Are populations of economically important bonefish and queen conch 'open' or 'closed' in the northern Caribbean Basin?

Running title: Northern Caribbean gene flow

Marlis R. Douglas[1] | Tyler K. Chafin[1] | Julie E. Claussen[2] | David P. Philipp[2,3] | Michael E. Douglas[1]

[1]Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas, 72701 USA

[2]Fisheries Conservation Foundation, Champaign, IL 61820 USA

[3]Cape Eleuthera Institute, Rock Sound, Eleuthera, The Bahamas

Correspondence Michael E. Douglas med1@uark.edu/ https://orcid.org/0000-0001-9670-7825

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Abstract(243)(280)

Demographics of co-occurring species can often be diagnosed through population genomic analyses of single nucleotide polymorphisms (SNPs). These data can define population structure, gene flow, plus candidate regions in the genome that potentially reflect local adaptations. Importantly, they can gauge if populations are demographically 'open' or 'closed' (i.e., with global or local recruitment). We derived SNPs from double-digest restriction-site associated DNA (ddRAD) to test the demographics of commercially important queen conch (*Lobatus gigas*) and bonefish (*Albula vulpes*) from two northeast Caribbean Basin islands (Grand Bahama to the north and Eleuthera to the south). Specifically, we tested the hypothesis that the strong west-to-east current in the Great Bahama Canyon forms a vicariant barrier separating the two islands. We conducted Bayesian assignment tests conducted on putatively neutral (*L. gigas*=64,863; *A. vulpes*=36,206 SNPs) and highly-differentiated outlier SNP datasets (*L. gigas*=51–88; *A. vulpes*=79–123, respectively). For conch, both analyses indicated weak structure, substantiating the vicariant hypothesis. However, results for bonefish suggested adult mobility and strong easterly currents as potential drivers for source-sink dynamics. These results, while preliminary, provide templates for future research endeavors with these impacted species. Outlier loci, for example, can potentially place populations of each within a demographic continuum, rather than within a dichotomous 'open'/'closed' framework, as well as diagnose ‘source’ and ‘sink’ populations, as herein. These methodologies can then be applies to co-distributed species with similar but less well understood ecologies so as to evaluate basin-wide trends in connectivity and local adaptation.

1 | INTRODUCTION

Connectivity among populations is a fundamental consideration for marine conservation (Bell et al. 2014) and management (Miller et al. 2014), with aspects that resonate both theoretically (Kool et al. 2010, Ellingson & Krug 2015) and functionally (Hameed et al. 2016, Krueck et al. 2017). Benthic marine invertebrates, for example, generally disperse as a component of the plankton so as to reach areas beneficial for growth and development. This often extends across temporally variable periods but with the end result being populations that are regarded as demographically 'open' (Domingues et al. 2010). Many marine fishes follow a similar life-history strategy (Williamson et al. 2016), but with an additional and innate capacity to 'self-recruit' back into their natal populations (Christie et al. 2010), a situation that serves to confound the traditional 'open' versus 'closed' dynamic. In a similar vein, larger-bodied marine vertebrates often exhibit philopatry, defined as the return of reproducing individuals to the locality from which they were spawned (Feldheim et al. 2014, Bonanomi et al. 2016, Salles et al. 2016). This, in turn, necessitates a capacity to home with great precision, in that the natal areas were previously experienced only during the egg or larval stage. When this behavior is manifested in both genders, a 'closed' population can result such that dynamics are driven not by long-distance immigration but rather by local reproduction/ recruitment (Bentzen & Bradbury 2016).

A variety of mechanisms have been employed to evaluate dispersal and connectivity in marine species, and consequently, to diagnose their open or closed status (Cowen et al. 2000, Cowen & Sponaugle 2009). In this regard, much contemporary evidence has been provided via indirect methods, with particular emphasis on genetic and genomic techniques that gauge 'effective dispersal' (i.e., that due to survival and subsequent reproduction), rather than strictly by movements identified among populations. The latter provide considerably greater resolution, such that results

establish larval relatedness (Ottmann et al. 2016), self-recruitment (Teske et al. 2016), panmixia
46 (Jasonowicz et al. 2017, Kensington et al. 2017, Tay et al. 2017), and adult dispersal (Veríssimo et al. 2017). Genomic assays have also been extended as well to estimate dispersal and connectivity
48 among deep-sea biodiversity, a group largely opaque to more traditional methods (Baco et al. 2016).

While methods of dispersal in marine biodiversity are many and varied, their variance can
50 often be a source of ambiguity, particularly when statistical tests of revelant hypotheses are conducted (Weersing & Toonen 2009). For example, several studies have displayed varying results
52 when population connectivity was tested against the temporal duration of the planktonic larval stage. In this sense, numeorus studies established a positive correlation between connectivity and
54 distance (Reisser et al. 2014, Ellingson & Krug 2015, Herrera et al. 2016, Morvezen et al. 2016, Tay et al. 2016, Van Wyngaarden et al. 2016, Jasonowicz et al. 2017, Kensington et al. 2017, Martinez et al.
56 2017). Yet, numerous others have demonstrated just the reverse, i.e. an inverse relationship between connectivity and distance (Kool et al. 2010, Jackson et al. 2014, Jorde et al. 2015, Cumming
58 et al. 2016, Gomes et al. 2016, Hameed et al. 2016, Teske et al. 2016). Clearly, many factors can constrain or accelerate dispersal, with the end result being the promotion or depression of
60 connectivity.

In a similar vein, other studies have established global interconnectedness but surprisingly, as
62 a complex matrix of locally-adapted populations with larval transport varying both spatially and temporally (Christie et al. 2010, Miller et al. 2014, Gould et al. 2017, McKeon et al. 2017, Segovia et
64 al. 2017). This, in turn, suggests a gradient in population structure, rather than a binary condition with available choices established as either 'open' versus 'closed.'

Here, we investigated the spatial population structure of two economically important species in the northeastern Caribbean Basin, queen conch *Lobatus gigas* and bonefish *Albula vulpes*. We did so by employing a double-digest restriction-site associated DNA (ddRAD) methodology that promotes the identification of single nucleotide polymorphisms (SNPs). Our study is the first to employ such techniques with these economically important study species, and we hypothesized that our assay of neutral loci so derived would reflect the homogenizing effects of gene flow in each, thus emphasizing their placement within the 'open' end of the demographic spectrum. We then sought to verify our general analyses of neutral loci within each species by deriving a more reduced and fine-grained series of outlier SNPs that have the potential to demonstrate local adaptation. In doing so, we tested the hypothesis that sharp environmental gradients can counterbalance gene flow and instead promote adaptive divergence.

Finally, we recognized that our study species comprise exploited stocks, each of which transects numerous national borders across the Caribbean Basin. As such, they experience varying levels of temporal and spatial exploitation. Thus, an understanding of coarse- and fine-grained dispersal in these species, and indeed if they display connectivity, is a necessary baseline from which to derive an ecologically meaningful framework for sustainable conservation. In this sense, the potential for local adaptation and source-sink dynamics between islands could seriously impact the management of conch and bonefish in the Caribbean.

2 | MATERIALS AND METHODS

2.1 | Study site

The Caribbean Basin extends west from Florida along the Gulf Coast of North America, then south along the coast of México and Central America, continuing eastward across the northern coast of South America, with end-points at the Greater and Lesser Antilles. Within this matrix, the Commonwealth of the Bahamas (Figure 1 top) represents a shallow series of carbonate banks (~104,000 km^2) situated on a submerged continental border east of Florida (Andrews et al. 1970). Our Bahamian study sites are located along the coasts of two islands: Grand Bahama (153 km west-east; 24 km north-south), and Eleuthera (~1.6 km west-east, 180 km north-south; Figure 1 top). Grand Bahama is located 86 km east of Palm Beach (FL) and represents the fourth largest island in the Bahamian chain, whereas Eleuthera is some 370 km distant with the Atlantic Ocean on its east side and the shallow (<3m depth) Great Bahama Bank immediately west (Figure 2 top). Approximately 1–3 km further west lie the abyssal waters of Exuma Sound (~1500m depth; "3" of Figure 2 top).

