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A Baseline Investigation into the Population Structure of White Seabass, *Atractoscion nobilis*, in California and Mexican Waters Using Microsatellite DNA Analysis

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Abstract.—The white seabass, *Atractoscion nobilis*, is a commercially important member of the Sciaenidae that has experienced historic exploitation by fisheries off the coast of southern California. For the present study, we sought to determine the levels of population connectivity among localities distributed throughout the species' range using nuclear microsatellite markers. Data from the present study have revealed distinct genetic breaks between the Southern California Bight, Pacific Baja California, and the Peninsula of Baja California.

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The white seabass, *Atractoscion nobilis*, is the largest species of croaker (Sciaenidae) occurring off the coast of southern California (Miller and Lea 1972) and has been highly prized historically by commercial and recreational fisheries. Declines in catches of white seabass have occurred historically to the point that population numbers had dropped to critically low levels (Pondella and Allen 2008). These declines have been followed by increases in commercial catches due to management strategies such as the prohibition of gill-nets along the southern California coast (Allen et al. 2007; Pondella and Allen 2008). Despite the economic importance of the white seabass and its history of over-exploitation and rebound, information on population structure life history has been limited.

What is known of the life history of the white seabass is that the species is a broadcast spawner, with males fertilizing eggs that females release into the water column. In regards to larval abundance, larvae are generally observed most frequently south of the Southern California Bight (SCB) (the faunal region of ocean extending from mid Baja California northward to Point Conception, CA) in the areas around Sebastian Viscaino and San Juanico bays off the coast of Baja California. (Moser et al. 1983). Donohoe (1990) and Franklin (1991) studied the abundance, distribution, age and growth, and food habits of young seabass from different regions of the SCB (the mainland coast between Point Conception to the Mexico border, and along the coastlines of four of the Channel Islands) and determined that the portion of the species' range that occurs within the SCB may be the northern extreme of the area where spawning can occur. It also appears that this portion of the SCB may support lower than expected successful settlement of seabass larvae. Allen and Franklin (1992) examined the settlement success of young seabass in this region and determined that recruitment success depends on larval availability as opposed to environmental factors (e.g., bottom water temperature, pH, lunar periodicity, etc.). In recent years, valuable information on spawning activity, sound production, and adult movements have been the subject of numerous studies (Aalbers 2008; Aalbers and Drawbridge 2008; Aalbers and Sepulveda 2012, 2015).

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The white seabass is distributed throughout the northeastern Pacific from Alaska to the tip of the Baja California peninsula and into the Gulf of California (Miller and Lea 1972; Eschmeyer et al. 1993). Numerous biogeographic and phylogeographic barriers have been described within the distribution of the white seabass (Rawson et al. 1999; Stepien et al. 2000; Dawson 2001; Dawson et al. 2001; Jacobs et al. 2004; Dawson et al. 2006; Robertson and Cramer 2009) with the most prominent being the San Quintín upwelling zone (Selkoe et al. 2007; Paterson et al. 2015) and the Peninsula of Baja California (Bernardi et al. 2003). As data indicate that the northernmost range of the white seabass along the Pacific coast of North America may be within the SCB and that the majority of breeding and recruitment within this region occurs off of the coast of Pacific Baja California, population substructure may exist within this species due to the effect of these barriers on population connectivity resulting in different stocks that may need to be managed separately. Recently, Romo-Curiel et al. (2016) used otolith isotope analyses to investigate the existence of distinct subpopulations of white seabass along the California and Pacific Baja California coastlines. Two distinct subpopulations of white seabass were observed and these authors suggested that the likely break occurs in the vicinity of Punta Eugenia (Romo-Curiel et al. 2016). Based on the distribution of the white seabass spanning several biogeographic barriers and the observation of two putative subpopulations by Romo-Curiel et al. (2016), the objective of this project was to use nuclear microsatellite loci, genetic markers with relatively high mutation rates and a bi-parental mode of transmission that makes them ideal for testing gene flow among populations (Avise 2004; Wang 2010), to establish a baseline estimate of the population connectivity within and among white seabass localities from throughout the range of this economically important species.

