Comparative phylogeography of a bathymetrically segregated pair of sister taxa of rockfishes (genus Sebastes): black rockfish, Sebastes melanops, and yellowtail rockfish, Sebastes flavidus

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Research Article

Keywords:

Posted Date: November 17th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-2203540/v1

Abstract

Twelve pairs of sister taxa in the speciose rockfish genus, *Sebastes*, overlap coastal distributions but are bathymetrically segregated. These pairs are ideal for comparative studies to understand how life-history traits, historical events, and environment interact to produce population genetic structure. Black rockfish, *Sebastes melanops*, forms one such pair. Its sister species, yellowtail rockfish (*Sebastes flavidus*), shows a genetic cline likely influenced by a dispersal barrier at Cape Mendocino, CA and northward range expansion. Due to geographic overlap and close systematic relationship, we predicted black rockfish was influenced by similar evolutionary processes and thus would show genetic pattern concordance with yellowtail rockfish. We analyzed ~ 1000 black rockfish from 22 sites spanning the species' range to test the null hypothesis of no structure, using the same markers that characterized yellowtail rockfish (i.e., 812 bp of the mitochondrial cytochrome b gene and six microsatellite loci). We reject the null hypothesis based on existence of at least three populations and microsatellite genetic divergence that separates the Alaskan and Continental U.S. populations (F_{CT}=0.021, p < < 0.001), and a mitochondrial genetic cline near Cape Mendocino (F_{CT}= 0.132, p < 0.01). We also found single collections genetically divergent from neighboring collections. Like yellowtail rockfish, oceanographic dispersal barriers and northern range expansion were inferred to influence black rockfish, however, unlike yellowtail rockfish, Cape Mendocino did not split the range into two stocks and was therefore inferred to be a less severe barrier. We hypothesize a higher frequency of extinction/recolonization events in black rockfish populations may have led to more complex genetic structure.

Introduction

Phylogeographic breaks have been observed across biogeographic breaks in both terrestrial and marine environments. In marine environments, the causes for these phylogeographic breaks have been linked to oceanographic currents and other factors that can limit exchange of migrants such as availability of suitable habitats. Although some species show concordant phylogeographic patterns (Goldstien et al. 2006, Martins et al. 2022), there can be discordant genetic structure across closely related taxa (e.g., DiBattista et al. 2012). The reasons for this variance are challenging to explain but are likely due to multiple processes that influence population structure including dispersal abilities (e.g., non-planktonic dispersers tend to share concordant phylogeographic breaks, Pelc et al. 2009). Studies have shown correlation of degrees of population structure with variation in life history characteristics (shallower depth preferences of adults leading to higher levels of population structure, Hickey et al. 2009). A population genetic study of a taxonomic group harboring high diversity of life history characteristics, such as the Pacific rockfishes (genus *Sebastes*) would be ideal to advance our understanding of how evolutionary processes interact with life history to produce population structure.

The rockfishes are the most species-rich and ecologically diverse group of marine fishes inhabiting the temperate rocky reefs of the west coast of North America (Love et al. 2002; Gunderson and Vetter 2006). Most species occupy discrete rocky habitats separated by soft sediments, thus fitting the definition of marine metapopulations (Hanski and Gilpin 1997; Gunderson and Vetter 2006; Kritzer and Sale 2006).

They are live-bearers with generally low adult movement and high site fidelity. They instead depend on pelagic dispersal of larvae and juveniles as a primary means of colonization and population connectivity (Love et al. 2002; Starr et al. 2002; Parker et al. 2007).

The subgenus *Sebastosomus*, as genetically redefined by Hyde and Vetter (2007), contains five species that form schools or aggregations associated with high-relief habitats. This assemblage is sometimes referred to as the “structure schooling ecological group” (Lenarz et al. 1995). In addition to the adult schooling behavior, the five species share pelagic larval and juvenile characteristics and inter-annual recruitment success tends to co-vary with oceanographic conditions such as the Pacific Decadal Oscillation (PDO) and El Nino-La Nina events (Lenarz et al. 1995). The subgenus contains two divergent evolutionary lineages. The first includes the shallow-dwelling pair of incipient species blue rockfish (*Sebastes mystinus*, (Burford and Bernardi 2008) and deacon rockfish (*S. diaconus*, Frable et al. 2015), and the deeper living widow rockfish (*S. entomelas*). The second lineage contains olive rockfish (*S. serranoides*), black rockfish (*S. melanops*), and yellowtail rockfish (*S. flavidus*). Of the three species, black and yellowtail rockfishes are most closely related (Hyde and Vetter 2007; Hess et al. 2011) but differ ecologically in bathymetric distribution. As adults, black rockfish remain in near-shore rocky habitats, whereas yellowtail rockfish migrate to deeper waters and are most common over rocky reefs at depths from 90–180 m (Love et al. 2002). Both species are highly resident as adults (Stanley et al. 1994; Lea et al. 1999; Parker et al. 2007), in fact the average home range size of black rockfish was recently estimated to be 55 ± 9 ha (Parker et al. 2007). Black and yellowtail rockfishes share a broadly overlapping latitudinal range from northern Baja California, Mexico to southeastern Alaska but black rockfish continue west to the tip of the Aleutian Archipelago. Both species have peak parturition of larvae in winter (Moser 1996), co-occur as pelagic juveniles for three to four months (Love et al. 2002), and share settlement timing and macro- and micro settlement habitat preferences for the kelp canopy and for artificial settlement collectors (Ammann 2004).

Studies on the phylogenetic relationships within the genus (Rocha-Olivares et al. 1999; Hyde and Vetter 2007) provide an evolutionary context for examining the processes of dispersal, gene-flow, and speciation by a comparative genetic approach that examines closely related sister taxa within a subgenus. Examining species that share a common lineage and most but not all key life history characteristics can provide insights into the role of bathymetry, oceanography, and climate in determining dispersal patterns, gene-flow, population structure, and speciation. Although some rockfish sister taxa appear to show expected allopatric signals of speciation (e.g., north and south species on either side of a biogeographic boundary), it is a recurrent theme among *Sebastes* that many sister taxa overlap across their latitudinal distributions but are bathymetrically segregated into a shallow and deep living species pair. Even more interesting, these species pairs often share a similar time of parturition, a similar pelagic phase, followed by shared juvenile settlement preference for near-shore rocky reef habitat, but subsequent bathymetric segregation of the adults as one species migrates to deeper water while the other remains a lifetime resident in shallow water. At least twelve bathymetrically segregating sister taxa have been identified within the genus *Sebastes* (table 5, Hyde et al. 2008b). The study of bathymetrically segregating sister

taxa may provide comparative insights into life-stage specific dispersal and gene-flow, as well as the role of bathymetry in the speciation process (Hyde et al. 2008b).

Our goal was to compare the population genetic structure of black rockfish (*Sebastes melanops*) to the published population genetic dataset of its bathymetrically segregating sister species, *Sebastes flavidus* (Hess et al. 2011). Specifically, we tested whether black rockfish exhibited the following two main patterns found in the yellowtail rockfish study, 1) a genetic barrier to dispersal at Cape Mendocino, CA and 2) northern range expansion. We expect this concordance due to the close phylogenetic relationship, overlapping geographic distributions, and similar life-histories that result in similar evolutionary processes such as physical barriers to dispersal and climate fluctuations. However, these species have different depth distributions where adult black rockfish are found in shallower waters relative to yellowtail rockfish. Past studies hypothesized that the different depth distributions may result in greater population structure of the shallower dwelling species (Hickey et al. 2009, Von der Heyden et al. 2013). Thus, we expect higher levels of population structure and steeper isolation-by-distance gradients in the shallower-dwelling black rockfish compared to the deeper-dwelling yellowtail rockfish.

Although there have been multiple population genetic studies conducted on black rockfish showing significant genetic differences among collections (e.g., Miller et al. 2005, Seeb and Seeb 2005, Lotterhos et al. 2015), the genetic markers and geographic study areas were not ideal for comparing results with the yellowtail rockfish study (Hess et al. 2011). Differences in study designs make it difficult to conclude whether population genetic structure characterized by these black rockfish studies are due to marker mutation rates, unique geography, demographic fluctuations between different time periods, or variance due to sample size. Here, we used the same DNA markers, six nuclear microsatellite loci and mitochondrial cytochrome b, from the yellowtail rockfish study to characterize population structure of black rockfish. These two marker types are informative because they address different temporal scales of genetic structure; microsatellites represent contemporary time scales versus the ancient events resolved by mitochondrial DNA. By comparing our black rockfish study to a previous study on its sister taxa yellowtail rockfish (Hess et al. 2011) using similar markers, spatial scales of sampling, and sampling time frames; we have the ideal set of conditions to examine how shared environment affects species in similar ways and whether bathymetric preferences shape population structure in predictable ways.

Materials And Methods

Sampling

The tissue samples used for DNA extraction were muscle and fin clips stored in 95% ethanol. All collections were sampled during the 2005 fishing season (June-September) using the catches from various recreational charter boats. Collections from Alaska were obtained by ADFG through coordination with their port sampling program (Fig. 1, Table 1). DNA was extracted using DNeasy 96 Tissue Kits with a high throughput liquid-handling BioRobot 8000 (QIAGEN). Samples from each port were pooled into collections and GPS coordinates were calculated by averaging the coordinates of the individuals.

Molecular methods and data quality

Polymerase chain reaction (PCR) amplification was used to amplify an 833 bp region that includes the first 812 bp of the cytochrome b mitochondrial region using the primers described in Hess et al (2011). PCR conditions and extraction procedure are the same as in Hess et al (2011). Six microsatellite loci were genotyped using the methods of Hess et al. (2011).

The genotypic data was organized in MICROSOFT EXCEL and formatted for various population genetic statistical programs using the EXCEL MICROSATELLITE TOOLKIT version 3.1 (Park 2001). MICROCHECKER 2.2.3 (Van Oosterhout et al. 2004) was used to examine all collections and loci for microsatellite null alleles and scoring errors due to stuttering and large allele dropout. Estimates of F_{IS} were calculated according to Weir and Cockerham (1984). All collections were tested for deviations of Hardy-Weinberg equilibrium and all loci were tested for linkage disequilibrium using GENEPOP version 3.4 on the web (1000 dememorizations, 2000 batches, 1000 iterations per batch; (Raymond and Rousset 1995)). Fisher's method was used to combine probabilities across all loci for each collection and probabilities across all collections for each locus.

