Conservation Genetics (2022) 23:435–447
https://doi.org/10.1007/s10592-021-01426-2

RESEARCH ARTICLE

Genetic recruitment patterns are patchy and spatiotemporally unpredictable in a deep-water snapper (*Lutjanus vivanus*) sampled in fished and protected areas of western Puerto Rico

Stuart C. Willis[1,2] · Christopher M. Hollenbeck[1] · Jonathan B. Puritz[1,3] · David S. Portnoy[1]

Received: 12 May 2021 / Accepted: 20 December 2021 / Published online: 29 January 2022

Abstract
Marine protected areas (MPAs) have the potential to conserve biodiversity and improve fishery sustainability, but their efficacy depends on sound design and implementation, which requires an understanding of connectivity among reserves and between reserves and fished areas. Most studies of connectivity involving reserves focus on fishes with characteristics atypical for exploited species, making the results less applicable to fisheries management. Here, patterns of genomic diversity were assessed within and among geographic samples of juvenile of silk snapper, *Lutjanus vivanus*, collected in protected and fished areas on the western coast of Puerto Rico. The results indicate significant variation in spatiotemporal genetic recruitment patterns, with the two MPAs located off the shelf having partially decoupled recruitment processes from sites on the shelf. Spatial autocorrelation was found at distances less than 20 km within years, but the degree and pattern of spatial structure differed across years, suggesting that recruitment along the west coast of Puerto Rico originates from semi-independent units of spawners whose contribution varies in space and time. The results suggest that while MPAs may work to supplement fisheries where recruitment is spatiotemporally predictable, in species for which adult contribution is variable in space and time, other management strategies should be explored as well.

Keywords ddRAD · Fishery · Genomic · Dispersal · MPA

Introduction

Marine protected areas (MPAs) have been proposed as a tool for explicit spatial management of marine resources, both for the conservation of marine biodiversity and for promoting sustainability and profitability of coastal fisheries (Roberts et al. 2001; Gell and Roberts 2003; Brander et al. 2020; Cabral et al. 2020). However, proper MPA design is challenging and requires data on the ecology and population dynamics of species that an MPA could potentially protect (Gell and Roberts 2003; Sale et al. 2005; Kershaw et al. 2021). Given often competing fisheries and conservation objectives, as well as other socioeconomic factors that must be considered, it is no surprise that there are often no clear answers as to which MPA design, e.g., where, what size, how many, etc., is optimal (Halpern and Warner 2003; Hilborn et al. 2004; Gaines et al. 2010; Pittman and Heyman 2020).

The largest fishery benefits of MPAs are expected to accrue through the enhanced persistence and abundance of reserve-dwelling adults, whose larvae are exported into fished areas, as well as through spillover of individuals that recruit in reserves but disperse later in life (Roberts 1998; Hilborn et al. 2004; Gaines et al. 2010; Green et al. 2015; Lenihan et al. 2021). Establishing the degree of connectivity between MPAs and adjacent areas is thus a critical step in determining the potential for an MPA to supplement fished stocks (Botsford et al. 2001; Halpern and Warner 2003; Kershaw et al. 2021). Connectivity across networks of reserves is also an important factor for increasing the capacity of a population to persist in the face of natural or anthropogenic

✉ Stuart C. Willis
swillis4@gmail.com

[1] Marine Genomics Laboratory, Department of Life Sciences, Texas A&M University-Corpus Christi, Corpus Christi, TX, USA

[2] Hagerman Genetics Laboratory, Columbia River Inter-Tribal Fish Commission, Hagerman, ID, USA

[3] Department of Biological Sciences, University of Rhode Island, Kingston, RI, USA

disturbances, including exploitation (Watson et al. 2011; Berumen et al. 2012). Spatial models of connectivity between MPAs and fished area have emphasized the importance of protecting sites that are situated in up-current areas and/or are net exporters of larvae, so that larval subsidies are enhanced (Crowder et al. 2000; Figueira 2009; Jonsson et al. 2021). However, these models rely on a number of simplifying assumptions about the spatial extent and stability of dispersal kernels (Green et al. 2015; Jonsson et al. 2021; Kershaw et al. 2021). Empirical studies of connectivity in tropical coastal fishes have often found that larval dispersal is more limited than expected based on pelagic larval durations (Jones et al. 2005; Almany et al. 2013), and that the pattern and magnitude of connectivity varies across time and space (Berumen et al. 2012; Hogan et al. 2012). However, with few exceptions, studies of reserve connectivity have focused on fishes with short or no pelagic larval duration and/or with adults and recruits that have small home ranges and live in shallow water, allowing for visual surveys (Green et al. 2015). Much less is known about the function of MPAs in the context of recruitment dynamics of typical fishery species, such as snappers, with long pelagic larval durations and whose juveniles and adults may live at considerable depth.

Genetic markers have been extensively used to estimate levels of connectivity in marine species whose dispersal cannot effectively be measured directly, but there are several challenges to this approach (Thorrold et al. 2002; Krueck et al. 2020). In many marine species, local effective population sizes are in the thousands, slowing the rate at which independent populations diverge via genetic drift (Hauser and Carvalho 2008) and making connectivity difficult to estimate directly from allele frequencies (Waples 1998). Parentage analysis has been suggested as another means to measure connectivity when the proportion of recruits originating from different sets of spawners can be estimated (Christie et al. 2010). However, this technique requires nearly exhaustive sampling of potential parents, and, because of large census sizes and high variance in individual reproductive success, is impractical in most broadcast spawning marine species. Alternatively, analyses of genetic diversity and kinship can be used to test predictions of models of meta-population structure, in which sets of interdependent sub-populations act as 'sources' that supply recruits to 'sink' areas that have higher mortality or lower reproductive success (Kritzer and Sale 2004). Although a simplification, this model makes a number of testable predictions about genetic diversity for those areas sitting near the functional ends of the spectrum. For example, if protected areas serve as sources with relatively large, stable populations and are largely self-recruiting (Pulliam 1988; Crowder et al. 2000; Figueira 2009), they should show higher levels of, and lower variance in, genetic diversity among cohorts. Sinks, by contrast, would have smaller populations and unstable recruitment (e.g., from multiple sources), showing higher variance in genetic diversity among cohorts. Meta-population models of genetic diversity are therefore a practical framework for assessing and monitoring the efficacy of MPAs, but their application to MPAs with deepwater fishery species has not yet been extensively explored.

Some of the most extensively exploited deepwater fishery species in the U.S. territorial waters are snappers (Lutjanidae), but relatively little information about the spatial limits of and functional connectivity between snapper stocks exists (Reguera-Rouzaud et al. 2021). The distance that larvae, post-settlement juveniles, and adults disperse over time impacts connectivity (Paris et al. 2005) but is not well studied in most snapper species. The typical pelagic larval duration of snappers is roughly 3 to 6 weeks (Leis 1987; Zapata and Herrón 2002), and adults are relatively long-lived, large predators with low natural mortality (Musick 1999; Anderson 2003). These life-history attributes indicate considerable dispersal potential at multiple life-history stages. However, theoretical dispersal of pelagic larvae to distant sites may be diminished when only those larvae entrained in favorable currents have a reasonable chance of survival, a dynamic that may lead to more localized recruitment (Cowen et al. 2000; Schulzitski et al. 2016). Further, many adult snappers show site fidelity, with relatively few individuals engaging in long-distance movements (Patterson et al. 2001; Burns et al. 2006; Pittman et al. 2014; Reguera-Rouzaud et al. 2021). Thus, the spatiotemporal extent of connectivity or local retention in snappers, even over relatively small scales, may be difficult to predict from broad oceanographic patterns and pelagic larval durations alone, and more data about effective dispersal rates are needed.

