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Life history, ecology and the biogeography of strong genetic breaks among 15 species of Pacific rockfish, *Sebastes*

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Abstract Strong genetic change over short spatial scales is surprising among marine species with high dispersal potential. Concordant breaks among several species signals a role for geographic barriers to dispersal. Along the coast of California, such breaks have not been seen across the biogeographic barrier of Point Conception, but other potential geographic boundaries have been surveyed less often. We tested for strong-population structure in 11 species of *Sebastes* sampled across two regions containing potential dispersal barriers, and conducted a meta-analysis including four additional species. We show two strong breaks north of Monterey Bay, spanning an oceanographic gradient and an upwelling jet. Moderate genetic structure is just as common in the north as it is in the south, across the biogeographic break at Point Conception. Gene flow is generally higher among deep-water species, but these conclusions are confounded by phylogeny. Species in the subgenus *Sebastosomus* have higher structure than those in the subgenus *Pteropodus*, despite having larvae with longer pelagic phases. Differences in settlement behavior in the face of ocean currents might help explain these differences. Across similar species across the same coastal environment, we document a wide variety of patterns in gene flow, suggesting that interaction of individual species traits such as settlement behavior with environmental factors such as oceanography can strongly impact population structure.

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Introduction

For many marine species, larval dispersal is a critical part of migration ability, and life history differences between species can dramatically affect gene flow. Investigations of genetic differences among marine populations have been widely used to gauge levels of dispersal, which often scale with larval traits such as pelagic duration (e.g. Berger 1973; Bohonak 1999; Marko 2004). Species for which larval duration is short or absent have often been found to have strong genetic structure among invertebrates (McMillan et al. 1992; Hellberg 1994, 1996) and fishes (e.g. Waples 1987; Doherty et al. 1995; Riginos 2001; Purcell et al. 2006). However, unexpectedly strong structure has also been demonstrated for some species that are presumed to have long distance dispersal potential (e.g. Reeb et al. 2000; Barber et al. 2002; Burford and Bernardi 2008). Uncovering the reasons for strong genetic breaks in such species can potentially reveal a great deal about larval mechanisms that limit dispersal.

Some of the clearest explanations of strong genetic breaks derive from the observation that in some cases, these breaks are concordant with strong biogeographic boundaries. Taxa as diverse as coastal birds, tortoises, fish and invertebrates show strong geographic differentiation along the southeastern coast of the United States (Avise 1992, 1996). Other cases of the confluence of genetic and biogeographic breaks in the oceans have been found in Indonesia, the western Mediterranean, the East Pacific and the Red Sea

(Palumbi 1996, 1997; Sanjuan et al. 1996; Lessios et al. 2001). In these cases, the confluence of genetic breaks across the same geographic feature suggests that the genetic patterns do not derive from specific traits of these species alone, but also depend on barriers to dispersal created by geographic or oceanographic features (Avise 1996).

Though some well-known biogeographic breaks show genetic concordance, others do not. In particular, the major biogeographic break at Point Conception in California is a major region of genetic change in only a handful of species examined (Burton 1998; Dawson 2001). However, strong genetic change may occur in other sections of the coast for other species, and it is possible that genetic concordance occurs along the west coast of North America, near features other than Point Conception.

This region is home to a number of strong ecological gradients that could have an effect on population structure. Between northern California and Oregon, there is a shift in upwelling conditions that increase Oregon nearshore productivity, larval settlement and the growth of many adults of nearshore species (Roughgarden et al. 1988; Connolly and Roughgarden 1998; Connolly et al. 2001; Menge et al. 2004). The center of this shift is Cape Mendicino, a region of strong upwelling that creates persistent offshore movement of nearshore water masses.

Current information on the genetics of coastal populations along this coast offers conflicting data for different species. Intertidal mussels (*Mytilus californianus*) have no structure across a range of genetic markers (Addison et al. 2008), and the shallow water sea urchin *Strongylocentrotus purpuratus* has been shown to have similar mtDNA and allozyme patterns along this coast (Palumbi and Wilson 1990; Edmands et al. 1996; Flowers et al. 2002). Some rockfish show mild genetic differentiation in an isolation-by-distance pattern along the coast (Buonaccorsi et al. 2002). By contrast, the blue rockfish *Sebastes mystinus* shows striking genetic changes near Cape Mendicino despite having a long-term planktonic larval stage (Burford and Bernardi 2008).

Understanding the position and the strength of genetic breaks along the west coast of North America is an important component of understanding the dynamics of this complex ecosystem. Whether dispersal across upwelling jets is common, whether the species inhabiting the near-continuous coastal kelp forest recruit from a common gene pool, and whether other coastal features besides prominent biogeographic breaks can serve as concordant genetic breaks are all questions that might be answered by searching for strong genetic differentiation along this coast. This information also has implications for nearshore fisheries management and of marine protected area networks designed to function within ocean areas between upwelling jets.

Here, we compare population genetic patterns of 11 species of the rockfish genus *Sebastes* sampled in three areas along the west coast of the United States in order to probe for strong genetic structure, and to test the relationship of genetic patterns to adult and larval traits. Adults of *Sebastes* spp. are generally non-migratory and often have limited home ranges. However, these species have pelagic larval durations that last from 1 to 4 months. Previous studies have suggested that species inhabiting shallow water as adults may in general show more consistent genetic structure than do species inhabiting deep, offshore habitats (Rocha-Olivares et al. 1999; Buonaccorsi et al. 2002, 2004).