Putative genetic barriers to dispersal

We performed a principal component analysis (PCA) on the microsatellite allele-frequency data with the program PCAGEN 1.2.1 (Goudet 1999), for heuristic identification of major genetic differentiation among collections (i.e., genetic discontinuity along the linear coastal distribution of collections). A multidimensional scaling (MDS) method was performed on the mtDNA pairwise F_{ST} matrix using the software package SPSS 11.0.2 (SPSS for MAC OSX, 2003).

STRUCTURE v. 2.3.2 (Pritchard et al. 2000) was used to determine how many populations might be represented among our collections. An initial burn-in of 50 000 iterations followed by 500 000 iterations of the Markov Chain Monte-Carlo method was used to generate posterior probabilities. We used the feature in STRUCTURE that takes into account spatial information (i.e., from which collection an individual was sampled) to modify the prior distribution for each individual's population assignment to increase the ability to detect structure at low levels of divergence (Hubisz et al. 2009). We ran 10 iterations of K values, 1 through 9, and averaged the estimated log-likelihoods [ln(PrK)] to determine the most likely value of K. We calculated DK using the method described by Evanno et al. (2005). After selection of $K = 2$, 40 iterations were run and the 10 iterations with the highest ln(PrK) were averaged using the *FullSearch* algorithm in CLUMPP (Jakobsson and Rosenberg 2007), which finds the best configuration of those 10 iterations by optimizing pairwise similarity (H).

FSTAT 2.9.3.2 (Goudet 2001) and ARLEQUIN 3.1 (Excoffier et al. 2006) were used to measure F-statistics for the genotype and sequence data respectively. Where the heuristic methods above detected a regional genetic discontinuity, we divided collections into regions separated by the center of the genetic cline and contrasted the regions using an analysis of molecular variance (AMOVA, Excoffier et al. 1992), a feature

in ARLEQUIN 3.1 (Excoffier et al. 2006). ARLEQUIN 3.1 was used to estimate gene-diversity, nucleotide diversity, and Tajima's D.

F_{ST} was calculated for all pairwise comparisons of collections. Isolation-by-distance regressions were examined at the following three spatial scales: 1) range-wide, 2) regional (dividing the ranges at points where a genetic discontinuity is centered), and 3) a four-collection sliding window across adjacent collections. Collections were considered linear and geographical distances were calculated along the coastline rather than as the crow flies. Only collections with a sample size of ten or greater individuals were used to test for isolation by distance by regressing pairwise F_{ST} comparisons with pairwise geographic distance. The "four-collection sliding window" was used to examine how isolation-by-distance changes across the range. For this approach, we started by calculating an isolation-by-distance regression with the first four southernmost collections. Each subsequent isolation-by-distance regression required shifting the window by one collection to the north, while excluding the southernmost collection to maintain a grouping of four neighboring collections for the new isolation-by-distance regression. The regional IBD tests were useful to understand whether an isolated regional break may be confounding a true signal of IBD gene flow. To remove these potentially confounding effects from our IBD signal, we tested IBD separately for the collections located on either side of the center of genetic breaks.

PASSAGE 1.0 (Rosenberg 2001) was used to perform a series of basic mantel and partial mantel tests for comparing the correlation coefficients of a model of isolation-by-distance gene-flow versus a model of fragmentation. Two basic mantel tests and two partial mantel tests were performed for each species. The basic mantels compared a matrix of genetic distance $F_{ST}/(1-F_{ST})$ (Rousset 1997) to either a matrix of pairwise geographical distances (used to assess the overall fit of an isolation-by-distance pattern) or a matrix of ones and zeros used to categorize collections on the same side or opposite sides of the center of a genetic cline (used to assess the overall fit of a genetic regional break). The partial mantels compared the matrix of genetic distance with one of the other two matrices while holding the remaining matrix constant. Significance for these mantel tests was tested using 9,999 permutations.

Range expansion and other demographic patterns

BOTTLENECK 1.2.02 (Cornuet and Luikart 1996) was used to test all collections for recent effective population size reduction or expansion. Three mutation models are available in this program: infinite allele model (I.A.M.), stepwise mutation model (S.M.M.), and two-phased model of mutation (T.P.M). The first two are considered the extremes over the range of models. FSTAT version 2.9.3.2 was used to calculate allelic richness, gene-diversity (Hs), and pairwise F_{ST}. P-values for population differentiation were calculated by permutation.

Effective population size based on linkage disequilibrium at all six microsatellite markers was calculated with LDNE which uses Burrows method to calculate , a measure of linkage disequilibrium (see Waples and Do in review, (Waples 2006)). LDNE was run using the three default p critical values 0.05, 0.02, and 0.01 and with confidence intervals using parametric and jackknifing over loci methods.

Nested Clade Phylogeographical Analysis (NCPA) is a type of population genetic approach that separates historical patterns from contemporary gene flow. NCPA makes use of the geographic distribution and genealogy of haplotypes to make inferences concerning the role of recurrent gene flow and historical phenomena such as fragmentation events and range expansions in shaping genetic structure (Templeton et al. 1995). The NCPA does not require a prior phylogeographic model but instead relies on statistically significant inferences that are built up from the data. This feature allows this method to reveal phylogeographic events that otherwise may not have been anticipated. Past criticisms of this method (Knowles and Maddison 2002; Panchal and Beaumont 2010) have been flawed and corrections of the misrepresentations showed the type I and type II errors of NCPA to be extremely low (Templeton 2009, 2015, Allen et al. 2021). In this study, the application of NCPA is ideal because it allows us to directly compare results across the black rockfish and yellowtail rockfish (Hess et al. 2011) studies using the same markers and methodology.

In the first step of the NCPA, haplotype trees were estimated using statistical parsimony (Templeton et al. 1992) using the program TCS v. 1.21(Clement et al. 2000). The haplotype trees were used to define a series of hierarchically nested clades following the nesting rules given in Templeton et al. (1987)and Templeton and Sing (1993). The program GeoDis v. 2.4 (Posada 2000) was used to calculate the various NCPA measures and test the null hypothesis of no association of a haplotype in a cladogram with geographical position. The results were interpreted using the GeoDis inference key (updated November 11th, 2005) on the website, http://darwin.uvigo.es/.

NCPA was applied using the parsimonious rooting of haplotypes based on their proximity to the network of the outgroup species (yellowtail rockfish) and using their outgroup probabilities performed by the method described by Castelloe and Templeton (1994). Outgroup probabilities offer a reliable alternative method for rooting networks when the differences between species are large with respect to the differences within. In these scenarios, there is often a lack of statistical resolution of the root, making it difficult to place a well-differentiated haplotype into a network of minimally differentiated haplotypes (Castelloe and Templeton 1994).

Results

Basic statistics

The total haplotype network that connects all haplotypes sequenced in black rockfish and includes a connection to a sister species outgroup (yellowtail rockfish) is displayed in Fig. 1. There were 56 haplotypes found in black rockfish (Genbank accession nos. FJ664347; OP718400 – OP718454).

The six microsatellite loci did not show any significant linkage disequilibrium using Fisher's method to combine p-values for each locus pair across all collections. However, using sequential Bonferroni correction to examine pairs of loci within collections, showed a single locus pair (Spi4 and Sal3) within

one black rockfish collection (collection 3, San Francisco n = 55) as being significant at the 0.05 alpha level.

Two black rockfish collections, pop 7 (Crescent City n = 11) and pop 13 (La Push n = 63) had significant positive F_{IS} values after sequential Bonferroni correction (0.448 and 0.147 at Sra16-5 and Sal3 respectively). However, Fisher's method indicated only pop 7 as having an overall trend in departure from HWE across loci ($p < 0.01$). Analysis with Fisher's method across all collections, Spi10 was found with significant departure from HWE ($p < 0.01$).

MICROCHECKER version 2.2.3 showed evidence of null alleles at locus Spi10 for three collections (Black rockfish collections 3, 15, and 19). Also, one collection (13) showed evidence of null alleles at locus Sal 3.

Putative genetic barriers to dispersal

A multidimensional scaling (MDS) plot was generated from pairwise F_{ST} comparisons based on mtDNA gene frequencies in collections of $n \geq 10$ (Supplemental Fig. 1). This plot helped to visualize the trends in the pairwise F_{ST} matrix (Table 2). We found that collections 2, 3, and 4 diverged from most of the other collections except for collection 9 which clustered with collections 2, 3, and 4. The haplotypic compositions of the collections reveal a large increase in clade 1–6 haplotypes at these collections compared to relatively higher percentages of the ancestral clade 1–1 haplotypes at neighboring sites (Fig. 2). Collections 2, 3, 4, and 9 formed most of the significant pairwise F_{ST} comparisons with the full dataset. The mtDNA dataset shows an overall F_{ST} of 0.11. AMOVA results show most of the genetic variation (89.3%) is captured within collections. When the black rockfish range is divided into two regions at the center of the genetic cline between collections 4 and 5, these regions represent 13.15% of the genetic variation and yield an F_{CT}=0.132, that is significant ($p < 0.01$). Making a third region that consists of the single divergent collection 9 increases the percent of genetic variation (16.9%) and increases F_{CT} (0.169, $p << 0.001$).

We performed a principal components analysis (PCA) on the black rockfish microsatellite allele frequency data of all collections with sample size $n \geq 10$ (Supplemental Fig. 2) and identified two regional groups (Alaska collections 15–22 versus continental U.S. collections 2–14) along the primary axis. Further, there was a single collection 8 that appeared to be separated from all other collections on the y-axis. The patterns in this PCA plot were consistent with the significant F_{ST} values that were observed in the genetic distance matrix (Table 2). I.e., there were significant F_{ST} values between Alaskan and U.S. continental collections as well as between the single collection 8 with most other collections. Analysis of the six microsatellites across all collections yields an overall F_{ST} value of 0.017 with 95% confidence intervals (C.I.) from bootstrapping over loci (0.011–0.022). These values were the same even when only collections with ten or greater individuals were considered. Exclusions of the locus and collection shown to deviate from HWE do not significantly alter these values for either species. For example, when Spi10 is excluded, the F_{ST} value is 0.018 (95% C.I.: 0.012–0.023).