Most deep-water snappers are managed as Snapper Unit 1 (silk, *Lutjanus vivanus*, black, *Apsilius dentatus*, vermillion, *Rhomboplites aurorubrens*, blackfin, *Lutjanus buccanella*, and wenchmen, *Pristipomoides aquilonaris*) in the U.S. Caribbean, and as recently as 2013 have been considered overfished (NOAA 2010, 2011; CFMC 2013). The majority of commercial landings of Snapper Unit 1 in Puerto Rico (~ 84%) are silk snapper, and most landings (mean 71%, 1971–2000) have historically come from the shelf off the western coast (SEDAR 2003). On or adjacent to this shelf, which lies next to the Mona Passage (separating Puerto Rico and the Dominican Republic), three areas, each ~ 30 km^2, have been designated as seasonal no-take zones (Dec-Feb), and a fourth area (Desecheo; 6.8 km^2) as a full-time no-take zone (Fig. 1). The seasonal closures, while ostensibly protecting all species found therein, were created primarily to protect the spawning aggregations of red hind (*Epinephelus guttatus*; Matos-Caraballo 2008). The efficacy of these protected areas in enhancing other Puerto Rican fisheries is, therefore, an important but open question. These four MPAs lie in proximity (tens of kilometers) to major fishing grounds

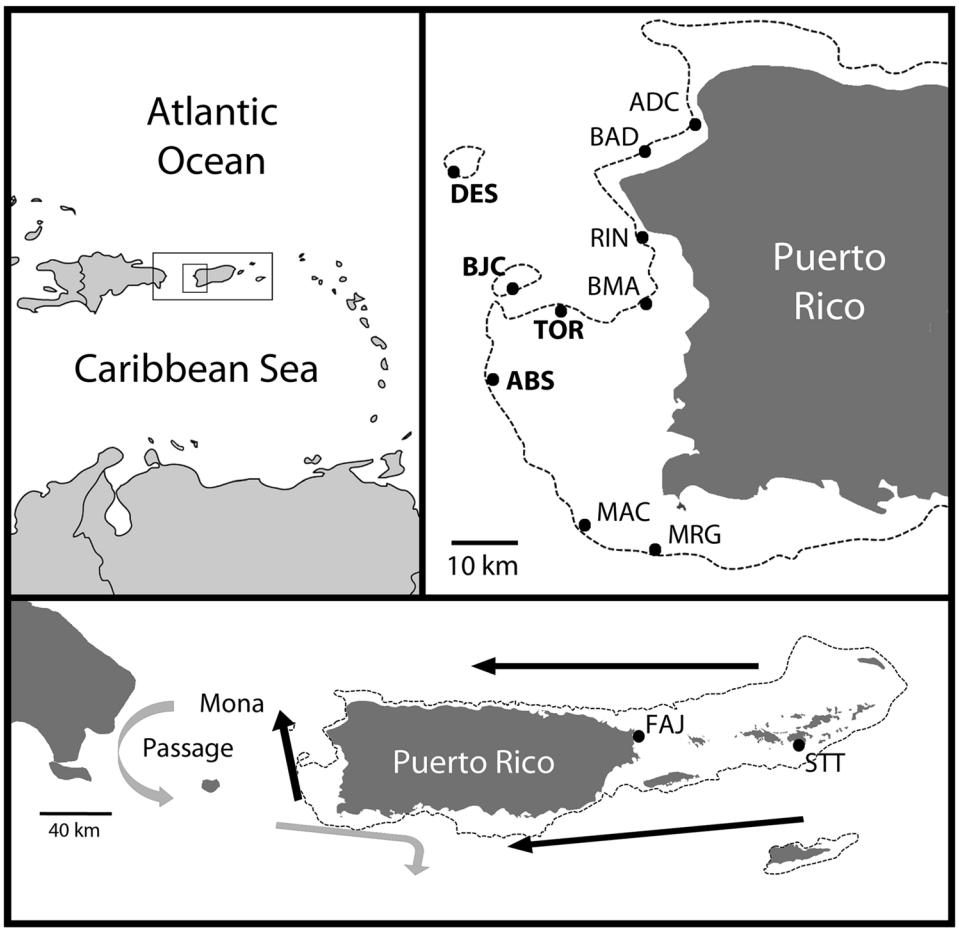

Fig. 1 Map of study area showing sampled sites. The 100 fathom (183 m) contour is shown by a dotted line. In the lower inset, major current patterns are indicated with black arrows, and intermittent currents are shown with grey arrows. Site codes follow Table 1, with marine protected sites indicated in bold (seasonal) or bold-underline (year-round)

along the west and southwest coasts of Puerto Rico where deep-water snapper have historically been caught (D. Matos-Caraballo, personal communication). While the broad scale patterns of recirculating currents in and around the Mona Passage could be conducive for local retention of larvae in the area, this area is also notorious for its rapidly-changing and heterogeneous current patterns (Johns et al. 1999; Rosario-Llantín 2000; Baums et al. 2006), many of which could advect larvae away from appropriate shelf habitat (Fig. 1). Thus, despite the proximity of these protected and fished areas, it remains to be seen if connectivity among these sites is strong and stable enough for protected areas to supplement one of the largest commercial finfish fisheries in Puerto Rico (Cummings and Matos-Caraballo 2003; SEDAR 2003).

A high-resolution, microhaplotype-based genomics approach (Willis et al. 2017; Baetscher et al. 2018) was used to assess patterns of genetic variation within and among spatiotemporally discrete samples of juvenile silk snapper collected inside and outside of protected areas across 3 years along the western coast of Puerto Rico. Relatively little natural history information is available for silk snapper to distinguish them from other snappers, except that adults generally inhabit deep water (50–200 m), and spawn in relatively small, local aggregations of individuals throughout the year, with notable increases in spring and late summer (Sylvester 1974; Boardman and Weiler 1979; Sylvester et al. 1980; Tabash and Sierra 1996; Rosario et al. 2006). Genetic diversity was assessed for patterns consistent with source or sink dynamics among sites and across years, as well as for evidence that protected areas near the Mona Passage acted differently than non-protected sites, including patterns indicated higher connectivity or more stable recruitment relative to non-protected sites. Sources or sinks may present different patterns of relative levels of genetic diversity and relatedness depending on the dynamics of connectivity and spatial distribution of spawners. For example, sites with strong recruitment (sources) might be expected to show high relative genetic diversity relative to sites where recruitment is more sporadic or from a more limited set of spawners (sinks). Sinks that sporadically receive recruits from multiple distinct spawning groups could actually exhibit higher genetic diversity than sources with strong and consistent recruitment from fewer spawning groups but would likely feature greater temporal variance in genetic diversity. Thus, analyses focused on spatiotemporal patterns

of variation in genetic diversity rather than comparing absolute values. Specifically, it was expected that potential recruitment sources would show lower variation in genetic diversity and higher relatedness across years than other sites, indicating consistent recruitment patterns, while sink sites would show higher variation in genetic diversity and lower relatedness across years, indicating more spatially variable recruitment sources and/or variance in reproductive success of spawners. Furthermore, sites that were connected demographically, either through animal movement or correlated recruitment patterns (synchrony), would show consistent patterns of spatial genetic structure across years.

Methods

Sample collection and sequencing

Fin clips from silk snapper were obtained from ten sites (Fig. 1) in western Puerto Rico including the four MPAs. Juvenile fish (median fork length 197 mm, max 410 mm) were sampled in 2012, 2013, and 2014 from each site at multiple times during each year using small, baited circle hooks deployed between 50 and 100 m. Tissue samples of adult silk snapper were also obtained from commercial fishermen working throughout the Mona Passage in 2015, but the explicit location of catch for every individual was not provided. Fin clips were preserved in 20% DMSO-0.25 M EDTA-saturated NaCl buffer (Seutin et al. 1991). Only sites with greater than ten fish collected within a year (site-years) were included in subsequent analyses.

DNA was extracted using Mag-Bind DNA extraction kits (Omega Bio-Tek). Approximately 500 ng of genomic DNA was used in a modified version of the double-digest restriction site associated DNA (ddRAD) genomic library preparation method (Peterson et al. 2012). Barcoded adaptors were ligated to individual extractions which had been digested with *Eco*RI and *Msp*I; ligated digestions were then pooled in approximately equal numbers into indexed groups (40–44 individuals per index). Each indexed group was size selected using a Pippin Prep (Sage Science) at 375 bp (300 bp fragment + 75 bp adapter), PCR amplified for 12 cycles with NEB Phusion polymerase, and up to four indexed groups were pooled together and sequenced on the Illumina HiSeq 2000 and 2500 platforms (paired-end, 2 × 100 bp). Individuals from each site in each year (hereafter, site-year) were divided and sequenced across multiple indexed groups and sequencing lanes, where possible. A subset of ten juvenile silk snappers from eight of the sites in the Mona Passage, and 12 adults, were also sequenced using on an Illumina MiSeq (paired-end, 2 × 300 bp) for de novo reduced representation genome creation.

