THE GENETIC DIVERSITY AND POPULATION STRUCTURE OF BARRED SAND BASS, *PARALABRAX NEBULIFER*: A HISTORICALLY IMPORTANT FISHERIES SPECIES OFF SOUTHERN AND BAJA CALIFORNIA

CORINNE N. PATERSON, CHRIS L. CHABOT, AND JEANNE M. ROBERTSON
Department of Biology
California State University, Northridge
Northridge, CA 91330-8303

BRAD ERISMAN
Department of Marine Science
University of Texas at Austin
Port Aransas, TX 78373-5015

JUAN JOSE COTA-NIETO
Centro para la Biodiversidad Marina
y la Conservación A.C.
La Paz, BCS, 23090, México

LARRY G. ALLEN
Department of Biology
California State University, Northridge
Northridge, CA 91330-8303
ph: (818) 677-3356
larry.allen@csun.edu

ABSTRACT

We examined the contemporary genetic structure of the barred sand bass, *Paralabrax nebulifer*, a commonly fished species in southern California and Baja California, Mexico. Populations of barred sand bass in southern California have experienced severe declines in numbers over the last decade subsequently leading to severely depressed status of the recreational fishery. Such large population declines can lead to an overall decrease in genetic diversity. The present study examined the genetic diversity in this species (N = 365) using both the control region of the mitochondrial DNA and microsatellite markers for locations throughout California and Baja California. Both markers showed a high degree of genetic diversity and genetic mixing however there is some evidence of structuring between locations north and south of the San Quintin upwelling zone. Despite the weak structuring observed around the upwelling zone, barred sand bass throughout the northeastern Pacific likely comprise a single large population.

INTRODUCTION

Molecular genetic techniques have become more widespread in oceanic systems and in fishery management (Ryman 1991; Ensing et al. 2013) due to the ability to identify distinct genetic stocks, the genetic health, and connectivity between stocks (Palsbøll et al. 2007; Dudgeon et al. 2012; Ovenden et al. 2015). Fishery stocks are identified using various life history parameters that do not necessarily reflect the genetic population or stock (Shaklee et al. 1999; Hutchinson et al. 2003; Hutchinson 2008; Reiss et al. 2009). Additionally, boundaries established by state or international borders can divide a biological stock into multiple fishery stocks (Shaklee et al. 1999). Therefore, it is important to understand what constitutes a biological stock to better manage fisheries. A high degree of genetic variation facilitates the adaptation of a species to a variety of environmental or anthropogenic conditions and thus, species (or population) survival (Carvalho and Hauser 1994; Kenchington et al. 2003). Connectivity between populations or stocks is also important for fishery management because it can identify source and sink populations and the potential for replenishment of depleted stocks (Palsbøll et al. 2007). Therefore, it is essential to quantify genetic variation and connectivity within a species to inform management decisions that maintain that variation (Ryman 1991; Airame et al. 2003; Pérez-Ruzafa et al. 2006; Palsbøll et al. 2007).

The barred sand bass, *Paralabrax nebulifer*, ranges from Santa Cruz, CA to the southern tip of the Baja California peninsula in Mexico (Love et al. 1996) and is fished in both countries. Barred sand bass form large spawning aggregations along the coast from late spring to early fall with a peak in July (Love et al. 1996; Baca-Hovey et al. 2002; Mason and Lowe 2010). Individuals exhibit site fidelity during non-spawning months and some exhibit site fidelity year round, not participating in spawning aggregations (Jarvis et al. 2010; Mason and Lowe 2010). The majority of barred sand bass also exhibit a preference for spawning locations from year to year (Jarvis et al. 2010). Barred sand bass migrate moderate distances (average of 15 km ranging from 1 km to 40 km) (Jarvis et al. 2010) to reach spawning locations; however, individuals with overlapping home ranges do not necessarily migrate to the same spawning grounds (Jarvis et al. 2010).

Because of these characteristics of its mating system, barred sand bass comprise one of the most important recreational fisheries in southern California. The species was commercially fished until the 1950s, and since then, it has been recreationally fished off the coast of southern California (Young 1963). The recreational fishery for barred sand bass experienced a collapse in 2003 due to the targeting of spawning aggregations and a decline in landings and biomass estimates (Erisman et al. 2011). In addition to the recreational fishery in California, there is a small scale commercial fishery in Baja California, Mexico. This small scale fishery has the highest catch in tons of any fished species along the Pacific Coast of

Baja California (Rosales-Casian and Gonzalez-Camacho 2003; Erisman et al. 2011).

Several aspects of the biology of the barred sand bass have been studied including life history (Baca-Hovey et al. 2002; Sadovy and Domeier 2005; Jarvis et al. 2010; Cota-Gomez et al. 2013), ecology (Mason and Lowe 2010) and the fishery (Erisman et al. 2011; Miller and Erisman 2014); however, the genetic diversity and population structure of barred sand bass off both southern and Baja California is unknown. One concern for barred sand bass populations is a decline in the genetic diversity due to the fishery collapse in southern California (Smith et al. 1991; Hutchinson et al. 2003) and the potential for reduction in the body size at first reproduction (van Wijk et al. 2013; Alós et al. 2014). In order to determine potential effects of the fishery collapse on the genetic diversity of barred sand bass, we must first determine what the genetic diversity and population structure of barred sand bass is.

Based on what is known about other species of *Paralabrax*, we expect to see a high degree of connectivity due to its reproductive mode and the potential for the larvae to be transported considerable distances via the currents (Selkoe and Toonen 2011). Barred sand bass have a pelagic larval duration (PLD) of 21–30 days (Allen and Block 2012) that is comparable to two congeners: the kelp bass, *P. clathratus*, and the spotted sand bass, *P. maculatofasciatus*. In both of these species there was a high degree of connectivity throughout the region (mtDNA control region; Phalen 1999; Salomon 2005); however, the spotted sand bass shows some evidence for divergent populations between southern California and Baja California that may be due to the San Quintin upwelling zone in Baja California, Mexico (Salomon 2005). Population genetic structure was also low in the kelp bass using microsatellites with a greater degree of structuring in southern California compared with Baja California (Selkoe et al. 2006; Selkoe et al. 2007). This upwelling zone is a known biogeographic barrier for migratory species (Bernardi 2000; Terry et al. 2000; Bernardi et al. 2003; Olivares-Banuelos et al. 2008). The upwelling zone is thought to also be a barrier for larval dispersal (Butler et al. 1982; Shanks and Eckert 2005). Thus, we expected to show a genetic break around the San Quintin upwelling zone in barred sand bass given that this division is seen in its sister species the spotted sand bass.