Most of the microsatellite genetic variation (97.3%) is captured within collections, however, there is also a significant portion of variation that is captured by dividing the sampled ranges according to the genetic cline indicated by the heuristic examinations with PCA. Separating the range into two regions between the Alaska and the continental U.S. range captures a significant amount of variation (2.1%; F_{CT}=0.021, p < < 0.001). Making a third region that consists of a single collection (collection 8 at Brookings, OR) increases this percent genetic variation (2.4%) and F_{CT} value (0.024, p < < 0.001). There are clearly two different regions that appear to be important in the microsatellite data versus the mitochondrial data for black rockfish. The relatively large genetic divergence between neighboring collections (i.e., genetic break) detected in the heuristic analyses indicated a location in California centered between collections 4 and 5 for the mitochondrial dataset but the only genetic break in the continental U.S. coast observed in the microsatellite data was centered on collection 8. Further, a larger genetic regional break appears in the microsatellite dataset between the continental U.S. and Alaskan collections. In contrast, for the black rockfish mtdna data, this continental U.S. versus Alaska division yields a lower percentage of the genetic variation (4.4%, F_{CT}=0.044, p < 0.05) than was found when we divided by the Californian cline (13.15%, F_{CT}=0.132, p < 0.01).

Isolation by distance

Range-wide level:

At the range-wide level, we detected a significant isolation-by-distance regression for both DNA marker datasets (Table 3). The black rockfish mtDNA dataset showed a significant pattern but the R^2 and slope were low: 0.024 linearized F_{ST} per 1000 km (R^2 = 0.076, p < 0.001, Fig. 3a). These values for the black rockfish mtDNA IBD regression were only slightly improved by omitting collection 9, which was genetically divergent from its neighbors. For the microsatellite dataset the range wide IBD equates to 0.007 linearized F_{ST} per 1000 km (R^2 = 0.270, p < 0.001; Fig. 3b). When we excluded the black rockfish collection 8 at Brookings, OR (highly genetically divergent from all other collections) we observed an IBD regression with a higher R^2: 0.008 linearized F_{ST} per 1000 km (R^2 = 0.648, p < 0.001).

Regional level:

We next examined IBD regressions on the regional level by examining IBD patterns on either side of the steep genetic clines that were identified in the heuristic analyses. The two regions examined for the mtDNA dataset included collections north and south of the break between collections 4 and 5. Neither region showed a significant IBD regression, unless collection 9 was excluded from the northern region, in which case the IBD regression was significant and yielded the following values: 0.007 linearized F_{ST} per 1000 km (R^2 = 0.105, p = 0.001; Table 3).

The microsatellite data were split into regions separating the continental U.S. and Alaska. The continental U.S. was not significant, and the Alaskan range showed a significant negative slope: -0.004 F_{ST} per 1000 km (R^2 = 0.365, p = 0.004). When collection 8 (Brookings, OR) was excluded, the continental U.S.

collections showed a weak, but significant IBD pattern: 0.004 linearized F_{ST} per 1000 km (R^2 = 0.059, p = 0.050).

Four-collection sliding window:

The four-collection sliding window isolation-by-distance regressions for the mtDNA dataset showed the 3-4-5-6 collection group had the highest IBD slope value, 0.799 $F_{ST}/(1-F_{ST})$ per 1000 km, which also had the highest R^2 (0.957) and was significant at the $p < 0.01$ alpha level (Table 3). The 6-7-8-9 collection group also had a significant IBD regression at the $p < 0.001$ alpha level: 0.206 $F_{ST}/(1-F_{ST})$ per 1000 km. The genetic cline at 3-4-5-6 appears to be a regional transition whereas the cline at 6-7-8-9 appears largely driven by one genetically divergent collection (9). Furthermore, we find that the center of the cline within the 3-4-5-6 region is between collections 4 and 5 which were the two neighboring collections that appeared separated with the greatest distance on the MDS plot.

The four-collection sliding window isolation-by-distance regressions for the microsatellite dataset showed the 4-5-6-7 collection group had the highest IBD slope value, 0.046 $F_{ST}/(1-F_{ST})$ per 1000 km, which also had the highest R^2 (0.749) and was significant at the $p < 0.05$ alpha level (Table 3). All other sliding window groups that showed significant trends were groups of collections straddling the continental U.S. and Alaskan range: groups 12-13-14-15, 13-14-15-17, and 14-15-17-18. Of those three groups, the group that was exactly centered between continental U.S. and Alaskan range (13-14-15-17) was the one with highest linearized F_{ST}: 0.015 (R^2 = 0.904, p = 0.004). Collections 14 and 15 were the two neighboring collections separated with the greatest distance on the primary axis of the PCA plot (Supplemental Fig. 2).

Mantel correlations are higher for regional divisions versus isolation by distance

We found that using both mtDNA and microsatellite datasets, the basic Mantel comparing regional affiliation versus genetic distance matrix yielded a higher correlation, which is the result expected if a regional genetic break were a better fit to the data compared to a model of isolation-by-distance. For example, the black rockfish mtDNA Mantel test of pairwise geographical distance versus pairwise linearized F_{ST} yields a significant correlation of 0.28 (right-tailed and two-tailed $p < 0.05$). In contrast, the Mantel test of the two regions north and south of collections 4 and 5, yields a correlation of 0.51 (right-tailed and two-tailed $p < 0.01$). The black rockfish microsatellite Mantel test of pairwise geographical distance versus pairwise linearized F_{ST} yields a correlation of 0.52 (right-tailed and two-tailed $p < 0.001$). Whereas, the Mantel test of Alaska and the continental U.S. regions versus pairwise linearized F_{ST} yields an improved correlation of 0.55 (right-tailed and two-tailed $p < 0.001$).

Structure

The STRUCTURE results were consistent with other microsatellite analyses. For example, in black rockfish no more than three populations could be interpreted (Table 4). Moreover, it appeared that high proportions

of membership in the three population clusters identified by STRUCTURE were geographically restricted to Alaska, continental, and collection 8 at Brookings, OR respectively (Fig. 4). This result corroborates our previous findings that the regions of Alaska and the continental U.S. are significantly genetically divergent from each other and our finding that collection 8 is significantly genetically divergent from all other collections. Finally, when we removed collection 8 from the STRUCTURE analysis, the results supported no more than two populations (Table 4), indicating that without collection 8 only the regional break between Alaska and the continental U.S. would be present.

Range expansion and other demographic patterns

Black rockfish had low mitochondrial gene diversity in the northern portion of its range. Gene diversity was consistently low from the coast of Washington at collection 12 and continuing north through the Alaskan range (Fig. 5). The significant pairwise F_{ST} values (Table 2) correspond with the collections that have a large discrepancy in mtDNA gene diversity. The low gene diversity was not exclusive of the Alaskan collections and was variable across the continental U.S. collections including 6, 7, 10, 12, 13, and 14 (Fig. 5).

We used two parameters (allelic richness and gene diversity) to characterize levels of diversity of the microsatellite variation. These parameters were estimated for each collection and plotted versus latitude to test for any significant correlations. There were no consistent trends across loci. A single locus (Spi 6) showed a significant negative trend in allelic richness with latitude using all collections with a minimum sample size of 10 ($y = -0.0368x + 9.3298$, $R^2 = 0.4523$, $p < 0.01$). Further, there was an opposite trend with locus Spi 4; i.e., a positive trend in allelic richness with latitude ($y = 0.0323x + 3.4495$, $R^2 = 0.269$, $p < 0.05$). The only locus to show a significant trend using gene diversity with latitude was Sra15-8, and in this case the trend was significantly negative ($y = -0.0032x + 0.8516$, $R^2 = 0.6331$, $p << 0.001$).

We also split the collections into two groups according to whether they were in the continental U.S. or Alaska and estimated whether these parameters were significantly different between these regions. Over all loci, neither allelic richness nor gene diversity was significantly different between these regions. However, when each locus was considered separately Sra 15 − 8 showed significantly greater gene diversity in the continental U.S. compared to Alaska (Hs = 0.72 vs 0.59 respectively, two sided $p < 0.01$) and Spi 4 showed the opposite pattern (Hs = 0.42 vs 0.53 for continental U.S. vs Alaska respectively, two sided $p < 0.05$). For allelic richness (AR), only locus Spi 6 was significant: (AR = 6.2 vs 5.6 for continental U.S. vs AK respectively, two sided $p < 0.05$).

The BOTTLENECK results suggest collection 8 is different from the others indicated by a deficit of heterozygosity that corresponds across all six loci (Fig. 6). Four loci (Spi6, Spi10, Spi4, and Sal3) showed significant ($p < 0.01$) deficits of heterozygosity under the SMM model. The only range wide trend in the difference in observed versus expected heterozygosity was found at Sra15-8, which is lower in Alaska compared to the continental U.S. collections. In fact, all Alaska collections except for collection 22 had significant deficits of heterozygosity at locus Sra15-8. This result reflects the finding that Sra 15 − 8 has significantly lower gene diversity in Alaska as we reported above.

Phylogeographical inferences

The nested haplotype network of black rockfish (Fig. 1) and each 1-step group is color coordinated with the chart showing the 1-step clade frequencies across all collections shown (Fig. 2). The details of specific numbers of haplotypes found in each collection are given in Supplemental Table 3. There were two significant (based on a chi square calculation in Geodis) phylogeographical inferences for the NCPA of black rockfish cytochrome b sequences. The chain of inferences based on the Dc and Dn values calculated by Geodis and interpreted by the Templeton inference key are presented in Table 5. The first significant inference involves haplotype H nested within clade 1–1. Clade 1–1 is dominated by one haplotype (A) which represents 812 individuals; haplotype A is likely the ancestral haplotype with an outgroup probability greater than 95%. Haplotype H (n = 21) is the only other haplotype within this clade that had greater than n = 5. Haplotype H is restricted geographically to Alaskan collections west of collection 15 in Yakutat, AK (Fig. 1). The geographical center of haplotype H is located significantly far from the center of its nesting clade (i.e. its Dc value was significantly small, while Dn was significantly large) which may indicate range expansion if more than one clade had shown this pattern. Therefore, the inference indicates that there is insufficient genetic resolution to discriminate between range expansion and colonization versus restricted dispersal and gene flow. The inference key also recommends filling in the gap in sampling between the continental U.S. and Alaska to discriminate between isolation by distance (short distance movements) versus long distance dispersal.

The only other significant inference for black rockfish is that of restricted gene flow with isolation by distance which is at the highest (Total cladogram) level involving clades 2 − 1 and 2–2. The tip clade 2–2 was restricted to the continental U.S. coast, primarily south of Washington State. Clade 2 − 1 is well supported as the most ancestral clade, due to it being the closest connection to other species and having the highest outgroup probability (Clade 2 − 1 outgroup probability = 81.3%, Clade 2–2 = 18.7%).