Bioinformatics and variant filtering

Raw sequence data were processed using the dDocent v2.18 pipeline (Puritz et al. 2014). Full details of bioinformatics procedures are included in the supplemental information (Supplemental File 1). Briefly, Illumina MiSeq data were used to create contiguous sequences (contigs) representing a reduced representation genomic reference for silk snapper that included putatively orthologous (single-copy) fragments, using optimized assembly parameters. Illumina HiSeq reads were mapped to the reference and single nucleotide polymorphisms (SNPs) and other variants scored by comparing alignments across individuals. Results were compiled into a variant call file (VCF) and filtered using a combination of VCFtools v0.1.11 (Danacek et al. 2011), vcflib (https://github.com/vcflib/vcflib), and custom BASH and Perl scripts. Contigs were filtered for SNP quality relative to depth, allele balance, consistency of scoring in forward and reverse reads, relative quality of the reference and alternate alleles, and asymmetric read pairing of the reference and alternate alleles (O'Leary et al. 2018). The dataset was then phased into numbered microhaplotypes (representing one or more SNPs) using a custom Perl script, and loci containing non-allelic fragments (paralogs) removed based on high read depth, excess heterozygosity, and number of inferred haplotypes within an individual (Willis et al. 2017). Loci and individuals were filtered for missing data with final cutoffs of 50% per individual (mean 91%, median 99%) and 90% per locus (mean 91%, median 92%) across all samples, and no cutoff for minor-allele frequency. To ensure that any missing data was randomly distributed across loci rather than the result of systematic genotyping errors (i.e. null alleles), genotypes from duplicate individuals were compared to estimate genotyping error and identify and remove loci where systematic errors were evident. Loci were tested for significant deviation from Hardy–Weinberg expectations within site-years, using Genodive v2.0b27 (Meirmans and Van Tienderen 2004). The final dataset consisted of numbered, multi-allelic, SNP-containing loci genotyped across individuals. Data were screened for outlier loci using the Bayesian modeling approach implemented in Bayescan v2.1 (Foll and Gaggiotti 2008), and identified outliers removed from downstream analysis. Outlier loci are potentially under positive or diversifying selection, and while they can provide evidence of localized selective pressure and adaptations, they may also provide misleading signal with regards to background demography (Funk et al. 2012).

Patterns of genetic diversity in recruits

Homogeneity of allele and genotype distributions among juvenile fish grouped by site-year was tested using exact G tests in Genepop v4.5.1 (Raymond and Rousset 1995), with 10,000 dememorization steps and 100 batches of 5000 steps per batch. Estimates of pairwise F_{ST} were made between site-years, sites (pooled across years) and years (pooled across sites) in Genodive, and significance tested by permuting individuals between groups 10,000 times. Correction for multiple testing was made using the false discovery rate procedure described by Benjamini and Hochberg (1995).

Spatial autocorrelation of genetic variation among individuals was assessed following the method of Smouse and Peakall (1999) as implemented in Genalex (Peakall and Smouse 2006). Each annual sample was analyzed separately. Geographic distances were calculated in kilometers and coordinates were jittered ± 10 m from the center of a given collection event, eliminating identical positions among individuals. Autocorrelation was estimated for eight distance classes chosen to represent biologically meaningful distances. These included (i) the distance across individual sites (0–1 km), (ii) the distance between sites and their nearest neighbors (1–15 km), and (iii) the distances between consecutively wider groupings of collection sites (six distance classes at increments from 15 to 70 km). Confidence intervals around the autocorrelation coefficient (r) were tested using 1000 bootstrap replicates; significance of r was tested using 999 permutations of individuals among distances. The program Barrier v2.2 (Manni et al. 2004) was used to visualize patterns of genetic variation among sites within years. In the context of this study the analysis was not used to infer barriers to gene flow, but rather to look for genetic similarity between sites that might suggest common sources for recruits. Strength of detected genetic discontinuities were assessed by generating 1000 bootstrapped matrices of F_{ST} (Weir and Cockerham 1984) using hierfstat (Goudet and Jombart 2015) and a custom R script (Supplemental File 2). This analysis was not conducted on samples from 2012 because too few sites had sufficient sample size.

Within sample genetic diversity was estimated for each locus at each site-year as rarefied allelic richness (El Mousadik and Petit 1996) and unbiased gene diversity (expected heterozygosity, H_E; Nei 1973), using PopGenReport (Adamack and Gruber 2014) and Adegenet (Jombart 2008), respectively, as implemented in R (R Corp). In addition, local F_{ST} (*beta*) was calculated for each locus for each site-year as 1-(gene diversity / total heterozygosity) in hierfstat (see also Weir and Hill 2002). Mixed model analysis of variance (Anova) was used to assess the contribution of site, year, and protection status (MPA vs. open) to observed patterns of within sample diversity, using rank-transformed values. Two different mixed-effects models were constructed, with year and site or year and protection-status as fixed effects; locus identity and global allelic richness (total number of alleles per locus across all samples) were set as random effects in both models. Models were constructed using the R package lme4 (Bates et al. 2015), and analysis of variance tests were conducted as Wald type-III χ^2 tests using the R package car (Fox et al. 2011). *Post-hoc* Tukey's tests, adjusted for multiple comparisons, were used to determine which, if any, specific pairwise comparisons between sites (across years), between years (across sites), and between protected and non-protected areas (across and within years) were driving significant results, as implemented in the R package multcomp (Hothorn et al. 2017). Additional post-hoc tests of homogeneity between sites within years was made using pairwise Wilcoxon's tests, corrected for multiple comparisons with custom R code, using the R Stats package.

Estimates of relatedness between individuals were generated using the triadic likelihood method (Wang 2007), as implemented in the R package Related (Pew et al. 2015). This approach applies a likelihood algorithm that compares the genotypes of any pair of individuals against the genotypes of 100 other individuals (when available). Pairs of individuals with relatedness values in the range expected for full- ($r \approx 0.5$) or half-siblings ($r \approx 0.25$) were identified to assess direct dispersion of recruits from a single source across sites and years. Confidence intervals for these relationships were calculated using the moment estimator of Wang (2002), and were assessed for overlap with confidence intervals determined through simulation, to evaluate whether full-, or half-sibling relationships could be assigned with confidence using this data set. Confidence intervals for empirical pairs of individuals were calculated by bootstrapping loci 1000 times, while simulated confidence intervals were made by calculating coefficients from 500 simulated pairs each of full- and half-siblings using empirical allele frequencies. Wilcoxon signed-rank-tests, implemented in R, were used to test homogeneity in pairwise relatedness within sites vs. among sites, within years vs. among years, and within protected vs. within non-protected sites. Kruskal–Wallis tests were used to test for homogeneity of relatedness among years (sites pooled) and among site-years. *Post-hoc* Conover-Iman tests (Conover and Iman 1979), with correction for multiple comparisons, were used to make pairwise comparisons between site-years, using the R package PMCMR (Pohlert 2014).

The effective number of breeders (N_b) was estimated for each site-year using the linkage disequilibrium approach (Waples 2006) as implemented in NeEstimator v2 (Do et al. 2014). Minor alleles at a frequency of 0.05 or less in each respective site-year were excluded; confidence intervals were determined parametrically (Waples 2006).

Table 1 Sample sizes for each sampling site in each year for juvenile and adult silk snapper

Site	Code	'12	'13	'14
Abrir la Sierra	**ABS**	0	32	40
Aguadilla City	ADC	22	19	20
Bahia Aguadilla	BAD	27	19	20
Bajo de Cico	**BJC**	26	17	20
Bahia Mayagüez	BMA	32	19	20
Desecheo	**DES**	0	50	38
Macamba	MAC	4	29	20
Margarita	MRG	2	19	15
Rincon	RIN	6	20	20
Tourmaline	**TOR**	25	21	20
Mona Passage adults				166*

Marine protected areas are indicated in bold font

*2015

Finally, all measures of within sample diversity, mean relatedness and N_b were calculated for all adults pooled into a single sample for comparison with the juvenile data sets.