The goal of this study was to determine the genetic diversity, population structure, and connectivity among localities of barred sand bass to inform the conservation management of genetic stocks. This study used both mitochondrial DNA markers and nuclear DNA markers (microsatellite loci) to determine the population structure of barred sand bass in southern California and Baja California, Mexico. The mitochondrial DNA control region is a common marker for population structure analysis due to the high variability of the region (Magoulas 2005), while microsatellite markers are ideal for population studies due to their high variability (Wirgin and Waldman 2005).

MATERIALS AND METHODS

Collection and Extractions

Tissue samples from either the fin, gill rakers, muscle, or liver tissues of individual barred sand bass were collected using sterile techniques and stored in 95% ethanol and subsequently frozen in a –4°C freezer at California State University, Northridge. Samples from southern California were collected using hook and line from five locations (Ventura, Marina Del Rey, Los Angeles/Long Beach Harbor, San Clemente, and San Diego) and from commercial fishers from eight sites in Baja California, Mexico (Popolta, San Quintin/Camalu, Santa Rosalita, Laguna Manuela, Isla Cedros, Punta Abreojos, and Bahia Magdalena) (fig. 1). Samples from Ventura, Marina Del Rey, Los Angeles/Long Beach Harbor, San Diego, Santa Rosalita, San Quintin, Popolta, Laguna Manuela, and Camalu were collected during the non-spawning season while samples from San Clemente, Isla Cedros, Punta Abreojos, and Bahia Magdalena were sampled during the spawning season. For each site, 7–30 individuals were sampled (Ventura, n = 21; San Quintin, n = 9; Laguna Manuela, n = 9; Popotla, n = 7; all other sites n = 30).

Additional barred sand bass samples that were collected from 1997 to 1999 from Santa Barbara, California to Isla Cedros, Mexico (San Diego, n = 9; Platform Gina, n = 1; Los Angeles/Long Beach Harbor, n = 37; San Quintin, n = 13; Isla San Martin, n = 6; Isla Cedros, n = 2). The samples from Isla San Martin and Isla Cedros were collected during the non-spawning season while the sample from Platform Gina in Santa Barbara was collected during spawning season. Samples from Long Beach were collected in both non-spawning and spawning season. Extractions were carried out using a DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol.

Mitochondrial DNA Amplification and Sequencing

The mitochondrial DNA control region was amplified in 25 µl polymerase chain reactions (PCR) containing ~100 ng DNA, 1 uM of primer (FWD 5'-TTCCACCTCTAACTCCCAAAGCTAG-3') and reverse (REV 5'-ACGCTGGAAAGAACG CCCGGCATGG-3'; Lee et al. 1995), and 1X EconoTaq® PLUS 2X Master Mix (Lucigen). PCR conditions consisted of an initial denaturation at 94°C for two minutes, followed

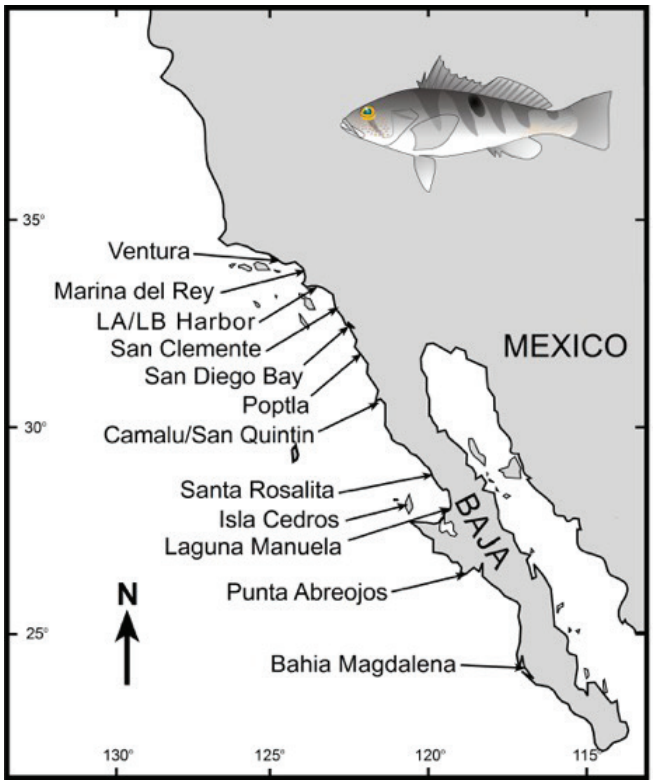

Figure 1. Map of sampling locations of *Paralabrax nebulifer*. Sampling covers the range in which *Paralabrax nebulifer* is commonly found. Sampling was performed using hook and line or from small scale trap fishermen.

by 30 cycles of 94°C denaturation for 30 seconds, 58°C annealing for 30 seconds, 72°C extension for 30 seconds, and a final extension of 72°C for 10 minutes. Amplicons were purified and sequenced by BigDye v3.1 (Applied Biosystems) dye-determination using nested primers from Lee et al. (1995; FWD 5'-GGGCGGATCCCAC-CACTAGCTCCCAAA-3'; REV 5'-CCTGAAGTAG-GAACCAGATG-3') at Laragen, Inc. (Culver City, CA).

Mitochondrial DNA Analysis

For each sample, the forward and reverse sequences were aligned and manually cleaned up using Sequencher 5.2 (Gene Codes Corporation). Each sequence was assigned a haplotype (1–164) and all sequences were aligned in MEGA 6 (Tamura et al. 2013). Corrections to the alignment were done using Mesquite (Maddison and Maddison 2011). All haplotypes were uploaded to GenBank (NCBI) (KJ935922-KJ936085).