Effective Population Size

Several collections had relatively low effective population sizes as indicated by finite confidence interval (C.I.) bounds calculated with LDNe software. The only collections that had finite C.I. bounds with both parametric and jackknifing methods were collections 8 and 13. Collection 8 had of 163 (CI: 76-2526 and 81-1072, parametric and jackknifing loci respectively) using all alleles above the critical frequency of 0.01 (i.e., pcrit = 0.01). Collection 13 had of 93 (CI: 46–410 and 54–215) with pcrit of 0.05.

After excluding the single locus found out of HWE in black rockfish, Spi10, there were four collections found with finite C.I. bounds (Collections 8, 13, 14, and 19). Collection 8 had of 75 (CI: 31-1511 and 34–499) with pcrit0.05 and of 117 (CI: 59–570 and 70–280) with pcrit0.01. Collection 13 had of 68 (CI: 33–262 and 41–144) with pcrit0.05 and of 139 (CI: 62-8650 and 68–910) with pcrit0.02. Collection 14 had of 7 (CI: 2-132 and 2–32) with pcrit0.05. Collection 19 had of 96 (CI: 50–400 and 48–501) with pcrit0.02.

Discussion

Comparison of genetic barriers for black and yellowtail rockfishes

Our population genetic study of black rockfish found evidence of more than one stock. In fact, based on microsatellites, there may be at least three populations along the species range; one concentrated in the south (U.S. West Coast), one that is concentrated at a single collection (Brookings, OR), and one that is concentrated in the north (Western Alaska). Our analyses of both mitochondrial sequences and nuclear microsatellite genotypic data from black rockfish collections reveal the presence of abrupt genetic clines (i.e., short isolation-by-distance trends) centered on three different geographic locations. Two genetic clines occur on relatively small geographic scales within the U.S. West Coast of our study (within 2–3 degrees latitude) and all three are significant isolation-by-distance correlations using a minimum of four neighboring collections. A relatively steep genetic cline based on high $F_{ST}/(1- F_{ST})$ revealed by our mtDNA dataset was centered between latitudes 38 to 42 (collections 3 to 7). This is similar to the pattern in yellowtail rockfish which exhibited a trend from between those same latitudes that appeared centered at Cape Mendocino (Latitude 40.5; Hess et al. 2011). However, unlike yellowtail rockfish, this genetic cline was not as steep [0.8 versus 1.8 $F_{ST}/(1- F_{ST})$ per 1000 km], it did not divide the region into two separate regional stocks, and it may be centered slightly further south (between collections 4 and 5, Point Arena). Further, the composition of mitochondrial haplotypes that comprise this cline resemble a staircase that begins in the southernmost range (San Francisco, CA) as relatively high frequency of southern haplotypes, which then decrease rapidly going northward (Crescent City, CA), and then again increase rapidly to a high frequency of southern haplotypes (Charleston, OR). These two transitions represent the two clines exhibited in the mitochondrial structure. The microsatellite genetic structure also shows a cline equal to the value [0.5 $F_{ST}/(1- F_{ST})$ per 1000 km] and the location (between collections 5 and 6 near Cape Mendocino) of that displayed in yellowtail rockfish structure. However, this black rockfish microsatellite cline is similar to the mitochondrial clines in the way it resembles an upward/downward staircase and does not split the U.S. West Coast range into two stocks unlike the cline in yellowtail rockfish.

Finally, a second significant microsatellite genetic cline was centered on the region between the Alaskan and continental U.S. collections. This cline appeared to be less steep than the US West Coast genetic cline but it is unclear whether this is simply due to a lack of samples between Neah Bay, WA and Yakutat, Alaska. The entire Canadian range is unsampled and may reveal more abrupt transitions if data were available.

Northward range expansion

The microsatellite data from the yellowtail rockfish study (Hess et al. 2011) had provided some indication that northern range expansion may have been part of the historical processes affecting population structure in the species. We would generally expect low genetic diversity in the northern collections of a species that has experienced rapid range expansion. This analysis provides evidence of a recent expansion of black rockfish into Alaska. First, the cytochrome gene diversity in this study was consistently lower in Alaskan collections vs continental U.S. collections. In fact, mtDNA gene-diversity

appears significantly lower in the northern portion of the species range starting north of the Columbia River at the border of Oregon and Washington and continuing into Alaska. Second, in a previous microsatellite study by Seeb and Seeb (2005) they find a decreasing allelic richness going west into Alaska. In contrast, we did not find a decreasing trend over all loci with regards to allelic richness in our microsatellite data (we used a different set of loci than Seeb). At most there was a single locus 15 – 8 that showed a decreasing trend of gene diversity in Alaska, but a different locus showed a significant opposite trend. We would expect low gene diversity in more recently expanded areas compared to areas that have maintained relatively stable effective population size over a longer time. These results may indicate longer population stability in the south as compared to the north.

The NCPA could not resolve whether isolation by distance or range expansion/colonization explains mtDNA variation due to insufficient genetic variation. The haplotype H was shown to be distributed relatively far from its parent haplotype (A) at the extreme end of the range in Western Alaska, which is a pattern typical of range expansion. However, robust testing requires more than just a single haplotype to show this pattern before it can be confidently interpreted. The NCPA did show a role for the process of restricted gene flow by isolation by distance. At the oldest temporal level (i.e. total cladogram level), isolation by distance gene flow explains the distribution of genetic variation.

Glaciation cycles have been hypothesized to affect genetic structure and speciation in other rockfish species. First, Rocha-Olivares et al. (1999) discussed how the presence of rosethorn rockfish (*S. helvomaculatus*) in Alaska may be the result of a northward expansion from a subgeneric center of the radiation south of 38 N. Second, copper rockfish population structure showed evidence of range expansion into Puget Sound after marine conditions were reestablished (Buonaccorsi et al. 2002). Third, speciation of thornyhead rockfishes (genus *Sebastolobus*, closely related to *Sebastes*) may have resulted from glacial cycles inducing vicariant events (Stepien et al. 2000).

Similar to our microsatellite results, an abrupt genetic cline was described in black rockfish within Alaska. Seeb and Seeb (2005) found support for a genetic discontinuity at the Alaska Gyre and suggested the direction of ocean currents in the Gulf of Alaska (GOA) restricts dispersal. The main results were: 1) significant pairwise F_{ST} values between all western GOA collections and every southeastern Alaska and Pacific Northwest collection, and 2) a trend toward decreasing allelic richness starting from the Pacific Northwest to the western GOA collections. However, ocean currents acting as gene flow barriers would not fully explain the second result. An alternative explanation is the western GOA collections were founded by a relatively small group of individuals (lacking in genetic variation), thus resulting in the observed decrease in allelic richness. One reason for expecting this founder scenario in the Alaskan range of this species is due to the last glacial maximum (LGM) that occurred just 20,000 years ago, which may have made this northern coastal habitat unsuitable to nearshore species. Glaciers and their associated ice shelves are hypothesized to have covered much of the continental shelf between the Alaska Peninsula and British Columbia (Mann and Hamilton 1995).

Extinction and recolonization events

So far, we have emphasized short isolation-by-distance trends along the U.S. West Coast in the genetic structure of black rockfish. However, a couple collections are genetically divergent from neighboring collections in mtDNA (collection 9) and microsatellite (collection 8) datasets. These collections had relatively large sample numbers ($n \geq 50$); yielded consistently high F_{ST} levels across a majority of collections in the dataset, including their nearest neighboring collections; and were both located in southern Oregon on either side of Cape Blanco.

The collections 8 and 9 do not appear to be part of any regional isolation-by-distance trends but appear to be isolated events at small spatial scales. These single divergent collections that lacked isolation-by-distance trends with surrounding collections are unlikely to be explained by sampling error, rather they were likely the result of local extinction and recolonization events. As few collections that had low effective population size, including collection 8 at Brookings, OR, provides evidence of local extinction and recolonization events. Additionally, collection 8 shows a deficit in heterozygosity across several loci that may be indicative of a recent increase in population growth from low effective population size. Collection 8 was genetically differentiated from all other collections in the species range according to the microsatellite data. Interestingly, a previous study of black rockfish identified Brookings, OR as a location with aberrant collections (Miller et al. 2005). Miller et al. (2005) found HWE deviations at microsatellite loci Spi4 and Spi10. In our study, collection 8 at this location of Brookings was differentiated from surrounding collections, however, none of the p-values were significant in tests for deviation of HWE. Results from BOTTLENECK simulations showed only collection 8 had significant heterozygosity deficit at more than four loci. We suggest that this area near Brookings, OR may have undergone a recent increase in population size from a small group of founders that could account for collection 8 being highly genetically differentiated from all other collections in this study and the fact that there are deficits of heterozygosity across multiple loci.

Despite these extinction and recolonization events, the overall population structure of black rockfish compared to yellowtail rockfish was not substantially higher as measured by overall F_{ST}. For example, based on microsatellites black rockfish had an overall F_{ST} of 0.017 (95% C.I: 0.011–0.022) compared to yellowtail 0.011 (95% C.I: 0.008–0.015). Based on mitochondrial DNA black rockfish data showed that splitting the dataset between collections 4 and 5 and making collection 9 into a third region yielded an F_{CT} (0.169, $p << 0.001$) that was lower than the F_{CT} represented by splitting the yellowtail rockfish range at Cape Mendocino ($F_{CT} = 0.32$, $p << 0.001$; Hess et al. 2011). Whether the depth preference differences between these species led to an overall greater number of extinction and recolonization events in black rockfish is an interesting question worth further consideration. However, regardless of possible higher frequency of these extinction and recolonization events, these events did not lead to greater overall genetic differentiation across the range but rather greater localized differentiation of neighboring sites. For example, the concentration of southern haplotypes at the southern end of the range appears suddenly absent near Point Arena (between collection 4 and 5) then continues to be absent until further north around collection 8 and 9 at Cape Blanco, before disappearing again at northern neighboring collection at

Newport, OR (10). Stochasticity from recurrent extinction and recolonization events would tend to create a disrupted pattern of haplotypic composition along the coast.