Results

A total of 15 or more juveniles were obtained for 2 consecutive years of silk snapper at all ten sites and for 3 consecutive years at five sites, for a total sample of 622 juveniles after filtering (Table 1; Supplemental Table 1). Tissues were also sampled from 166 adults from throughout the sampling area. After filtering and removing four outlier loci, a total of 1130 haplotyped loci, containing 2780 SNPs, with 2 to 24 alleles per locus (1 to 15 SNPs), were retained. The genotyping error rate, based on 55 duplicate individuals, ranged from 0.14 to 2.69% per individual, with a mean of 1.12% of conflicting genotypes within SNPs. This value is likely an overestimate, since many duplicate individuals were repeated because of poor coverage or low-quality DNA, factors that produce an increased rate of genotyping error.

All exact tests of homogeneity between juvenile fish grouped by site-year were significant ($p \leq 0.0003$). The magnitude of pairwise divergence between samples, as measured by $F_{ST,}$ was low, ranging from zero to 0.004. Forty-seven (out of 300) pairwise comparisons were significant before correction and one comparison, between the 2013 sample from Macamba (MAC) and the 2014 sample from Rincon (RIN), was significant after correction ($F_{ST} = 0.0044$, $p < 0.0001$; Supplemental Table 2). For sites pooled across year, MAC was divergent from RIN and Bajo de Cico (BJC) from Desecheo (DES), before, but not after, correction (Supplemental Table 3). For years pooled across site, 2014 was

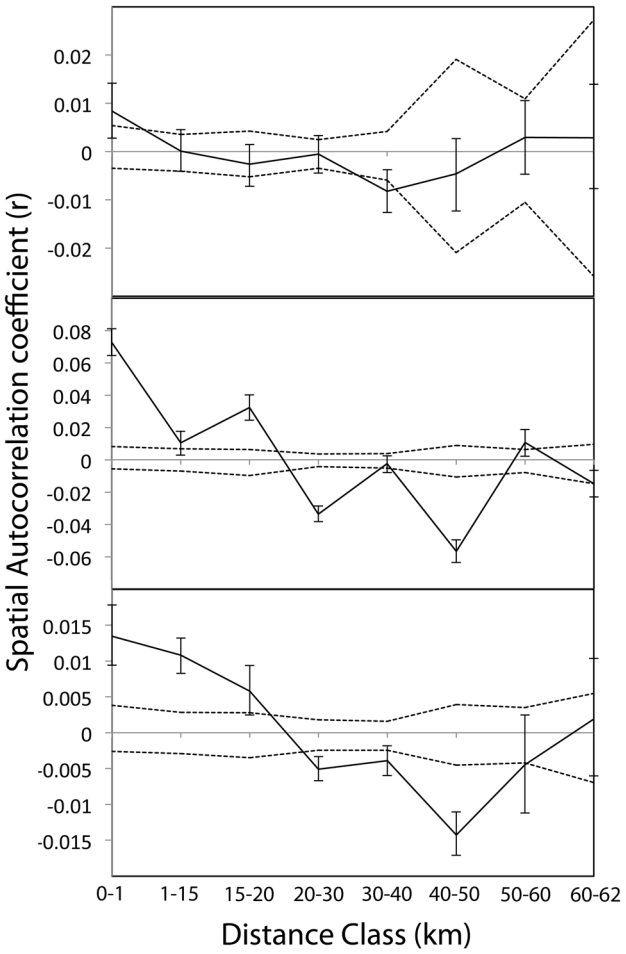

Fig. 2 Spatial autocorrelation of annual samples of silk snapper: 2012 (**A**), 2013 (**B**), 2014 (**C**). Black lines denote estimated spatial autocorrelation coefficient for that distance class, with bars denoting the 95% confidence interval from bootstrapping across loci. Dotted lines denote 95% confidence interval for autocorrelation from permuted samples among localities. Significant autocorrelations fall outside the dotted lines and have bootstrap intervals that do not include zero

significantly different from 2012 and 2013 before, but not after, correction (Supplemental Table 4).

Spatial autocorrelation analyses revealed significant, positive autocorrelation within sites (0–1 km), and significant, positive autocorrelation across nearest-neighbor sites (1–15 km and 15–20 km) in 2013 and 2014 (Fig. 2). At greater distances spatial autocorrelation became negative or non-significant with the exception of 50–60 km in 2013. While the pattern of spatial autocorrelation was largely congruent across years, the magnitude of autocorrelation was considerably higher in 2013 than 2014 and 2012. Consistent with results of spatial autocorrelation, bootstrapped estimates of F_{ST} revealed disjunctions between more sites in 2013 than 2014 (Fig. 3). In both 2013 and 2014, the two northern shelf sites Aguadilla City (ADC) and Bahia

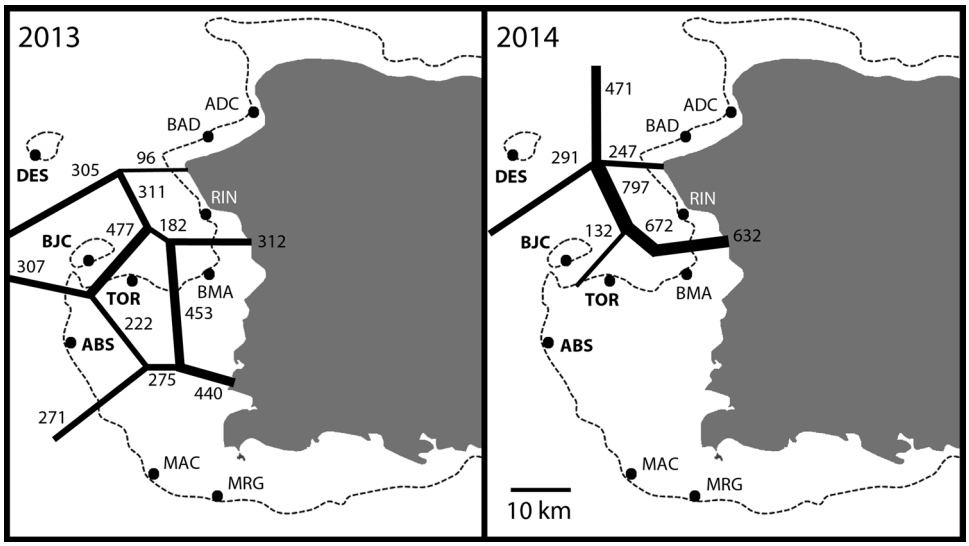

Fig. 3 Barriers inferred from F_{ST} distances (Weir and Cockerham 1984) calculated from 1000 bootstrapped locus matrices from silk snapper samples in 2013 and 2014. Sites and features are as in Fig. 1. Width of the barrier is proportional to the number of times that barrier was inferred out of 1000; values are also shown. Barriers with values between 7 and 67 are not shown. Within each panel, strength of the barrier is proportional to width, but these values are not comparable between panels, since even a weak barrier may show a high consistency if it represents the strongest barrier in that year. Rather, these barriers show the spatial extent of genetic disjunction in a given year. See also Fig. 2

Table 2 Analysis of variance of linear mixed-effects model fit to allelic richness, gene diversity, or local F_{ST} data from juvenile snapper, with site-years classified by site and year

Factor	χ^2	df	*P*
Allelic richness			
Site	50.456	9	$\mathbf{8.84\times10^{-8}}$
Year	29.124	2	$\mathbf{4.74\times10^{-7}}$
Site:year	43.763	13	$\mathbf{3.36\times10^{-5}}$
Gene Diversity			
Site	52.942	9	$\mathbf{3.00\times10^{-8}}$
Year	13	2	**0.0015**
Site:year	43.947	13	$\mathbf{3.13\times10^{-5}}$
Local F_{ST}			
Site	44.955	9	$\mathbf{9.40\times10^{-7}}$
Year	22.459	2	$\mathbf{1.33\times10^{-5}}$
Site:year	25.593	13	**0.0193**

Significant p-values in bold

Table 3 Analysis of variance of linear mixed-effects model fit to allelic richness, gene diversity, or local F_{ST} data from juvenile silk snapper, with site-years classified by year and protection status

Factor	χ^2	df	*P*
Allelic richness			
Year	28.3391	2	$\mathbf{7.02\times10^{-7}}$
Protection	2.8782	1	0.0898
Year:protection	19.6883	2	$\mathbf{5.31\times10^{-5}}$
Gene diversity			
Year	15.9057	2	**0.0004**
Protection	7.7041	1	**0.0055**
Year:protection	17.3005	2	**0.0002**
Local F_{ST}			
Year	18.9729	2	$\mathbf{7.59\times10^{-5}}$
Protection	2.8452	1	0.0917
Year:protection	8.1767	2	**0.0168**

Significant p-values in bold

Aguadilla (BAD) grouped together as did the two southern shelf sites Macamba (MAC) and Margarita (MRG).

