review.” *Agricultural Sciences*. 2014; 5(12):1152-1158. doi:10.4236/as.2014.512125.
50. Kenchington E, Heino M. Maintenance of Genetic Diversity: Challenges for Management of Marine Diversity. IIASA Interim Report. IR-03-005, Laxennurg, Austria: IIASA. 2003. <http://pure.iiasa.ac.at/7076/>.
51. Stoner AW, Davis MH, Booker CJ. Negative consequences of allele effect are compounded by fishing pressure: Comparison of queen conch reproduction in fishing grounds and a marine protected area. *Bull. Mar. Sci*. 2012; 88(1): 89-104.
52. Stoner AW, Ray-Culp M. Evidence for allee effect in an over-harvested marine gastropod: Density-dependent mating and egg production. *Marine Ecology Progress Series*. 2000; 202: 297-302. doi: 10.3354/meps202297
53. Roberts CM. Connectivity and management of Caribbean coral reefs. *Science*. 1997; 278: 1454-1457.
54. Campton DE, Berg CJ Jr , Robison LM, Glazer RA. Genetic patchiness among populations of queen conch *Strombus gigas* in the Bimini. *Fishery Bulletin, U.S.* 1992; 90: 250-259.

55. Cowen RK, Sponaugle S. Larval dispersal and marine population connectivity. Annual Review of Marine Sciences. 2009; 1: 443-466.
56. Kitson-Walters KA, Candy AS, Truelove NK, Roye ME, Webber MK, Aiken KA, Box SJ. Fine-scale population structure of *Lobatus gigas* in Jamaica's exclusive economic zone considering hydrodynamic influences. Fisheries Research. 2018; 199: 53-62.
57. Villegas-Sanchez CA, Rivera-Madrid R, Arias-Gonzalez JE. Small-scale genetic connectivity of bicolor damselfish (*Stegastes partitus*) recruits in Mexican Caribbean reefs. Coral Reefs. 2010; 29: 1023-1033. doi:10.1007/s00338-010-0643-0.
58. Schill SR, Raber GT, Roberts JJ, Treml EA, Brenner J, Haplin PN. No reef is an island: integrating coral reef connectivity data into the design of regional scale marine protected area networks. PLoS ONE. 2015; 10(12): e0144199.
<https://doi.org/10.1371/journal.pone.0144199>.
59. Webber MK. Annual structure and production of the copepod community in a tropical oceanic area. Ph.D. thesis, University of the West Indies, Mona. 1993.
60. Baldwin EK, Schill S, Zenny N, Blake D. Developing ecosystem-based information for marine spatial planning on the Pedro Bank, Jamaica. Proc Gulf Carib Fish Inst. 2014; 67: 12.
61. Tewfik A, Appeldoorn RS. 1997 queen conch (*Strombus gigas*) abundance survey and potential yield estimates for Pedro Bank, Jamaica. Fisheries Division, Ministry of Agriculture, Kingston Jamaica. 1998.
62. Stoner AW, Mehta N, Ray-Culp M. Mesoscale distribution patterns of queen conch (*Strombus gigas* Linne) in Exuma Sound, Bahamas: Links in recruitment from larvae to fishery yields. Journal of Shellfish Research. 1998; 17(4): 955-969.

63. Jones DB, Jerry DR, McCormick ML, Bay LK. The population genetic structure of a common tropical damselfish on the Great Barrier Reef and eastern Papua New Guinea. Coral Reefs. 2010. 29:455-467.
64. Heller KA. Efficient Bayesian methods for clustering. Ph.D thesis, University of London. 2007.
65. Kalinowski ST. The computer program STRUCTURE does not reliably identify the main genetic clusters within species: simulations and implications for human population structure. Heredity. 2010; 106(4): 625-632. doi 10.1038/hdy.2010.95
66. NOAA. Endangered and threatened wildlife and plants: Notice of 12 month finding on a petition to list the queen conch as threatened or endangered under the Endangered Species Act (ESA). The Daily Journal of the United States Government, Federal Register. 2014; 79 FR 65628: 16.
67. Marquez E, Landinez-Garcia RM, Ospina-Guerrero SP, Segura JA, Prada M, Castro E, Correa JL, Borda C. Genetic analysis of queen conch *Strombus gigas* from the Southwest Caribbean. Proc Gulf Carib Fish Inst. 2013; 65: 410-416.
68. Chakalall B, Cochrane LK. The queen conch fishery in the Caribbean – An approach to responsible fisheries management. Proc Gulf Carib Fish Inst. 1997; 49:531-554.
69. CFMC/CFRAMP. Queen conch stock assessment and management workshop report. Belize City, Belize, March 15-22, 1999.
70. CITES. Regional cooperation on the management of and trade in the queen conch (*Strombus gigas*). CoP17 Doc. 72. Seventeenth meeting of the Conference of the Parties Johannesburg, South Africa. 2016. https://cites.org/eng/prog/queen_conch.

