



Conservation genetics and management of yellowtail snapper, *Ocyurus chrysurus*, in the US Caribbean and South Florida

E. A. SAILLANT

Department of Coastal Sciences, The University of Southern Mississippi Gulf Coast Research Laboratory, Ocean Springs, MS, USA

M. A. RENSHAW

Center for Biosystematics and Biodiversity, Texas A&M University, College Station, TX, USA

N. J. CUMMINGS

Southeast Fisheries Science Center, National Marine Fisheries Service, Miami, FL, USA

J. R. GOLD

Center for Biosystematics and Biodiversity, Texas A&M University, College Station, TX, USA

Abstract Population-genetic structure and average long-term effective size of yellowtail snapper, *Ocyurus chrysurus* (Bloch), sampled offshore from the Florida Keys and four localities in the US Caribbean, were investigated using nuclear-encoded microsatellites and a fragment of the mitochondrially encoded ND-4 gene. Analysis of spatial genetic variation revealed occurrence of up to four groupings (stocks) of yellowtail snapper: one in the Florida Keys, one along the west coast of Puerto Rico, one that includes the east coast of Puerto Rico and St. Thomas and one offshore of St. Croix. The observed genetic differences among localities are not strong, and additional sampling to examine whether the observed patterns of population structure are temporally stable is warranted. Levels of genetic variability and estimates of average, long-term effective size (N_e) indicate that yellowtail snapper at all five localities have, at present, sufficient genetic variation to maintain long-term integrity and sustainability.

KEYWORDS: connectivity, conservation genetics, *Ocyurus chrysurus*, population structure, US Caribbean, yellowtail snapper.

Introduction

Yellowtail snapper, *Ocyurus chrysurus* (Bloch), is a reef-associated lutjanid fish found throughout coastal waters of the tropical and subtropical western Atlantic shelf (Allen 1985; Cummings 2004a). The species supports important fisheries in the southeastern United States (principally southern Florida) and in the Caribbean Sea (Johnson 1983; Manooch & Drennon 1987; Matos-Caraballo 2000; Cummings 2004b; Claro *et al.*

2009). Management of reef fish resources, including yellowtail snapper, in the US Caribbean fishery (Puerto Rico, the US Virgin Islands, and the surrounding EEZ) has been of concern (SEDAR8 {Southeast Data, Assessment, and Review} 2005) and is limited by a critical absence of information on individual species (http://www.sefsc.noaa.gov/sedar/download/CaribData_Final.pdf?id=DOCUMENT). Among the pressing needs are: (1) delineation of different management units (stocks) within the fishery,

Correspondence: Eric Saillant, Department of Coastal Sciences, The University of Southern Mississippi, Gulf Coast Research Laboratory, 703 East Beach Drive, Ocean Springs, MS 39564, USA (e-mail: eric.saillant@usm.edu)

should they exist; (2) information on population demography (i.e. growth/decline, size and density distribution) across the region; and (3) patterns of migration and movement. Although supporting data are limited, a general decline in all reef fish fisheries (combined) in waters off both Puerto Rico and the US Virgin Islands was suggested by Appeldoorn *et al.* (1992) and Matos-Caraballo (2000).

An assessment of yellowtail snapper in the US Caribbean generated during the SEDAR8 {Southeast Data, Assessment, and Review} (2005) process employed a two-stock model that was based primarily on: (1) length (approximately 35–40 days) of the planktonic larval phase (Lindeman 1997; Lindeman *et al.* 2001) and data on prevailing surface currents (Roberts 1997; Watson & Munro 2004); (2) indications of restricted post-larvae and adult movement (Randall 1968; Watson *et al.* 2002); and (3) existence within the region of two geological platforms (a northern Puerto Rico Platform that includes the islands of Puerto Rico, St. Thomas, St. John, and the British Virgin Islands, and a southern St. Croix Platform that includes the island of St. Croix) that are separated by a deep oceanic trench that extends to approximately 4000 m (CFMC {Caribbean Fisheries Management Council} 2004). Primary physical factors affecting gene flow (migration) and potential isolation of different stocks within the region are surface current patterns that would affect hydrodynamic transport of pelagic larvae and the deep trench that separates the two geological platforms. Roberts (1997) assessed surface current patterns in the Caribbean and attempted to map potential dispersal routes of pelagic larvae. He suggested that with a 2-month envelope of larval drift, areas off of Puerto Rico and the US Virgin Islands could represent a core group. There are, however, a number of caveats to the notion that surface current patterns and existence of pelagic larvae equates to unrestricted movement (and gene flow) across a geographical surface. Shulman and Bermingham (1995) showed that neither egg type nor length of larval life is necessarily an effective predictor of gene flow in structure-associated fishes. In addition, flow models coupled with mortality estimates (Cowen *et al.* 2000, 2006) indicated that larval exchange rates of marine species may be significantly overestimated and that ecologically relevant larval-dispersal distances may lie within a 10–100 km range. Finally, empirical studies in the region have shown that the magnitude of dispersal can differ substantially between windward (high dispersal) and leeward (low dispersal) sides of islands (Swearer *et al.* 1999) and that species with the capacity for long-range larval dispersal often exhibit

high levels of larval retention (Taylor & Hellberg 2003).