The Great Bahama Canyon (length=225 km, max width=37 km, max depth=6.9 km) is located northeast of the Great Bahama Bank ("1" of Figure 2 top), and effectively separates Grand Bahama and Andros islands (to the north) from Eleuthera (to the south). It is divided into two main branches: ‘Northwest Providence Channel’ extending north and west towards Grand Bahama Island, with ‘Tongue of the Ocean’ reaching south and east of Andros Island, towards Exuma Sound. The Northwest Providence Channel also absorbs a small but significant easterly contribution from the Gulf Stream (Richardson & Finlen 1967), with currents extending west-to-east in the Canyon (green arrow, Figure 2 bottom). The occasionally turbid currents within the Great Bahama Canyon deposit a large sediment fan as it merges with the Antilles Current of the Atlantic Ocean ~65km to the north-

northeast (red arrow, Figure 2 bottom) (Andrews 1970). The direction and extent of these currents offer the potential for a vicariant separation between Grand Bahamas and Eleuthera islands.

2.2 | Bonefish

A complex of four bonefish species occur within the Atlantic Ocean/ Caribbean Basin: Bonefish (*Albula vulpes*), Threadfin bonefish (*A. nemoptera*), Channel bonefish (*A. goreensis*), and an as yet undescribed form *A. sp. cf. vulpes*. The three nominate species are partitioned non-geographically in the Basin (Wallace & Tringali 2016). We restricted our evaluation to *A. vulpes*, a species that reflects an elevated home range fidelity within the shallow flats proximate to Bahamian islands (Murchie et al. 2013). However, deeper channels that separate the shallow flats can serve as conduits for travel, or as refugia from rapid changes in water temperature (Humston et al. 2005). Inshore/nearshore habitat are somewhat distant from home ranges, yet allow pre-spawning adults to congregate during October-May. In this sense, pre-spawning bonefish are found on the south side of Grand Bahama island where deeper waters are available for spawning (Murchie et al. 2015). Spawning movements to offshore waters (>300 m) then occur on the full moon (Danylchuk et al. 2011). However, specific spawning locations and actual spawning activities have yet to be identified/observed. Bonefish produce leptocephali larvae that are planktonic, and subsequently drift for ~41–71 days before eventually recruiting to inshore nurseries (Adams & Cook 2015).

A Basin-wide genetic analysis of *A. vulpes* (Wallace & Tringali 2016) revealed two somewhat intermixed genetic populations. However, the extent of larval drift from local or distant sources remains unknown for each. In this sense, populations of *A. vulpes* may reflect a situation found in other high gene flow species, such as cardinalfish *Siphamia tubifer*, where genetic homogeneity

effectively conceals a high population turnover and a variable accumulation of larvae from divergent sources (Gould et al. 2017). Brown crab *Cancer pagurus* displays a similar condition in the English Channel and North Sea, where high levels of dispersal and gene flow effectively mask a genetic patchiness due to recruitment that is both spatially and temporally variable (McKeon et al. 2017).

2.3 | Queen conch

Queen conch (*Lobatus gigas*) is not only the largest of six species in the Caribbean Basin, but also an icon of considerable economic and cultural importance (Kough et al. 2017). It feeds on micro-and macro-algae, but with habitat shifts that occur ontogenetically from shallower seagrass habitat into deeper-water macroalgae plains (~40m) (Doerr & Hill 2013). Harvest (and over-harvest) are promoted by a density-dependent reproductive strategy in which both genders not only reduce movements but also aggregate along open sandy bottoms for broadcast spawning (Stoner 1997).

Spawning extends from April through October, with peak larval abundance in late June-August when temperatures in the northeastern Caribbean Basin exceed 28°C (Stoner & Davis 1997a). Planktonic larvae drift for ~60–75 days (Ballantine & Appeldoorn 1983), but with high natural mortality and with distances controlled by oceanic conditions. For example, the surface environment dictates the vertical distribution of larvae in the water column, with >80% of larvae occurring at 0.5-5.0 m depth (Stoner & Davis 1997b).

In 1992, *L. gigas* was recognized by the Convention on International Trade of Endangered Species (CITES: https://cites.org/eng/prog/queen_conch/introduction) and, in 1994, was added to the Red List maintained by the International Union for the Conservation of Nature (IUCN;

148 http://www.fao.org/docrep/006/Y5261E/y5261e07.htm). A review of the *L. gigas* fishery is provided by Brownell & Stevely (1981).

150 A broad-ranging spatial genetic study of *L. gigas* across the greater Caribbean (Truelove et al. 2017a,b) found that isolation-by-oceanic-distance dictated Basin-wide gene flow and pannmixia, but 152 surprisingly, not within the Bahamas. Similarly, a more regional study in the Mesoamerican Caribbean again rejected panmixia (Machkour-M'Rabet et al. 2017), whereas a more homogeneous 154 gene flow was suggested for the Bahamas (Mitton et al. 1983). Also of note is the fact that overall genetic homogeneity among populations (per the Bahamas) can be masked by the annual variation 156 in numbers of larvae that emerge from over-fished source populations.

2.4 | Collection, extraction, and amplification of samples

158 During 2014, we sampled fin clips from 57 adult bonefish collected by rod and reel from three locations on the west and south sides of Eleuthera Island (EW, ES1, ES2; Table 1) and one from the 160 Atlantic Ocean (east) side (EEB; Table 1). Muscle samples were also gathered from 60 adults at Grand Bahama Island, with 30 taken from the south (Flats) side (GSB) and 30 from the north (Atlantic) side 162 (GNB) (total N=117). Sampling was in compliance with the U.S. National Research Council Guide for the Care and Use of Laboratory Animals (https://grants.nih.gov/grants/olaw/Guide-for-the-Care-and-164 use-of-laboratory-animals.pdf). We also collected 30 individuals of queen conch from the south side of Grand Bahama Island (GSC), and 30 from the Flats (or west) side of Eleuthera Island (EWC) (Table 166 1, Figure 1 bottom). Fin clips and muscle plugs were preserved on WHATMAN® FTA® Classic DNA cards, with genomic DNA subsequently extracted using a GENTRA® Puregene DNA Purification Kit and stored 168 in hydrating solution (per manufacturer instructions). The quality of DNA was visualized on 2%

agarose gels, then quantified using a Qubit fluorometer (Thermo-Fisher Scientific, Inc.). Subsequent
170 library preparation followed previously published protocols (Peterson et al. 2012, as modifed in Bangs et al. 2018).

172 Restriction digests were performed using 1µg of genomic DNA with PstI (5'-CTGCAG-3') and MspI (5'-CCGG-3') in CutSmart buffer (New England Biosciences) for 20 hours at 37°C, after first
174 optimizing restriction enzyme and size selection choices using an *in silico* approach (FRAGMATIC; Chafin et al. 2018). Digests were visualized on 2% agarose gels, purified using AMPure XP beads, and
176 quantified with a Qubit fluorometer. Digested samples were normalized to 0.1 µg of DNA and subsequently ligated with barcoded Illumina adaptors, using custom oligos (Peterson et al. 2012).
178 Inline barcodes were designed to differ by at least 2 bases so as to minimize mis-assignments. Pooled ligations were size-selected at 350-400 bps using the Pippin Prep automated size fractionator (Sage
180 Sciences). Adaptors were extended by PCR (10 cycles) with Phusion high-fideltiy DNA polymerase (New England Biosciences). Size distribution and successful amplification of purified libraries was
182 then confirmed on the Agilent 2200 TapeStation. Indexed libraries were multiplexed with 100-bp single-end sequencing on the Illumina HiSeq 2500 lane at the University of Oregon Genomics and Cell
184 Characterization Core Facility.

2.5 | Processing and assembly of ddRAD data

186 Raw reads were demultiplexed and processed in the PyRAD pipeline (Eaton 2014) using a 90% identity threshold for clustering homologous reads. Read clusters representing putative loci within
188 individuals were filtered when alleles were > two (i.e., potentially overmerged or representing paralogs), or when sequencing depth was <10. Following assembly, additional loci were discarded if

190 they exhibited: 1) <50% presence across individuals; 2) >60% heterozygosity per site among individuals; 3) >10 heterozygous sites per consensus sequence; or 4) >10 consensus N bases. Further
192 data processing was performed using custom scripts (available at: github.com/tkchafin/scripts).

2.6 | Detection and spatial structure of local selection

194 We first sub-sampled all SNPs to a maximum of one per locus. We then utilized a Bayesian method (BAYESCAN v.2.1, Foll & Gaggiotti 2008) with a burn-in period of 50,000 followed by 100,000
196 iterations to calculate per-locus F_{ST}, to determine a candidate list of potential loci under selection. We used F_{ST}-etimates to derive three additional datasets per taxon: (1) All unlinked SNPs (=ALL); (2)
198 SNPs >2 standard deviations (sd) above mean F_{ST} (=SD2); and (3) SNPs >3 sd above the mean (=SD3).

