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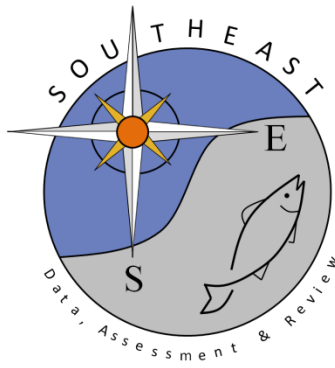
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Spatial connectivity in an adult-sedentary reef fish with extended pelagic larval phase

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Abstract

Understanding the spatial scale of demographic connectivity in marine reef fishes dispersing pelagic larvae is a challenging task because of the technical difficulties associated with tagging and monitoring the movements of progeny at early life stages. Several studies highlighted a strong importance of local retention with levels of dispersal of ecological significance restricted to short distances. To date little information is available in species where pelagic dispersal lasts for long periods of time. In this work, population structure and connectivity were studied in the grey triggerfish, *Balistes capriscus*. Grey triggerfish larvae and juveniles remain associated with floating *Sargassum* sp. beds for an estimated period of 4–7 months before settling on benthic habitats where they remain sedentary as adults. Analysis of genetic variation among populations along the continental shelf of the northern Gulf of Mexico and U.S. east coast, encompassing over 3,100 km of coastline, revealed homogeneous allele frequencies and a weak isolation-by-distance pattern. Moment and maximum-likelihood estimates of dispersal parameters both indicated occurrence of large neighbourhoods with estimates of the dispersal distribution parameter σ of 914 and 780 km, respectively. Simulated distributions of dispersal distances using several distribution functions all featured substantial fractions of long-distance dispersal events with the 90% percentiles of travel distance prior to settlement averaging 1,809 km. These results suggest a high dependency of local recruitment on the output of nonlocal spawning stocks located hundreds of kilometres away and a reduced role of local retention in this species.

KEYWORDS
Balistes capriscus, connectivity, dispersal, grey triggerfish, population genetics-Empirical

1 | INTRODUCTION

Characterizing genetic and demographic connectivity among geographic populations is essential to design effective conservation strategies (Lowe & Allendorf, 2010). The marine environment is a priori open to migrations (Avise, 1998), and many marine species display a continuous distribution across large portions of their range, sometimes encompassing several thousand kilometres, leading to the assumption that connectivity occurs across these large geographic areas, promoted by free dispersal. The spatial scale of the actual genetic connectivity is, however, influenced by several factors including the dispersal capability of organisms, the density of populations and the strength of local adaptation. The dispersal itself is determined by several factors including the occurrence of barriers to gene flow resulting from discontinuities of suitable habitat, the duration of the physical transport of eggs and larvae, the velocity of currents involved for species with pelagic planktonic phases, and the movement behaviour and capabilities of adults. In reef fishes, movements of adults are often limited, and when this is the case, the larval transport processes are assumed to be the major determinants of dispersal (Jones et al., 2009; Leis & McCormick, 2002; Shanks, 2009).

Under the island model, genetic connectivity can be maintained even when only a few effective migrants are exchanged per generation (Waples, 1998) which is often enough to rapidly ensure the spread of advantageous mutations across a metapopulation (Lowe & Allendorf, 2010). However, management is also concerned with local demographic change of populations, in particular the relative role of local recruitment and migration in determining local demographic dynamics, or the potential for local replenishment through migration from external populations (Kritzer & Sale, 2004). The spatial scale of this demographic connectivity is often different from that of the genetic connectivity and is also more difficult to determine because it requires estimating rates of migrations. Obtaining direct estimates of the spatial scale of demographic connectivity requires data on local recruitment as well as quantitative estimates of migrations from and to other demes (Lowe & Allendorf, 2010). This information is particularly challenging to obtain when boundaries between demes are not clearly defined as is the case in many marine species that are structured in large continuous metapopulations. In such cases, tag and recapture studies or studies of elemental signatures in otoliths can provide information on juvenile and adult movements but are not adapted to measure dispersal in most reef fishes that are sedentary as adults but disperse planktonic eggs and larvae that cannot easily be tagged (Thorrold et al., 2002). Particle tracking may be used to predict larval envelopes (e.g., Cowen, Paris, & Srinivasan, 2006; Johnson, Perry, Lyczkowski-Shultz, & Hanisko, 2009; Roberts, 1997), but this approach can also be challenging in species that cannot be modelled by a simple particle including, for example, those utilizing pelagic habitats that are fluctuating over time in size and shape such as floating *Sargassum* beds.

Paternity analysis inferred from molecular marker data and tracking of the maternal origin of settling juveniles through the analysis of stable isotopes transmitted from mother to offspring have been used successfully to demonstrate occurrence of local recruitment (e.g., Almany, Berumen, Thorrold, Planes, & Jones, 2007; Christie, Stallings, Johnson, & Hixon, 2010), but these approaches are limited when populations are large and dispersal occurs across broad geographic areas. Genetic estimation of contemporaneous rates of gene flow through assignment tests has been used in several species (Lowe & Allendorf, 2010), but this approach requires migrants to be exchanged between discrete and differentiated populations. When there is isolation by distance in a continuous population this method is irrelevant but inferences on dispersal can be made using the isolation-by-distance theoretical framework (Puebla, Bermingham, & Guichard, 2009; Rousset, 1997). Recent developments of this approach using individual models and maximum-likelihood algorithms (Rousset & Leblois, 2007, 2012; Watts et al., 2007) allowed assessing dispersal in metapopulations showing high degree of genetic connectivity (and homogeneity) across large geographic areas (e.g., Puebla, Bermingham, & McMillan, 2012).