In this study, nuclear-encoded genetic markers (microsatellites) and a mitochondrial (mt)DNA coding gene were used to answer three questions: (1) Are there multiple, genetically defined stocks of yellowtail snapper in US waters of the Caribbean Sea? (2) What are the patterns of genetic migration of yellowtail snapper in the region? (3) What are the effective population sizes of yellowtail snapper at each sampling locality and what is the magnitude of spatial variability in effective size? Knowledge of genetic stock structure and connectivity in a managed fishery is critical to both assessment and allocation (Hilborn 1985; Sinclair *et al.* 1985) in that different stocks (populations) within a fishery may possess novel genetic resources that promote distinct differences in critical life-history traits (Stepien 1995). Conservation of unique genetic resources is especially critical in the context of species or populations under exploitation, as erosion of genetic resources via depletion of (unrecognised) constituents of spawning components can directly impact immediate and long-term recruitment potential and adaptability (Lynch *et al.* 1995). Knowledge of genetic demography, including effective size, of an exploited species is also of critical importance to accurate assessment and allocation because fundamental fishery parameters, such as population growth, natural and fishing mortality, density, reproductive potential and recruitment, may differ significantly across the range of a single genetic stock and impact long-term adaptability and sustainability. Prior genetic data on yellowtail snapper in the US Caribbean is limited to a study by Wallace *et al.* (2003), who assayed a 404-base-pair fragment of the mitochondrial (mt)DNA D-loop region and eight nuclear-encoded microsatellites from 310 yellowtail snapper sampled off the east coast of Florida, the Florida Keys, and Puerto Rico. Although they found no evidence of spatial population structure in sample pairwise exact tests, a significant isolation-by-distance effect, indicating restricted genetic migration or gene flow, was evident.

Materials and methods

A total of 511 yellowtail snapper were collected between 2005 and 2007 from the Florida Keys and four localities within the US Caribbean (Fig. 1). Samples from the Florida Keys (KEYS) were obtained both from head boats and fish houses in Key West and by angling off Long Key. Samples from the west coast of Puerto Rico (PR-WEST) were obtained from fish houses in or near Mayaguez, while samples from the

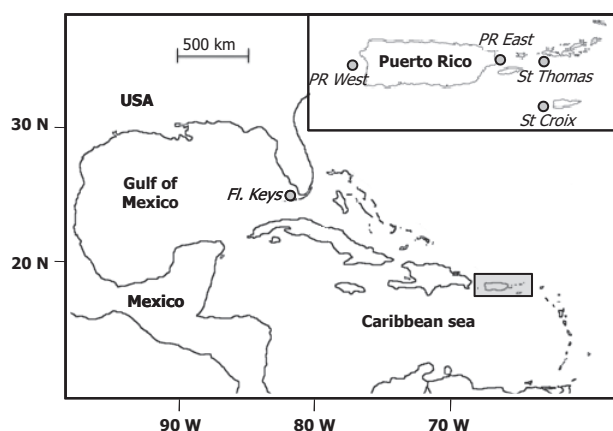


Figure 1. Approximate sample localities for *Ocyurus chrysurus* in the Florida Keys and the Caribbean Sea.

east coast (PR-EAST) were obtained at fish houses in or near Fajardo. Samples from St Thomas (ST) were obtained at the Gustave Quétel Fish House in Frenchtown (Charlotte Amalie) and from local fishermen. Samples from St Croix (SC) were obtained from artisanal fishers operating off the west coast (near Fredericksted). Sample sizes were 100 specimens per locality except for the Florida Keys where 111 specimens were obtained. Tissue samples (fin and/or muscle) from each fish were preserved immediately in molecular grade 95% ETOH. DNA was isolated using a standard phenol–chloroform protocol, following proteinase K digestion (Sambrook *et al.* 1989). All fish sampled were assayed for genotypes at 19 nuclear-encoded microsatellites, using polymerase chain reaction (PCR) primers designed from genomic libraries developed for *O. chrysurus* and other lutjanids (*Lutjanus analis* Cuvier, *Lutjanus campechanus* Poey, *Lutjanus synagris* Linnaeus and *Rhomboplites aurubens* Cuvier). Details regarding PCR primers are found in Bagley and Geller (1998), Gold *et al.* (2001) and Renshaw *et al.* (2007). Microsatellites were assayed using three multiplex panels. Amplification followed the Touchdown II protocol described in Renshaw *et al.* (2006), but with different annealing temperatures.