We employed multiple methods to examine population structure for both species across all
200 three datasets. Hierarchical iterative clustering analysis using STRUCTURE v.2.2.4 (Pritchard et al. 2000) was run in parallel (Besnier & Glover 2013) on the Jetstream cloud computing platform (Hancock et
202 al. 2019) using the GNU Parallel shell tool (Tange 2011). STRUCTURE was run for 250k repetitions with a burn-in period of 100k, and with potential clusters for K-values ranging from 1-20. Optimal K for each
204 dataset was ascertained using the delta-K method (Evanno et al. 2005), as implemented and visualized in the CLUMPAK pipeline (Kopelman et al. 2015). Differentiation among sampling localities
206 was also examined with Discriminant Analysis of Principal Components (DAPC) in the R package ADEGENET (Jombart 2008, Jombart et al. 2008), with a minimal number of principal components
208 retained to explain 50% variance.

2.7 | Asymmetric migration among populations

210 Physical processes such as water current and tidal fluxes often create patterns of asymmetric gene flow among populations, and consequently impact patterns of genetic diversity. Given our initial
212 hypothesis, we were interested in gauging the amount and direction of gene flow among the six study populations of bonefish, and two of queen conch. In contrast to STRUCTURE, which employs a
214 Bayesian probabilistic model to assign individuals to ancestry clusters, we instead wished to estimate the posterior probability of individual migratory histories, thereby allowing the direction and
216 magnitude of dispersal among populations to be dissected.

To do so, we employed a revised software optimized for large SNP datasets (i.e., BA3-SNPs,
218 Mussmann et al. 2019). We first tuned MCMC acceptance parameters using an automated iterative procedure, then generated posterior estimates of migration rates using 250,000 iterations with a
220 burn-in period of 50,000. We further tested the hypothesis of source-sink dynamics by computing net emigration rates as a sum of immigration rates subtracted from summed emigration rates
222 (Andreasen et al 2012), with positive numbers indicating a genetic source populations wheras negative values indicated a sink population.

224 3 | RESULTS

After filtering, we obtained 56,046 loci for bonefish (*Albula vulpes*), of which 68.7% (N=36,206) were
226 parsimoniously informative (Table 2). Average number of loci per individual was 35,443, at a mean depth of 77x. Subsampling only unlinked SNPs produced a matrix of 25,205 SNPs, from which SD2
228 and SD3 datasets were derived, and which contained 123 and 79 SNPs, respectively.

For queen conch (*Lobatus gigas*), 30,697 loci were available post-filtering, and represented
230 64,864 SNPs, of which 68.4% (N=44,334) were parsimony informative. Individuals were sequenced at

a depth of 58.6x, averging 33,409 loci per individual (Table 2). Subsampled unlinked SNPs totaled
232 19,716, from which 88 and 51 SNPs were derived as input to the SD2 and SD3 datasets.

3.1 | Spatial structure in Bonefish and Queen Conch

234 STRUCTURE runs for *A. vulpes* employing the ALL dataset (=neutral differentiation) revealed scant differentiation among sample sites (Figure 3). The most highly-supported models for SD2 for SD3
236 were K=2 and K=3 groupings, both of which depicted GSB (Grand Bahama, south side) as clustereing with EWB (Eleuthera, west side) and ES2 (south and west side of Eleuthera). The second cluster
238 placed GNB (Grand Bahama north side) with EEB (Eleuthera east or Atlantic side) and ES1 (south and west side of Eleuthera) (Figure 3). The K=3 STRUCTURE run with SD2 and SD3 datasets was a bit mixed,
240 with GSB and EWB linked as one group, ES1, ES2, and EEB as a second group, with GNB as the third. Subsequent K-groups were decidedly more mixed which rendered them indecipherable.

242 However, the DAPC clustering of the ALL dataset for bonefish (Figure 4 left) displayed considerable overlap among sites (per STRUCTURE plot in Figure 3). Three populations with scant
244 separation were grouped within the center of the graph (i.e., ES1, ES2 and EEB). Three others were somewhat more peripheral and reflected greater within-group variability (i.e., GNB, GSB, and EWB).
246 The same type of analysis, but employing the SD2 dataset (Figure 4 middle), separated GNB, EWB, EEB, and ES1 without overlap, while grouping GSB with ES2. These relationships were maintained in
248 the DAPC clustering of the SD3 dataset, but with more overlap between the previously separated EEB and ES1, whereas ES2 and GSB maintained their linkage. GNB and EWB remained distinct (Figure 4
250 right).

The STRUCTURE analysis of *L. gigas* populations using the ALL dataset revealed little genetic differentiation, with mean F_{ST} (all SNPs) =0.0129. However both EWC and GSC showed significant separation when both SD2 and SD3 datasets were evaluated (Figure 5). The DAPC clustering of the ALL dataset (Figure 6 left) again showed considerable overlap between the two islands, whereas each separated with considerably less overlap when SD2 was analysed, and became even more distinct based upon the SD3 (Figure 6, middle, right).

3.2 | Asymmetric migration

The BAYESASS3 analysis of *L. gigas* found very high demographic independence among populations, with 'self-migration' (e.g., recruitment) rates estimated at >98% for both Grand Bahama and Eleuthra populations (Table 3). Results for bonefish revealed highly variable and asymmetric migration rates, with EEB and EWB depicted as source populations, with outward migration rates to both Grand Bahama and flats-side Eleuthra populations. This varied from 8.5-17.9% for EEB and 7.5-14.6% for EWB (Table 3; Figure 7). Notably, the remaining populations lacked any strong signal of outward migration, and all showed negative rates of net emigration (Figure 8), suggesting a sink dynamic.

4 | DISCUSSION

Populations are frequently classified as to the manner by which they are replenished. In this sense, closed populations are defined as having recruitment via local reproduction, whereas open populations are independent of source (Pinsky et al. 2012). This dichotomy underscores several ecological, evolutionary, and conservation-based research agendas: Exploitation or protection (Yau et al. 2014, Krueck et al. 2017); Life history and taxonomy (Mora & Sale 2002, Baco et al. 2016);

Recovery from disturbance (Bell et al. 2014); and Extent to which populations are locally adapted
272 (Jorde et al. 2015, Salles et al. 2016, Segovia et al. 2017). It also has obvious implications for how populations are managed, yet with considerable resolution provided by the advent of genomic
274 techniques, and particularly with the estimation of local adaptation (Reisser et al. 2014).

4.1 | *FST* outliers for queen conch

276 For non-model organisms (as herein), two approaches are most often utilized: The first identifies loci that display unusually high genetic differentiation among populations (i.e., *FST* outlier approach),
278 whereas the second (i.e., gene-environment association) seeks correlations between the allele frequencies of populations and their local environments. We employed the first approach in this
280 study, and by so doing, found that outlier loci did indeed discriminate sessile populations of queen conch *Lobatus gigas* separated by a potential vicariant barrier (the Great Bahama Canyon).

282 This is aptly demonstrated in Figure 5, where the south side of Grand Bahama Island and the west side of Eleuthera Island are clearly discrete one from another. This condition is reinforced by
284 the DAPC analysis (Figure 6), where distributions for SD2, and SD3 datasets consistently diverge from that depicted for the ALL dataset. *FST* values for these two populations are not significantly different
286 when computed from the ALL data, but are when compiled from the SD2 and SD3 datasets (Table 3). Of interest is the fact that whereas neutral loci showed little differntiation across the study area, a
288 smaller proportion reflected strong patterns of differentiation consistent with local adaptation. This scenario has also been manifested in other marine species that were similarly investigated using SNP
290 analyses (Cure et al. 2017, Thomas et al. 2017).

4.2 | *FST* outliers for bonefish

292 A similar analysis employing data for bonefish *Albula vulpes* failed to group samples on either side of the Canyon into geographically congruent groups, suggesting instead a distribution more panmictic
294 in format (per STRUCTURE analysis and DAPC plot for the ALL data). Furthermore, STRUCTURE plots for K=2 and K=3 groupings (Figure 3) deviated but little. For K=2, both SD2 and SD3 datasets linked the
296 south side of Grand Bahama Island (GSB) with the west side of Eleuthera (EWB) and with one (of two) ES locations (i.e., ES2). This, in turn, suggests a level of connectivity across the Great Bahama
298 Canyon, a conjecture supported by Figure 4. However, the north side of Grand Bahama Island (GNB) grouped with the eastern (Atlantic) side of Eleuthera (EEB) and with the second ES site in the K=2
300 grouping (i.e., ES1). This relationship separates at K=3, with GSB remaining linked with EWB, whereas EEB and ES2 separate. These relationships are difficult to interpret biologically, particularly given
302 what we know of geomorphic and current patterns in the northeast Basin (Figure 2). A more parsimonious explanation would point to the considerable mobility of adult bonefish superimposed
304 onto a lack of site specificity.