One possible cause of extinction and recolonization may be related to levels of anoxia observed in the Oregon range of black rockfish (Chan et al. 2008). Dissolved oxygen measured from 0–800 meters depth during upwelling season (mid-April to mid-October) between 42–46° N latitude (approximately the area between collection 7 and 11, Fig. 1) crossed the severe hypoxia threshold (below 0.5 ml L^{-1}) in 2006, which was a rare event from 1950–1999 but has increased from 2000–2005 (Chan et al. 2008). Chan et al. (2008) reported that this severe hypoxic event affected all their cross-shelf transect lines between 44.25°N and 45.00°N (approximately the area between collection 9 and 11, Fig. 1), extending from the shelf break to the inner shelf (under 100 m depth) and encompassing at least 3000 km^2. Further, Chan et al. (2008) showed there was a complete absence of all fish from the rocky reefs normally occupied by rockfishes when they conducted submersible surveys in August 2006. This particular event would have been most likely to affect collection 10 that was obtained in the summer of 2005 within the hypoxic region and before that area was found in summer 2006 to be vacant of rockfishes (Chan et al. 2008). Black rockfish would have been one of the species impacted by this phenomenon as adults mostly occur in less than 55 m depth (Love et al. 2002). Interestingly, collection 10 had significant pairwise F_{ST} based on mtDNA, and lower mtDNA gene diversity compared to its two neighboring collections 9 and 11. Fish may not suffer direct lethal effects from these hypoxic conditions since they can move to avoid them, but the effects can be similar to extinction and recolonization events. When a large area of habitat becomes unsuitable, periods of displacement can be followed by replacement, but not necessarily by a representative sample of the displaced individuals.

It is possible that aspects of the reproductive biology of black rockfish, particularly bet-hedging strategies (e.g., Sogard et al. 2008) combined with sweepstakes type recruitment mechanisms (e.g., Markel et al. 2006), have influenced the genetic disruptions we have observed. The period of parturition (when larvae are extruded) occurs between mid-January and mid-March with a peak in February and older females tend to release larvae earlier than younger females (Bobko and Berkeley 2004). It also appears that faster growth and higher survival was linked to older females likely due to contributing a larger energy storage oil globule to larvae (Berkeley et al. 2004). In this way, localized areas may receive segments of larval recruitment originating from a relatively small numbers of adults.

The influence of seascape on genetic structure

The three locations of steep genetic clines from this study (two in Central California close to Point Arena and Cape Mendocino and one in the region between Alaska and Continental U.S.) have all been discussed previously as locations of putative mesoscale oceanographic dispersal barriers in population genetic studies of rockfish (reviewed by Gunderson and Vetter 2006, Hyde and Vetter 2009). The complete list of barriers includes Alaska Gyre, Queen Charlotte Sound, Puget Sound, the Cape Mendocino jet (e.g., yellowtail rockfish, Hess et al. 2011), and the Southern California Eddy (e.g. cowcod rockfish, Hess et al. 2014; sunset rockfish, Longo et al. 2022) and these locations have all been shown to correlate

to genetic discontinuities in rockfishes (Gunderson and Vetter 2006). Even outside of the rockfish genus, other marine taxa (fishes and invertebrates) also show genetic discontinuities at these locations (Hare and Avise 1996; Arndt and Smith 1998; Lecomte et al. 2004; Marko 2004; Cimmaruta et al. 2005; Hickerson and Cunningham 2005; Hickerson et al. 2006; Wilson 2006; Petersen 2007). Besides correlative evidence from genetic studies, Point Conception and Cape Mendocino (Briggs 1974, Williams and Ralston 2002, Cope 2004) are observed to be biogeographic breaks where species ranges terminate. In addition, Cape Mendocino and Cape Blanco are regions where groundfish species assemblage structure has been found to shift (Tolimieri and Levin 2006).

The possible mechanisms responsible for the way in which these locations could act to limit dispersal may be due to currents (Magnell et al. 1990; Marchesiello et al. 2003, Longhurst 2007) or bathymetric features such as submarine ridges and canyons (Williams and Ralston 2002). Longhurst (2007) defined a series of geographic compartments within the California Current Ecological Province and these coast upwelling regions explained genetic patterns in the vermillion rockfish species complex (Hyde and Vetter 2009). At various capes along the west coast and particularly at Cape Mendocino, there are major upwelling quasi-permanent eddies (Marchesiello et al. 2003) and they are strongest in spring and summer when rockfish juvenile recruitment occurs. For regions around Monterey and Cape Mendocino California there is also a decrease in total habitat in waters shallower than 200 m, which affects the common depths inhabited by both yellowtail and black rockfish (Williams and Ralston 2002).

The collections that were genetically divergent from neighboring collections (collection 8 at Brookings, OR and collection 9 at Charleston, OR) do not appear to be a result of a major dispersal barrier that disrupts connectivity in a way that splits this species into two separate stocks. However, Cape Blanco is located in between Brookings and Charleston, OR and there may be a localized isolating effect of currents in the vicinity of Cape Blanco that are sufficient in cutting off recruitment from neighboring areas to produce a recruitment sink. In addition, a large swath of sandy habitat between Charleston and Newport separates rocky habitat that is more suitable for black rockfish. Copper rockfish also show a genetic discontinuity between Charleston and Newport, Oregon (Buonaccorsi et al. 2002; Johansson et al. 2008). Aside from rockfish, four species of Pacific salmonids, *Oncorhynchus mykiss* (steelhead trout), *O. clarki* (cutthroat trout), *O. kisutch* (coho salmon), and *O. tshawytscha* (Chinook salmon) share similar Evolutionarily Significant Unit (ESU) designations and the northern border of ESU III is demarcated at Cape Blanco, OR.

Past genetic studies on black rockfish

There have been several genetic studies conducted across portions of the range of black rockfish. Four of these studies found significant genetic structure based on F_{ST} values calculated overall collections: F_{ST} = 0.011 ($P < 0.001$), ten microsatellites, eleven collections from Oregon to Aleutian islands (Seeb and Seeb 2005); $F_{ST} = 0.018 \pm 0.004$ ($p < 0.001$), seven microsatellite loci, four collections from Oregon and Washington (Miller et al. 2005); and F_{ST} = 0.013 ($P < 0.05$), fourteen allozyme loci, eight collections from northern Oregon (Don Bodenmiller, ODFW pers. comm.); and F_{ST} = 0.002 ($p < 0.001$), eight microsatellite loci, eight collections from Oregon to Vancouver Island, B.C. (Lotterhos et al. 2014). Additionally, a stock

identification study conducted in 1995–1997 by WDFW genotyped ten collections from northern California to southern British Columbia for twenty allozyme loci (Farron Wallace, WDFW pers. comm.). Multidimensional scaling (MDS) analysis of genetic distances (Nei, 1978) revealed three major geographical groupings: 1) north of Cape Falcon, 2) south of Cape Falcon off the Oregon coast, and 3) a single collection from northern California (Farron Wallace, WDFW pers. comm.).

These studies provide evidence that black rockfish exhibits some degree of structure throughout the range and some of the stock divisions that have been identified are shared across studies. The main conclusions of Miller et al. (2005) were that the collection from southern W.A. was genetically divergent from all other collections from southern Oregon. Seeb and Seeb (2005) concluded that a discontinuity occurred between Southeastern A.K. and Western G.O.A collections. Farron Wallace (pers. comm.) found a genetic boundary at Cape Falcon (just south of collection 11). No significant pairwise F_{ST} values were found in the smaller geographic scale study confined to northern Oregon including collections located on either side of Cape Falcon (Don Bodenmiller, pers. comm.). Finally, Lotterhos et al. (2014) found that the collection at the extreme southern end of their study region, near Cape Blanco, was divergent from the rest of the range.

Implications for fisheries management of black rockfish

Stock assessments are critical for management of marine fishes including black rockfish, as their purpose is to collect and analyze demographic data to characterize changes in abundance of fishery stocks. In the most recent stock assessment of black rockfish (Cope et al. 2016), Black rockfish was divided into three stocks stratified by the borders of California and Oregon and the borders of Oregon and Washington along the continental U.S. coast. The northern portion of the range is assessed and managed by Alaska Department of Fish and Game (ADFG) and by Department of Fisheries and Oceans for the portions of the range in Alaska and Canada, respectively. ADFG assesses the species as three separate stocks in the Western Region: Kodiak, Chignik, and the South Alaskan Peninsula Area-Eastern District (Mattes and Sagalkin 2007).

The continental U.S. black rockfish assessments have in the past used a tagging study and allozyme genetic study (Wallace et al. 2007) as a basis for assessing black rockfish as two different stocks separated by Cape Falcon, OR (between collections 10 and 11). The more recent assessment considers three stocks and uses the state borders (CA and OR border is between collections 7 and 8; OR and WA border is between collection 11 and 12), however, our genetic results provide basis to break California into two stocks at Point Arena (between collections 4 and 5). In addition, our genetic results within Oregon provide support for another stock boundary near Cape Blanco (between collections 8 and 9). Alaska is already managed separately from the continental U.S., and until more work can be performed, results from Seeb and Seeb (2005) showing a stock boundary west of Yakutat seem reasonable. A greater level of stratification along these suggested boundaries would create five black rockfish stocks along the U.S. continental coastline which may complicate stock assessments. However, the potential for gene-flow barriers identified as genetic breaks in this study may indicate that abundance trends of rockfish

populations on either sides of these genetic breaks may be behaving in independent ways and could benefit by being assessed separately.

Concluding remarks

Our population genetic study on black rockfish establishes this species as an example of a marine species having more genetic structure on both fine and coarse spatial scales than would be expected given the large dispersal potential of their pelagic larval and juvenile life stages. We demonstrated how evolutionary processes such as restricted gene-flow with isolation by distance, range expansion, and extinction and recolonization appear to have influenced the observed genetic patterns. While black rockfish and yellowtail rockfish have overlapping ranges, these sister taxa are bathymetrically segregated. The hypothesis that black rockfish population genetic structure would resemble that of yellowtail rockfish was partially supported by this study. Both mitochondrial and microsatellite genetic structure shows discontinuities in similar regions of California near Cape Mendocino. These data, as well as a previous study (Seeb and Seeb 2005), support northern range expansion. However, black rockfish did not have a substantially higher degree of population structuring based on F_{ST} as might be expected given a preference for shallower depths as compared to yellowtail rockfish. Black rockfish may, however, be more prone to extinction and recolonization events resulting in localized genetic differentiation between neighboring collections to a degree not observed in yellowtail rockfish.

Declarations

Acknowledgements

The following employees at state agencies (ADF&G, WDFW, ODFG, and CDFG) helped collect samples as part of their regular port sampling programs-Lynne Mattes, J. Daniel Urban, Charlie Trowbridge, Charlie Stock, Scott Meyer , James Latimer, Rhonda Coston, Kris Widdows, Eric Eisenhardt, Eric Shindler, Don G. Bodenmiller, Allen Palacios, Hans Bruning, Deb Wilson Vandenberg, Todd Phillips, Erin Nakada, David Ono, and Michelle Horeczko.