A 650-base-pair (bp) fragment of the mitochondrial gene encoding for the ND-4 subunit of the NADH dehydrogenase was amplified using primers ND4LB (Bielawski & Gold 2002) and NAP2 (Arevalo *et al.* 1994). Polymerase chain reaction conditions followed methods outlined in Gold *et al.* (2011). Amplification products were purified using the Exo-SAP-IT PCR clean-up kit (GE Healthcare, Piscataway, NJ, USA) and sequenced using the Big-Dye Terminator v3.1 Sequencing kit (Applied Biosystems, Foster City, CA,

USA), following the manufacturer's protocol. Sequencing reaction products were run on an ABI-3130 capillary sequencer (Applied Biosystems). Sequence chromatograms were edited in SEQUENCHER 3.0 (Gene Codes Corporation, Ann Arbor, MI, USA); a total of 590 bp were reliably scored in all sequences obtained and were used in data analysis.

Summary statistics, including number of alleles, allelic richness and unbiased gene diversity, were computed for each microsatellite in all five samples, using F-STAT (Goudet 1995; v. 2.9.3, <http://www2.unil.ch/popgen/softwares/fstat.htm>). Homogeneity of allelic richness and gene diversity among samples was tested via Friedman rank tests as implemented in PROC FREQ of SAS® (SAS Institute, Cary, NJ, USA). Departure of genotypic proportions from Hardy–Weinberg (HW) equilibrium expectations in each sample was measured as Weir and Cockerham's (1984) *f* statistic. The probability that *f* differed significantly from zero (P_{HW}) was estimated using an exact probability test as implemented in GENEPOP v. 4.0.7 (Raymond & Rousset 1995; <http://kimura.univ-montp2.fr/~rousset/Genepop.htm>). Parameters of the Markov Chain employed in estimation were 10 000 dememorisations, 500 batches and 5000 iterations per batch. Genotypic disequilibrium between pairs of microsatellites within samples was tested by exact tests, in GENEPOP, and employing the same Markov chain parameters as mentioned previously. Sequential Bonferroni correction (Rice 1989) was applied for all multiple tests performed simultaneously. Possible occurrence of stuttering, large allele dropout and/or null alleles was evaluated for each microsatellite in each sample, using the software MICROCHECKER (van Oosterhout *et al.* 2004).

Summary statistics for mtDNA sequences, including number of haplotypes, haplotype diversity and nucleotide diversity, were computed in DNASP (Rozas *et al.* 2003; v. 5.10.01, <http://www.ub.edu/dnasp/>). Homogeneity among samples in number of mtDNA haplotypes and haplotype diversity was tested using a bootstrap resampling approach (Karlsson *et al.* 2008). Under the null hypothesis (homogeneity), the number of haplotypes or haplotype diversity observed in one sample does not differ significantly from that in a random subsample of the same size from the overall dataset. POP TOOLS (a free-add in software for EXCEL, available at <http://www.cse.csiro.au/poptools/index.htm>) was used to generate random samples of 25 and 26 haplotypes from the overall dataset. Random sampling was performed 10 000 times, and the average number of observed haplotypes and average haplotype diversity and their upper (97.5) and lower (2.5) percentiles

were recorded. Observed values in each sample were considered to differ significantly from expected values under the null hypothesis if they fell outside the obtained 95% confidence intervals. Selective neutrality of mtDNA in each sample was tested via Fu's (1997) F_S statistic and Fu and Li's (1993) D^* and F^* statistics, as implemented in DNASP. Significance of F_S , D^* , and F^* was assessed from 10 000 coalescent simulations. A statistical parsimony network of mtDNA haplotypes was constructed as described by Templeton *et al.* (1992) and implemented using TCS v. 1.21 (Clement *et al.* 2000).

Homogeneity of allele and genotype distributions (microsatellites) was tested using exact tests as implemented in GENEPOP and using the same Markov chain parameters as above for tests of HW equilibrium. The degree of divergence between pairs of samples was estimated as Weir and Cockerham's (1984) θ , as computed in F-STAT. Sequential Bonferroni correction (Rice 1989) was applied for all multiple tests performed simultaneously. Population structure was examined using spatial analysis of molecular variance (SAMOVA, Dupanloup *et al.* 2002), using the software Samova 1.0 available at <http://web.unife.it/progetti/genetica/Isabelle/samova.html>. SAMOVA employs a simulated annealing algorithm to optimise allocation of N geographic populations into K groups ($2 < K < N$) to maximise the proportion of total genetic variance due to genetic variation among the inferred groups. One hundred simulated annealing processes were used to determine optimal allocation of the five geographic samples into two, three or four groups. Homogeneity of mtDNA haplotype distribution was tested using analysis of molecular variance (AMOVA, Excoffier *et al.* 1992) as implemented in ARLEQUIN (Excoffier & Lischer 2010; v. 3.5.1.2., <http://cmpg.unibe.ch/software/arlequin35/>) and using the number of pairwise differences between haplotypes as a molecular distance. Significance of the genetic variance among localities and of Φ_{CT} was assessed using 10 000 permutations of haplotypes. Population structure was assessed using SAMOVA, employing the same parameters as used for the microsatellite data.