Studies in reef fishes to date have revealed relatively small (less than 100 km in most cases) larval dispersal envelopes (Cowen et al., 2006; Puebla et al., 2012; Roberts, 1997; Shanks, 2009), but the species considered were characterized by short-dispersal durations, usually less than a month. On another hand, data on the spatial scale of demographic connectivity are lacking for species where larval dispersal lasts longer. In those species, rare successful long-distance dispersal events could maintain genetic connectivity across long distances even if the majority of dispersal events are restricted to local areas; in that situation, the local spawning biomass would retain a strong influence on recruitment. Alternatively, longer larval transport could result in high proportion of dispersal events at long distances and a reduced contribution of local spawning stocks to recruitment. Distinguishing between these scenarios is essential to determine effective conservation and management strategies.

The grey triggerfish, *Balistes capriscus*, is a reef fish that inhabits subtropical and temperate waters on both sides of the Atlantic Ocean. This species is highly sedentary as adult where it is found associated with benthic structures of the continental shelf (Ingram, 2001) at depths ranging between 0 and 100 m (Harmelin-Vivien & Quéro, 1990). Dispersal is thought to occur primarily during the larval and juvenile stages (Franks et al., 2007; Wells & Rooker, 2004) when the species is pelagic. This pelagic phase (4–7 months, Simmons, 2008) lasts longer than in most other reef fishes, and, during that period, larvae and juveniles are found associated with floating seaweeds and flotsam (mostly *Sargassum* sp.) until they settle on hard benthic structures. Grey triggerfish reach sexual maturity at a length of 250 mm fork length (FL) and the age of 1 year for males and 2 years for females (Ingram, 2001; Wilson, Nieland, & Stanley, 1995). Females produce on average 13,809 oocytes per gram of ovary (range 6,318–24,188, Hood & Johnson, 1997). Grey triggerfish can live up to 16 years in the Gulf of Mexico (NMFS 2006), and their generation time is estimated between 4 and 8 years (Jing et al., 2015). Their centre of abundance is located in the southeast United States (Gulf of Mexico and southeast U.S. coast) where they approach a continuous distribution along shelf habitats. The life history features of this species predict structuring according to an isolation-by-distance model as discussed above where dispersal is limited by the spatial scale of the pelagic larval transport. The extended pelagic phase could promote long-distance movement, but it has also been hypothesized that larvae could be retained in local eddies and recruit close to their spawning location (NMFS 2006). The availability of a large continuously distributed population in the southeastern U.S. provides the opportunity to describe the isolation-by-distance model and assess quantitatively the spatial scale of demographic connectivity resulting from larval dispersal in this species.

In this work, 17 microsatellite markers were used to survey genetic variation among grey triggerfish in the northern Gulf of Mexico and along the east coast of the United States. The data set was used to characterize patterns of population structure and provides first estimates of dispersal parameters and connectivity in the species.

2 | MATERIALS AND METHODS

2.1 | Sampling

Samples of grey triggerfish were obtained during the summer and fall of 2008, 2009 and 2010. Sampling focused on subadult and

adult specimens settled on benthic continental shelf habitats where they are known to display high site fidelity (Ingram, 2001). Specimens from across the northern Gulf of Mexico were obtained in conjunction with the summer and fall groundfish SEAMAP surveys conducted by the National Marine Fisheries Service (NOAA-Fisheries). The survey employs a stratified randomized design to sample benthic shelf habitats used by triggerfish juveniles and adults, (10–100 m depth) by trawling from Pensacola to the U.S./Mexico border (Nichols, 2004). Additional samples from the northern Gulf were collected at recreational fishing docks (Mississippi and vicinity of Panama City, Florida) and during fishery-independent reef fish monitoring surveys conducted by the NOAA-Fisheries Panama City laboratory in west Florida (east of Pensacola) using traps. Sampling in the northern Gulf (1,400 km of coastline, Figure 1) yielded 430 specimens and resulted in minimal gaps in this section of the studied range except for the shelf nearing the Mississippi estuary delta and a small portion of the Texas shelf north of Corpus Christi.

Two hundred and thirty-five additional samples were obtained from southwest Florida (SWF, $n = 77$ collected by trawling), from southeast Florida (SEF, $n = 80$ collected by angling) and South Carolina (SC, $n = 78$ collected by trapping) bringing the total sampling size to 665 specimens.

Specimens were preserved frozen on board (SEAMAP samples) or kept on ice until fish were landed. Muscle tissue and fin clips were collected and stored in 95% alcohol or a Dimethyl Sulfoxide (DMSO) salt-saturated storage buffer (0.25 M EDTA, 20% DMSO, NaCl) prior to DNA extraction except for the samples from South Carolina which were preserved in a Sarkosyl urea lysis buffer (1% N-lauroylsarcosinate, 20 mM NaPO4, 8 M urea, 1 mM EDTA).

2.2 | Laboratory assays

DNA extraction was performed following a phenol–chloroform protocol (Sambrook, Fritsch, & Maniatis, 1989). The fish were genotyped at 17 microsatellite markers described in Antoni and Saillant (2012). To improve the cost-effectiveness of genotyping, microsatellites were assayed in four multiplex panels developed during the study. Detailed multiplexed PCR protocols including microsatellite

loci identification, primers concentration, fluorescent labelling and specific T_a are presented in Appendix S1. PCR products were loaded on a 6% acrylamide gel and run on an ABI Prism 377 DNA Sequencer (Applied Biosystems, Foster City, CA, USA) following instructions from the manufacturer. Electropherograms were analysed in the software GENESCAN v.3.1.2 (Applied Biosystems), and alleles were called in the software GENOTYPER v.2.5 (Applied Biosystems).