4.3 | Potential problems with *FST* outlier analyses

306 One potential issue with detecting selection via departure from neutrality is that each locus may manifest an independent response that can hinge upon population structure and demography. This is
308 particularly problematic when the average level of differentiation among populations is relatively high (Hoban et al. 2017). However, pairwise *FST* values for bonefish are neither elevated nor
310 significant (Table 3), suggesting this concern may not apply in our situation. An additional concern is that some loci may demonstrate false signatures of selection, such as when small populations found
312 on the leading edge of an expansion are contributing disproportionately to observed frequency

differences. Again, our study populations are already established and thus the concept of a leading edge of expansion is not a viable consideration. Similarly, cryptic hybridization and introgression can invoke confounding effects as well, but again, these are not apparent in our data.

4.4 | Asymmetrical migration in bonefish and queen conch

The structure of the physical environment can promote differential movements in aquatic organisms, and thus promote a metapopulation structure within a species (i.e., a source–sink dynamic). This in turn can skew estimates of genetic differentiation among populations, and consequently promote erroneous management decisions, particularly when the organisms are anthropogenically harvested such that active management is based on an economic model. In this sense, we employed genetic estimates of population migration so as to ascertain potential source-sink considerations in our study organisms, and to determine if indeed movements between them were asymmetrical.

In this study, populations of conch were found to be highly demographically independent, as seen in both estimates of contemporary migration (BA3-SNPs) and from estimates of population structure using highly-differentiated SNPs. On the other hand, bonefish showed strong signals of source-sink dynamics across islands. The two Eleuthra populations (EEB and EWB) seemingly act as genetic sources, as evidenced by their high net emigration rates derived from BayesAss3 (Figure 8). Their genetic differentiation may suggest the presence of discrete genetic stocks, reflecting either spatial or temporal asynchrony with regards to spawning. Given a tendency for bonefish to move into deeper waters for spawning (Danylchuk et al 2011), the differentiation between the two Eleuthera populations may indicate spawning site-fidelity, with subsequent intermingling of

ancestries in flat-side feeding grounds. The latter may also explain the cryptic intra-site structure as recorded in the assignment tests of Fst outlier SNP datasets (Figure 3).

4.5 | Dispersal and connectivity within the Caribbean Basin

We hypothesized that the population demographics of our study species would be impacted by the currents passing through the Grand Bahama Canyon. Prior to test, we sought data from othere species that might potentially shed light on this conjecture. Jackson et al. (2014) investigated genetic differentiation among 19 spawning aggregations of Nassau grouper *Epinephelus striatus* in the Basin. The life history of this species parallels that of bonefish (above) in that spawning aggregations are cued by water temperature and phases of the moon over a 3-month period. As with bonefish, breeding aggregations develop some distance from individual home ranges, with larvae drifting for a similar duration (~40 days) before settling. Four Basin-wide genetic groups were identifed, to include the Bahamas, but with little within-group differentiation, again in parallel with that found for bonefish (per Wallace & Tringali 2016). A major barrier to larval dispersal was the separation of the Basin into eastern and western regions (Jackson et al. 2014, Figure 3). These results implicate the Great Bahama Canyon (Figure 1 top) as a vicariant barrier, similar to what was found herein with conch.

In a second study, Kool et al. (2010) coupled results from a matrix-based projection model with those based on a bio-physical approach to examine genetic dispersal among coral reef patches in the Basin. Allele frequencies were found to shift along the length of the Bahamas, with the sharpest demarcation occurring at the separation between Grand Bahama Island and the southern Bahamas. This separation was not recognized in the original publication but indeed juxtaposes with

354 the presence of the Grand Bahama Canyon (Figure 1). Again, the results from Kool et al. (2010) promote the Canyon as a major vicariant feature in the region.

356 ## 5 | CONCLUSIONS

An understanding of genetic connectivity within exploited species is a crucial aspect, such that 358 appropriate geographic units can be subsequently designated for management purposes. This includes the establishment of quotas for 'take,' as well as the delineation boundaries for marine 360 protected areas (MPAs). Furthermore, an understanding of Basin-wide linkages (or lack thereof) among populations of commercially exploited species (as herein) promotes the realization among the 362 numerous stakeholders that fisheries management is a complex and continually evolving geopolitical problem.

364 Understanding adaptive (i.e., ecologically relevant) variation potentially allows the incorporation of such information into conservation and management practices (Allendorf 2017). For 366 instance, it could be used to define adaptive-based management units that, in high gene flow species, may represent subsets within more traditional neutral-based units (Funk et al. 2012). Outlier 368 SNPs could also identify illegal conch fishing and help define stock boundaries and potential management units (Milano et al. 2014).

370 These aspects cut to the definition of conservation genomics, which (in the narrow sense) is defined as those approaches that differ conceptually and quantitatively from traditional genetics. 372 This, in turn, allows genome-wide signals of adaptation to be detected, and this in turn subsequently provides answers to those questions impossible to address using genetic data alone (Garner et al. 374 2016). Importantly, such data can provide genomic evidence for potential heat tolerance (or the lack

thereeof), an issue that has serious reverberations for sessile marine invertebrates in particular (as herein) (Thomas et al., 2017). These issues loom large as oceans acidify and their heat profiles expand in lockstep with global climate change (Hurd et al., 2018).

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AUTHOR'S CONTRIBUTIONS

MRD/ JEC/ DPP/ MED designed the study; JEC/ DPP contributed to fieldwork; MRD/ TKC/ MED contributed to lab work; TKC performed bioinformatic work and statistical analyses; MRD/ TKC/ MED interpreted results and generated figures; MRD/ TKC/ MED drafted the manuscript; All authors gave final approval for publication.

ORCID

Michael E. Douglas https://orcid.org/0000-0001-9670-7825

DATA ACCESSIBILITY

DNA SNP loci: Dryad Digital Repository (http://dx.doi.org/upon-acceptance).

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TABLE 1 Collection data for bonefish (*Albula vulpes*) and queen conch (*Lobatus gigas*). Listed are: Species, Island, Side (of island with compass direction in parentheses), Locality, Date, N, and Sample label).

Species	Island	Side	Locality	Date	N	Label
Bonefish	Grand Bahama	Flats (N)	North	26-Jan-14	30	GNB
Bonefish	Grand Bahama	Ocean (S)	South	25-Jan-14	30	GSB
Bonefish	Eleuthra	Flats (W)	Broad Creek	2-Mar-14	30	EWB
Bonefish	Eleuthra	Ocean (E)	Half Sound	8-Mar-14	10	EEB
Bonefish	Eleuthra	Flats (SW)	Plum Creek	8-Mar-14	10	ES1
Bonefish	Eleuthra	Flats (SW)	Sound Side	10-Mar-14	7	ES2
Conch	Grand Bahama	South	Freeport	1-Jan-14	30	GSC
Conch	Eleuthra	Flats (W)	Schooner Cay 2	1-Mar-14	30	EWC

TABLE 2 Study species (= bonefish *Albules vulpes*; queen conch *Lobatus gigas*) evaluated in this study. Also provided are number of genetic loci greater than 50% retention (= Loci > 50%); Average number of loci per individual (= Av loci/ind); Average depth of coverage (= Av coverage); Number of SNPs generated (= N SNPs); and Number of parsimonious-informative SNPs (= PI SNPs).

Species	**Loci > 50%**	**Av loci/ind**	**Av coverage**	**N SNPs**	**PI SNPs**
Bonefish	38,221	39,502	73X	36,797	25,039
Conch	30,697	33,409	59X	64,863	44,334

TABLE 3 BAYESASS3 results for bonefish (*Albula vulpes*) and queen conch (*Lobatus gigas*) sampled at Grand Bahama and Eleuthera islands. Values are expressed as proportion of individuals expected to be of a given migrant or non-migrant origin. Migration rates along the diagonal are analogous to a self-recruitment rate, with high values representative of demographic independence. Sample site abbreviations per Table 1.