Genetic diversity statistics for site-cohorts are presented in Supplemental Table 5. Mixed model analysis of variance revealed significant heterogeneity in allelic richness, gene diversity, and local F_{ST} attributable to site and year, and to an interaction between site and year (Table 2). There was also significant heterogeneity in all three measures attributable to protection status and/or the interaction between protection status and year, (Table 3). In *post-hoc* pairwise comparisons between sites (years pooled), BJC, a protected site, had significantly lower allelic richness than the other nine sites, significantly lower gene diversity than six other sites, and significantly higher local F_{ST} than eight other sites (Supplemental Table 6). In *post-hoc* comparisons between years (sites pooled), the 2013 sample had significantly lower allelic richness and higher local F_{ST} than both the 2012 and 2014 samples, and significantly lower gene diversity than the

Table 4 Tukey post-hoc tests of equal means in allelic richness, gene diversity, or local F_{ST} among annual samples of silk snapper juveniles

	Years	Estimate	SE	Z	*P*
Allelic richness	13–12	– 665.3	209.5	– 3.176	**0.0034**
	14–12	– 481.5	209.5	– 2.298	**0.0465**
	14–13	183.8	39.6	4.644	$\mathbf{<1\times10^{-5}}$
Gene diversity	13–12	– 401.3	194.8	– 2.059	0.0835
	14–12	– 285.6	194.8	– 1.466	0.2778
	14–13	115.7	36.8	3.141	**0.0038**
Local F_{ST}	13–12	1576.3	568.3	2.774	**0.0123**
	14–12	1137.3	568.3	2.001	0.0954
	14–13	– 439.0	107.4	– 4.087	**0.0001**

Significant p-values in bold

2014 sample (Table 4). Comparisons between the protected and non-protected sites revealed significantly lower gene diversity in protected sites across years ($P=0.006$; Table 3), and when compared within the same year, protected sites had significantly lower allelic richness and higher local F_{ST} in 2012 (Tukey's $P=0.013$) and significantly lower gene diversity in both 2012 and 2013 (Supplemental Table 7). By contrast, in 2014 protected sites had significantly higher allelic richness and gene diversity than non-protected sites (Supplemental Table 7). In post-hoc tests, the two offshore protected sites appeared to be driving this pattern: BJC and DES (Supplemental Table 8).

Only one pair of juveniles were identified as full-siblings, both collected in 2014, one at BAD and the other at Bahia Mayagüez (BMA; Supplemental Table 9). Twelve pairs of juveniles were half-siblings, none of which were from the same site-year, though one pair was from the same site Tourmaline (TOR) in consecutive years. Wilcoxon tests revealed that mean relatedness within sites (across years) was significantly greater than among sites, greater within years (across sites) than among years, and greater in protected areas than in non-protected areas (Supplemental Table 10). Kruskal–Wallis tests revealed that relatedness also differed among years ($H=255.29$, $P<2.2\times10^{-16}$), with relatedness among silk snapper in 2013 > 2012 > 2014 (Supplemental Table 11). Kruskal–Wallis tests also revealed significant heterogeneity in mean relatedness among site-years ($H=129.66$, $P<1\times10^{-14}$), with *post-hoc* testing revealing that BJC in 2012 and DES in 2013, both offshore protected sites, had elevated mean relatedness and accounted for 27 out of 33 significant site-year comparisons (Supplemental Table 12).

The effective number of breeders (N_b) for site-year of each species generally had infinite upper confidence intervals, indicating that the sample size was insufficient relative to N_b (e.g., the 10% rule; Waples 2005). In all but 2 cases, the lower confidence interval was above 1000, and the remaining above 500 (Supplemental Table 13).

Comparisons of adult and juvenile data was also instructive. While there were no significant pairwise F_{ST} values between Mona Passage adult and any juvenile cohort ($P>0.38$; Supplemental Table 4), all 3 years (pooled across sites) had higher mean relatedness than the adult sample ($P<0.03$; Supplemental Table 14), suggesting that juveniles originate from a subsample of available adult breeders. Similarly, adult silk snapper exhibited greater rarefied allelic richness ($P<0.0001$), higher gene diversity ($P<0.002$), and lower local F_{ST} ($P<0.001$) than the cohort samples of juveniles, indicating that, even with larger sample sizes in 2 years, juveniles still represented a subset of the genetic variation in the adult population (Supplemental Table 15). Consistent with this, the point estimate of N_b (29,449; 95% CI 20,794–50,309) for all YOY silks did not fall within the lower confidence limit of the estimate of N_b for adults (34,596-inf), likely indicating a smaller N_b for juveniles relative to adults. Only a single first-order (offspring-parent or full-sibling) relationship was observed, as well as two second order relationships (half-sibling or avuncular) between adults and juveniles, and one between two adults.

Discussion

For juvenile silk snapper in western Puerto Rico, heterogeneity in allele and/or genotype distributions was detected across spatial and temporal scales, but there was no clear evidence the protected sites (Desecheo, Bajo de Cico, Tourmaline, or Abrir la Sierra) showed elevated estimates of within-site genetic variation, or temporal stability in genetic diversity, as might be expected for sources. Instead, patterns of within site-year variation for silk snapper at Desecheo (an offshore island) and Bajo de Cico (an offshore bank) relative to all other sites were consistent with a decoupling of local recruitment at offshore sites from recruitment in the sites along the Puerto Rican shelf. Recruits at the two offshore protected sites were less diverse genetically in 2012 and 2013 than shelf non-protected sites and more diverse than shelf non-protected sites in 2014. Further, both had significantly higher mean relatedness than most shelf sites in at least some years (Bajo de Cico in 2012 and Desecheo in 2013), suggesting that at times Desecheo and Bajo de Cico received immigrants from a more limited (and perhaps different) set of sources than sites along the Puerto Rican shelf. There was no clear evidence that juveniles of this species at the protected sites on the shelf exhibited divergent patterns from those at the non-protected sites, indicating that they may be integrated into the same, spatiotemporally variable recruitment processes.

The finding of temporal and spatial heterogeneity in allele/genotype frequencies among juveniles is contrary to expectations based on dispersal potential of snappers, with a larval period on the order of 3 to 6 weeks (Leis 1987; Szedlmayer and Conti 1999; Zapata and Herrón 2002), and the relative geographic scale of this study (10 s of kilometers between sites) (Reguera-Rouzaud et al. 2021). However, such a pattern, often referred to as genetic patchiness, is not uncommon even in marine species with significant pelagic larval periods (Broquet et al. 2013; Deli et al. 2020). While genetic patchiness is sometimes ascribed to large variances in reproductive success among adults (Hedgecock 1994; Flowers et al. 2002; Vendrami et al. 2021), estimates of N_b for site-years were large and no full-sibling or half-sibling pairs were detected within site-years, suggesting that large variance in reproductive success alone may not explain the observed pattern. Genetic patchiness can also result from spatiotemporal variation in larval sources for recruitment, as well as cohesion of larvae from the same source during dispersal (Eldon et al. 2016; Rueger et al. 2020; Vendrami et al. 2021), an idea supported by elevated mean relatedness within site-years, sites and years, as well as positive spatial autocorrelation within years at the distances across sites and between neighboring sites (< 20 km). Silk snapper differs from some other lutjanids in that they spawn throughout the year and likely in small ephemeral groups (Boardman and Weiler 1979; Tabash and Sierra 1996; Rosario et al. 2006), rather than in large, annual or semi-annual aggregations (Carter and Perrine 1994; Claro and Lindeman 2003). If adults show site fidelity, as predicted for similar species (Patterson et al. 2001; Burns et al. 2006; Pittman et al. 2014), then the spawning stock could be composed of semi-independent spawning units whose contribution to recruitment on local scales could differ both temporally and spatially due to biophysical processes (Reguera-Rouzaud et al. 2021). Contrary to expectations based on simple particle diffusion, cohesion of individuals from a common source during long-distance larval dispersal may be common (Bernardi et al. 2012; Ottmann et al. 2016) and such a dynamic has been suggested in red snapper, *Lutjanus campechanus*, in the northern Gulf of Mexico, where genetic heterogeneity occurs in young-of-the-year at small spatial scales (Saillant et al. 2010; Puritz et al. 2016). Currents in the Mona Passage have regular features such as a countercurrent movement to the north along the West Puerto Rican shelf, but there is also complex spatial and temporal variation in currents, including the formation of small and meso-scale eddies (Johns et al. 1999; Rosario-Llantín 2000; Baums et al. 2006). Oceanographic features, such as eddies, can concentrate and enhance fishery productivity by facilitating larval survival (Cowen et al. 2000; Schulzitski et al. 2016), but can also facilitate cohesion and movement of larvae from a common source (Ottmann et al. 2016). Further, because pelagic larvae are in fact not passive particles, their behavior can also influence patterns of recruitment (Jones et al. 2005; Paris et al. 2005; Berumen et al. 2012), perhaps contributing to cohesion.