A number of charter boat captains and crew gave crucial support for this project:

Captain Joe Siggy G charter; Betty Kay Charter, Taylor Freeland of Tidewind Charters, Sea Hawk Charter with Captain Tim, Rumblefish Captain Kirk, Telstar Captain Randy, Flying Fish Charter, Captain Hook Charter, Larry the Fisherman on Chris' Charter fishing, and Captain Jason Diamond of Stardust. Discussions with Eric Iwamoto, Anna Elz, Kanegy Lab, Robin Waples. Carol Kimbrell and Russ Vetter at SWFSC provided samples for this project, details on molecular markers, and feedback on study design. Rick Stanley and Ruth Withler at DFO collected and extracted yellowtail collection 17 from northern Vancouver Island, B.C. The moving window of IBD slopes was an idea suggested by Lorenz Hauser at University of Washington.

Funding

This work was supported by the National Research Council post doctoral fellowship program as well as the conservation biology division resources at the NOAA Northwest Fisheries Science Center in Seattle.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

Jon E. Hess designed the study, collected and analyzed the data, and wrote the manuscript. Paul Moran provided input in the study design, analysis, and edits to the manuscript. John R. Hyde provided input in the study design, development of molecular markers, and edits to the manuscript.

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request. The 56 mitochondrial haplotype sequences are available in Genbank (accession nos. FJ664347; OP718400 – OP718454).

Ethical approval

No approval of research ethics committees was required to accomplish the goals of this study because tissue samples were taken from specimen that were legally harvested by recreational fishers. Tissue samples for this research study were granted by the express approval of the fishers.

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Tables

Table 1. Sample sizes and locations of black rockfish collections.

				Sample N	
Collection	Location	Latitude	Longitude	mtDNA	msat
1	Morro Bay, CA	35.35964	-121.00406	9	9
2	Santa Cruz, CA	36.95498	-122.01917	54	54
3	San Francisco, CA	37.80807	-122.54988	55	55
4	San Francisco, CA	38.34133	-123.09333	32	32
5	Fort Bragg, CA	39.52958	-123.82794	51	51
6	Trinidad, CA	41.05568	-124.14717	49	49
7	Crescent City, CA	41.70833	-124.15833	11	11
8	Brookings, OR	42.05409	-124.27666	64	64
9	Charleston, OR	43.34557	-124.32566	50	50
10	Newport, OR	44.61467	-124.08150	60	60
11	Cannon Beach, OR	45.86861	-123.96917	51	51
12	Westport, WA	47.11790	-124.28321	81	81
13	La Push, WA	47.91064	-124.64604	65	63
14	Neah Bay, WA	48.36667	-124.61667	13	11
15	Yakutat, AK	59.59438	-140.04813	32	32
16	Prince William Sound	60.26333	-147.55778	6	6
17	Seward, AK	59.86363	-149.08163	80	80
18	Nuka Bay, AK	59.28333	-150.71667	49	49
19	N. Kodiak Is., AK	58.36955	-152.03211	50	50
20	S. Kodiak Is., AK	56.88333	-153.55000	50	49
21	Shumagin Is., AK	55.28304	-159.90230	81	81
22	Akutan, AK	54.04907	-159.90230	4	30
Total				997	1018

Tables 2 to 5 are available in the Supplementary Files section.

Figures

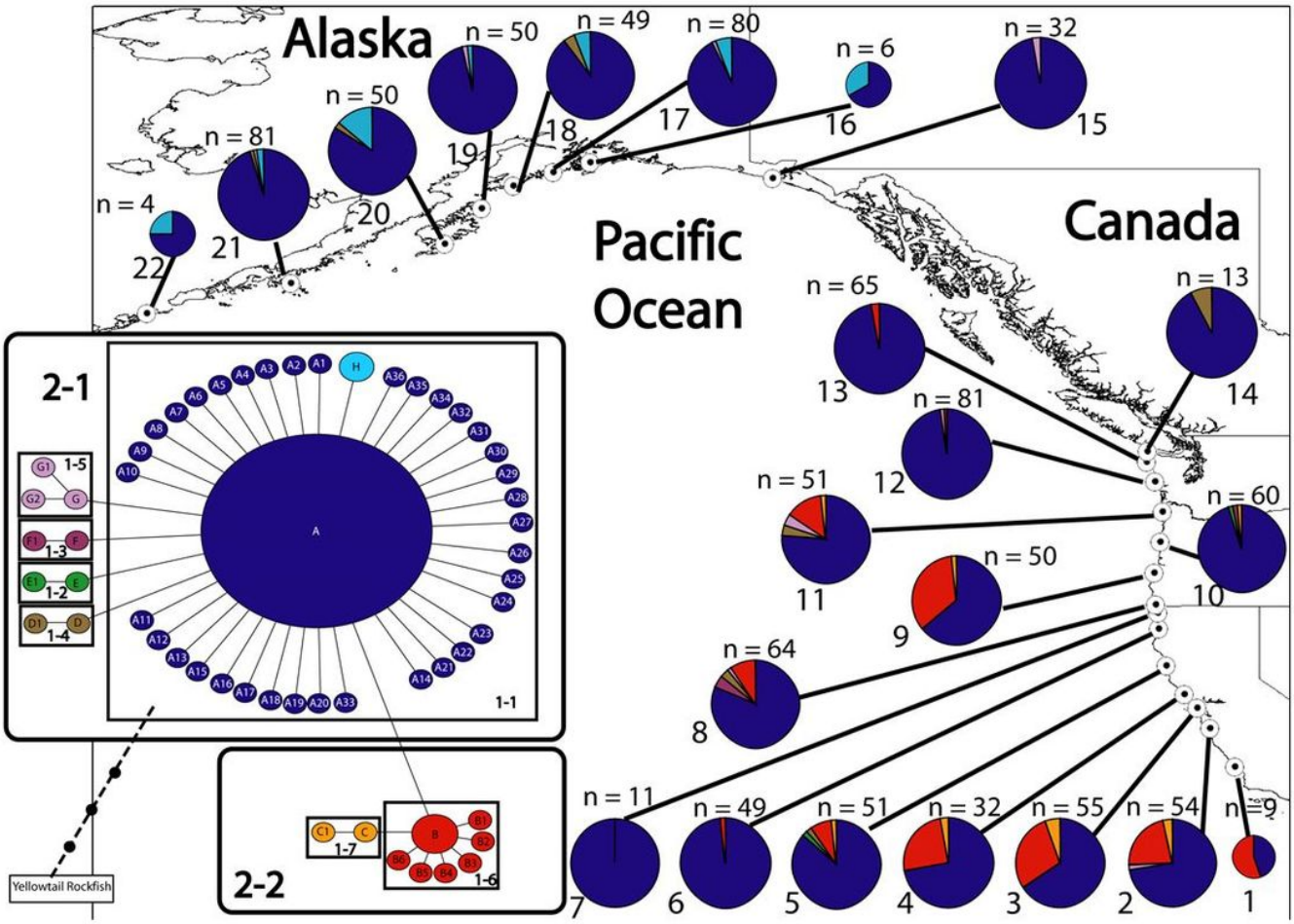


Figure 1

Map of black rockfish sample sites, haplotype frequency charts, and nested clade. Circles with notations represent observed haplotypes. The notation indicates the name of the haplotype. Each line connecting haplotypes represents a single mutation. Small solid circles represent unobserved haplotypes. Groups of haplotypes were nested according to rules in NCPA and assigned a clade number (indicated within the outlined nested group). The square represents the mtDNA haplotypes from a sister species (yellowtail rockfish) used as an outgroup, and indicates clade 1-1 as ancestral. Colors in the pie charts correspond to those colors used in the haplotype network.

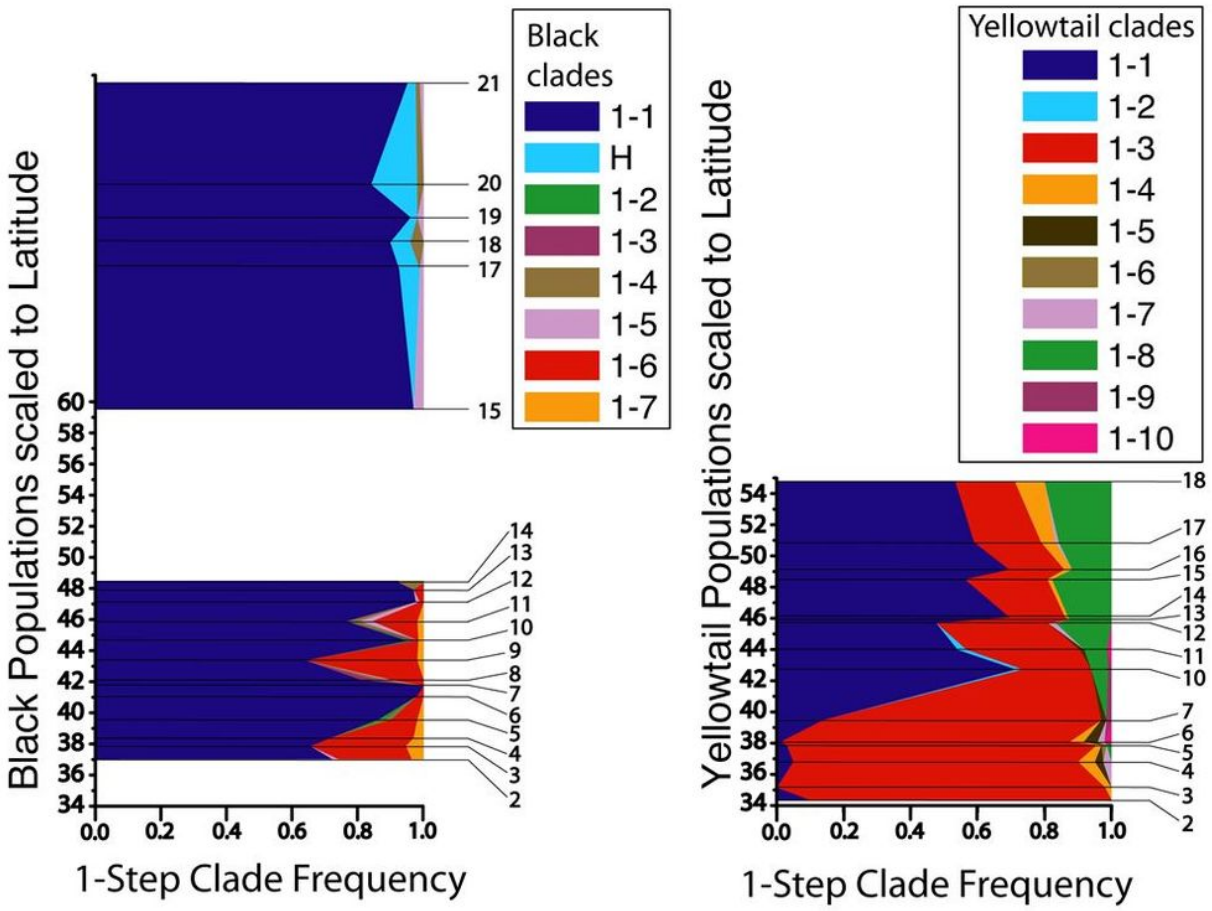
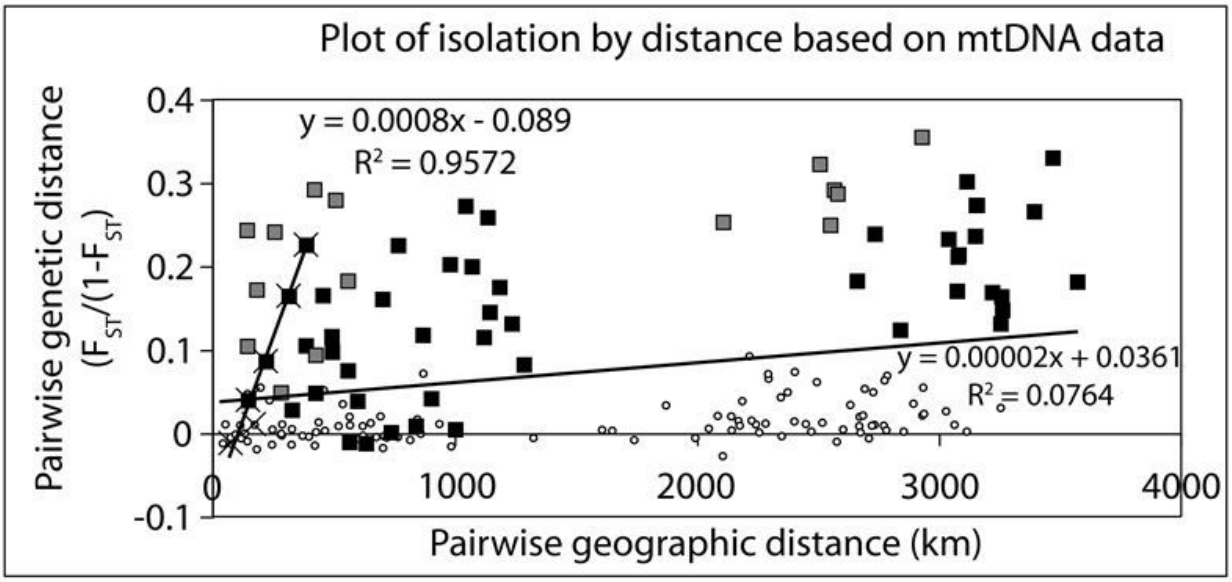