	EWB	**EEB**	**ES1**	**ES2**	**GNB**	**GSB**	**GNC**	**EWC**
EWB	0.884	0.039	0.020	0.019	0.021	0.018	-	-
EEB	0.085	0.833	0.020	0.021	0.020	0.020	-	-
ES1	0.104	0.146	0.689	0.020	0.020	0.021	-	-
ES2	0.127	0.106	0.026	0.693	0.025	0.025	-	-
GNB	0.104	0.075	0.016	0.016	0.774	0.015	-	-
GSB	0.179	0.077	0.015	0.016	0.016	0.698	-	-
GNC	-	-	-	-	-	-	0.987	0.013
EWC	-	-	-	-	-	-	0.013	0.988

FIGURE LEGENDS

FIGURE 1 (Top) Map depicting The Commonwealth of Bahama (insert top right). The islands of Grand Bahama, Abaco, Eleuthera and Andros (northeastern Basin) are depicted. Blue dots represent sample sites for queen conch, whereas those for bonefish are designated with red dots. (Bottom) Sample sites at Eleuthera Island for queen conch and bonefish. Colors as above. Labels as in Table 1.

FIGURE 2 (Top) Bathymetry map of the northwest Carribean Basin (modified from http://oceanexplorer.noaa.gov/explorations/09deepseacorals/logs/summary/media/bahamas_region_600.html). Red ellipse designates Eleuthera Island; 1 = Great Bahama Canyon; 2 = Great Bahama Flat; 3 = Exuma Sound. (Bottom) Oceanic currents in the northern Caribbean Basin (modified from: University of Miami Rosenthiel School of Marine and Atmospheric Science, http://oceancurrents.rsmas.miami.edu/caribbean/caribbean-maps.html). Black lines depict currents; Yellow arrow designates direction of Gulf Stream (east coast of Florida); Green arrow indicates direction of current in Grand Bahama Canyon; 2 = Eleuthera Island; Red Arrow indicates direction of the Antillean Current (Atlantic Ocean).

FIGURE 3. STRUCTURE plots for bonefish (*Albula vulpes*) sampled at Grand Bahama and Eleuthera islands, The Bahamas. K=2 represent a 2-group analysis employing (1) the SD2 dataset containing single nucleotide polymorphisms (SNPs) >2 standard deviations (sd) above mean Fst (N=99), and (2)

692 the SD3 dataset containing SNPs >3 sd above mean Fst (N=64). K = 3 represents a 3-groupl analysis
involving the same two datasets. GN = Grand Bahamas Flats North (Flats or North side); GS = Grand
694 Bahamas Ocean Side (South or Bahamian side); EW = Eleuthera Flats Broad Creek (West side); EE =
Eleuthera Ocean Half-Sound (Atlantic Ocean or East side); ES1 = Eleuthera Ocean Plum Creek (Flats or
696 Southwest side); ES2 = Eleuthera Ocean South Side (Flats or Southwest side). More details on sample
sites provided in Table 1.

698

FIGURE 4. Plots depicting discriminant analysis of principal components (DAPC) for six populations of
700 bonefish (*Albula vulpes*) along discriminant functions one (=DF1) and two (=DF2). ALL = plot utilising
All loci (N=38,221); SD2 = plot depicting single nucleotide polymorphisms (SNPs) > 2 standard
702 deviations (sd) above mean Fst (N=99); SD3 = plot employing SNPs > 3 sd above mean Fst (N=64). GN
= Grand Bahamas Flats North (Flats or North side); GS = Grand Bahamas Ocean Side (South or
704 Bahamian side); EW = Eleuthera Flats Broad Creek (West side); EE = Eleuthera Ocean Half-Sound
(Atlantic Ocean or East side); ES1 = Eleuthera Ocean Plum Creek (Flats or Southwest side); ES2 =
706 Eleuthera Ocean South Side (Flats or Southwest side). More details provided in Table 1.

708 FIGURE 5. Structure plots for queen conch (*Lobatus gigas*) sampled as Grand Bahama and Eleuthra
islands, the Bahamas, with individuals represented by vertical lines. Two groups are depicted [GBS =
710 Grand Bahama South Freeport (Flats or South side); EW = Eleuthera Flats Schooner Cay 2 (Flats or
West side)]; ALL = Plot employing all single nucleotide polymorphisms (SNPs) (N=30,697); SD2 = SNPs

712 > 2 standard deviations (sd) above mean Fst (N=88); and SD3 = plot depicting SNPs > 3 sd above mean Fst (N=51).

714

FIGURE 6. Plots depicting discriminant analysis of principal components (DAPC) for two populations

716 of queen conch (*Lobatus gigas*), with GBS = Grand Bahama South Freeport (Flats or South side) and EW = Eleuthera Flats Schooner Cay 2 (Flats or West side) plotted along discriminant function one

718 (=DF1). All = Plot employing all single nucleotide polymorphisms (SNPs) (N=30,697); SD2 = SNPs > 2 standard deviations (sd) above mean Fst (N=88); and SD3 = plot depicting SNPs > 3 sd above mean

720 Fst (N=51).

722 FIGURE 7. Graph depicting relative migration rates for six populations of bonefish (*Albula vulpes*), where nodes represent populations, and edges are weighted according to the level of direction

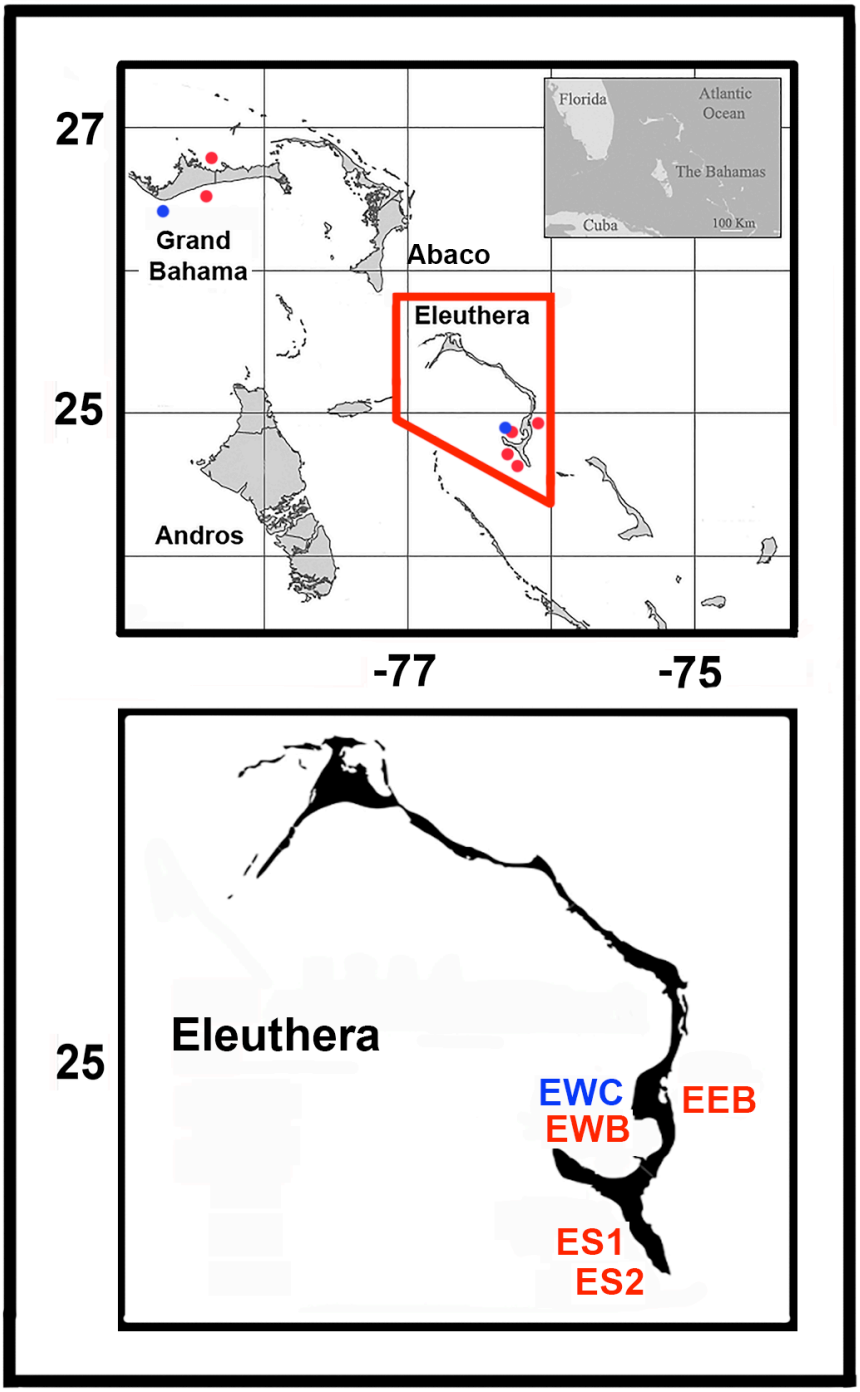
724 relative migration rates (*m*), as derived from BA3-SNPs results. All edges below 0.02 were omitted. Full results shown in Table 3. GN = Grand Bahamas Flats North (Flats or North side); GS = Grand