We used JModelTest (Guindon and Gascuel 2003; Darriba et al. 2012) to determine the best evolutionary model for the control region. We used a Tamura Nei model with a gamma correction in MEGA 6 (Tamura et al. 2013). Nucleotide divergence between sampling locations was calculated in MEGA 6. Estimates of pairwise genetic differentiation (pairwise Φ_{ST}) between sampling locations was calculated in Arlequin 3.5 (Excoffier and Lischer 2010) with significance being determined by permutation (10,000 replicates) and the false discovery rate used to correct for multiple tests (Narum 2006).

The genetic structure of barred sand bass populations was determined using nested AMOVAs (Analysis of MOlecular Variance) in Arlequin 3.5 (Excoffier and Lischer 2010). The first AMOVA compared the samples collected in 1997–99 and those collected 2010–13 to determine if samples could be pooled. We then used an AMOVA to compare all sampling locations of barred sand bass. Finally, we quantified genetic differentiation for all barred sand bass samples between the north and south of the San Quintin upwelling zone (north: Ventura, CA to San Quintin, B.C.; south: Santa Rosalita, B.C. to Bahia Magdalena, B.C.). To determine significance, 10,000 permutations were performed for all AMOVAs and the false discovery rate was used to correct for multiple tests. A median-joining haplotype network (Bandelt et al. 1999) was generated using all DNA sequences in NETWORK 4.6.11 (Fluxus-engineering.com). Post processing analysis was carried out to clean up the network (Polzin and Daneschmand 2003).

The relative nucleotide composition, number of polymorphic loci, haplotype diversity (*h*), nucleotide diversity (π), the number of pairwise nucleotide differences, the co-ancestry coefficient (θ_S), Tajima's D (Tajima 1989) and Fu's F_S (Fu 1997) were calculated using Arlequin 3.5 (Excoffier and Lischer 2010). In addition, a Mantel test for an estimate of isolation by distance was done across the range of barred sand bass using GeneAlEx 6.5 (Peakall and Smouse 2006, 2012).

Microsatellite Loci Selection

A microsatellite library for *Paralabrax nebulifer* was generated using 454 sequencing by Cornell University using extracted barred sand bass DNA and tissue samples from California and Mexico. We amplified 12 polymorphic loci using a three primer system where a nucleotide tag was added to the 5' end of each primer (Brownstein et al. 1996; Schuelke 2000). The third primer was fluorescently labeled using 6-FAM or 5-HEX. Each PCR contained 2 µl of the 10 µM pig tail primer, 0.15 µl of the 10 µM long tail primer, 0.05 µl of 10 µM 6-FAM (or 5-HEX), 1X EconoTaq® PLUS 2X Master Mix (Lucigen) and 100 ng of template DNA (10–990 µM). We used a touchdown PCR with the following conditions. An initial denaturation of 95°C for 5 minutes, followed by 35 cycles of denaturation at 95°C for 40 sec; annealing temperatures starting at 61°C for 45 sec with a decrease by 1°C for each of 7 subsequent cycles and the remaining 28 cycles performed at 55°C for 45 sec; extension of 72°C for 45 sec, with a final elongation step

TABLE 1
Microsatellite loci generated for use in *Paralabrax nebulifer*. All loci are in Hardy-Weinberg equilibrium and have no null alleles.

Locus	Forward primer 5'–3'	Reverse primer 5'–3'	Motif	N	Size (bp)	A	H_O	H_E	F_{IS}
*Pne*01CCK17	TGGCCAGTAATTATAATACGCACG	CTTCCTTTCATCATCTACCACCC	$(ATCC)_n$	341	217–273	27	0.876	0.837	–0.047
*Pne*2102	CTTCCCTCTGCCACTTCTTCAC	TCAGAGATCAGAGATGGTTTCGG	$(AACAT)_n$	315	163–203	12	0.712	0.713	0.002
*Pne*01CVDJQ	TTCTTTATAGCACCAGACGCAAC	TTTCTCTTGCTCTTTCTTGGGC	$(AGCC)_n$	317	146–200	13	0.820	0.799	–0.027
*Pne*02IMIH6	GGCAGTTTGAAGTGTGTCCTAG	TCTCATATTCAGCCTTCCTCACC	$(ATCC)_n$	340	150–208	14	0.859	0.830	–0.035
*Pne*5053	ACTTCTTGCATGATAGTTCTGGC	GTCTTTATCCTCAATCCCGAAGC	$(AAAG)_n$	341	384–474	32	0.546	0.609	0.102
*Pne*02JMRK5	ACGGTCAGGGTAAGATTATCAGG	TAGTAAGGTGTCGGGTCATCAAG	$(ATCC)_n$	330	234–462	40	0.898	0.932	0.036

*indicates significant value

at 72°C for 5 min. All PCR products were electrophoresed on an Applied Biosystems 3130XL Genetic Analyzer at California State University, Northridge. Allele sizes were scored by comparison with 500 LIZTM ladder (GeneScan™ ABI) and scored manually in GeneMarker (Softgenetics). To validate the dataset, 14% of the PCRs were reanalyzed for all loci.

Additionally, each locus was tested for applicability in two congeners (*P. clathratus* and *P. maculatofasciatus*) using the same protocols for amplification as described previously. Successful amplification and genotypes were determined using GeneMarker (Softgenetics). All 12 of the microsatellite primers successfully amplified in both *P. clathratus* and *P. maculatofasciatus*.

Microsatellite Analysis

Deviations from Hardy-Weinberg equilibrium for each sampling location were calculated using GenePop (Raymond and Rousset 1995; Rousset 2008) and significance was determined after Bonferroni correction for multiple tests. Each sampling location was checked for null alleles using Micro-Checker (van Oosterhout et al. 2004) and tests of disequilibrium between all pairs of loci over all populations and within populations were calculated using FSTAT 2.9.3.2 (Goudet 2003). Loci not in Hardy-Weinberg equilibrium and with possible null alleles were eliminated from the final analysis. A total of six loci were used for the analysis (*Pne*01CCK17, *Pne*2102, *Pne*02IMIH6, *Pne*5053, *Pne01CVDJQ* and *Pne*02JMRK5) (table 1). Observed heterozygosity (H_O) and expected heterozygosity (H_E) for the loci were calculated using GenAlEx 6.5 (Peakall and Smouse 2006, 2012).