2.3 | Data analysis

Samples were initially grouped in six regional populations based on gaps in sampling (Figure 1). The occurrence of scoring errors due to null alleles, stuttering bands and large allele dropout in each regional population-sample was tested in MICROCHECKER v.2.2.3 (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). The conformance of genotype proportions to Hardy–Weinberg (H-W) equilibrium expectations was tested using exact tests in GENEPOP v.4.2 (Raymond & Rousset, 1995; Rousset, 2008a). Probability-value estimates were based on 10,000 dememorizations, 500 batches and 5,000 iterations per batch. Departure from H-W equilibrium (F_{IS}) measured as Weir and Cockerham's (1984) f, the number of alleles, allelic richness (El Mousadik & Petit, 1996) and gene diversity (expected heterozygosity calculated as described in Nei, 1987) were computed for each regional sample in FSTAT v.2.9.3 (Goudet, 1995).

2.4 | Analysis of spatial genetic variation

Homogeneity in allelic richness and gene diversity among samples was tested using the Friedman ranks test, as implemented in SPSS v.20 (IBM Corp., Armonk, NY, USA). The degree of population differentiation (F_{ST}) among regions was estimated as Weir and Cockerham (1984) θ as calculated in FSTAT and homogeneity of allele distributions among regional samples was tested using exact tests in GENEPOP. Pairwise comparisons were performed by computing estimates of pairwise θ between individual regions and performing associated pairwise exact homogeneity tests. Markov chain parameters during exact homogeneity tests were the same as above (Exact tests of H-W equilibrium). The False Discovery Rate (FDR, Benjamini &
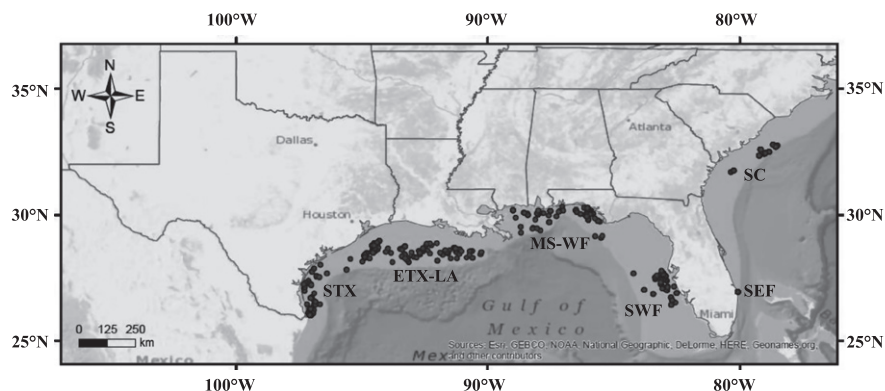

FIGURE 1 Sampling localities for gray triggerfish, *Balistes capriscus*, in US waters. STX, south Texas; ETX-LA, east Texas-Louisiana; MS-WF, Mississippi-west Florida; SWF, southwest Florida; SEF, southeast Florida; SC, South Carolina

Hochberg, 1995) procedure was used to determine the significance threshold for p-values when multiple independent tests were conducted simultaneously.

Isolation by distance due to limited dispersal potential and barriers to gene flow (genetic discontinuities) may both account for divergence among geographic samples. Spatial genetic variation within the region was, therefore, further explored using the Bayesian clustering approach implemented in the software TESS v.2.3.1 (Chen, Durand, Forbes, & François, 2007; Durand, Chen, & François, 2009). TESS aims to detect genetic discontinuities within continuously distributed populations of a species based on the distribution of multilocus genotypes. This approach accounts for the decay of spatial autocorrelation that occurs due to isolation by distance, and is therefore well suited for populations displaying spatially restricted dispersal and a predicted isolation-by-distance pattern. One hundred runs were performed using a conditional autoregression (CAR) admixture model, allowing for correlated allele frequencies among populations. Each Monte Carlo simulation included 250,000 sweeps with the first 50,000 sweeps discarded as burn-in. The 20 runs showing the lowest Deviance Information Criteria (Spiegelhalter, Best, Carlin, & van der Linde, 2002) were retained to make inferences, as recommended by Durand, Jay, Gaggiotti, and François (2009).

Structuring according to an isolation-by-distance mechanism was examined within ranges where no evidence of genetic discontinuity was found. The method developed by Rousset (2000) and Leblois, Rousset, and Estoup (2004) was employed as it allows estimating dispersal parameters based on existing theory of isolation by distance (Rousset, 1997).

The genetic distance between pairs of individuals was estimated as the ê statistics (Watts et al., 2007) computed in the software GEN-EPOP. The ê statistics is more powerful in cases where the spatial pattern of population structure is weak (Watts et al., 2007), as is the case in the present study (see Section 3). The analysis of isolation by distance focused on data obtained on specimens (n = 430) collected between south Texas and west Florida (1,400 km) because this portion of our sampling design approached best a continuous sampling along the coastline as recommended to infer parameters of the model (Leblois et al., 2004). Considering the shelf habitat used by grey triggerfish, two approaches were used to compute individual coordinates and calculate geographic distances between individuals and isolation-by-distance statistics. In a first approach, a one-dimensional lattice (mid-shelf transects following the coastline, 1D model) was used thus assuming dispersal in a one-dimensional linear habitat. In a second approach, a two-dimensional habitat spanning from Texas to west Florida was considered (2D model). The 2D model was only evaluated using the likelihood approach in MIGRAINE.

Because estimation of the parameters of the isolation-by-distance model is biased when the geographic distance between samples being compared is greater than $0.56\,\sigma/\sqrt{2}\mu$, where σ is the standard deviation of parental position relative to offspring position and μ is the mutation rate (Rousset, 1997), a bootstrap resampling approach was used to investigate the effect of the spatial scale of sampling on estimates of the slope of the isolation-by-distance

relationship and σ. Subsamples were drawn by resampling sets of 100 individuals located within subsections of the lattice of various lengths using the software POPTOOLS v.3.2.5 (Hood, 2010), and the slope of the 1D linear regression between genetic and geographic distance (b) was estimated for each resampled data set.