Though not exclusive, the majority of temporal differences in genetic diversity were observed among the off-shelf (Desecheo and Bajo de Cico) and the remaining, on-shelf sites, suggesting that the former are decoupled from the recruitment dynamics of the latter. Oceanographic features of the Mona Passage and the western Puerto Rican shelf may also explain this apparent decoupling. For example, the western side of Puerto Rico is the leeward side of the island, and local larval retention may be enhanced in nearer-shore, leeward locations due to hydrodynamic drag (Swearer et al. 1999; Krueck et al. 2020). In addition, the northward countercurrent on the eastern side of the Mona Passage is disrupted at times north of Rincon, resulting in a clockwise circulation pattern (Baums et al. 2006). This clockwise circulation could facilitate larval connectivity between southwestern insular shelf sites while at the same time excluding sites further offshore. Further, the insular shelf is separated from Desecheo by waters greater than 500 m in depth and Bajo de Cico by waters greater than 300 m in depth (Chaytor and ten Brink 2010), depths which exceed the lower depth preference (~ 200 m) of adult silk snapper (McEachran and Fechhelm 2005) and therefore, likely limit movement of juveniles, and perhaps adults between offshore and shelf sites. Finally, ephemeral, seasonal circulation patterns have been shown to facilitate movement of larvae from eastern and central parts of the Mona Passage to western Puerto Rico (Baums et al. 2006). Due to proximity, offshore sites may be more likely to receive recruits from sources to the west than shelf sites.

Excluding the off-shelf sites, it appears likely that recruitment processes across the western insular shelf are fairly coupled demographically, as indicated by the similarity in genetic diversity within years. However, it remains unclear if these factors also produce correlation in the magnitude of recruitment (recruit abundance) across on-shelf sites, a pattern known as synchrony (Roughgarden et al. 1988; Oken et al. 2021). Determining the spatiotemporal extent and variance of synchrony in the magnitude of recruitment is important because it indicates the spatial scale of forces determining recruitment and assists with identifying the forces themselves (Myers et al. 1997; Lagos et al. 2007). Synchrony also has implications for resilience and MPA design, since populations that fluctuate synchronously may be more at risk of extirpation (Heino et al. 1997; Moore et al. 2021; Ong et al. 2021). Generally, there are two processes expected to produce synchrony: environmental forcing by shared environmental factors (Moran 1953) and recruitment from a common pool, i.e. dispersal (Kendall et al. 2000). At scales where local populations are linked

by demographically significant migration, both recruitment from a common pool and environmental forcing can contribute to synchrony, but as the distance between sites increases and migration between them declines, environmental forcing becomes more important. Thus, determining the extent and influence of dispersal is important for discriminating the contribution of these two factors to synchrony. If correlations in genetic diversity are indicative of some degree of synchrony in deep water snapper recruitment e.g. years of high genetic diversity across sites indicates strong regional recruitment success, it seems unlikely that post settlement dispersal contributes to this pattern at all but the smallest scales, since positive spatial autocorrelation was detected only among juveniles within sites and their nearest-neighbors (Fig. 2). This would suggest a greater role for mesoscale or regional environmental factors in producing synchrony (Lagos et al. 2007), however, additional data on recruit abundance across sites and time should be examined to determine the extent of synchrony.

The results also indicate that our juvenile samples, both separated by site and year and in aggregate, represent only a subset of the genetic diversity of the adult population. Yearly samples represent collections made across several trips to each site over the course of a given year, while spawning in these species appears to happen largely year-round, with peaks in spring and late summer (Boardman and Weiler 1979; Tabash and Sierra 1996). Moreover, as silk snapper are known to grow quickly (Tabash and Sierra 1996) and some of our samples were > 300 mm, the possibility of some post-recruitment dispersal of age 1 + fish cannot be dismissed. Thus, it is likely that the degree of temporal variation in genetic patchiness and the heterogeneity in larval sources are underestimated relative to what would be seen if only new recruits (young-of the year) were sampled.

The efficacy of MPA networks depend crucially on understanding meta-population dynamics, the rates of dispersal and retention of larvae and older age classes, habitat suitability and carrying-capacity of each area, as well as other density-dependent processes (Figueira 2009). However, because important demographic parameters vary widely among species, it is unlikely that any single MPA will equally serve all co-distributed species (Hilborn et al. 2004; Green et al. 2015). Recruitment processes of silk snapper in the waters of western Puerto Rico, and perhaps other deep-water snappers as well, may be dependent on subsets of the available adult spawners whose contribution to recruitment varies in space and time. Further, genetic recruitment at the shelf and off-shelf sites seems to be decoupled. Therefore, it may be that the current MPA arrangement (with restricted fishing at Desecheo and Baja De Cico) off the western Puerto Rico shelf is not the optimal strategy for promoting sustainability of silk snapper resources on the shelf. While additional MPAs could theoretically be erected to protect a larger portion of the adult spawners on the shelf, it remains unclear where or how large these would need to be. Coordinating alternative management strategies, such as a region-wide catch quotas or seasonal closures, with the current MPAs could be more effective. However, closures will only be effective if they are strictly enforced and if fishing pressure is reduced rather than simply displaced to the open season (Roberts et al. 2001; White et al. 2020).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10592-021-01426-2.

Acknowledgements The authors appreciate the contributions of J. Gold, N. Cummings, D. Matos-Caraballo, M. Figuerola and F. Lentz, including helpful discussions about Puerto Rico 'chillo' fisheries and biooceanography. We also acknowledge the contributions of T. Krabbenhoft (U. Buffalo) to library preparation and sequencing of some individuals utilized in this study. This is publication 32 Hof the Marine Genomics Laboratory and 125 of Genetic Studies in Fishes (Genetic Studies in Marine Fishes).

Funding National Marine Fisheries Service, National Oceanic and Atmospheric Administration (CRP Grant No. NA12NMF4540082).

Data availability Sequence reads for each species have been deposited with NCBI Short Read Archive with accession number PRJNA800815. Scripts to process the sequence data are available at: https://github.com/jpuritz; https://github.com/stuartwillis; https://github.com/chollenbeck.

References

Adamack AT, Gruber B (2014) PopGenReport: simplifying basic population genetic analyses in R. Methods Ecol Evol 5:384–387

Almany GR, Hamilton RJ, Matawai M, Bode M, Potuku T, Saenz-Aguadelo P, Planes S, Berumen ML, Rhodes KL, Thorrold SR et al (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. Curr Biol 23:626–630

Anderson WD (2003) Lutjanidae. In: Carpenter KE (ed) The living marine resources of the western central Atlantic. pp 1479–1504

Baetscher DS, Clemento A, Ng TC, Anderson EC, Garza JC (2018) Microhaplotypes provide increased power from short-read DNA sequences for relationship inference. Mol Ecol Resour 18:296–305

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw. https://doi.org/10.18637/jss.v067.i01

Baums IB, Paris CB, Chérubin LM (2006) A bio-oceanographic filter to larval dispersal in a reef-building coral. Limnol Oceanogr 51:1969–1981

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J Roy Stat Soc B 57:289–300

Bernardi G, Beldade R, Holbrook SJ, Schmitt RJ (2012) Full-sibs in cohorts of newly settled coral reef fishes. PLoS ONE 7:e44953

Berumen ML, Almany GR, Planes S, Jones GP, Saenz-Aguadelo P, Thorrold SR (2012) Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. Ecol Evol 2:444–452

Boardman C, Weiler D (1979) Aspects of the life history of three deep water snappers around Puerto Rico, vol 32. Gulf and Caribbean Fisheries Institute, Marathon, pp 158–172

Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett 4:144–150

Brander LM, Beukering P, Nijsten L, McVittie A, Baulcomb C, Eppink FV, Amrit J, van der Lelij C (2020) The global costs and benefits of expanding Marine Protected Areas. Marine Policy 116:103953

Broquet T, Viard F, Yearsley J (2013) Genetic drift and collective dispersal can result in chaotic genetic patchiness. Evolution 67:1660–1675

Burns KM, Brown-Peterson NJ, Overstreet RM, Gannon JG, Sprinkel JM, Robbins BD, Weaver CA (2006) Geographic comparison of age, growth, reproduction, movement, and survival ofred snapper offthe state ofFlorida. Mote Marine Laboratory Technical Report

Cabral RB, Bradley D, Mayorga J, Goodell W, Friedlander AM, Sala E, Costello C, Gaines SD (2020) A global network of marine protected areas for food. Proc Natl Acad Sci USA 117:28134–28139

Carter J, Perrine D (1994) A spawning aggregation of dog snapper, Lutjanus Jocu (Pisces: Lutjanidae) in Belize, Central America. Bull Mar Sci 55:228–234

CFMC (2013) Fact sheet: annual catch limits for US Caribbean species. F. S. 2. CFMC, San Juan

Chaytor JD, ten Brink US (2010) Extension in mona passage, Northeast Caribbean. Tectonophysics 493:74–92

Christie MR, Tissot BN, Albins MA, Beets JP, Jia Y, Ortiz DM, Thompson SE, Hixon MA (2010) Larval connectivity in an effective network of marine protected areas. PLoS ONE 5:e15715

Claro R, Lindeman KC (2003) Spawning aggregation sites of snapper and grouper species (Lutjanidae and Serranidae) on the insular shelf of Cuba. Gulf Caribb Res 14:91–106

Conover WJ, Iman RL (1979) On multiple-comparison procedures. Los Alamos Scientific Laboratory, New Mexico

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? Science 287:857

Crowder LB, Lyman SJ, Figueira WF, Priddy J (2000) Source-sink population dynamics and the problem of siting marine reserves. Bull Mar Sci 66:799–820

Cummings NJ, Matos-Caraballo D (2003) Summarized reported commercial landings in Puerto Rico from 1969–2001 with specific notes on the silk snapper landings category. Sustainable Fisheries Division Contribution No. SFD 2003-0023 and Caribbean Deepwater SEDAR Data Workshop Report 4 SEDAR

Danacek P, Auton A, Abecasis G, Albers CA, Banks E, DePristo MA, Handsaker R, Lunter G, Marth G, Sherry ST et al (2011) The variant call format and VCF tools. Bioinformatics 27:2156–2158

Deli T, Guizeni S, Ben Abdallah L, Said K, Chatti N (2020) Chaotic genetic patchiness in the pelagic teleost fish *Sardina pilchardus* across the Siculo-Tunisian Strait. Mar Biol Res 16:280–298

Do C, Waples RS, Peel D, Macbeth GM, Tillett BJ, Ovenden JR (2014) NeEstimator V2: re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. Mol Ecol Resour 14:209–214

El Mousadik A, Petit RJ (1996) High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theor Appl Genet 92:832–839

Eldon B, Riquet F, Yearsley J, Jollivet D, Broquet T (2016) Current hypotheses to explain genetic chaos under the sea. Curr Zool 62:551–566

Figueira WF (2009) Connectivity or demography: defining sources and sinks in coral reef fish metapopulations. Ecol Model 220:1126–1137

Flowers JM, Schroeter SC, Burton RS (2002) The recruitment sweepstakes has many winners: genetic evidence from the sea urchin *Strongylocentrotus purpuatus*. Evolution 56:1445–1453

Foll M, Gaggiotti O (2008) A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. Genetics 180:977–993

Fox J, Weisberg S, Adler D et al (2011) Car: companion to applied regression. CRAN, p. R package version 2.1-4

Funk WC, McKay JK, Hohenlohe PA, Allendorf FW (2012) Harnessing genomics for delineating conservation units. Trends Ecol Evol 27:489–496

Gaines SD, White C, Carr MH, Palumbi S (2010) Designing marine reserve networks for both conservation and fisheries management. Proc Natl Acad Sci USA 107:18286–18293

Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol Evol 18:448–455

Goudet J, Jombart T (2015) hierfstat: estimation and tests of hierarchical F-statistics. p. R package version 0.04-22

Green AL, Maypa AP, Almany GR et al (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol Rev (Camb) 90:1215–1247

Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. Proc R Soc Lond B 270:1871–1878

Hauser L, Carvalho GR (2008) Paradigm shifts in marine fisheires genetics: ugly hypotheses slain by beautiful facts. Fish Fish 9:333–362

Hedgecock D (1994) Does variance in reproductive success limit effective population sizes of marine organisms? In: Beaumont A (ed) Genetics and evolution of aquatic organisms. Chapman and Hall, London, pp 122–134

Heino M, Kaitala V, Ranta E, Lindstrom J (1997) Synchronous dynamics and rates of extinction in spatially structured populations. Proc R Soc Biol Sci Ser B 264:481–486

Hilborn R, Stokes K, Maquire JJ et al (2004) When can marine reserves improve fisheries management? Ocean Coast Manag 47:194–205

Hogan JD, Thiessen RJ, Sale PF, Heath DD (2012) Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. Oecologia 168:61–71

Hothorn T, Bretz F, Westfall P, Heiberger RM, Schuetzenmeister A, Scheibe S (2017) multcomp: simultaneous inference in general parametric models. CRAN, p. R package version 1.4-8

Johns E, Wilson WD, Molinari RL (1999) Direct observations of velocity and transport in the passages between the Intra-Americas Sea and the Atlantic Ocean, 1984–1996. J Geophys Res 104:25805–25820

Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405

Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. Curr Biol 15:1314–1318

Jonsson PR, Hammar L, Wåhlström I, Pålsson J, Hume D, Almroth-Rosell E, Mattsson M (2021) Combining seascape connectivity with cumulative impact assessment in support of ecosystem-based marine spatial planning. J Appl Ecol 58:576–586

Kendall BE, Bjornstad ON, Bascompte J, Keitt TH, Fagan WF (2000) Dispersal, environmental correlation and spatial synchrony in population dynamics. Am Nat 155:628–636

Kershaw F, McClintock W, Andrews KR, Riet-Sapriza FG, Caballero S, Tetley MJ, Notarbartolo di Sciara G, Hoyt E, Goldberg G, Chou E et al (2021) Geospatial genetics: Integrating genetics into marine protection and spatial planning. Aquat Conserv 31:2440–2458

Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: from Levin's model to marine ecology and fisheries science. Fish Fish 5:131–140

Krueck NC, Treml EA, Innes DJ, Ovenden JR (2020) Ocean currents and the population genetic signature of fish migrations. Ecology 101:e02967

Lagos NA, Tapia FJ, Navarrete SA, Castilla JC (2007) Spatial synchrony in the recruitment of intertidal invertebrates along the coast of central Chile. Mar Ecol Prog Ser 350:29–39

Leis JM (1987) Review of early life history of tropical groupers (Serranidae) and snapper Lutjanidae. In: Polovina JJ, Ralston S (eds) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, pp 189–237

Lenihan HS, Gallagher JP, Peters JR, Stier AC, Hofmeister JKK, Reed DC (2021) Evidence that spillover from Marine Protected Areas benefits the spiny lobster (*Panulirus interruptus*) fishery in southern California. Sci Rep 11:2663

Manni F, Guérard E, Heyer E (2004) Geographic patterns of (genetic, morphologic, linguistic) variation: how barriers can be detected by "Monmonier's algorithm." Hum Biol 76:173–190

Matos-Caraballo D (2008) Lessons learned from the Puerto Rico's Commercial Fishery, 1988–2008. 61st Gulf and Caribbean Fisheries Institute. Proceedings of the 61st Gulf and Caribbean Fisheries Institute

McEachran J, Fechhelm JD (2005) Fishes of the Gulf of Mexico: scorpaeniformes to tetraodontiformes. University of Texas Press, Austin

Meirmans PG, Van Tienderen PH (2004) GENOTYPE and GENODIVE: two programs for the analysis of genetic diversity of asexual organisms. Mol Ecol Notes 4:792–794

Moore JW, Connors BM, Hodgson EE (2021) Conservation risks and portfolio effects in mixed-stock fisheries. Fish Fish 22:1024–1040