Genetic demes were determined using STRUCTURE 2.3.4 (Pritchard et al. 2000) using an admixture model. The model was run for K = 1–12 with a burn-in length of 100,000 and Monte Carlo Markov Chain of 1,000,000 steps and was repeated 20 times for each K. The Evanno method was implemented using STRUCTURE HARVESTER (Earl and VonHoldt 2012) to determine the best K for barred sand bass (Evanno et al. 2005). Proportion of ancestry for each individual based on the best value of K was visualized in Excel (Microsoft Corporation).

POWSIM 4.1 (Ryman and Palm 2006) was used to estimate the statistical power of the microsatellite loci to detect differentiation among localities. Burn-in consisted of 1,000 steps with 100 batches and 1,000 iterations per batch. A Fisher's and Chi-square test were used to test for significance of a F_{ST} value for each run. Pairwise tests of differentiation (F_{ST}) were calculated using GeneAlEx 6.5 (Peakall and Smouse 2006, 2012). As F_{ST} has been shown to underestimate divergence when estimated from highly polymorphic loci (Hedrick 1999),

TABLE 2
Summary statistics for a) mitochondrial DNA control region and b) microsatellite DNA markers for all locations of *Paralabrax nebulifer*.

a) Mitochondrial DNA control region statistics showing haplotype number, haplotype diversity (h), nucleotide diversity (π), mean pairwise difference, coancestry coefficient (θ_S), Tajima's D and Fu's F_S for all populations

Location	Haplotype no.	h	π	Mean pairwise difference	θ_S	Tajima's D	Fu's F_S
Platform Gina	1	1.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000	0.000
Ventura	20	0.995 ± 0.017	0.014 ± 0.008	7.448 ± 3.625	14.496 ± 5.149	–1.934*	–13.072*
Marina Del Rey	23	0.984 ± 0.013	0.013 ± 0.007	6.919 ± 3.341	12.167 ± 4.018	–1.608*	–13.794*
LA/LB Harbor	45	0.989 ± 0.005	0.010 ± 0.006	5.557 ± 2.703	10.649 ± 3.098	–1.616*	–25.374*
San Clemente	22	0.994 ± 0.013	0.011 ± 0.006	6.169 ± 3.030	11.353 ± 3.629	–1.664*	–16.287*
San Diego	30	0.988 ± 0.009	0.012 ± 0.006	6.250 ± 3.032	11.353 ± 3.629	–1.650*	–24.603*
Popolta	7	0.964 ± 0.077	0.006 ± 0.004	3.464 ± 1.974	4.242 ± 2.154	–1.210	–2.842
Camalu/San Quintin	30	0.989 ± 0.010	0.013 ± 0.007	7.127 ± 3.422	14.710 ± 4.673	–1.897*	–20.915*
Santa Rosalita	29	1.000 ± 0.009	0.013 ± 0.007	7.042 ± 3.040	13.496 ± 4.508	–1.817*	–25.082*
Isla Cedros	27	0.990 ± 0.011	0.011 ± 0.006	5.966 ± 2.921	9.684 ± 3.854	–1.400	–22.931*
Laguna Manuela	9	1.000 ± 0.052	0.012 ± 0.007	6.444 ± 3.369	8.463 ± 3.854	–1.312	–4.037*
Isla San Martin	4	0.900 ± 0.161	0.006 ± 0.004	3.000 ± 1.874	3.360 ± 2.001	–0.747	–0.331
Punta Abreojos	26	0.994 ± 0.011	0.011 ± 0.006	5.712 ± 2.810	9.932 ± 3.342	–1.612*	–25.345*
Bahia Magdalena	21	0.974 ± 0.019	0.009 ± 0.005	4.902 ± 2.462	7.966 ± 2.819	–1.444	–14.865*
All samples	164	0.998 ± 0.000	0.011 ± 0.006	6.148 ± 2.931	19.449 ± 4.139	–2.059*	–24.568*

b) Microsatellite DNA marker statistics showing number of alleles (A), observed (H_O) and expected (H_E) heterozygosity.

Location	A	H_O	H_E
Ventura	11	0.8781	0.786
Marina Del Rey	13	0.8797	0.824
LA/LB Harbor	15	0.7876	0.822
San Clemente	14	0.8499	0.835
San Diego	13	0.7690	0.779
Popolta	7	0.6458	0.777
Camalu/San Quintin	13	0.7424	0.806
Santa Rosalita	10	0.8617	0.752
Isla Cedros	13	0.8460	0.817
Laguna Manuela	6	0.6852	0.675
Punta Abreojos	13	0.7181	0.780
Bahia Magdalena	12	0.7585	0.791
All samples	12	0.7852	0.787

* indicates significant value

G'_{ST} (Meirmans and Hedrick 2011) and Jost's D (Jost 2008) were also calculated in GenAlEx 6.5 (Peakall and Smouse 2006, 2012). For all pairwise comparisons, 9,999 permutations were performed to determine significance and the false discovery rate was used to correct for multiple tests.

Genetic structure was determined by three AMOVAs performed within GeneAlEx 6.5 (Peakall and Smouse 2006, 2012). The first AMOVA tested the samples collected between 1997 and 1999 to those collected between 2010 and 2013. The second AMOVA compared the variation across the entire range of the species. Finally, the third AMOVA tested the effect of the San Quintin upwelling zone on population connectivity by grouping sampling locations into two large populations north and south of the zone (north: Ventura, CA to San Quintin, B.C.; south: Santa Rosalita, B.C. to Bahia Magdalena, B.C.). To determine significance, 9,999 permutations were performed for all AMOVAs and the false discovery rate was used to correct for multiple tests.

RESULTS

Mitochondrial DNA

We amplified 365 mitochondrial control region sequences and detected 164 unique haplotypes from the study region. Sequences ranged from 382 to 545 base-pairs in length and contained approximately 50 base-pairs of the tRNA-Pro gene at the beginning of the sequence (average composition = 22.06% cytosine, 30.01% thymine, 32.61% adenine, and 15.32% guanine). Barred sand bass haplotypes contained a total of 126 variable sites (table 2a; GenBank Accession Number KJ935922–KJ936085). Of the 164 haplotypes, 53 were shared among locations and 111 were unique to a single individual location.