Materials and Methods

Tissue samples of white seabass (gill filaments or fin clips) were obtained by gillnets, spear, and hook-and-line from the three putative regions spanning the distribution of the species within the northeastern Pacific: two groups of localities within Southern California (SC) north of the San Quintín upwelling zone including the California Channel Islands (Anacapa Island, Santa Cruz Island, Santa Rosa Island, Santa Barbara Island, Santa Catalina Island, and San Clemente Island; n = 69) and along the California mainland coast (Santa Barbara, Ventura, Hermosa Beach, Long Beach, Newport Bay, and Mission Bay; n = 57), along the mainland coast south of the San Quintín upwelling zone (Pacific Baja California; n = 16), and within the northern Gulf of California (GC) (San Felipe, Baja California and the Midriff Islands; n = 17) (Fig. 1) between the summers of 1990 and 1993. All samples were preserved in NET* (2.5 M NaCl, 0.25 M EDTA, 0.25 M Tris base, pH 8.5) and placed on wet ice in the field followed by long-term storage at $-20°C$ at the California State University, Northridge.

Nuclear DNA was isolated by phenol-chloroform-isoamyl alcohol extraction followed by cold ethanol/ammonium acetate precipitation (Sambrook et al. 1989). Five species-specific microsatellite loci, ATRNOB-D, ATRNOB-E, ATRNOB-F, ATRNOB-K, and ATRNOB-R (Appendix 1), were used to genotype white seabass individuals following the protocols of Franklin (1997). Departures from Hardy-Weinberg Equilibrium (HWE), observed heterozygosity (H_O), and expected heterozygosity (H_E) were estimated for each sample locality in GENE-POP 4.0 (Raymond and Rousset 1995; Rousset 2008). Linkage disequilibrium (LD) was tested in FSTAT 2.9.3.2 (Goudet 2003). FSTAT was also used to determine the total number of alleles and to estimate average allelic richness (A_R). STRUCTURE 2.3.3 (Pritchard et al. 2000; Falush et al. 2003; Falush et al. 2007) was used to assign individuals to putative clusters/subpopulations (K) of white seabass that minimize linkage disequilibrium and deviations from Hardy Weinberg equilibrium. Number of subpopulations was estimated with
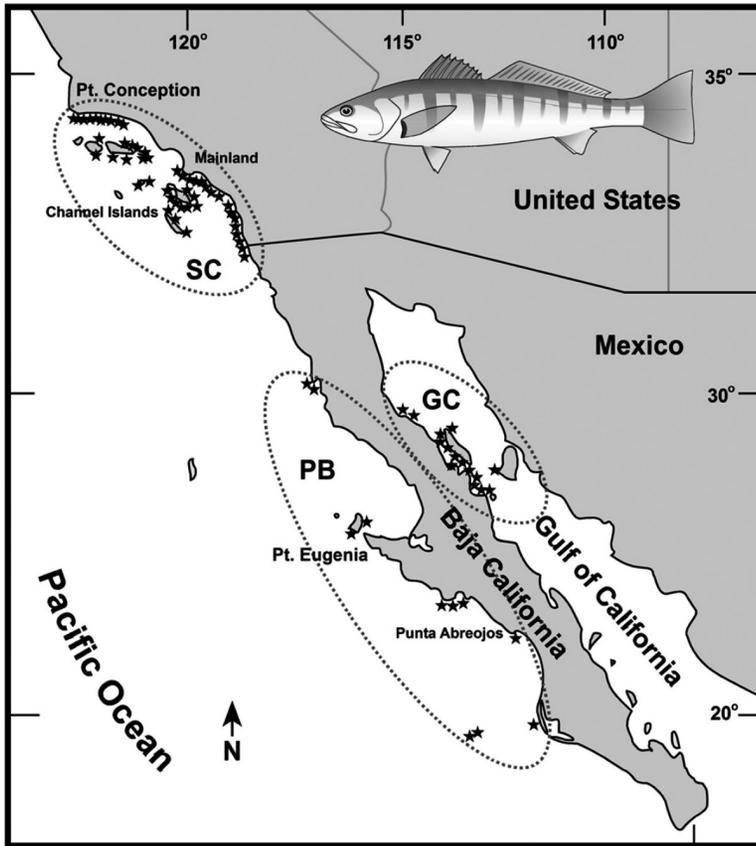
Fig. 1. Locations where genetic samples of *Atractoscion nobilis* were obtained within the three general regions (Southern California – SC; Pacific Baja California – PB; and Gulf of California – GC) of the Northeast Pacific Ocean.