This slope was then used to calculate σ, given the effective population density (D), using the relationship (Rousset, 1997)

$$\sigma = \sqrt{\frac{1}{4Db}} \qquad (1)$$

Inferences on σ thus require information on population density. Two approaches were taken to obtain values for D and discuss values of σ and the distribution of dispersal distances. An upper bound for D is given by the census population density (D_c). The census density of grey triggerfish was estimated based on average landing data in the Gulf of Mexico during the sampling period obtained from the recreational fisheries statistics database of the Fisheries Statistics Division of the National Marine Fisheries Service (personal communication, database accessed 08 January 2016) and accounting for estimates of fishing mortality rates that range between 0.435 and 0.53 (NMFS 2011). The obtained estimate of the census number of adults was applied to the Gulf section of the lattice (2,035 km) to derive estimates of census density for the 1D model and to estimates of the area of the shelf habitat for grey triggerfish approximated as a strip surrounding the 1D lattice for the 2D model.

Effective density (D_e) was also estimated using genetic data. Considering the observed homogeneity in allele frequencies across the sampling surface (see Section 3), an estimate of the effective size for the overall metapopulation was generated using the maximum-likelihood (ML) coalescent approach in the software MIGRAINE v.0.4.1 (Leblois et al., 2014; Rousset & Leblois, 2007, 2012). The OnePopVar-Size demographic model allowing accounting for historical change in population size was used in the estimation (Appendix S2). The parameter N that represents an estimate of the current effective population size was calculated assuming an average mutation rate across microsatellites of 5×10^{-4} (Estoup & Angers, 1998). N was also calculated considering mutation rates of 10^{-3} and 10^{-4} in order to evaluate the sensitivity of parameter estimates to the mutation rate. The obtained estimate of N was applied to the entire lattice length/surface to derive an estimate of effective density.

Estimates of contemporaneous N_e by the linkage disequilibrium method were also generated for each of the six regional populations using the software LDNE (Waples & Do, 2010).

Because the genetic consequences of dispersal depend on the shape of the distribution of dispersal distance (Rousset, 2008b), a simulation approach after Puebla et al. (2012) was taken to determine the parameters of dispersal distance distributions yielding isolation-by-distance slopes consistent with that estimated from the empirical data set. Coalescent simulations were implemented in the software IBDSIM v.2.0 (Leblois, Estoup, & Rousset, 2009) considering various distribution functions (Geometric, Pareto and Sichel). Simulations employed a one-dimensional lattice of 10,000 km with absorbing boundaries; samples were generated from a 1,400 node

subsection of the lattice to match the length of the portion of the northern Gulf of Mexico (south Texas to west Florida, approximately 1,400 km of coastline) used in the empirical study and at most one individual was sampled per node. Simulated data sets included 17 unlinked loci following a GSM mutation model with a mean mutation rate of 5×10^{-4} and a geometric variance of multi-step mutations with parameter estimated during N_e estimation in MIGRAINE (Appendix S2). The simulated data sets were processed for isolation-by-distance analysis as described above. Parameters for each of the dispersal distribution functions were adjusted to determine ranges of values leading to isolation-by-distance slopes b similar to those obtained with the empirical data set. Series of simulations were then conducted in triplicates within this range to identify the parameter values (or combination of parameter values) that led to isolation-by-distance slopes closest to the estimates from the empirical data set. The influence of the mutation rate on the dispersal distribution parameters was evaluated by considering mutation rates of 10^{-3} and 10^{-4} used as an upper and lower bound of the average mutation rate for the 17 microsatellites used in the study, respectively.

Finally, Maximum-likelihood estimates of σ were generated using both linearIBD and planarIBD demographic models implemented in MIGRAINE. These methods provide an estimate of the neighbourhood size parameter (Nb) from which an estimate of σ can be derived. The planarIBD model accounts for a two dimensional habitat while the linearIBD model assumes dispersal along a one dimension (linear) lattice. Estimates were generated during three replicate runs employing the Product of Approximate Conditional (PAC) likelihoods algorithm with 2,000 points and 100 runs per point.

Estimates of the parameter σ were derived from Nb using the relationships Nb = $2D\sigma^2$ (Equation 2) and Nb = $2D\pi\sigma^2$ (Equation 3) for the linear and the two dimensional model, respectively, where D was set to the census or the effective population density value determined as above.

An exclusion approach in the software GENECLASS v.2.0 (Piry et al., 2004) was used to test the influence of possible migrants from divergent grey triggerfish populations on estimates of isolation-by-distance parameters. Sampled individuals were assigned to a locality based on their multilocus genotype using the Bayesian method of Rannala and Mountain (1997); the probability that an individual belonged to a given locality was calculated using the resampling algorithm of Paetkau, Slade, Burden, and Estoup (2004) and was based on 10,000 simulated individuals. Putative migrants were identified as those showing p-value of assignment below 0.05 for all six regional samples. The slope of the isolation-by-distance model and sigma were recalculated as described above after removing the detected possible migrants from the data set.

3 | RESULTS

Four of 102 tests (6 geographic samples $\times$ 17 loci) of Hardy–Weinberg equilibrium were significant before FDR correction for multiple tests performed simultaneously. None of the test remained significant after correction. MICROCHECKER analyses indicated possible occurrence of null alleles at locus BC14 in the ETX-LA region, locus BC17 in the SEF region and stuttering and/or null alleles at locus BC3 in the SWF region. Because the scoring artefacts at these three loci were found in one region (of six) only and did not lead to significant departure from Hardy–Weinberg expectation, all 17 markers were kept for further analysis.

Summary statistics per locus and per region including number of alleles, allelic richness, gene diversity, inbreeding coefficient and probability of significance of tests of Hardy–Weinberg equilibrium are presented in Appendix S3. The number of alleles (A) per locus averaged 25.6 and ranged between 9 (locus BC16) and 45 (locus BC46). Gene diversity ranged between 0.27 (locus BC16 in the SEF region) and 0.969 (locus BC46 in the SWF region). Allelic richness and gene diversity did not differ significantly among localities (p = .240 and p = .083 respectively).