Over all sampling locations haplotype diversity was high ($h = 0.999 \pm 0.000$) and nucleotide diversity was relatively low ($\pi = 0.011 \pm 0.006$). Haplotype diversity remained high across all sampling sites ranging from 0.900 ± 0.161 to 1.000 ± 0.009 while nucleotide diver-

TABLE 3
Results of three hierarchical AMOVA's for Paralabrax nebulifer based on the mitochondrial control region.

a) For samples collected between 1997-1999 and 2010-2013.

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation
Among groups		1	2.88	–0.0020	–0.07
Among populations within groups		17	52.72	0.0015	0.05
Within populations		347	1066.68	3.074	100.02
Total		365	1122.28	3.073	
Fixation index (Φ_{CT})	–0.001				

$p > 0.025$

b) For all sampling locations.

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation
Among Populations		13	43.914	0.01244	0.400
Within Populations		352	1078.122	3.06285	99.600
Total		365	1122.036	3.075	
Fixation index (Φ_{CT})	0.004				

$p > 0.05$

c) Comparing locations north and south of the San Quintin upwelling zone.

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation
Among groups		1	10.90	0.048	1.56
Among populations within groups		12	33.01	–0.013	–0.410
Within populations		352	1078.12	3.039	98.84
Total		365	1122.04	3.099	
Fixation index (Φ_{CT})	0.016				

$p < 0.025$

TABLE 4
Pairwise Φ_{ST} values between all sampling locations of *Paralabrax nebulifer*. Pairwise Φ_{ST} values below and corresponding p-values above. Significant p-values indicated by +. PG = Platform Gina, VE = Ventura, MD = Marina Del Rey, LA = Los Angeles/Long Beach Harbor, SC = San Clemente, SD = San Diego, PO = Popolta, SQ = San Quintin, SR = Santa Rosalita, IC = Cedros Island, LM = Laguna Manuela, ISM = Isla San Martin, PA = Punta Abreojos, and BM = Bahia Magdalena.

	PG	VE	MD	LA	SC	SD	PO	SQ	SR	IC	LM	ISM	PA	BM
PG		—	—	—	—	—	—	—	—	—	—	—	—	—
VE	–0.251		—	—	—	—	—	—	—	—	—	—	—	—
MD	–0.210	–0.012		—	—	—	—	—	—	—	—	—	—	—
LA	–0.118	0.003	–0.007		—	—	—	—	—	—	—	—	—	—
SC	–0.179	–0.026	–0.021	–0.014		—	—	—	—	—	—	—	—	—
SD	–0.128	–0.022	0.002	0.004	–0.003		—	—	—	—	—	—	—	—
PO	0.044	–0.035	–0.021	–0.019	–0.016	–0.029		—	—	—	—	—	—	—
SQ	–0.216	0.002	0.003	0.001	–0.005	0.004	–0.026		—	—	—	—	—	—
SR	–0.326	–0.001	0.014	0.008	–0.001	0.008	–0.011	0.008		—	—	—	—	—
IC	–0.143	0.016	0.052	0.026	0.024	0.025	0.028	0.018	–0.003		—	—	—	—
LM	–0.160	0.007	–0.001	0.004	–0.009	0.011	0.007	0.003	0.014	0.032		—	—	—
ISM	0.000	–0.056	–0.015	–0.005	–0.011	–0.019	–0.074	–0.038	–0.027	0.007	0.029		—	—
PA	–0.150	0.003	0.040	0.012	0.019	0.010	–0.022	0.014	–0.006	0.005	0.027	–0.022		—
BM	–0.056	0.003	0.024	0.001	0.002	0.018	0.018	0.013	–0.007	–0.007	0.010	0.030	0.001	

$p < 0.001$

sity remained low ranging from 0.006 ± 0.004 to 0.014 ± 0.008 (table 2a). Sequence divergence was low within sampling locations (6.148 ± 2.931) and ranged from 0.000 ± 0.000 to 7.448 ± 3.625 (table 2a). Tajima's D for all populations was –2.059 and ranged from –0.717 to –1.934, indicating a population expansion. Nine of the 14 sampling locations show significant deviation from neutrality and potential population expansion (table 2a). Deviation from neutrality was also seen overall for barred sand bass (F_S = –24.568; $p < 0.02$) as well as in 11 of the 14 sampling locations indicating a rapid expansion (table 2a).

Barred sand bass samples collected from our two time points, 1997–99 and 2010–13, showed high within-populations variation and were not different from one another in a pairwise test of genetic differentiation (Φ_{CT} = 0.001; p = 0.660) (table 3a). All samples were pooled together by sampling site for the remaining analysis. Testing for differentiation among all sampling locations indicated no significant differences (Φ_{CT} = 0.004; p =