20 independent runs of $K = 1$-10 with each run consisting of 10^6 MCMC repetitions and a burn-in of 10^5 steps under the admixture model with correlated allele frequencies. The optimal number of subpopulations was estimated using ΔK of Evanno et al. (2005) as implemented in STRUCTURE HARVESTER (Earl and vonHoldt 2012). Similarity among STRUCTURE replicates was assessed using CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) utilizing the greedy algorithm.

Global population structure was estimated by Analysis of Molecular Variance (AMOVA) (Excoffier et al. 1992) as implemented in GENALEX 6.501 (Peakall and Smouse 2006). To determine the effect of the San Quintín upwelling zone and the Peninsula of Baja California in restricting population connectivity, a hierarchical AMOVA based on three regions corresponding to areas adjacent to either side of these potential barriers (Mainland/Channel Islands — Pacific Baja California — Gulf of California) was performed in GENALEX. Pairwise population estimates of F_{ST} were generated for all pairs of sample localities in GENALEX. F_{ST} is commonly used to assess population subdivision, however, due to the high mutation rate of microsatellites resulting in elevated heterozygosities, F_{ST} may underestimate population subdivision (Rousset 1996). Therefore, Hedrick's G''_{ST} (Hedrick 2005; Meirmans and Hedrick 2011) and Jost's D (Jost 2008) were estimated in GENALEX. Both estimators produce values between

Table 1. Summary microsatellite statistics for *Atractoscion nobilis*. *N*, number of individuals, H_O avg. observed heterozygosity; H_E avg. expected heterozygosity; *A*, number of alleles; A_R, avg. allelic richness; *PA*, private alleles.

Locality	N	H_O	H_E	A	A_R	PA
Overall	159	0.719	0.733	69	-	-
Mainland	57	0.686	0.738	58	7.12	3
Channel Islands	69	0.739	0.743	65	7.39	5
Pacific Baja	16	0.713	0.582	18	3.43	3
Gulf of California	17	0.882	0.636	27	4.97	14

0 and 1 with 0 indicating complete panmixia and 1 being indicative of a lack of migration. All estimates of divergence were tested non-parametrically (9,999 bootstrapped replicates) and significance was tested via permutation and corrected for multiple testing by the sequential Bonferroni correction. Statistical power of the microsatellite loci used in the present study to detect genetic divergence and to reject the null hypothesis of panmixia among sampled white seabass localities was determined by power simulations conducted in POWSIM 4.1 (Ryman & Palm 2006). Settings for simulations were a minimum F_{ST} of 0.05, a value indicated by Balloux and Lugon-Moulin (2002) to be the upper threshold of weak divergence for microsatellite loci, 500 replicates, and sample sizes from populations after the simulated drift process equal to those of the present study.

Results

White seabass loci were all in Hardy-Weinberg equilibrium for each sample locality and did not demonstrate any evidence of linkage disequilibrium. All loci were polymorphic for all localities with the number of alleles ranging between 18 and 65 (69 overall) (Table 1), observed and expected heterozygosities ranged between 0.686-0.882 (0.719 overall) and 0.582-0.743 (0.733 overall) (Table 1), respectively. When taking into account sample size, allelic richness ranged between 3.43-7.39 (Table 1) with Pacific Baja California demonstrating the lowest allelic richness and Channel Islands the highest. Private alleles were observed in all localities with the Gulf of California possessing the greatest number (Table 1).