Spatial genetic variation was further assessed by use of spatial autocorrelation analysis (Smouse & Peakall 1999), as implemented in GENALEX (Peakall & Smouse 2006; v.6.0, <http://www.anu.edu.au/BoZo/GenAlEx/>). The spatial autocorrelation coefficient (r) was computed using the geographic distance between localities inferred from longitudes and latitudes and the multilocus genetic distance described in Smouse and Peakall (1999). With isolation by distance, estimated values of r differ significantly from zero for

geographically proximal samples and decrease with increasing geographic distance between samples. The distance between samples at which r no longer differs significantly from zero provides an approximation of the maximum distance at which population structure can be detected (Peakall *et al.* 2003). Distance class sizes were determined based on observation of the distribution of pairwise geographic distances between sample localities to ensure that at least two pairs of localities were included in each distance class. The distribution of r values under the null hypothesis of random spatial distribution of genotypes was estimated by randomly permuting microsatellite genotypes among localities. One thousand permutations were implemented, and the distribution of r values obtained was used to determine the probability of significance of observed values of r according to a one-tailed test (i.e. r is significant if it lies beyond the upper 95% bound of the distribution). The significance of r also was tested by generating bootstrap 95% confidence intervals for r . Bootstrap values were obtained by sampling, with replacement, pairs of comparisons within a given distance class. Bootstrap resampling was performed 1000 times, and the significance of r inferred when the 95% confidence interval did not overlap zero.

Occurrence of barriers to gene flow was assessed using the approach implemented in BARRIER 2.2, available at <http://www.mnhn.fr/mnhn/ecoanthropologie/software/barrier.html> (Manni *et al.* 2004). The method employs a Delauney triangulation and a modified version of Monmonier's maximum-difference algorithm to identify boundaries, areas where differences between pairs of sample localities are largest, within a set of spatially distributed sample localities. Briefly, BARRIER constructs a Voronoi diagram that defines the boundaries of each locality neighbourhood by enclosing it in a polygonal cell. Barriers are initiated by the edge of the Voronoi diagram that corresponds to the highest pairwise divergence estimate and continue through adjacent edges according to the Monmonier's algorithm until the border of the overall area studied is reached or the barrier closes around a set of localities. A second barrier can then be initiated as the edge of the Voronoi diagram that corresponds to the maximal pairwise divergence measure between the remaining localities. Divergence between pairs of sample localities was assessed using Weir and Cockerham's (1984) θ . Support for inferred barriers was assessed via bootstrapping over microsatellites. POP TOOLS was used to generate 1000 bootstrap matrices of pairwise θ values between all sample localities by resampling the 16 microsatellites with replacement and

computing the weighted estimate of θ over the 16 resampled microsatellites, as described in Weir and Cockerham (1984). The 1000 resampled matrices were used as input into BARRIER to compute support of the barriers between individual pairs of sample localities. Support in this case was the proportion of the resampled dataset where the boundary between two sample localities was included in one of the barriers inferred.

Average, long-term effective population size (N_e) was estimated using the maximum-likelihood coalescent approach implemented in the program MIGRATE (Beerli & Felsenstein 1999, 2001; v 3.03, <http://popgen.scs.fsu.edu/Migrate-n.html>). Maximum-likelihood estimates (and 2.5% and 97.5% bounds of the likelihood distribution) of the parameter theta (Θ) were generated; Θ is defined as $4N_e\mu$ when based on biparentally inherited markers such as microsatellites. The parameter μ is the average, per-gene mutation rate and was derived from the Bayesian coalescent approach of Beaumont (1999) and Storz and Beaumont (2002), as implemented in MSVAR ver. 1.3 (<http://www.rubic.rdg.ac.uk/cgi-bin/MarkBeaumont/dirlist1.cgi>). N_e estimated by this method represents an average estimate of effective size integrated over the time to the common ancestor of all sampled alleles. Because simulations in MIGRATE are computationally demanding, parameter estimates were based on a random sample of 25 individuals from each location (125 individuals total). Markov Chain Monte Carlo (MCMC) coalescent simulations of gene trees were used to compute estimates, accounting for migration between populations. Parameter estimates were derived based on the results of three replicate runs. Each replicate run employed 10 initial short chains (10^4 trees sampled) and 4 long chains (5×10^6 trees sampled).