726 Bahamas Ocean Side (South or Bahamian side); EW = Eleuthera Flats Broad Creek (West side); EE = Eleuthera Ocean Half-Sound (Atlantic Ocean or East side); ES1 = Eleuthera Ocean Plum Creek (Flats or

728 Southwest side); ES2 = Eleuthera Ocean South Side (Flats or Southwest side).

730 FIGURE 8. Asymmetric immigration recorded for bonefish (*Albula vulpes*) from Grand Bahama and Eleuthra islands. Values are expressed as net emigration rates (summed emigration - summed

732 immigration) for each population, with positive values indicating ‘source’ populations and negative values indicating ‘sink’ populations.


27
25
-77
-75
Grand
Bahama
Abaco
Eleuthera
Andros
Florida
Atlantic
Ocean
The Bahamas
Cuba
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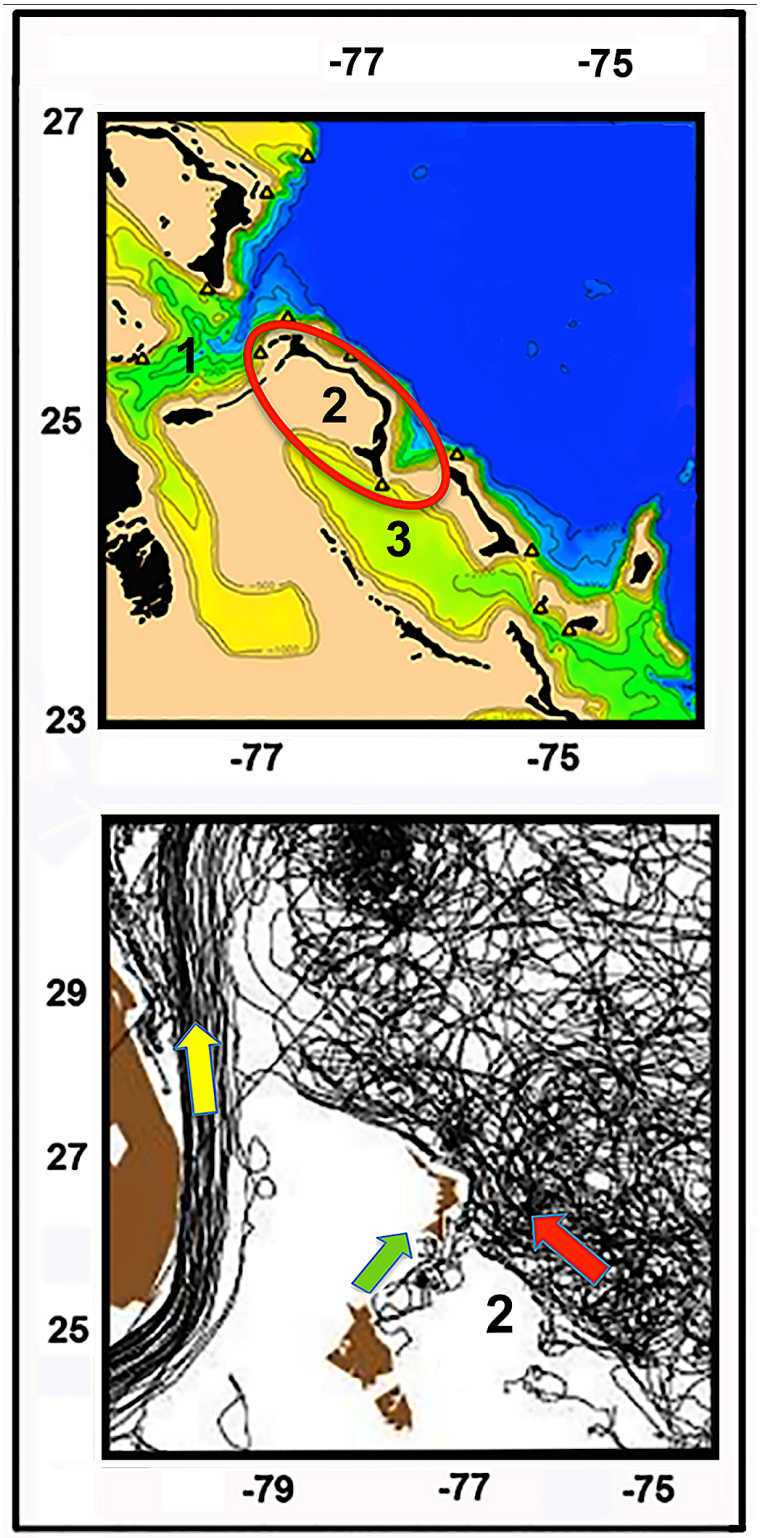
Eleuthera
EWC
EWB
EEB
ES1
ES2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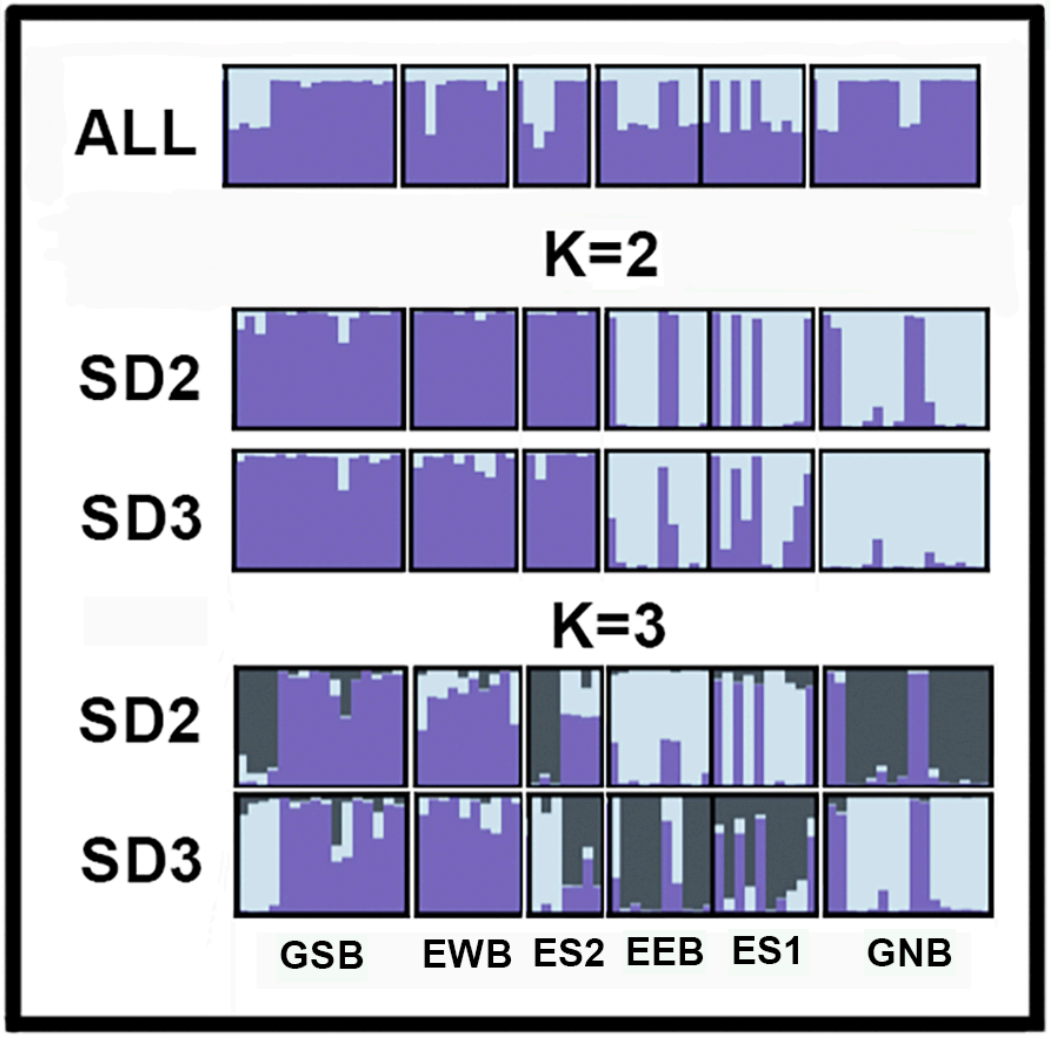
-75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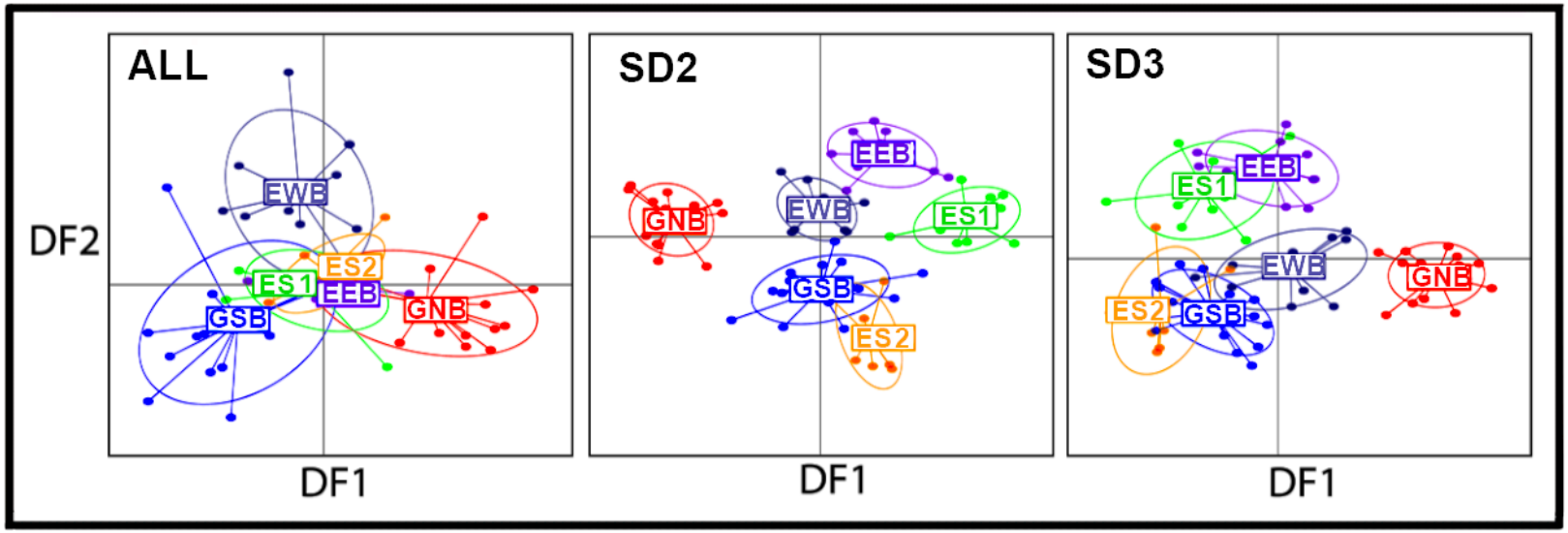
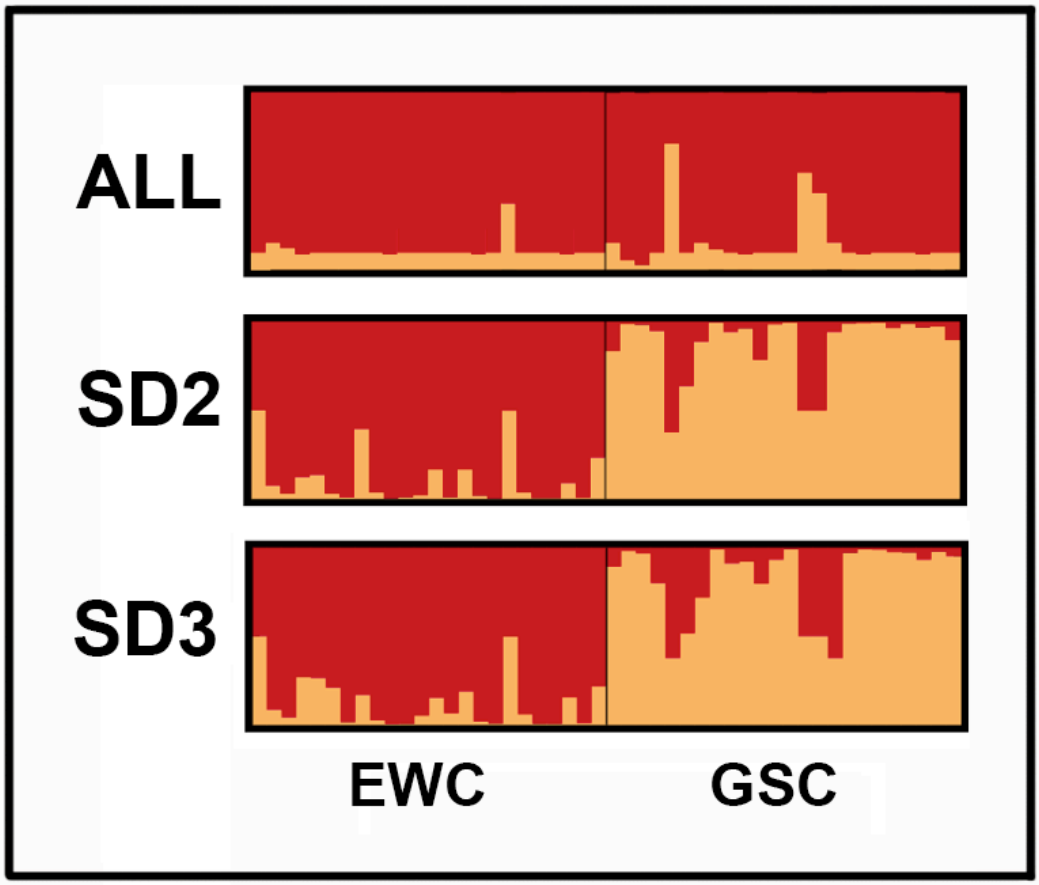
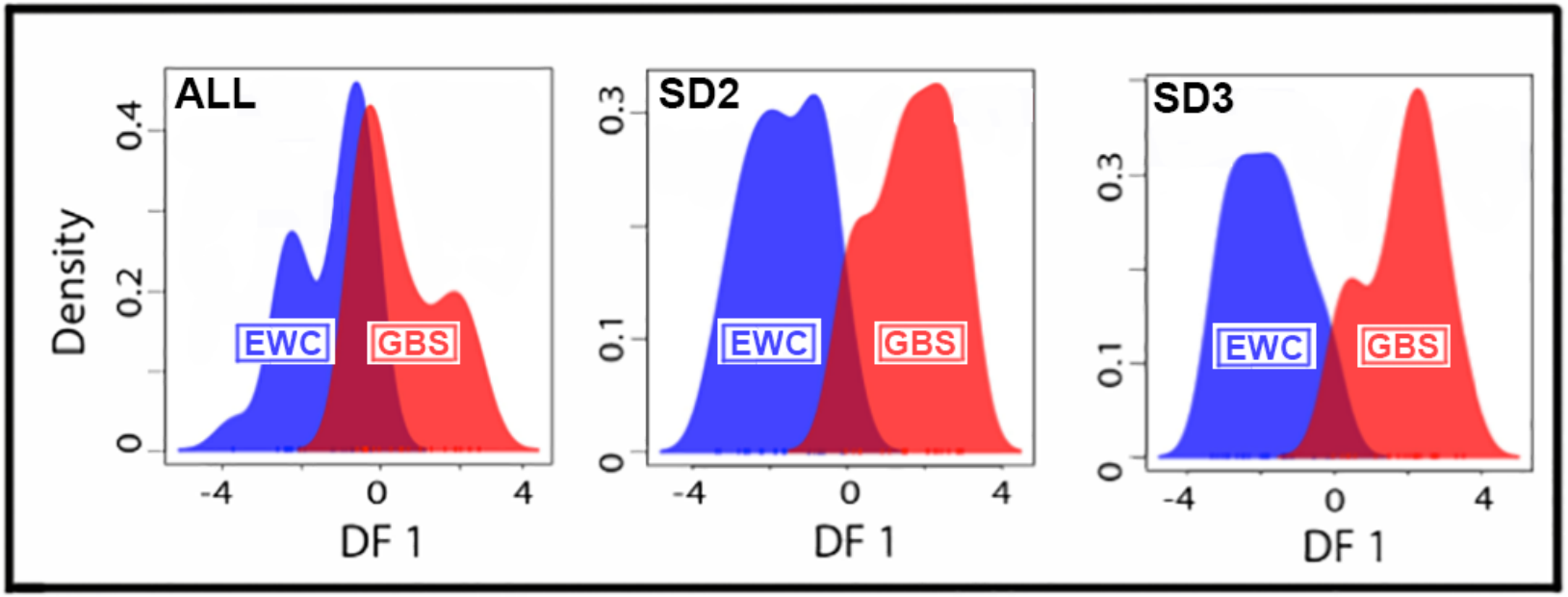
SD3
K=3
SD2
SD3
GSB
EWB
ES2
EEB
ES1
GNB