Based on results from both the log-likelihood and Evanno methods, a *K* of two had the greatest posterior support from the STRUCTURE analysis and a break was evident at Pacific Baja California between the Southern California (Mainland/Channel Islands) and the Gulf of California (Fig. 2). Significant genetic divergence was observed globally among all four localities (Table 2; $F_{ST} = 0.04$, $p < 0.005$). Results of the hierarchical AMOVA also revealed significant divergence between Mainland/Channel Islands — Pacific Baja California — Gulf of California (Table 3; $F_{CT} = 0.09$, $p < 0.0001$). Similarly, pairwise estimates of divergence also demonstrated two significant disjunctions in population connectivity corresponding to the breaks recovered by the hierarchical AMOVA (Table 4).

Discussion

Data from the present study of the white seabass demonstrate subpopulation structuring indicating three main sub-groups/populations within the northeastern Pacific: one in the north including the Southern California Bight, another in the south including Pacific Baja, and the last subgroup consisting of the members from the Gulf of California. This pattern of diversity has been supported by the STRUCTURE analysis (Fig. 1) and divergence estimates based on allele frequencies (Table 2) and pairwise comparisons of sample localities (Table 3). A note on the STRUCTURE analysis, although STRUCTURE is generally used to assign individuals to
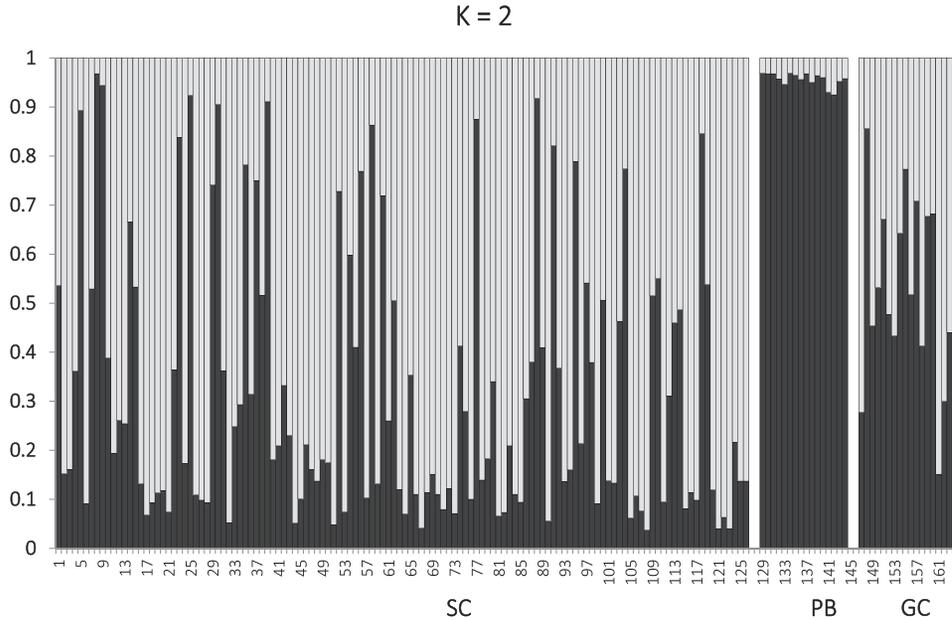
Fig. 2. STRUCTURE analysis of *Atractoscion nobilis*. Localities (Mainland (MD), Channel Islands (CI), Pacific Baja California (PB), and Gulf of California (GC)) are separated by whitespace from left to right. Overall analysis of allelic frequencies suggested that a strong break exists at Pacific Baja California separating Southern California (MD, CI, and EN) from Pacific Baja (PB), and the Gulf of California (GC).

subpopulations and to therefore infer population subdivision indirectly from these assignments, the methodology implemented in STRUCTURE has been demonstrated to have difficulties in assigning individuals when sample sizes are unequal (Kalinowski 2011) or when F_{ST} values are low (0.02-0.03 with 97% accuracy being attained at 0.05 or greater) (Latch et al. 2006). As sample sizes within the present study are skewed towards the Southern California Bight and pairwise estimates of divergence between the Gulf of California and the Mainland and Channel Islands are < 0.04 STRUCTURE may not have been capable of assigning Gulf of California individuals effectively or detecting the substructure that was identified by analyzing variances in allele frequencies (Tables 3 and 4). Based on this, the following discussion places greater weight on variance in allele frequencies than the results presented by STRUCTURE.