Historical (female) demography, based on mtDNA sequences, was examined using the maximum-likelihood coalescent approach implemented in LAMARC (Kuhner 2006), available at <http://evolution.genetics.washington.edu/lamarc/>. Initial attempts to estimate demographic parameters for individual samples did not converge to interpretable results. Considering the low level of divergence of mtDNA among the five samples (see Results), LAMARC runs were then carried out on haplotypes from all localities (pooled) to infer the overall average of the parameter g , the exponential population growth rate in females scaled by the mutation rate (μ), for yellowtail snapper in the region. A total of 30 initial short chains (10^4 trees sampled) and four long chains (10^6 trees sampled) were run, with the first 10 000 trees discarded as burn-in.

Results

Microsatellites *Prs248* and *Lan3* could neither be amplified consistently nor scored reliably for a large number of individuals, and microsatellite *Lan9*, based on initial data analysis, appeared to have a large frequency of null alleles in all five samples. Consequently, all three microsatellites were removed from data analysis. Genotypes at the 16 remaining microsatellites for each individual assayed in each sample are available at <http://agrillife.org/wfsc/doc/> under the file name 'Yellowtail snapper microsatellite genotypes'. The number of alleles detected ranged from one at *Lsy4* in the sample from PR-EAST to 26 at *Lan5* in the samples from SC and ST. Unbiased gene diversity ranged from zero at *Lsy4* in the sample from PR-EAST to 0.950 at *Lan5* in the samples from PR-EAST and ST. Neither allelic richness nor gene diversity differed significantly among samples [$Q_{(4)} = 4.14$, $P = 0.39$ and $Q_{(4)} = 2.15$, $P = 0.71$, respectively].

Significant departure from Hardy-Weinberg equilibrium expectations was found in three tests (*Lan13* in the sample from SC and *Och2* and *Ra1* in the sample from PR-EAST) prior to, but not following, Bonferroni correction. Estimates of F_{IS} ranged from -0.110 (*Lan12* in the sample from the Florida Keys) to 0.134 (*Och2* in the sample from PR-EAST). Analysis with MICROCHECKER indicated possible occurrence of null alleles only at *Lan13* in the sample from SC, and at *Och2* and *Ra1* in the sample from PR-EAST. There was no indication that possible null alleles affected scoring at these three microsatellites in the other samples. Consequently, all 16 microsatellites were used in subsequent analyses.

A total of 28 different mtDNA haplotypes were observed among the 126 individuals assayed. Haplotype #1 was the most common in all five sample localities and occurred in 59.5% of all individuals assayed. Observed number of haplotypes and haplotype diversity in each sample were included within the 95% confidence interval obtained during bootstrap resampling, indicating that observed values in each sample did not differ significantly from those expected in a random subsample of the overall dataset. Fu's (1997) F_S statistic and Fu and Li's (1993) F^* and D^* statistics in all of the samples except for SC were negative and differed significantly from zero prior to Bonferroni correction (Table 1). Following Bonferroni correction, all three neutrality tests remained significant only in the sample from the Florida Keys (Table 1). A statistical parsimony network of haplotypes (Fig. 2) revealed a star-like phylogeny.

Table 1. Fu's (1997) F_S and Fu and Li's (1993) D^* and F^* measures of selective neutrality among samples of *Ocyurus chrysurus* from the Florida Keys and the Caribbean Sea. Probabilities of significance (P) for each test were estimated using 10 000 coalescent simulations. Values in bold were significant after Bonferroni correction

| | F_S | P | D^* | P | F^* | P |
|--------------|--------------|---------------|--------------|---------------|--------------|---------------|
| Florida Keys | -7.97 | 0.0013 | -3.91 | 0.0003 | -4.03 | 0.0009 |
| PR-west | -4.40 | 0.0199 | -2.50 | 0.0292 | -2.69 | 0.0136 |
| Pr-east | -5.54 | 0.0146 | -2.40 | 0.0182 | -2.72 | 0.0161 |
| ST | -5.07 | 0.0172 | -1.88 | 0.0697 | -2.23 | 0.0347 |
| SC | -2.96 | 0.0817 | -0.84 | 0.2755 | -1.15 | 0.1561 |

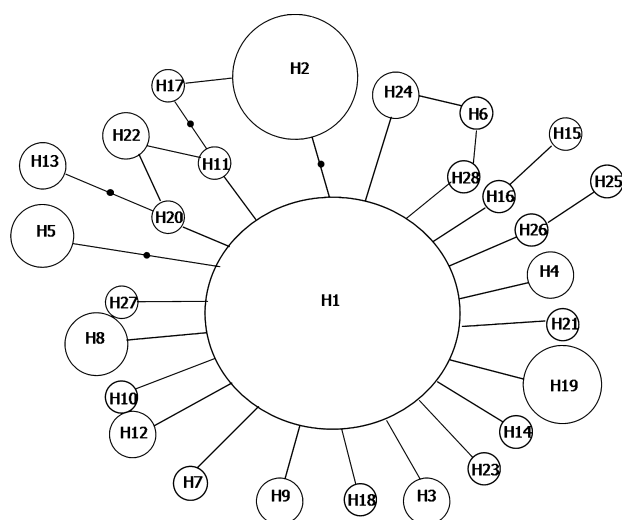


Figure 2. Parsimony network of *Ocyurus chrysurus* mtDNA haplotypes. Labels H1 to H28 correspond to individual haplotypes (Appendix S3). Sizes of circles are scaled to reflect their relative frequencies. Small, unnumbered (black) circles represent undetected intermediate haplotypes. Lines between haplotypes represent one base-pair substitution regardless of length.