- 717 71. Stoner AW, Davis MH, Kough AS. Relationships between fishing pressure and stock
718 structure in queen conch (*Lobatus gigas*) populations: Synthesis of long-term surveys and
719 evidence for overfishing in The Bahamas. Reviews in Fisheries Science & Aquaculture.
720 2018: 1-21. doi: 10.1080/23308249.2018.1480008.
- 721 72. Cochrane KL, Garcia SM. eds. A Fishery Manager's Guidebook. 2nd ed. Rome: FAO.
722 2009. <http://www.fao.org/3/i0053e/i0053e.pdf>.
- 723 73. Berg CJ, Olsen DA. Conservation and management of queen conch (*Strombus gigas*)
724 fisheries in the Caribbean. In: J.F. Caddy editor Marine invertebrate fisheries; their
725 assessment and management. NY: Wiley and Sons. 1989. pp.421-442.
- 726 74. Randall J. Contributions to the biology of the queen conch, *Strombus gigas*. Bull Mar Sci.
727 Gulf Carib. 1964; 14(2): 246-295.
- 728 75. Commission Regulation No. 1005/2008/EC. Establishing a community system to prevent,
729 deter and eliminate illegal, unreported and unregulated fishing. 2008.
730 https://ec.europa.eu/fisheries/cfp/illegal_fishing/info_en.

Pedro Bank Figures

Figure 1 Map of Pedro Bank: (a.) Highlighting location approximately 80 km SW of mainland Jamaica with major contour lines demarcating Artisanal zone (0-10 m) and Industrial Fishing zone (11-20 m) (Adopted from [Error! Reference source not found.]). (b.) VSD Monitoring zones 1-5 established across the bank for management purposes and straddling the depth zones 0-10 m in yellow (artisanal zone), 11-20 m in blue (industrial zone) and the 21- 30 m zone in red. (c.) Sampling locations within monitoring zones. Three sets of samples were located in zone 1 as differentiated by shades of green triangles. Diamond shapes were representative of samples in zone 3 while zones 2, 4 and 5 were grouped into one sample set (star shapes). Map produced using ArcGIS ver. 10.3.1

Figure 2 Sampling locations on Pedro Bank. (a.) Sites sampled in the 2015 conch abundance survey. (b.) All 80 sites from the 2015 survey with 47 highlighted to show samples taken for genetic studies in keeping with the 1:2:1 ratio associated with fishing pressure across all 3 depth zones while allowing for maximum coverage of Pedro Bank. Map produced using ArcGIS ver. 10.3.1

Figure 3 Individual conch samples: (a.) Showing tip of mantle collected for genetic analysis. (b.) Air dried on paper with coded sampling location from zones on Pedro Bank prominently displayed. (Photographs by author)

Figure 4 DARwin Neighbour-joining tree showing the admixture of 208 individuals based on estimates of average distances from nine polymorphic microsatellite loci used to characterize the genetic population of *L. gigas* across Pedro Bank. Each location sampled was assigned a colour which magnifies the level of admixture of individuals within and between populations. Below the dendrogram are four defined groups of individuals, while two clades are highlighted above indicating the most likely populations among the samples.

Figure 5 Determination of homogeneous populations (K) using the modal value of an ad hoc quantity (ΔK) which is based on the second order rate of change in the likelihood function [Error! Reference source not found.].

Figure 6 Bayesian clustering analysis of *Lobatus gigas* samples from five sampling sites across Pedro Bank as performed using STRUCTURE. Samples were assigned to four ($k=4$) population clusters represented by the lines below the bar graph. Lines above the bar plot represents the most reliable populations from the reassignment of individuals as reflected using samples collected from the Queen conch survey only (S4 Appendix D).