Hydrologic and zoogeographic data suggests that the Southern California Bight represents a faunal zone between Magdalena Bay, Baja California, to the south, and Point Conception to the

Table 2. F_{ST} values for *Atractoscion nobilis* from all four localities.

		F-Statistics		
Source of variation	d.f.	Sum of squares	Variance components	% variation
Among localities	3	20.877	0.076	4.33
Among individuals	155	250.953	−0.065	−3.68
Within individuals	159	278.000	1.748	99.35
Total	317	549.830	1.760	100
Fixation index (F_{ST})	0.04*			
$P = 0.005$				

Significant *P* values after Bonferonni correction indicated by *.

Table 3. F_{ST} values for *Atractoscion nobilis* from three major regions (Southern California, Pacific Baja California, and Gulf of California).

F-Statistics				
Source of variation	d.f.	Sum of squares	Variance components	% variation
Among groups	2	20.385	0.161	8.76
Among populations within groups	1	0.492	−0.009	−0.49
Among individuals within populations	155	250.953	−0.065	−3.52
Within individuals	159	278	1.748	95.25
Total	317	549.83	1.835	
Fixation index (F_{ST})	0.09*			
P = 0.0001				

Significant *P* values after Bonferonni correction indicated by *.

north (Briggs 1974). The white seabass population affinities implied by microsatellite DNA analysis generally reflect the degree of intermingling expected from the prevailing hydrographic patterns along the California and Baja coastline. Oceanic patterns within the Southern California Bight from April to October (Lynn et al. 1982) as determined by dynamic heights, feature a general southerly flow at the surface (California Current). Originating in the subarctic Pacific, the California Current moves cold water towards the equator at maximum velocities of about 10 cm s^{-1}, leaving the mainland at Pt. Conception in the spring and flowing outside the Santa Rosa-Cortez Ridge. Thus the current diverges near the US/Mexico border, splitting into the Southern California Countercurrent (strengthened by the underlying Rodriguez current) that flows east and then north to border the mainland coastline and run the length of the Southern California Bight, and a southerly branch, that parallels the Baja coastline. By July to October, the California Countercurrent forms a large eddy (Southern California Eddy) virtually enclosing the Southern California Bight with the San Diego region at its southwestern border. Geostrophic flow in the eddy is less than 5 cm s^{-1}. Drift bottle studies (for example see Schwartlose and Reid 1972) reveal smaller eddies within the Southern California Eddy (that cannot be detected by geostrophic flow analysis): especially, a counterclockwise flow between Catalina Island and the mainland, and a clockwise flow between San Clemente Island and Catalina Island. These eddies increase the retention time and mixing of waters within the Southern California Bight. The divergence of the Southern California Countercurrent creates upwelling north of and including Bahia San Quintín. Water flows up from below the thermocline and away from the coast to create a nearshore lens of cold water south of the divergence. The water mass introduced into the SCB at this point is primarily cold water, and is devoid of larvae from many coastal fishes that occur as breeding adults in the waters about the nearby islands of the Southern California Bight (for example, see Moser et al. 1993). After leaving

Table 4. Pairwise F_{ST}, G''_{ST}, and Jost's D values for *Atractoscion nobilis* for the four localities. F_{ST}/G''_{ST} values are presented below the diagonal and Jost's D values above.

	Mainland	Channel Islands	Pacific Baja	Gulf of California
Mainland	—	−0.009	0.216*	0.122*
Channel Islands	0.003/−0.012	—	0.263*	0.105*
Pacific Baja	0.062*/0.294*	0.071*/0.350*	—	0.373*
Gulf of California	0.038*/0.170*	0.033*/0.148*	0.126*/0.501*	—

* indicates significant *P* values after Bonferroni correction ($P \leq 0.001$).

the Southern California Bight, the California current flows around the upwelling at Bahia San Quintin to encroach on Punta Eugenia. Because of the current flows, larval white seabass in this region most likely do not move into the waters of the Southern California Bight to mix with local stocks. Although currents may influence the distribution of species that utilize pelagic larval dispersal such as the white seabass, the region around San Quintin and Punta Eugenia has also been implicated as a barrier to gene flow for species lacking a pelagic larval stage, such as the black surfperch, *Embiotica jacksoni* (Bernardi 2000), and demonstrates the impact of the region on population connectivity among various lineages with differing dispersal strategies.