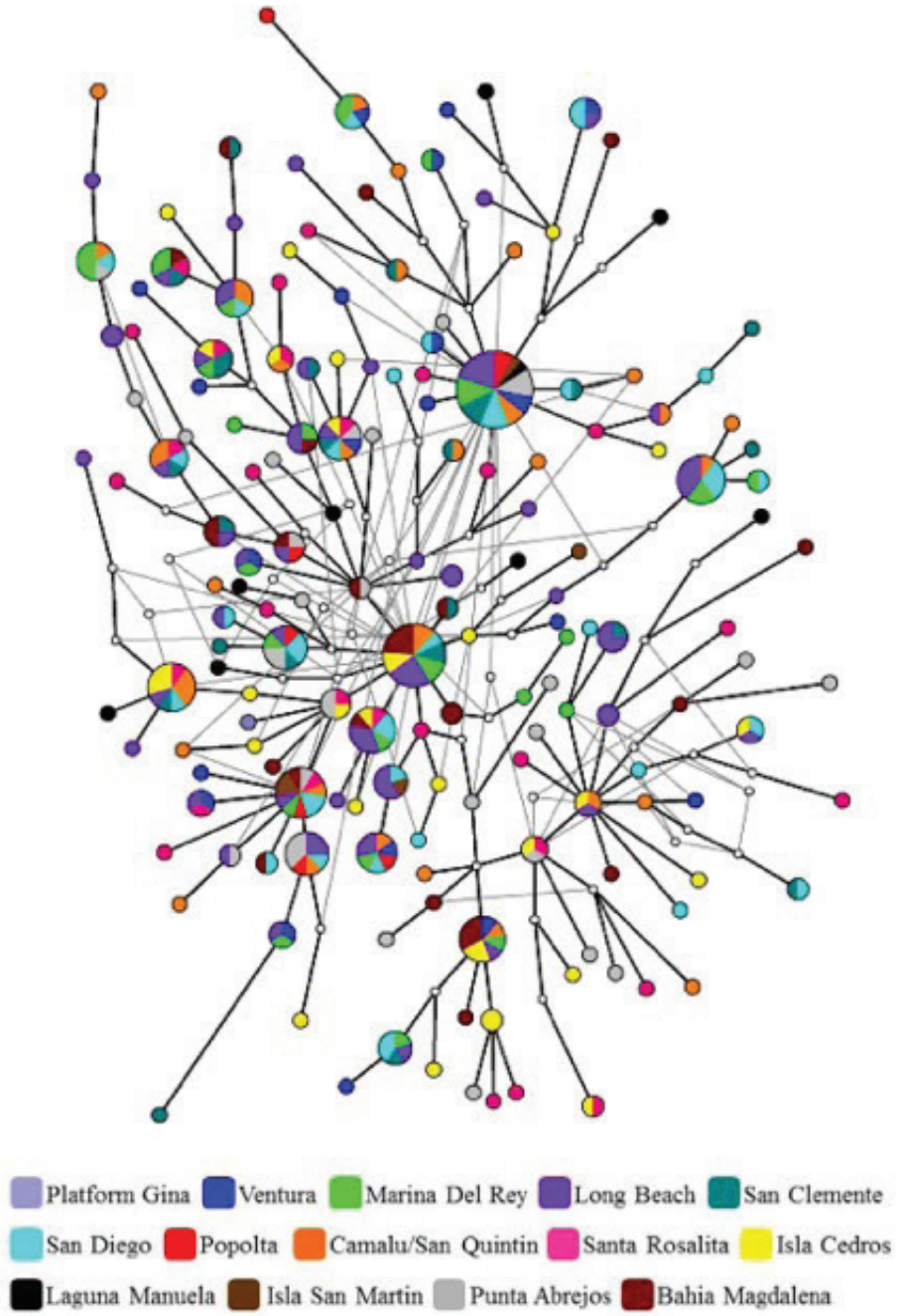

Figure 2. Haplotype network for *Paralabrax nebulifer* in California and Mexico. Each circle represents a haplotype and each color a sampling location found in this study. The bold line represent on of 53 possible Steiner trees while the grey lines represent all other possible trees. All trees are equally likely. A total of 189 haplotypes were found with 51 shared haplotypes. Platform Gina is near Ventura while Isla San Martin is near San Quintin (see fig. 1). Unsampled haplotypes shown as small open circles.

0.156) (table 3b). Similarly, pairwise Φ_{ST} comparisons showed no differentiation among all sampling locations (table 4). However, in testing for the presence of a genetic barrier of the San Quintin upwelling zone there appeared to be a weak but significant difference between samples north and south of the upwelling zone (Φ_{CT} = 0.016; $p < 0.001$) (table 3c). Barred sand bass showed no evidence of isolation by distance for mitochondrial DNA ($R^2 = 0.0002$; $p = 0.164$).

Haplotype network analyses revealed a total of 54 possible Steiner trees where each tree is equally likely (fig. 2). The network revealed no distinct clusters by sampling location or region (north and south of the San Quintin upwelling zone) and revealed no population structure in barred sand bass. This network shows the high number of singletons across the entire range of barred sand bass and historical connectivity among sampling locations.

Microsatellite Markers

The six loci used in the study were highly polymorphic with an average of 23 alleles per locus (range = 12 to 40 alleles). The average observed heterozygosity was 0.785 (0.546–0.898) while the average expected heterozygosity was 0.787 (0.609–0.932) (table 2b). POWSIM indicated that the six loci had the statistical power to detect a significant difference between samples when testing for $F_{ST} \leq 0.05$ (avg. $F_{ST} = 0.0487$ for simulations). Pairwise comparisons of divergence (G'_{ST} and Jost's D) show genetic differentiation between a few population pairs but a pattern of geographic divergence is not clearly discernable (table 5).

As seen with the mitochondrial DNA, samples collected from 1997–99 and 2010–13 were not differentiated from one another ($F_{CT} = -0.001$; $p = 0.777$) (table 6a). Therefore, all samples were pooled together for further analysis. In the AMOVA, we detected weak

TABLE 5

Pairwise G'_{ST} (below the diagonal) and Jost's D (above the diagonal) for all sampling locations of *Paralabrax nebulifer*. Significant p-values are indicated by ★. VE = Ventura, MD = Marina Del Rey, LA = Los Angeles/Long Beach Harbor, SC = San Clemente, SD = San Diego, PO = Popolta, SQ = San Quintin, SR = Santa Rosalita, IC = Isla Cedros, LM = Laguna Manuela, PA = Punta Abreojos, and BM = Bahia Magdalena.

	VE	MD	LA	SC	SD	PO	SQ	SR	IC	LM	PA	BM
VE		0.023	0.133★	–0.015	0.118★	0.103	0.068	0.063	0.036	0.040	0.152★	0.097★
MD	0.028		0.055★	–0.006	0.092★	0.013	0.076★	0.085★	0.020	0.152★	0.101★	0.037
LA	0.158★	0.065★		0.041	0.020	–0.038	–0.009	0.061★	0.020	0.253★	0.028	0.008
SC	–0.018	–0.007	0.049		0.034	–0.003	0.017	0.057★	–0.010	0.109	0.089★	0.025
SD	0.143★	0.110★	0.024	0.041		–0.061	–0.008	0.051★	0.016	0.247★	0.066★	0.022
PO	0.123	0.016	–0.046	–0.003	–0.076		–0.045	0.038	0.026	0.259★	0.046	–0.003
SQ	0.082	0.090★	–0.011	0.020	–0.010	–0.055		0.031	0.008	0.207★	0.021	0.010
SR	0.078	0.104★	0.076★	0.069★	0.064	0.048	0.038		0.029	0.150★	0.066	0.008
IC	0.044	0.024	0.023	–0.012	0.019	0.031	0.009	0.036		0.167	0.029	–0.012
LM	0.051	0.187★	0.304★	0.135★	0.303★	0.311★	0.254★	0.193★	0.206★		0.242★	0.226★
PA	0.183★	0.121★	0.034★	0.107★	0.082★	0.056	0.026	0.083★	0.035	0.296★		0.002
BM	0.117★	0.045	0.010	0.030	0.028	–0.004	0.013	0.010	–0.015	0.277★	0.003	