ALL
SD2
SD3
DF2
DF1
DF1
DF1
EWB
ES2
ES1
EEB
GSB
GNB
EEB
EWB
ES1
GNB
GSB
ES2
EEB
ES1
EWB
GNB
ES2
GSB


ALL
SD2
SD3
EWC
GSC


ALL
SD2
SD3
Density
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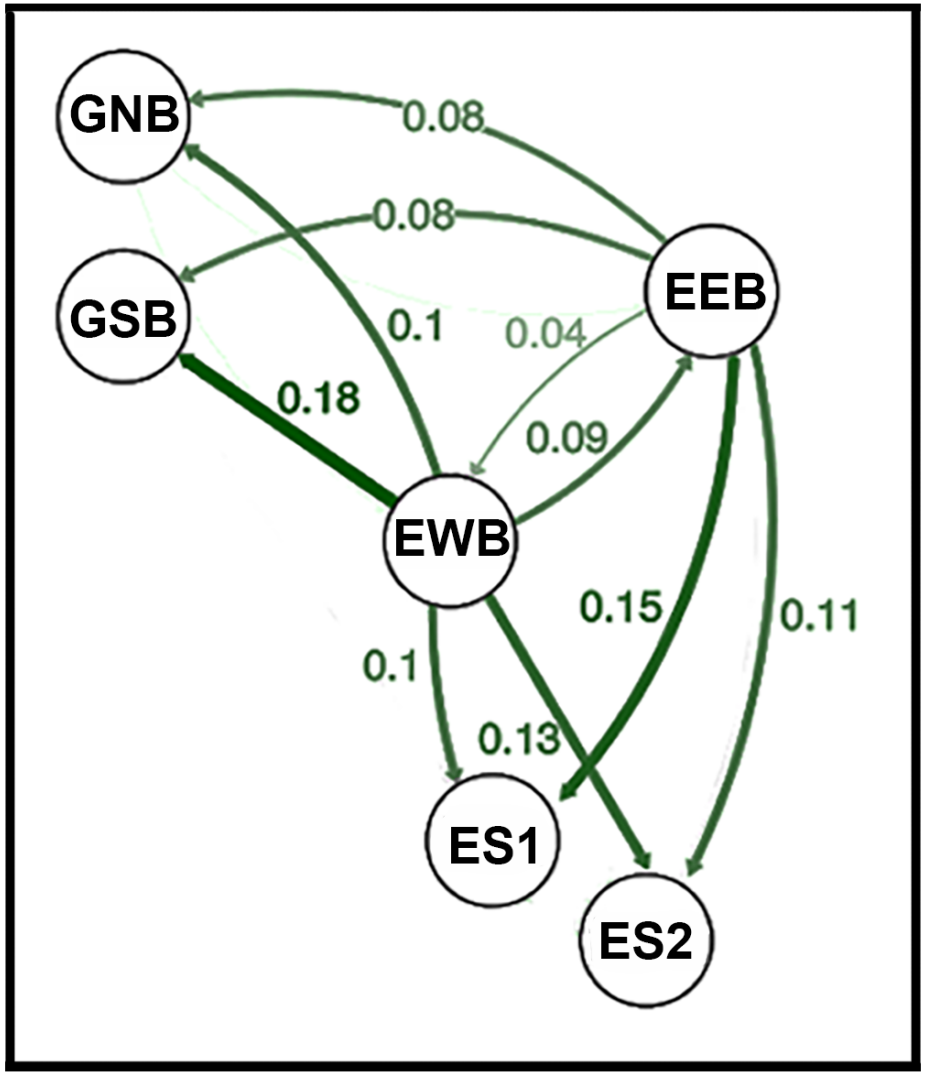
0.4
0.1
0.3
EWC
GBS
-4
0
4
DF 1


GNB
GSB
EEB
EWB
ES1
ES2
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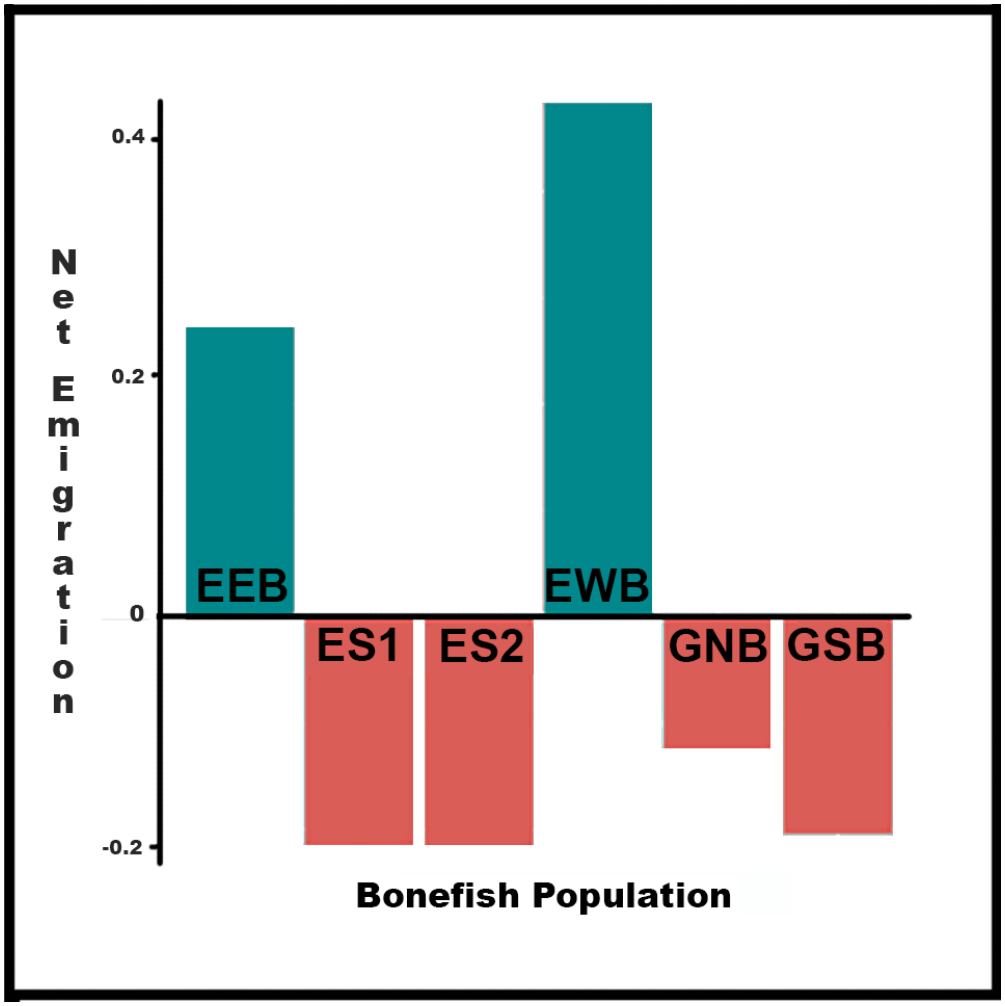
0.08
0.1
0.04
0.18
0.09
0.15
0.11
0.1
0.13


0.4
0.2
0
-0.2
Net Emigration
EEB
ES1
ES2
EWB
GNB
GSB
Bonefish Population