In addition to directional flow, the coastal upwelling and the subarctic origin of the California Current pose potential thermal barriers to larval fish. Upwelling around Bahia San Quintin in Mexico drops the water temperature in the area by as much as 8° C (11.0 vs. 19.0° C) in July (Alvarez-Borrego and Alvarez-Borrego 1982). The extent and annual duration of this temperature discontinuity is sufficient to significantly alter the ichthyofaunal assemblage of this region and has been indicated as a potential barrier to gene flow in the kelp bass, *Paralabrax clathratus* (Selkoe et al. 2007)*, the barred sand bass, *P. nebulifer* (Paterson et al. 2015), the spotted sand bass, *P. maculatofasciatus* (Chris L. Chabot pers. obs.), and the present study. While it seems that adult white seabass prefer cooler water temperature of 13-16° C (Aalbers and Sepulveda 2015), the temperatures that young-of-the-year (YOY) seabass encounter in areas of upwelling and in the California Current may restrict successful settlement. We found a positive correlation between YOY seabass occurrence, warm bottom temperature, and CPUE (Allen and Franklin 1988; Franklin 1991; Allen and Franklin 1992). Highest CPUE coincided with seasonally high temperature peaks for the three-year study and elevated bottom temperatures may be an important settlement cue for these fish as the number of larval seabass may be the most important factor that determines the success of settlement success. Although adult white seabass are capable of traveling great distances (up to 555 km) from the Southern California Bight north to central California (Aalbers and Sepulveda 2015), evidence that adults migrate between southern California and central Baja California is lacking at this time.

The divergence of the Gulf of California population of white seabass is consistent with the presence of a barrier to population connectivity originating somewhere in the vicinity of the Peninsula of Baja California. This warm-water region has been implicated in the divergence of several lineages with distributions on both sides of the Peninsula (Walker 1960; Stepien et al. 2000; Bernardi et al. 2003; Sandoval-Castillo et al. 2004; Bernardi 2014). As adult white seabass tend to prefer cooler waters, the warm tropical waters associated with the tip of the Peninsula are likely severing population connectivity between Pacific and Gulf populations resulting in the significant level of divergence observed in the present study.

Based on the results of the present study, three genetically distinct populations of white seabass have been observed within the northeastern Pacific. In support of this, recent ontogenetic comparisons of growth rates and otolith isotope analyses between Southern California Bight and southern Baja California white seabass populations have revealed significant differences between the two regions (Romo-Curiel et al. 2015; Romo-Curiel et al. 2016). As these populations demonstrate a lack of contemporary connectivity and are likely evolving independently, efforts to bilaterally manage US-Mexican white seabass fisheries should recognize the independent evolutionary trajectories of each population and manage them accordingly. Due to the isolated nature of these populations and their history of exploitation, any continued reduction in numbers will likely result in the loss of unique, possibly adaptive, genetic diversity and will place the species at risk in terms of future adaptive potential.

Acknowledgements

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Appendix 1.   Microsatellite primers and repeat motifs for *Atractoscion nobilis.*

Locus	Repeat	Forward	Reverse
ATRNOB-D	CA_{30}	5′- ACT CAG CGT CTT TGT TTC TCA C -3′	5′- TGG TCC GTT TGT GTT CAG A -3′
ATRNOB-E	AAT_{19}	5′-CCA CGA AAA CAG AGC ATC AG -3′	5′- CCC AAA ACT ACA ACA AGC CA -3′
ATRNOB-F	TAA_{15}	5′-GAA TGG TGC CTG ATT TCT T -3′	5′- AGG GGA TTG TGA GGG AAT -3′
ATRNOB-K	GAG_{9}	5′- TCT TCC CTC CTG ACC TG -3′	5′-ATG CTT GAA TGT GAT TGA A -3′
ATRNOB-R	TTA_{11}	5′- CCT CAA ACA GTT CTC TCG TC -3′	5′- TCT TCA GAT AAA AGC AGG TAG -3′