$p < 0.01$

TABLE 6

Results of three heirarchical AMOVAs for *Paralabrax nebulifer* based on microsatellite loci.

a) For samples collected between 1997-1999 and 2010-2013

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation	%
Among Regions		1	3.808	3.808	0.000	0%
Among Populations		14	54.929	3.923	0.030	1%
Among Individuals		331	885.280	2.675	0.199	8%
Within Individuals		347	790.000	2.277	2.277	91%
Total		693	1734.016		2.506	100%
Fixation index (F_{ST})	-0.001					

$p > 0.05$

b) For all sampling locations

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation	%
Among Populations		11	47.325	4.302	0.029	1%
Among Individuals		335	896.691	2.677	0.200	8%
Within Individuals		347	790.000	2.277	2.277	91%
Total		693	1734.016		2.505	100%
Fixation index (F_{ST})	0.012					

$p < 0.05$

c) Comparing locations north and south of the San Quintin upwelling zone.

Source of variation		d.f.	Sum of squares	Variance component	Percentage of variation	%
Among Regions		1	6.100	6.100	0.005	0%
Among Populations		10	41.226	4.123	0.026	1%
Among Individuals		335	896.691	2.677	0.200	8%
Within Individuals		347	790.000	2.277	2.277	91%
Total		693	1734.016		2.508	100%
Fixation index (F_{CT})	0.002					

$p < 0.05$

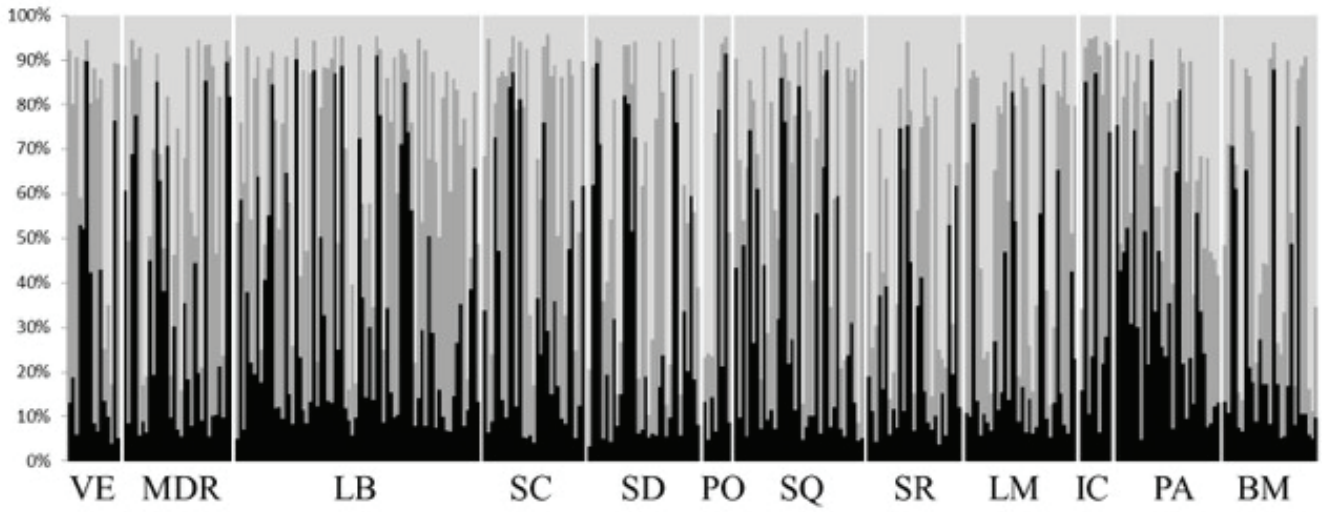

Figure 3. Structure diagram for *Paralabrax nebulifer* with K = 3.

differentiation for all sampling locations pooled together (F_{ST} = 0.012; p = 0.001) (table 6b). Testing specifically for the San Quintin upwelling zone as a genetic barrier showed that there, again, is weak but significant differentiation between sampling locations north and south of the upwelling zone (F_{CT} = 0.002; p = 0.011) (table 6c). The Evanno Method within STRUCTURE HARVESTER determined that three admixed genetic demes was the most probable value of K obtained from the STRUCTURE analysis (Mean LnP(K) = –8713.95; ΔK = 5.488) (fig. 3). However, standard errors associated with mean log likelihood values from the STRUCTURE analysis were highly variable and overlapping for all values of K indicating a failure of the STRUCTURE analysis to resolve the most probable value of K with any certainty.

DISCUSSION

This study found a high degree of genetic diversity for a single population of barred sand bass. While there was a weak but significant difference between sampling locations north and south of the San Quintin upwelling zone for both mitochondrial and nuclear markers, there is still a high degree of connectivity between the two regions. A single, panmictic population is further supported by the STRUCTURE results. While the Evanno method suggested a K of 3 as the most probable number of clusters, standard errors of the log likelihoods from the STRUCTURE analyses were highly variable and overlapped across all estimates of K. The Evanno method may not always determine the most likely K from a STRUCTURE analysis; instead, log likelihood values have been shown to provide reliable estimates of the number of clusters (Duncan et al. 2015). The STRUCTURE histogram generated from a K of 3 (fig. 3) is consistent with a large, single population with high migration as no clear clustering among individuals was observed.

The San Quintin upwelling zone is a seasonal upwelling event along the coast of the Baja California peninsula. This upwelling event occurs regularly in July coinciding with the peak in spawning for all three species of *Paralabrax* (Love et al. 1996; Hovey and Allen 2000; Allen et al. 1995). The San Quintin upwelling zone is also a known barrier to other summer spawning species with a pelagic larval stage such as opaleye, *Girella nigricans* (Terry et al. 2000), white seabass, *Atractoscion nobilis* (Michael P. Franklin pers. comm.), and purple sea urchins, *Strongylocentrotus purpuratus* (Olivares-Banuelos et al. 2008). However, the upwelling zone was not observed as a barrier for all fish along the California coast. Species with a pelagic larval stage that are not exclusively summer spawners like the California halibut, *Paralichthys californicus* (Craig et al. 2011), as well as those without a pelagic larval state such as the brown smoothhound (*Mustelus henlei*) (Chabot et al. 2015) and the round stingray (*Urobatis halleri*) (Plank et al. 2010), did not reveal the San Quintin upwelling zone as a genetic barrier. This suggests that possession of pelagic larvae alone does not predict movement patterns across all fish in this region. The timing of spawning is probably more important.