Figure 2

Spatially scaled comparison of the change in mitochondrial clade frequencies for a) black rockfish and b) yellowtail rockfishes. Species were analyzed separately, and the frequencies of the 1-step mitochondrial clades were calculated for each collection with greater than 10 individuals and then these average frequencies were interpolated between collections to create a continuous 100% stacked chart that was scaled to latitudinal position of each collection. Yellowtail rockfish data came from Hess et al. (2011).

a.)



b.)

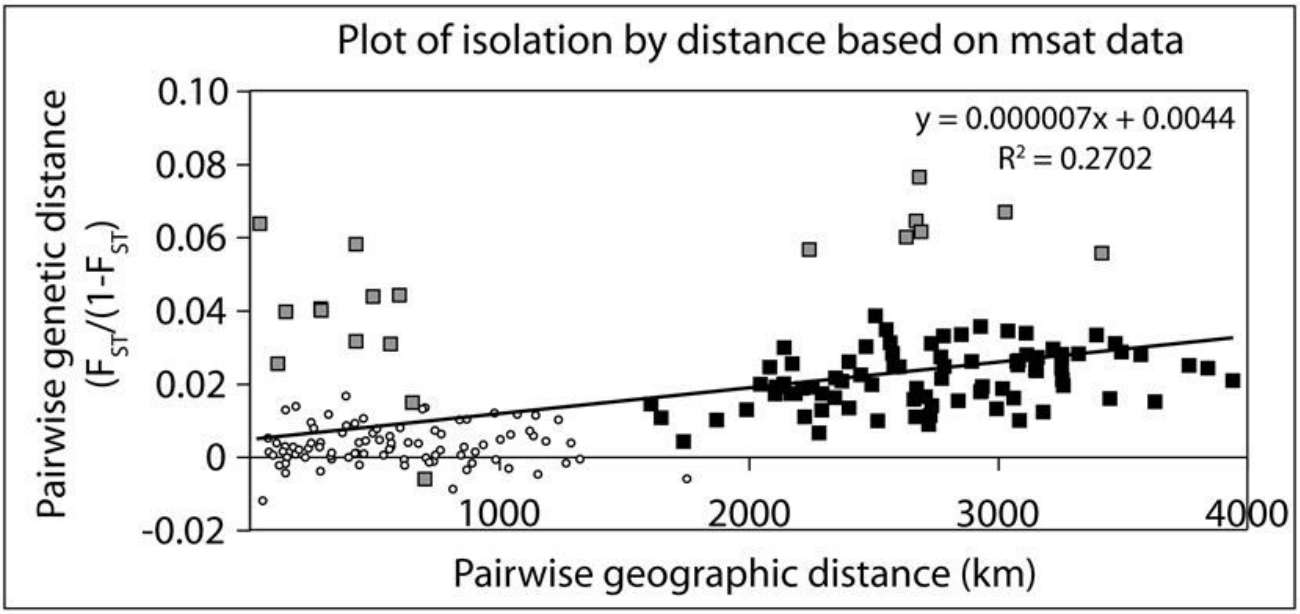


Figure 3

Isolation by distance regression plot based on (a) mtDNA and (b) microsatellite data. The regression of pairwise genetic versus geographic distance comparisons of all collections was significant ($p<0.001$). Pairwise comparisons of collections 2, 3, and 4 (South of Point Arena) versus all other populations are indicated by black squares. Pairwise comparisons of collection 9 with all other collections north of Point Arena are mostly outlier points (indicated by grey squares). Pairwise comparisons of all other collections within either of the two regions (south or north of Point Arena) are indicated as open circles. The small region centered on Point Arena (involving collections 3,4,5, and 6) produced a significant ($p<0.01$) and steep IBD regression which is indicated with X's.

The microsatellite regression of pairwise genetic versus geographic distance comparisons of all collections was highly significant ($p<<0.001$), however the large genetic divergence between continental U.S. and Alaskan collections appears to be the main factor causing this correlation. Pairwise comparisons of continental U.S. versus Alaskan collections are indicated by black squares. Pairwise comparisons of collection 8 with all other collections are mostly outlier points (indicated by grey squares). Pairwise comparisons of all other collections within either of the two regions (continental U.S. or Alaska) are indicated as open circles.

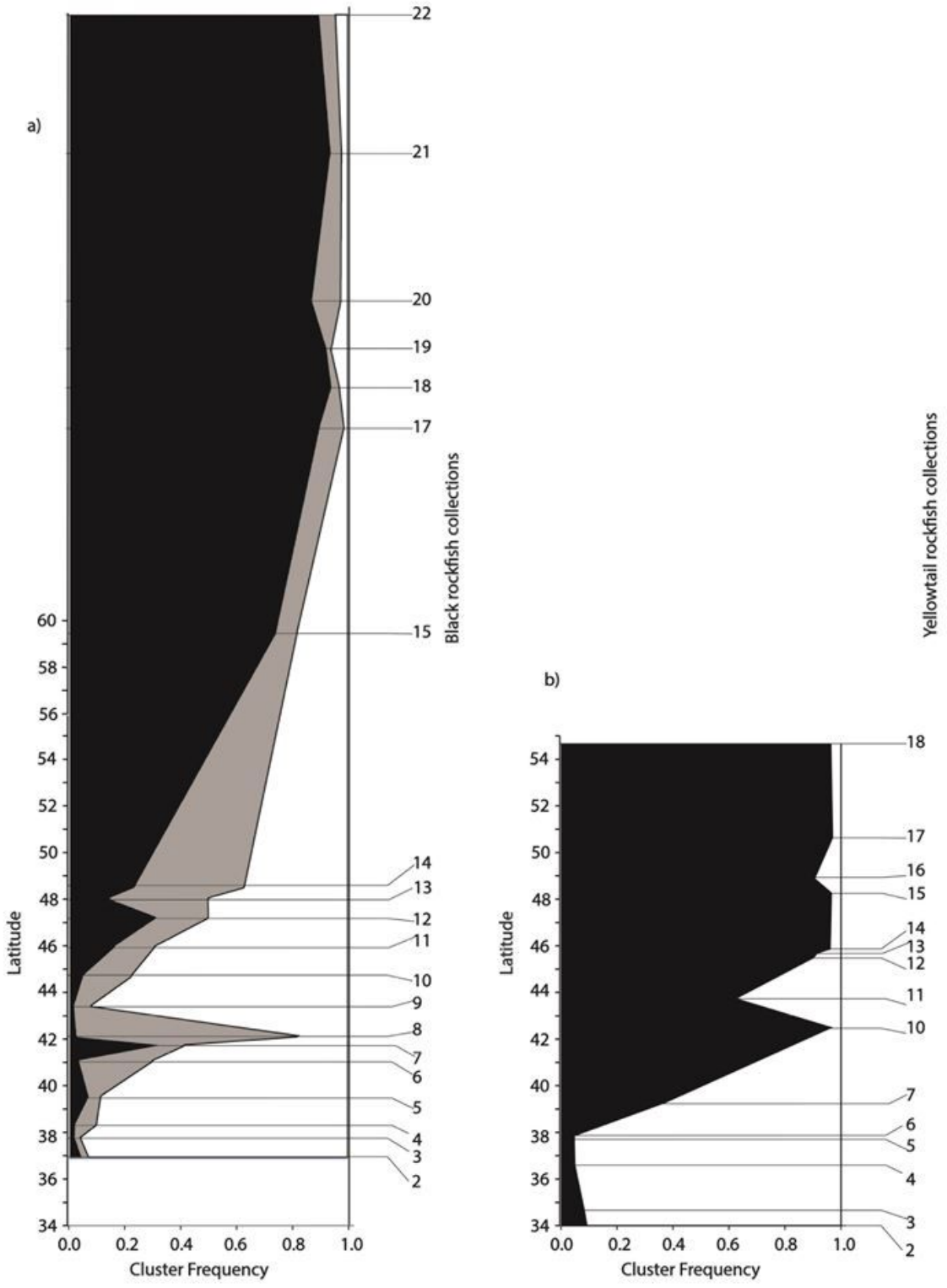
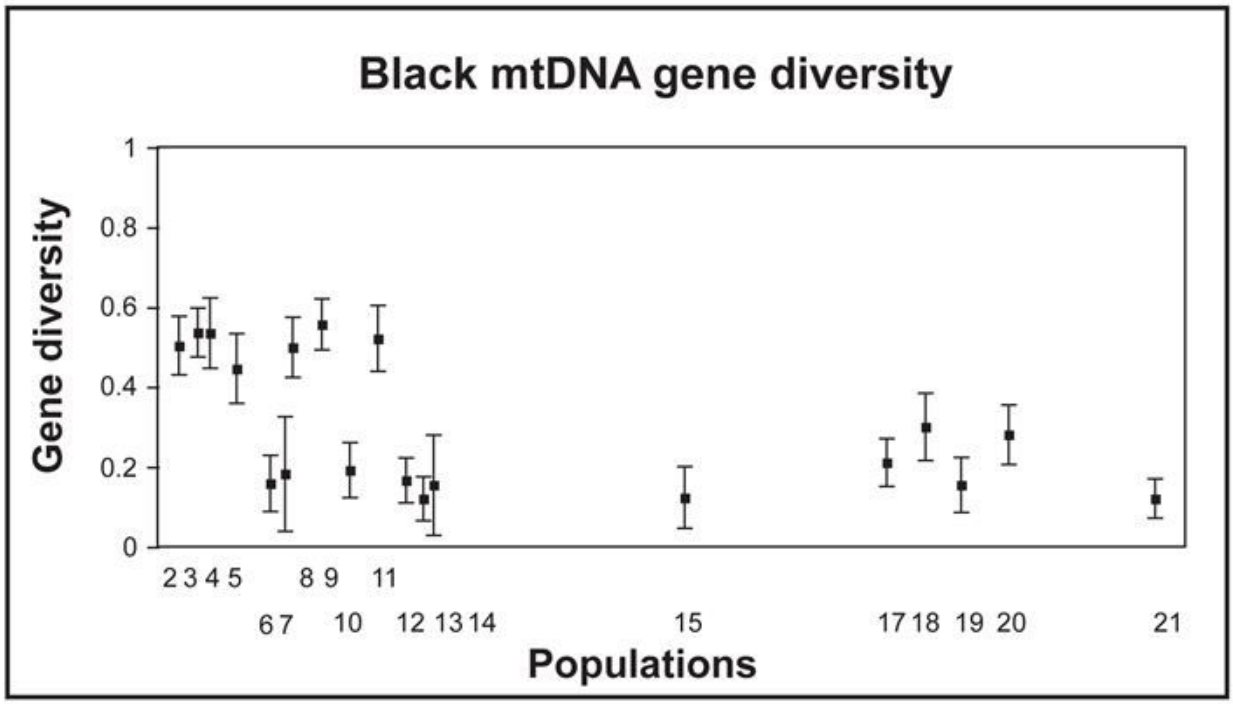