The estimate of θ was very low (0.0004, 95% bootstrapping Confidence Interval CI: 0–0.001), and the probably that θ differed from zero from exact homogeneity tests was 0.031. Homogeneity tests at individual loci did not reveal significant heterogeneity in allele frequencies among regions except for one locus, BC46, that showed significant heterogeneity (p = .042) before FDR correction but not after correction. Pairwise θ values between individual regions averaged 0.0006 (range −0.0006–0.0018, Table 1) and only two pairwise exact homogeneity tests (across loci) were significant before and after FDR correction (SWF vs. ETX-LA comparison: p = .0177, estimate of θ = 0.0008; SWF vs. SEF comparison: p = .0032, estimate of θ = 0.0018). Bayesian clustering runs in TESS all converged towards a single unit with no genetic discontinuity within the sampled range. Further analysis of isolation by distance proceeded under this assumption.

The estimate of the current effective size (N) derived assuming an average mutation rate of 5×10^{-4} was 29,940 individuals (95% CI: 18,570–62,630, Appendix S2). The genetic estimate of D_e was generated by applying the estimate of N to the entire one-dimensional lattice (from south Texas to South Carolina, 3,100 km) yielding a value of 9.66 individuals/km (95% CI: 5.99–20.20) for D_e for the 1D model. N was then applied to a 20-km wide strip surrounding the transect line (123,331 km^2) for the 2D model yielding a value of 0.24 ind./km^2 (95% CI: 0.15–0.51) providing an upper bound value for D_e under this model. The census density D_c for the Gulf of Mexico was 175 ind./km (1D model) or 2.89 ind./km^2 (2D model) giving a ratio of effective to census density of 0.055 (95% CI: 0.034–0.115) for the 1D model and 0.083 (95% CI: 0.052–0.176) for the 2D model.

All the obtained N_e estimates from the linkage disequilibrium method were infinite or very large (greater than 2,494, Appendix S4).

Estimates of the isolation-by-distance slope under the 1D model using subsets of the data encompassing increasing distance ranges revealed a high variance among slopes when resampled data sets were generated using genotypes found within short-distance ranges (<1,100 km, Appendix S5). The mean and standard error of slopes from resampled data sets stabilized between

TABLE 1 Estimates of F_{ST} (Weir and Cockerham θ) (upper diagonal) and probability that $F_{ST} = 0$ (lower diagonal) for pairwise comparisons of microsatellite allele distributions between grey triggerfish geographic samples. Probability values that differed significantly from zero following correction for multiple tests are in bold

	STX	ETX-LA	MS-WF	SWF	SEF	SC
STX		0.0007	0.0003	0.0004	0.0018	−0.0002
ETX-LA	0.182		0	0.0008	0.0006	−0.0006
MS-WF	0.543	0.048		0.0004	0.0012	−0.0006
SWF	0.163	**0.018**	0.259		0.0018	0.0003
SEF	0.220	0.203	0.297	**0.003**		0.0015
SC	0.514	0.618	0.323	0.265	0.098	

3.4×10^{-8} and 4.4×10^{-7} when the sampled range was between 1,400 and 1,700 km (Appendix S5). Accordingly, final estimates were generated based on all available data for the area between south Texas and west Florida where the high density of sampling locations with minimal gaps best reflected the near-continuous distribution of grey triggerfish along the continental shelf. The obtained estimate was 3.1×10^{-8} (lower and upper bounds of the slope -5.24×10^{-7} and 4.61×10^{-7}, Figure 2). Point estimates generated using greater portions of the data set (i.e., including localities in south Florida and South Carolina) were all included within the bounds of the confidence interval described above. Considering the genetic estimate of effective density and census density, the corresponding values of σ derived using

equation 1 were 914 (95% CI: 237−+∞) and 215 (95% CI: 56−+∞), respectively.

Estimates of σ derived from Nb values obtained from the maximum-likelihood approach in MIGRAINE using equations 2 and 3 were 780 (95% CI: 255–2517) for the 1D model and 740 (95% CI: NA-7,330) for the 2D model. Because dispersal along a coastline one-dimensional axis can be approximated more easily, and the ML estimates of dispersal using the 1D and 2D models were similar, further analysis of dispersal distributions via simulations focused on the 1D model.

The simulated dispersal distributions are presented in Table 2. All distributions compatible with the empirical isolation-by-distance regression involved mean dispersal distances greater than 123 km. Examination of cumulated distributions reveals that 10% of dispersal events occurred at distances greater than 326 km in all distributions generated and, on average, at distances greater than 1,809 km (Table 3).