Exact tests over all microsatellites revealed significant heterogeneity in allele and genotype distributions among the five samples ($P = 0.0005$, allele distributions; $P = 0.0058$, genotype distributions). Allele distributions differed significantly at four microsatellites (*Lan5*, *Lan12*, *Lan13* and *Ral*) before Bonferroni correction, but only at one (*Lan5*) after correction. The estimate of θ (weighted average across microsatellites) was 0.0013. Three of 10 exact tests between pairs of samples were significant before Bonferroni correction (KEYS vs PR-EAST, KEYS vs SC, and PR-EAST vs SC, Table 2), but only the test of KEYS vs SC remained significant following Bonferroni correction. Exact tests of homogeneity of mtDNA haplotype distributions were not significant (Table 2). Spatial analysis of molecular variance failed to resolve significant group-

Table 2. F_{ST} estimates for pairwise comparisons of microsatellite allele distributions (upper diagonal) and mtDNA haplotype distributions (lower diagonal) between *Ocyurus chrysurus* sampled from the Florida Keys and the Caribbean Sea. *and **: F_{ST} values that differed significantly from zero before and following Bonferroni correction, respectively

| | Florida Keys | PR-west | PR-east | St. Thomas | St. Croix |
|--------------|--------------|---------|---------|------------|-----------|
| Florida Keys | | 0.0018 | 0.0009* | 0.0007 | 0.0034** |
| PR-west | -0.0015 | | 0.0016 | -0.0005 | -0.0002 |
| PR-east | -0.0149 | -0.0123 | | 0.0008 | 0.0017* |
| St. Thomas | -0.0077 | -0.0077 | -0.0092 | | 0.0095 |
| St. Croix | 0.0222 | -0.0191 | 0.0020 | 0.0004 | |

ings in the microsatellite dataset (<0.2% of the total variance was explained by the among groups component of variance). Spatial analysis of molecular variance of the mtDNA dataset, however, revealed that the highest genetic variance among groups was explained when SC was isolated in one group with the other four samples classified in a second group. This partition explained 1.74% of the total variance.

Spatial autocorrelation analysis of the microsatellite dataset considering various distance class sizes revealed a significant positive correlation among genotypes sampled within 50–300 km from one another. This result was due primarily to the large distance between the sample locality in the Florida Keys and those in the US Caribbean, as no positive autocorrelations were found when the sample from the Florida Keys was excluded from the analysis. Bootstrap resampling of inferred barriers generated by BARRIER, however, indicated restricted gene flow among yellowtail snapper in the US Caribbean. Strong support (>95%) for a barrier to gene flow was indicated between PR-EAST and SC and between PR-EAST and PR-WEST, and moderate support (82.5%) was indicated for a barrier to gene flow between the Florida Keys and the sample localities in the US Caribbean (Fig. 3).

Estimates of average, long-term, effective population size (N_e) for each locality were derived from Θ values generated in MIGRATE ($N_e = \Theta/4\mu$), with μ equal to the modal mutation rate of 2.63×10^{-4} obtained from the Bayesian coalescent approach of Beaumont (1999) and Storz and Beaumont (2002). Estimates of N_e ranged from 1007 to 1084 and, based on estimated 95% confidence intervals, did not differ significantly among the five localities (Table 3). The estimate of g (95% CI), obtained from analysis of the mitochondrial DNA dataset, was 4545 (3372–7666). Based on base-substitution rates of 1.5 and 1.0% per million years, estimated for a variety of fishes, including lutjanids, by

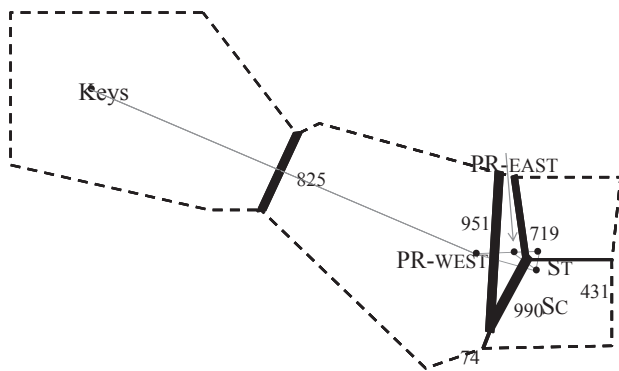


Figure 3. Voronoi diagram (dashed lines) displaying neighbourhoods of five localities (one in the Florida Keys and four in the Caribbean Sea); edges of the Voronoi diagram separating localities (outlined in black) are potential sections of a barrier to gene flow as inferred using the Monmonier's algorithm. The thickness of a neighbourhood edge is proportional to the number of times it was included in one computed barrier during analysis of 1000 bootstrap datasets. Numbers in blue indicate bootstrap support of each barrier section.