Figure 4

Spatially scaled frequencies of ancestry to STRUCTURE clusters for a) black rockfish and b) yellowtail rockfish collections. Species were analyzed separately and three clusters (black, white, and gray) were resolved for black rockfish and two clusters (shown in black versus white shading) were resolved for yellowtail rockfish (data from Hess et al. 2011). Only collections with N≥10 samples are included in this interpolation of individual probability of ancestry to each cluster which was averaged across individuals within each collection.



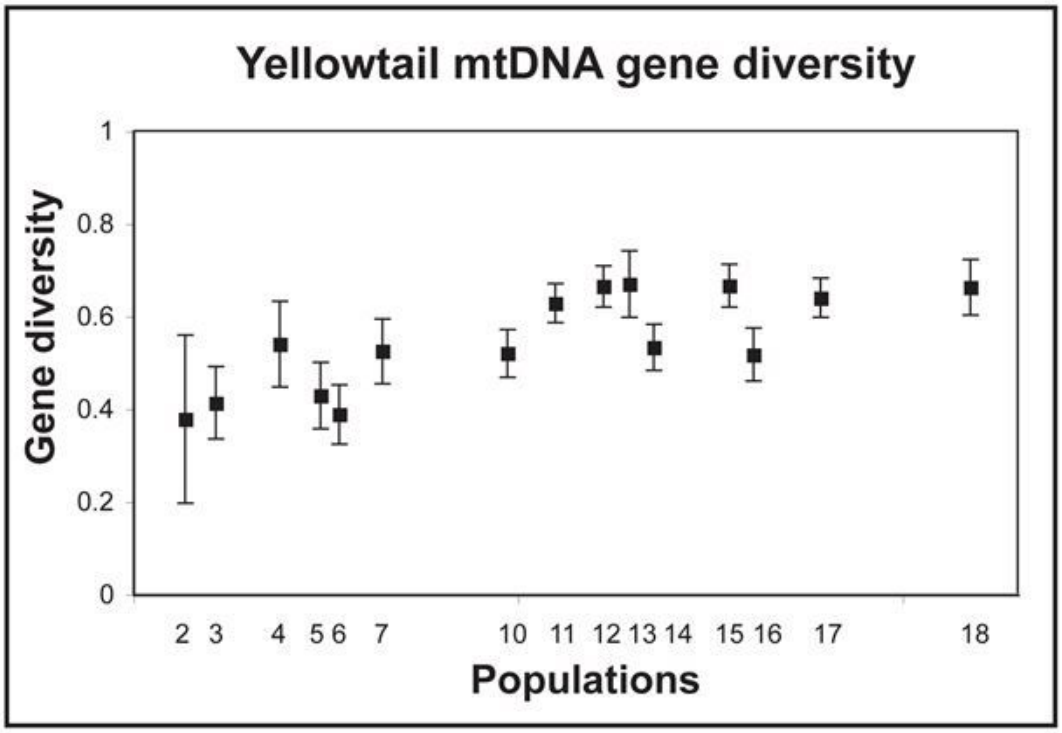


Figure 5

Gene diversity of collections of black rockfish (top) and yellowtail rockfish (from Hess et al. 2011, bottom) based on cytochrome b haplotypes. Each point represents a separate collection as labeled on the x axis and corresponds to population labels in Figure 1. Only populations with greater than n=10 are shown.

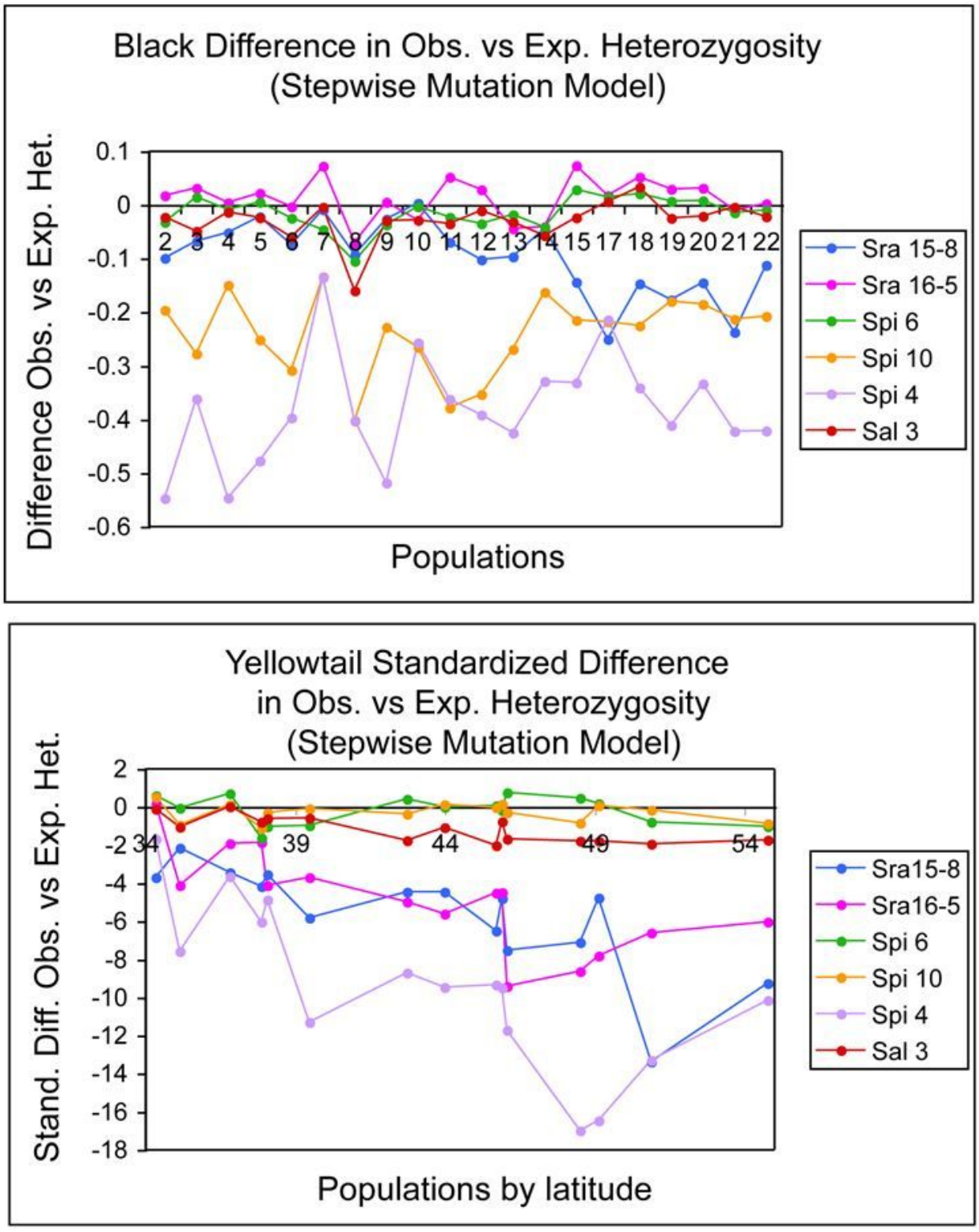


Figure 6

Black rockfish (top) and yellowtail rockfish (from Hess et al. 2011, bottom) difference in observed versus expected heterozygosity under a stepwise mutation model of microsatellite data. Microsatellite locus names shown in legend.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementalMaterial.docx
- Table.docx