The ML estimates of the standard deviation of the parent-offspring dispersal distance remained large when a low average mutation rate (10^{-4}) was considered with a point estimate at 349 km (95% CI: 114–1,126). The estimate using a high mutation rate scenario (average 10^{-3}) yielded substantially larger values for sigma (point estimate 1,103, 95% CI: 361–3,559). Simulated dispersal distributions accounting for the two mutation rates in IBDSIM all yielded an estimate of σ greater than 123 km ($\mu = 10^{-4}$) or 141 km ($\mu = 10^{-3}$) when the census density was used in calculations, or 231 ($\mu = 10^{-4}$) and 259 ($\mu = 10^{-3}$) when the estimate of effective density was used (Appendix S6).
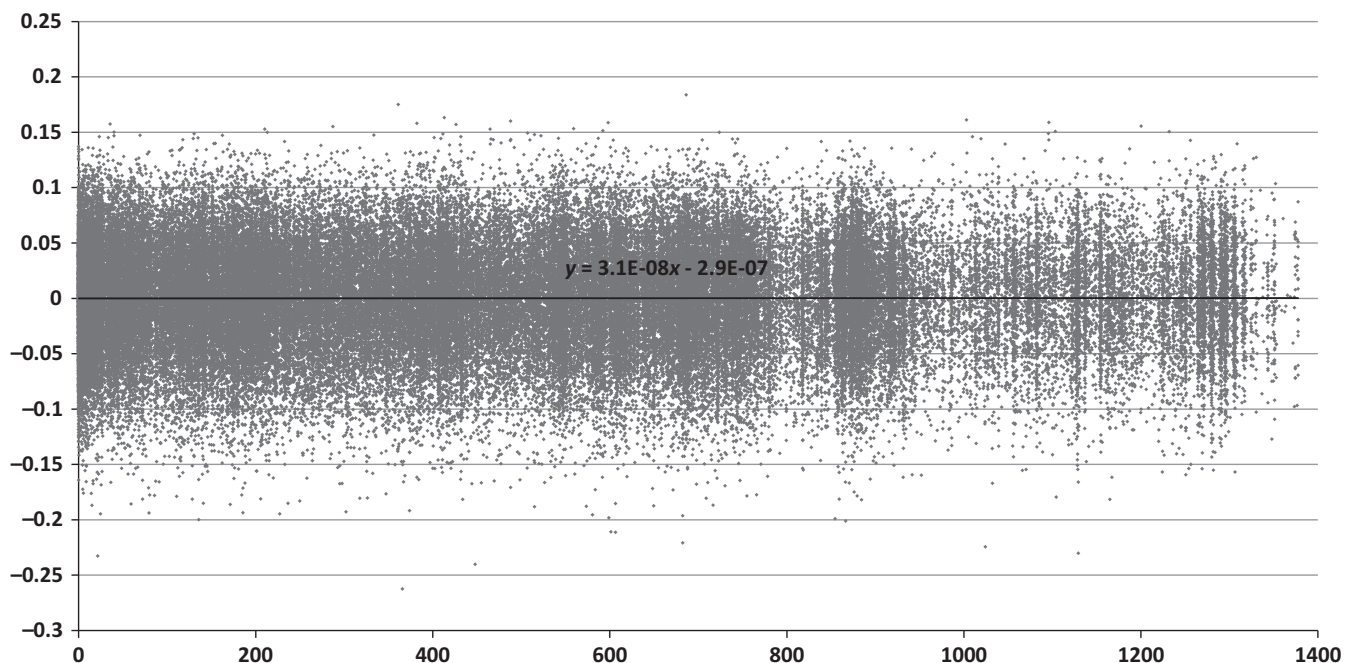

FIGURE 2 Plot of genetic versus geographic distance among individual gray triggerfish sampled in the northern Gulf of Mexico and equation of the regression under the 1D model of isolation-by-distance

TABLE 2 Parameters of simulated distributions yielding isolation-by-distance slopes comparable to that of the empirical data set (point estimate and upper bound). *D*: population density; μ_x: mean (simulated) dispersal distance; σ: standard deviation of parental position relative to offspring position; sim.: simulated; est.: estimated; *p*-value: Range of Mantel test *p*-values (10,000 permutations) in the three replicates

Model	μ	σ (sim./est.)	IBD slope	95%−	95%+	*p*-value
*D*e = 10 ind./km						
Empirical		914	3.10E-08	−5.24E-07	4.61E-07	.159
Pareto (M = 0.995; n = 1.16)	482	1,509/293	3.02E-07	1.25E-07	4.99E-07	.0000–.0002
Pareto (M = 0.97; n = 0.92)	1323	2,666/938	2.94E-08	−9.93E-08	1.88E-07	.0248–.0670
Geometric (m = 0.98; g = 0.993)	140	203/242	4.41E-07	2.50E-07	6.48E-07	.0000
Geometric (m = 0.95; g = 0.999)	950	1,400/1,031	2.43E-08	−1.02E-07	1.74E-07	.0000
Sichel (γ = −0.0005; ξ = 15000; Ω = 0.002)	420	1,037/318	2.56E-07	4.89E-08	6.64E-07	.0000–.0004
Sichel (γ = −0.002; ξ = 15000; Ω = 0.001)	505	1,263/806	3.98E-08	−8.92E-08	2.05E-07	.0113–.0794
*D*c = 175 ind./km						
Empirical		215	3.10E-08	−5.24E-07	4.61E-07	.159
Pareto (M = 0.95; n = 0.98)	1047	2,300/219	2.99E-08	−8.65E-08	1.51E-07	.0143–.1863
Geometric (m = 0.98; g = 0.992)	123	175/213	3.14E-08	−6.28E-08	1.45E-07	.0085–.0522
Sichel (γ = −0.001; ξ = 10,000; Ω = 0.004)	278	660/212	3.19E-08	−9.57E-08	1.69E-07	.0011–.1525

TABLE 3 Percentile distribution of the simulated functions compatible with the isolation-by-distance slope estimated during the study

	Percentile			
Distribution parameter	25	50	75	90
Pareto (M = 0.995; n = 1.16)	3	12	137	1,247
Pareto (M = 0.97; n = 0.92)	12	166	1,519	4,866
Geometric (m = 0.98; g = 0.993)	40	97	196	326
Geometric (m = 0.95; g = 0.999)	238	643	1,336	2,251
Sichel (γ = −0.0005; ξ = 15,000; Ω = 0.002)	14	67	356	1,205
Sichel (γ = −0.002; ξ = 15,000; Ω = 0.001)	12	65	403	1,485
Pareto (M = 0.95; n = 0.98)	6	75	912	3,889
Geometric (m = 0.98; g = 0.992)	35	85	172	286
Sichel (γ = −0.001; ξ = 10,000; Ω = 0.004)	13	54	241	726

Exclusion analysis in GENECLASS detected three putative migrants. The estimate of the 1D isolation-by-distance slope obtained after excluding those three individuals was 4.08×10^{-8} (lower and upper bounds of the slope -5.17×10^{-7} and 4.66×10^{-7}) and corresponded to sigma values of 795 (95% CI: 236−+∞) or 187 (95% CI: 55−+∞) when considering effective and census density, respectively.