Table 3. Estimates of average, long-term effective size (N_e) and their 95% confidence intervals for *Ocyurus chrysurus* sampled from the Florida Keys and the Caribbean Sea

| Sample locality | N_e | Lower 95% CI | Upper 95% CI |
|-----------------|-------|--------------|--------------|
| Florida Keys | 1023 | 945 | 1156 |
| PR-west | 1009 | 936 | 1089 |
| PR-east | 1032 | 953 | 1119 |
| St. Thomas | 1084 | 999 | 1166 |
| St. Croix | 1007 | 923 | 1085 |

Bermingham *et al.* (1997), the estimate of g corresponds to a one order of magnitude increase in female population size over the last 33 775 or 50 662 years, respectively.

Discussion

Genetic differentiation and population (stock) structure

Results of the analysis of spatial genetic variation provided evidence of significant although weak genetic differences among the five geographic samples. Global exact tests (microsatellites) revealed significant heterogeneity in both allele and genotype distributions and three of 10 pairwise exact tests were significant prior to Bonferroni correction (KEYS vs PR-EAST, KEYS vs SC, and PR-EAST vs SC); only one of these (KEYS vs SC) remained significant following Bonferroni correction. Spatial heterogeneity also was inferred from spatial analysis of molecular variance of the mtDNA dataset.

The sample from SC was isolated in one group, with the remaining four samples forming a second group. Occurrence of significant spatial genetic heterogeneity also was demonstrated by the significant, positive autocorrelation (r) of microsatellite genotypes among fish sampled from all five localities. No significant autocorrelation, however, was detected when only samples from the US Caribbean were used in the analysis. Because spatial autocorrelation generally reflects isolation by distance (Sokal & Wartenberg 1983), these results indicate first that there is insufficient gene flow in yellowtail snapper to maintain correlations among genotypes between the Florida Keys and the US Caribbean; and second that spatial genetic variation among the samples from the Caribbean cannot be explained by a simple isolation-by-distance model. Analyses using BARRIER gave strongest support to barriers to gene flow between PR-EAST and SC and between PR-EAST and PR-WEST. The finding of genetic differences and restricted gene flow among geographic samples of yellowtail snapper was not necessarily unexpected as Vasconcellos *et al.* (2008) reported significant differences in mtDNA control-region sequences between yellowtail snapper sampled along the coast of Brazil and those sampled off Belize, while Wallace *et al.* (2003) reported an isolation-by-distance effect in both microsatellites and mtDNA among samples of yellowtail snapper from the east coast of Florida, the Florida Keys, and Puerto Rico.

The foregoing indicates there potentially could be up to four groupings of yellowtail snapper in US waters: one in the Florida Keys, one along the west coast of Puerto Rico, one that includes the east coast of Puerto Rico and St Thomas and one offshore of St Croix. Based primarily on the isolation-by-distance effect reported by Wallace *et al.* (2003), yellowtail snapper along the southeastern coast of the US are now considered a separate stock distinct from those in the US Caribbean (Muller *et al.* 2003; Cummings 2004a). Existence of a distinct stock of yellowtail snapper in Florida waters also is supported in this study by results of homogeneity (exact) tests, spatial autocorrelation analysis and the restricted gene flow inferred from analysis using BARRIER. Given the distance (1600 km) between the US southeast coast and the US Caribbean, these findings are consistent with studies of yellowtail snapper that reported limited post-larval and adult movement (Randall 1968; Beaumariage 1969; Watson *et al.* 2002; Lindholm 2005) and with simulation studies of larval dispersal (Roberts 1997), based on prevailing current patterns, which indicate there is virtually no overlap in expected

larval-drift envelopes between peninsular Florida and the US Caribbean.