Moran P (1953) The statistical analysis of the Canadian lynx cycle II. Synchronization and meteorology. Aust J Zool 1:291–298

Musick JA (1999) Ecology and conservation of long-lived marine animals. Am Fish Soc Symp 23:1–10

Myers RA, Mertz G, Bridson J (1997) Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Can J Fish Aquat Sci 54:1400–1407

Nei M (1973) Analysis of gene diversity in subdivided populations. Proc Natl Acad Sci USA 70:3321–3323

NOAA (2010) Public hearing draft amendment 2 to the fishery management plan for the queen conch fishery of Puerto Rico and the U.S. Virgin Islands and amendment 5 to the reef fish fishery management plan of Puerto Rico and the U.S. Virgin Islands (with Draft Environmental Impact Statement and Regulatory Impact Review). National Oceanographic and Atmospheric Administration

NOAA (2011) National Marine Fisheries Service 2010 report to Congress on the status of U.S. Fisheries. National Oceanographic and Atmospheric Administration

O'Leary SJ, Puritz JB, Willis SC, Hollenbeck CM, Portnoy DS (2018) These aren't the loci you're looking for: principles of effective SNP filtering for molecular ecologists. Mol Ecol 27:3193–3206

Oken KL, Holland DS, Punt AE (2021) The effects of population synchrony, life history, and access constraints on benefits from fishing portfolios. Ecol Appl 31:e2307

Ong JJL, Walter JA, Jensen OP, Pinsky ML (2021) Global hotspots of coherent marine fishery catches. Ecol Appl 31:e02321

Ottmann D, Grorud-Colvert K, Sard NM, Huntington BE, Banks MA, Sponaugle S (2016) Long-term aggregation of larval fish siblings during dispersal along an open coast. Proc Natl Acad Sci USA 113:14067–14072

Paris CB, Cowen RK, Claro R, Lindeman KC (2005) Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. Mar Ecol Prog Ser 296:93–106

Patterson WF, Watterson JC, Shipp RL, Cowan J (2001) Movement of tagged red snapper in the Northern Gulf of Mexico. Trans Am Fish Soc 130:533–545

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295

Peterson BK, Weber JN, Kay EH, Fisher HS, Hoekstra HH (2012) Double digest RADseq: an inexpensive method for de novo SNP discovery and genotyping in model and non-model species. PLoS ONE 7:e37135

Pew J, Wang J, Muir P, Frasier T (2015) Related: an R package for analyzing pairwise relatedness data based on codominant molecular markers. CRAN

Pittman SJ, Heyman WD (2020) Life below water: Fish spawning aggregations as bright spots for a sustainable ocean. Conserv Lett 13:e12722

Pittman SJ, Monaco ME, Friedlander AM, Legare B, Nemeth RS, Kendall MS, Poti M, Clark RD, Wedding LM, Caldow C (2014) Fish with chips: tracking reef fish movements to evaluate size and connectivity of caribbean marine protected areas. PLoS ONE 9:e96028

Pohlert T (2014) The pairwise multiple comparison of mean ranks package (PMCMR). CRAN.

Pulliam HR (1988) Souces, sinks, and population regulation. Am Nat 132:652–661

Puritz JB, Hollenbeck CM, Gold JR (2014) dDocent: a RADseq, variant-calling pipeline designed for population genomics of non-model organism. PeerJ 2:e431

Puritz JB, Gold JR, Portnoy DS (2016) Fine-scale partitioning of genomic variation among recruits in an exploited fishery: causes and consequences. Sci Rep 6:36095

Raymond M, Rousset F (1995) GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. J Hered 86:248–249

Reguera-Rouzaud N, Díaz-Viloria N, Pérez-Enríquez R, Espino-Barr E, Rivera-Lucero MI, Munguía-Vega A (2021) Drivers for genetic structure at different geographic scales for Pacific red snapper (Lutjanus peru) and yellow snapper (*Lutjanus argentiventris*) in the tropical eastern Pacific. J Fish Biol 98:1267–1280

Roberts CM (1998) Sources, sinks, and the design of marine reserve networks. Fisheries 23:16–19

Roberts CM, Bohnsack JA, Gell FR, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. Science 294:1920–1923

Rosario A, Rojas J, Piñero E, Figuerola M, Peña N, Torres W (2006) Reproductive cycle and maturation size of silk snapper (*Lutjanus vivanus*). Caribbean Fishery Management Council.

Rosario-Llantín J (2000) Tidal currents in mona passage. Department of Marine Sciences, University of Puerto Rico, Mayagüez

Roughgarden J, Gaines SD, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241:1460–1466

Rueger T, Harrison HB, Buston PM, Gardiner NM, Berumen ML, Jones GP (2020) Natal philopatry increases relatedness within groups of coral reef cardinalfish. Proc R Soc Biol Sci Ser B 287:20201133

Saillant E, Bradfield SC, Gold JR (2010) Genetic variation and spatial autocorrelation among young-of-the-year red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico. ICES J Mar Sci 67:1240–1250

Sale PF, Cowen RK, Danilowicz BS et al (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20:74–80

Schulzitski K, Sponaugle S, Hauff M, Walter KD, Cowen RK (2016) Encounter with mesoscale eddies enhances survival to settlement in larval coral reef fishes. Proc Natl Acad Sci USA 113:6928–6933

SEDAR (2003) Data report of SEDAR 4, Atlantic and Caribbean deepwater snapper-grouper. South Atlantic Fishery Management Council, Charleston

Seutin G, White BN, Boag PT (1991) Preservation of avian blood and tissue samples for DNA analyses. Can J Zool 69:82–90

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. Heredity 82:561–573

Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef ®sh. Nature 402:799–802

Sylvester JR (1974) A preliminary study of the length composition, distribution, and relative abundance of three species of deepwater snappers from the Virgin Islands. J Fish Biol 6:43–49

Sylvester JR, Drew DW, Dammann AE (1980) Selective life history of silk and blackfin snapper from the Virgin Islands. Caribb J Sci 15:41–48

Szedlmayer ST, Conti J (1999) Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. Fish Bull 97:626–635

Tabash FA, Sierra LM (1996) Assessment of *Lutjanus vivanus* and *Lutjanus buccanella* in the north Caribbean coast of Costa Rica. Naga 19:48–51

Thorrold SR, Jones GP, Hellberg ME, Burton RS, Swearer SE, Neigel JE, Morgan SG, Warner RR (2002) Quantifying larval retention and connectivity in marine populations with artificial and natural markers. Bull Mar Sci 70:291–308

Vendrami DLJ, Peck LS, Clark M, Eldon B, Meredith M, Hoffman JI (2021) Sweepstake reproductive success and collective dispersal produce chaotic genetic patchiness in a broadcast spawner. Sci Adv 7:625

Wang J (2002) An estimator for pairwise relatedness using molecular markers. Genetics 160:1203–1215

Wang J (2007) Triadic IBD coefficients and applications to estimating pairwise relatedness. Genet Res 89:135–153

Waples RS (1998) Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J Hered 89:438–450

Waples RS (2005) Genetic estimates of contemporary effective population size: to what time periods do the estimates apply? Mol Ecol 14:3335–3352

Waples RS (2006) A bias correction for estimates of effective population size based on linkage disequilibrium at unlinked gene loci. Conserv Genet 7:167–184

Watson JR, Siegel DA, Kendall BE, Mitarai S, Rassweiller A, Gaines SD (2011) Identifying critical regions in small-world marine metapopulations. Proc Natl Acad Sci USA 108:E907–E913

Weir B, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370

Weir B, Hill WG (2002) Estimating F-statistics. Annu Rev Genet 36:721–750

White TD, Ong T, Ferretti F, Block BA, McCauley DJ, Micheli F, De Leo GA (2020) Tracking the response of industrial fishing fleets to large marine protected areas in the Pacific Ocean. Conserv Biol 34:1571–1578

Willis SC, Hollenbeck CM, Puritz JB, Gold JR, Portnoy DS (2017) Haplotyping RAD loci: an efficient method to filter paralogs and account for physical linkage. Mol Ecol Resour 17:955–965

Zapata FA, Herrón PA (2002) Pelagic larval duration and geographic distribution of tropical eastern Pacific snappers (Pisces: Lutjanidae). Mar Ecol Prog Ser 230:295–300