4 | DISCUSSION

Allele frequencies at the 17 microsatellites were homogeneous across the sampled area as indicated by the very low estimates of F_{ST}. Only two pairwise exact tests comparing the southwest Florida sample to the southeast Florida and east Texas/Louisiana samples, respectively, were significant. These three geographic samples did not differ significantly in allele frequencies from any other regional samples, leading to the interpretation that the marginal difference between these localities did not correspond to true barriers to gene flow. This finding was confirmed by the outcome of Bayesian

clustering using a spatially explicit approach in TESS which converged towards a single unit and no discontinuity.

The lack of divergence among regional samples is consistent with a preliminary assessment based on mitochondrial DNA conducted by Antoni, Emerick, and Saillant (2011). Genetic discontinuities within the sampled area have been evidenced in a variety of other marine and coastal species, in particular between the Gulf of Mexico and the U.S. east coast (Avise, 1992), or between populations east and west of Mobile Bay (Karlsson, Saillant, & Gold, 2009; Portnoy & Gold, 2012). These reported genetic breaks involved species occupying coastal or estuarine habitats, or species using offshore habitats but displaying characteristics prone to maintaining geographic structure such as limited dispersal abilities. In contrast, species occupying outer shelf habitats similar to those used by the grey triggerfish and dispersing pelagic larvae did not display clear genetic discontinuities across the same geographic area (e.g., red porgy, *Pagrus pagrus*, Ball, Beal, & Chapman, 2007; or the red snapper, *Lutjanus campechanus*, Saillant, Bradfield, & Gold, 2010; Hollenbeck, Portnoy, Saillant, & Gold, 2015).

The spatial scale of demographic connectivity in grey triggerfish was explored by estimating the parameters of the isolation-by-

distance model. Both the moment estimator of Watts et al. (2007) and the maximum-likelihood estimate in MIGRAINE (Rousset & Leblois, 2007, 2012) yielded large estimates of neighbourhood sizes with estimates of the parameter σ approaching 800 km. Simulated distributions of dispersal distances using different families of functions and different mutation rates yielded average dispersal distances between 123 and 1,323 km. Moreover, examination of the simulated distributions of dispersal distances indicated that 10% of dispersal events resulted in migrations across very long distances from origin (the average 90% percentile was 1,809 km). Interestingly, the relatively high frequency of long-distance dispersal events (90% percentile in the hundreds of kilometres) was observed in all simulations, including those where the census population size (which can be considered as an upper bound of effective density) was used, which indicates that the inference that demographic connectivity occurs across long distances is not affected by uncertainties on the value of effective population density. A fraction of immigrants of 10% is usually considered as a threshold below which connected populations are transitioning from demographic dependence to independence (Hastings, 1993; Waples & Gaggiotti, 2006). While gene flow cannot be easily quantified in terms of a percentage of immigrants in the case of isolation-by-distance, the long distances travelled by a substantial fraction of grey triggerfish before recruiting to benthic habitats and subsequently to breeding populations is consistent with a large degree of demographic dependency of local recruitment from nonlocal spawning stocks, including those located several hundreds of km from a given recipient benthic habitat. This result contrasts with finding in studies of the demographic connectivity of various reef fishes (e.g., Cowen et al., 2006; Puebla et al., 2012; Roberts, 1997) that concluded that dispersal of ecological significance was occurring within short distances (less than 100 km in most cases). The species considered in these studies dispersed larvae over a period limited to a few weeks and usually less than 40 days while grey triggerfish larvae and juveniles remain in the *Sargassum* habitat for 4 to 7 months (Simmons, 2008). Thus, although local spawners could contribute to recruitment in the same region if larvae are caught in local eddies (NMFS 2006), the present results indicate that such local retention, if it occurs, is limited and local recruitment is dependent for a large part on the output of spawning populations located at long distances from recipient habitats. An important consequence for management of grey triggerfish populations is that recruitment cannot be predicted from local spawning biomass as it depends for a large part on the output of nonlocal spawning populations. Instead, recruitment indices may need to be based on the abundance of newly settled juveniles in order to maintain healthy local populations.

Inferences based on the isolation-by-distance relationship imply that dispersal was symmetrical along a one-dimensional axis. Information on the movement and dynamics of *Sargassum* patches used by grey triggerfish larvae and juveniles is still limited. The peak of the grey triggerfish spawning season occurs in June and July (Simmons & Szedlmayer, 2011). During these months, *Sargassum* is found in abundance in the Gulf of Mexico and tends to move off the Florida coast and along the Gulf Stream in September (Gower & King, 2008). This could favour asymmetric dispersal rates from the Gulf to the Atlantic, a hypothesis that cannot be formally tested using currently available methods to analyse isolation by distance. Improved data on the accumulation and movement of *Sargassum* would also be helpful to develop more accurate dispersal models for grey triggerfish in the region. Another limitation of the 1D model used in this study is that shorter dispersal routes across open water were not accounted for leading to potential bias during inference of long-distance dispersal events in particular in the Gulf of Mexico. Considering dispersal across sections of the open Gulf (e.g., from south Texas to West Florida) in a 2D framework is challenging because grey triggerfish larvae cannot settle in the middle of the Gulf thus violating assumptions of the model. Estimating density is also challenging because the adult habitat is limited to the shelf. An upper bound of density was obtained considering a 20 km wide strip surrounding the 1D lattice and led to estimates of σ consistent with those of the 1D model yet likely underestimating σ. Thus, while further developments of isolation-by-distance models to allow accounting for the specific characteristics of habitats used by grey triggerfish and the dispersal process would be needed, the inference of large neighbourhood sizes and long-distance dispersal seems supported under the two models. Another underlying assumption made during inferences on connectivity based on population genetics models is that the population has reached an equilibrium situation. While this cannot be determined easily, repeated temporal sampling could be conducted to confirm the temporal stability of patterns described in this study.