Seasonal upwelling zones are more effective barriers to larvae than to adults (Gaithier et al. 2009). Eggs of barred sand bass were shown to successfully hatch at a wide range of temperatures, but developed much slower at low temperatures and failed to develop or died at 12°C (Gadomski and Caddell 1996), the mean temperture in July off of San Quintin in July from 1950 to 1978 (Lynn et al. 1982). Furthermore, this was an area of consistently low abundance of serranid larvae in general from 1951 to 1984 (Moser et al 1993). Together these

findings imply that barred sand bass larvae are less likely to cross this barrier during the summer months when they are most abundant accounting for the weak, yet significant genetic structuring north and south of the barrier as found in this study. However, all three species of *Paralabrax* off California have a pelagic larval duration of approximately 21–37 days (Allen and Block 2012) and can be in the currents before and after this upwelling event. As a result, the limited larval transport before and after the establishment of the seasonal San Quintin upwelling zone could account for the high degree of gene flow and genetic diversity for barred sand bass. The California Countercurrent generates eddies within the Southern California Bight (Harms and Winant 1998) that has been shown to transport larvae along the coast of southern California and the Channel Islands (Shanks and Eckert 2005; White et al. 2010). Similar patterns of current flow have been shown along Baja California (Bograd and Lynn 2003; Di Lorenzo 2003). Shanks and Eckert (2005) suggested that larvae of nearshore fish species that are pelagic broadcast spawners off the coast of southern California and Baja California were transported widely via the currents and eddies along the eastern Pacific.

In addition to the larval mediated transport, at least some high genetic diversity and site connectivity in barred sand bass can also be attributed to adult migration patterns. Jarvis and colleagues (2010) found that barred sand bass show high spawning site fidelity however not all individuals return to the same spawning site every year and some visit multiple spawning sites in a single spawning season. This migration of just a few individuals per generation can keep the genetic diversity of a population stable (Ryman 1991).

Currently barred sand bass are part of a larger recreational fishery in southern California that includes the kelp and spotted sand bass. All three species are managed together with collective bag limits of 5 fish and a minimum size limit of 14 inches (CDFW). These regulations were increased in March 2013 in response to declining numbers of kelp and barred sand bass, however these regulations do not account for differences in genetic diversity or population structure between the three congeners. A comparison of the diversity of barred sand bass in this study to previous studies of the other two bass species shows that barred sand bass and kelp bass both exhibit high haplotype diversity in the mitochondrial control region (Phalen 1999) while the spotted sand bass shows the opposite (Salomon 2005). However, nucleotide diversity is low for barred sand bass and the spotted sand bass (Salomon 2005) and is high for the kelp bass (Phalen 1999). The differences in haplotype and nucleotide diversity reflect differences in the genetic diversity of the three congers.

Populations that have undergone historic reductions in the past are expected to demonstrate high mitochondrial haplotype diversity and low nucleotide diversity after a demographic expansion from a population of small effective size (Grant and Bowen 1998). Within barred sand bass, high haplotype diversity and low nucleotide diversity were observed in the present study (table 2). Furthermore, significantly negative Tajima's D and Fu's F_S values from the present study (table 2) would seem to support a rapid increase in population size at some point in the past. However, it is important to note that the haplotype network generated in the present study (fig. 2) does not reflect the starburst pattern that is rapidly expanding population. It is possible that the high haplotype diversity observed in barred sand bass in the present study may be a result of the highly mutable nature of this region in teleosts resulting in extreme variability. As a result, the high variability of barred sand bass control region sequences may be masking population structure in the species. Bradman and colleagues (2011) found that the control region in broadbill swordfish, *Xiphias gladius*, was unable to detect population structure on as fine a scale as the NADH dehydrogenase subunit 2 (ND2) region. Based on the limitations imposed by the high variability of the mtCR, this marker may not be the best choice of for detecting population structure in barred sand bass.

Differences in life histories among the congeners of *Paralabrax* appear to have resulted in these observed differences in population genetic structure and diversity. All three species are aggregate broadcast spawners (Allen et al. 1995; Baca-Hovey et al. 2002; Erisman and Allen 2006), however each species differs in where it spawns. Barred sand bass migrate to open soft bottom substrate off the coast (a few km) to spawn (Baca-Hovey et al. 2002) while kelp bass do not migrate large distances to spawn (Erisman and Allen 2006). Spotted sand bass are found within bays and spawn at the mouth of those bays (Hovey and Allen 2000; Allen et al. 1995) which can limit the dispersal of larvae (Levin 1983, 2006).

The barred sand bass is a heavily fished species in both southern California, USA (Erisman et al. 2011) and in Baja California, Mexico (Cota-Nieto et al. 2014; B. Erisman unpublished results). Understanding the life history of the species as well as its population structure is important in the management of both fisheries. Genetic diversity and population structure which informs management of populations and the degree of connectivity between those populations (Shaklee and Bentzen 1998; Airame et al. 2003; Pérez-Ruzafa et al. 2006; Palsbøll et al. 2007). The life history characteristics of barred sand bass have been well studied in southern California (Baca-Hovey et al. 2002; Jarvis et al. 2010; Mason and Lowe 2010) and are underway in Baja California,

Mexico (B. Erisman unpublished results). The results of the present study suggest that barred sand bass consist of one large, panmictic population. This suggests the need for a binational management plan for barred sand bass.

Currently the barred sand bass population exhibits very high genetic diversity (table 2). There is no evidence of a decline in genetic diversity over the last 13 years. Because barred sand bass can live up to 24 years (Love et al. 1996), the genetic consequences to the recreational fishery crash off California in 2004 may simply not have had enough time to manifest. Further sampling 20 or more years after the fishery decline in 2004 may be necessary to reflect any decline in genetic diversity. The present study does provide a baseline for the genetic diversity of barred sand bass that can then be used to monitor and detect any future declines in diversity.

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