Genetic differences observed in the current study among yellowtail snapper in the US Caribbean are much weaker and more subtle. While results of homogeneity tests (microsatellite alleles and genotypes) prior to Bonferroni correction, and spatial analysis of molecular variance of mtDNA haplotypes, suggested differences involving yellowtail snapper sampled off St Croix, analysis with BARRIER indicated restricted gene flow between fish on the west and east coasts of Puerto Rico and between fish on the east coast of Puerto Rico and St Croix. A recent stock assessment of yellowtail snapper in the US Caribbean (SEDAR8 {Southeast Data, Assessment, and Review} 2005) employed a two-stock model separating yellowtail snapper off Puerto Rico and St Thomas from those off St Croix. The model was based primarily on length of the planktonic larval phase and prevailing surface currents that would impact larval drift, data indicating restricted post-larvae and adult movement, and occurrence of two geological platforms (one containing Puerto Rico and St Thomas and one containing St Croix) that are separated by a approximately 4000-m trench. The distances between St Croix and St Thomas and between St Croix and the east coast of Puerto Rico, however, are approximately 65 km and 110 km, respectively, well within the one- and 2-month larval-dispersal envelopes suggested by Roberts (1997), and within or near the ecologically relevant larval-dispersal distances suggested by Cowen *et al.* (2000, 2006). Further, the locality sampled off St Croix is on the leeward side of the island and may be prone to larval retention (Swearer *et al.* 1999). In addition, the major surface currents in the region, including the Anegada Passage that runs between St Thomas and St Croix (Johns *et al.* 2002), generally run east to west (Roberts 1997). These considerations are consistent with the possibility that gene flow from yellowtail snapper off St Croix to localities on the Puerto Rican platform may be restricted.

Significant barriers to gene flow between the east and west coasts of Puerto Rico were inferred from analysis with BARRIER. Considerations of factors that might affect gene flow between the two localities are mixed. As noted previously, the few data available on movement of post-larval and adult yellowtail snapper indicate relative site fidelity. Alternatively, the distance between the two sample localities is approximately 175 km, within the 2-month envelope of larval drift suggested by Roberts (1997), but beyond the 10–100 km range of ecologically relevant larval-dispersal distances suggested by Cowen *et al.* (2000, 2006).

Although surface currents in the region generally run east to west, the prevailing near-shore surface current along the southern coast of Puerto Rico runs west to east (Roberts 1997; Fig. 1a). In addition, the locality on the west coast is on the leeward side of the island where the majority of recruitment may be local (Swearer *et al.* 1999). Overall, these considerations are not incompatible with reduced gene flow between the two coasts. The data supporting this, however, are limited to the analysis with BARRIER; additional studies directed specifically towards assessing direction and magnitude of gene flow along the southern coast of Puerto Rico certainly are warranted.

Genetic diversity and effective population size

Levels of genetic variability (microsatellites and mtDNA) were homogeneous at all five sample localities and easily commensurate with levels of genetic variability in other species of exploited snapper (Saillant & Gold 2006; Gold *et al.* 2009; Karlsson *et al.* 2009). The star-like phylogeny observed for mtDNA haplotypes is consistent with demographic population expansion (Calafell *et al.* 2002), as are the results from analysis with LAMARC (where the estimate of female population growth rate (g) was significantly greater than zero), and, to a lesser extent by the results from tests of selective neutrality of mtDNA variants where all test values were negative and most tests were significant prior to Bonferroni correction. Estimates of average, long-term effective size (N_e), based on microsatellites and assuming an average mutation rate of 2.63×10^{-4} , ranged among the five localities between 1007 and 1084 and did not differ significantly from one another. A minimum effective size of 500–1000 has been suggested variously as baseline levels necessary to avoid mutational meltdown and preserve genetic variation at quantitative traits involved in fitness (Higgins & Lynch 2001; Rieman & Allendorf 2001). The estimates of N_e obtained here are higher than those minimum benchmarks, suggesting that yellowtail snapper at all five localities have, at present, sufficient genetic variation to maintain long-term integrity and sustainability; the estimates of N_e , however, are barely higher than the minimum recommended, indicating that continued monitoring of yellowtail snapper genetic resources in the region is warranted.

Finally, estimates of historical female population growth rate (g) indicated that a one order of magnitude increase in female population size has occurred over at least the last 33 000–50 000 years. In all likelihood, this reflects an historical increase in female effective

size, perhaps since glacial times, as has been suggested (Pruett *et al.* 2005; Saillant *et al.* 2010) for red snapper in the Gulf of Mexico.

In closing, it is noted that the range of genetic divergence among the localities is fairly low ($F_{ST} < 0.0034$ across microsatellites and < 0.02 at mtDNA) and that results of various analyses were at best mixed. Given that only single samples were obtained at each locality, it is theoretically possible that the differences observed could stem from 'chaotic patchiness' (Hedgecock 1994) or 'chaotic temporal variation' (P. Bentzen, personal communication). Additional sampling could test this possibility.

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Supporting Information

The following supplementary material is available:

Appendix S1. Multiplex panels used to assay 16 microsatellites in *Ocyurus chrysurus*.

Appendix S2. Summary statistics for 16 nuclear-encoded microsatellites and mtDNA ND-4 sequences in yellowtail snapper, *Ocyurus chrysurus*, sampled from the Florida Keys and the Caribbean Sea.

Appendix S3. Spatial distribution of mtDNA haplotypes among yellowtail snapper, *Ocyurus chrysurus* sampled from the Florida Keys and the Caribbean Sea.

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