The analysis conducted in this work also implicitly neglected the effects of immigration from geographic populations in other portions of the species' range. Grey triggerfish are reported in Central and South America, in Europe and the Mediterranean Sea and in western Africa (Robins, Ray, Douglass, & Freund, 1986; Sazonov & Galaktionova, 1987). Migrations of grey triggerfish from populations located in the east Atlantic or South America are unlikely considering the long distances involved and large sections of unsuitable habitats for adults in the open Atlantic; Caribbean habitats are closer to the Gulf but the species appears extremely rare in that region (L. Antoni and E. Saillant, Unpublished results). However, the impact of rare migrants from divergent populations on estimates of isolation-by-distance parameters cannot be excluded and was evaluated by omitting possible migrants identified in an exclusion analysis in GENECLASS. The parameters obtained were very similar to those generated using the entire data set suggesting that estimates are robust to this departure of the 1D model.

Grey triggerfish are also present in the southern Gulf of Mexico (e.g., the Bay of Campeche). Populations from the southern Gulf would be expected to be connected to the studied populations and follow the isolation-by-distance pattern described in this study with the additional implication that the effective density estimate would be lower depending on the geographic extent of grey triggerfish south of Texas and the limitations of the 1D model discussed above. Genetic characterization of grey triggerfish in the southern Gulf and study of their abundance is warranted to evaluate this hypothesis and refine current estimates of dispersal parameters.

The ratio of effective to census population density was approximately 5.5×10^{-2}. This value is intermediate between the extremely low ratios of effective to census population size (10^{-3} to 10^{-5}) reported in studies of some other marine fishes (Hauser, Adcock, Smith, Ramirez, & Carvalho, 2002; Saillant & Gold, 2006; Turner, Wares, & Gold, 2002) and the range (>0.1) expected in most situations based on demographic models (Nunney & Elam, 1994). Estimating effective population size/density is particularly challenging in marine species structured in large connected populations as is the case for grey triggerfish (Hare et al., 2011). Methods based on coalescent simulations such as the model used in the present study tend to estimate the size of the overall metapopulation that includes all demes connected to one another by migrations as long as migration is not too low (Hare et al., 2011). These methods also integrate the various historical events experienced by the metapopulation over time meaning that it is difficult to determine an appropriate census number that can be matched with the obtained estimates of N_e. The model used in the present study accounted for historical population growth rate of grey triggerfish and thus the estimate of N generated is expected to reflect current/recent N_e, after the detected recent change in population size event (Leblois et al., 2014). Very recent changes in population size might not be reflected in the coalescent estimate, and the ratio D_e/D_c may be biased if the estimates of census and effective size, respectively, correspond to different time periods. Alternative methods to estimate contemporaneous effective size such as the linkage disequilibrium (Waples, 2006; Waples & Do, 2010) would have been preferable to match directly census and effective numbers for the same cohorts (Hare et al., 2011), but these methods are very imprecise when N_e is greater than 1,000 as was found in the present study. When there is isolation by distance, estimates of N_e by the linkage disequilibrium based on samples collected within a breeding window tend to reflect the neighbourhood size (Neel et al., 2013). This suggests that, even though results from the linkage disequilibrium method lack of precision in the present case, the infinite or very large estimates are consistent with the very large neighbourhood size inferred during isolation-by-distance analysis. The census density estimate was derived based on catch data available from the NOAA Office of Science and Technology database for the period that matched genetic sampling and approximates the density of adults present on benthic habitats. This value can be considered an upper bound for population density as it was uncorrected for potential factors likely to lower N_e such as biased sex ratio and variance in reproductive success (Nunney & Elam, 1994).

5 | CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This study used a genetic approach to estimate demographic connectivity among geographic populations of the grey triggerfish, an adult-sedentary reef fish with extended pelagic dispersal. Estimates of the dispersal parameters in an isolation-by-distance framework were consistent with large neighbourhoods and dispersal events spread-out over long sections of the shelf habitat used by the species. These estimates suggest a reduced role of local retention in determining local recruitment and a high dependency on the reproductive output of nonlocal spawning stocks potentially located hundreds or even thousands of kilometres away from recipient benthic habitats. This result contrasts with findings in reef fishes that disperse pelagic larvae over shorter periods (and distances) and suggests that the longer dispersal in this species is associated with a reduced importance of local retention. Implications for management of populations are significant in that fisheries harvest cannot be managed under the assumption that local biomasses are the major determinant of recruitment. Divergence among geographic regions is insufficient to implement classical mixed stock fisheries models in this case and alternative approaches would need to be developed. Further information on dispersal distribution would be useful to better characterize demographic connectivity and develop appropriate models for management of regional fisheries. Studies of the dynamics of formation and movement of *Sargassum* patches in particular will be useful to develop more accurate models predicting dispersal and could then be used to study dispersal in other species that utilize this habitat at early life stages. Contemporaneous estimates of effective population density would also be needed, but it will be challenging to generate those estimates based on genetic data. Improved data on life history traits of grey triggerfish would be useful to estimate population size using demographic methods.

DATA ACCESSIBILITY

Genotypes of all individual samples at 17 microsatellites: uploaded on the Aquila repository of the University of Southern Mississippi as part of the grey triggerfish genetics project. https://doi.org/10.18785/gtg.ds.01.

AUTHOR CONTRIBUTIONS

E.S. and L.A. designed the study. E.S. coordinated sample acquisition. L.A. performed data acquisition. E.S. and L.A. analysed the data and wrote the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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