We designed a sampling scheme encompassing species with different adult habitat requirements by including nearshore demersal species (copper rockfish, *Sebastes caurinus*; gopher rockfish, *S. carnatus*; brown rockfish, *S.auriculatus*; black rockfish, S. *melanops*; olive rockfish, *S. serranoides* and blue rockfish, *S. mystinus*) as well as species that occur in deeper waters (bocaccio, *S. paucispinis*; widow rockfish, *S. entomelas*; yellowtail rockfish, *S. flavidus*; starry rockfish, *S. constellatus*; and vermilion rockfish, *S. miniatus*). These species also fall into subgenera that differ in potential dispersal abilities. The subgenus *Sebastosomus* (Eigenmann and Beeson 1893) was defined on the basis of skull and spine traits, and consists of five species, namely black, olive, yellowtail, widow and blue rockfish, all of which have a relatively long larval period (3–4 months). By contrast, the subgenus *Pteropodus* (including kelp, gopher, copper, brown, grass and black-and-yellow rockfish) has shorter a pelagic development period (1–2 months; Carr and Syms 2006).

Comparing many species at many loci often precludes fine-grained geographic detail. Here, we adopt a coarse sampling strategy that focuses on only three areas: the Oregon coast (hereafter OR), Monterey Bay (MB), and the southern California shore near Santa Barbara (SB; Fig. 1). These three sites span the biogeographic boundary at Point Conception between Monterey and Santa Barbara, and span the ecological gradient between Monterey and Oregon. They are also nested within different oceanic regimes (Parrish et al. 1981), being separated by upwelling jets at Cape Mendocino and Point Conception. We use this design to determine what species show genetic distinctions across these boundaries. Clearly, such a sampling strategy cannot uncover genetic differentiation at small spatial scales. Its strength, instead, lies in a highly comparative data set of differences at the same genetic loci for a range of different species in different areas. Starting from this base, we also collected data from the literature on structure of other *Sebastes* species from the west coast of North America and conducted a metadata analysis to evaluate the impact of adult habitat, phylogeny and larval duration on genetic differentiation.

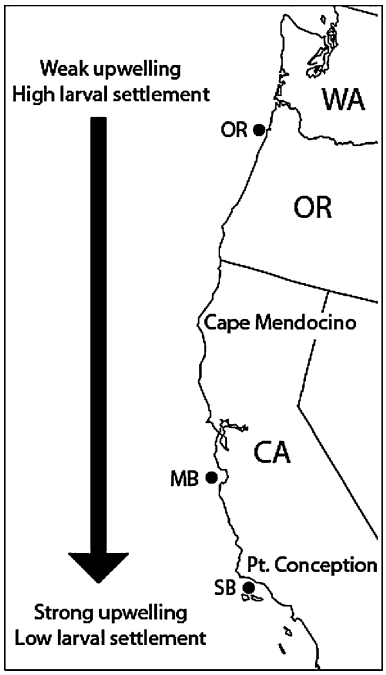


Fig. 1 Map of California and Oregon showing the location of sampling of new populations analyzed here, along with the locations of the biogeographic barrier at Pt. Conception and the ecological gradient along the coast

Methods

Samples and data collection

Fin clips from individuals of all species were collected on board sport-fishing vessels in Santa Barbara, CA (hereafter SB), Monterey, CA (MB) and Garibaldi, OR (OR). Clips were sorted by species and immediately stored in 70% ethanol. Genomic DNA was extracted from fin clips by boiling a small piece of tissue in 10% Chelex (Bio-Rad Laboratories). A portion of the mitochondrial control region was amplified by PCR using the forward primer L15876 (5′-AAGCACTTGAATGAGCTTG) and the reverse primer H16498 (5′-CCTGAAGTAGGAACCAGATG) (Meyer et al. 1990). In some cases where amplification failed, the forward primer K (5′-AGCTCAGCGCCAGAGCGCCGG TCTTGTAAA) was used instead (Lee et al. 1995). PCR products were sequenced in one direction using the forward PCR primer. Sequences were assembled and aligned using Sequencher 4.6 (Gene Codes Corporation).

Microsatellite loci developed in various species of *Sebastes* were also amplified from these samples. The loci *Sal1*, *Sal2* and *Sal3* from *S. alutus* (Miller et al. 2000), *Sma2*, *Sma4*, *Sma5* and *Sma10* from *S. maliger* (Wimberger 1999) and *Sra5-9*, *Sra7-2*, *Sra7-7* and *Sra7-25* from *S. rastrelliger* (Buonaccorsi et al. 2004; Westerman et al. 2005) were screened using the primers and protocols described in those studies. Amplifications were performed using 5′ fluorescently labeled primers (Applied Biosystems) and genotyped on an ABI-3730 DNA Analyzer (Applied Biosystems). Allele calls were made using GeneMapper 4.0 (Applied Biosystems) and inspected visually for accuracy.

Statistical analyses

Genetic differentiation among populations of each species was estimated as Φ_{ST} from control region sequences using Arlequin 2.001 (Schneider et al. 2000) using the Kimura 2-parameter model of DNA substitution. Relationships among individuals and populations were also estimated by constructing a neighbor-joining tree for each species using PAUP 4.0b (Swofford 1998).

The degree of population subdivision within species was estimated using the mitochondrial control region sequences based on standard Φ_{ST} analysis as well as multilocus microsatellite genotypes. For the microsatellites, in addition to standard estimates of population differentiation based on F_{ST} and R_{ST}, we used a non-parametric test for population structure based on assignment probabilities that asks whether individuals are assigned back to their native population more often than strictly due to chance. A visual examination of the plots for each population comparison provides an estimate of how frequently individuals were assigned back to the population they were sampled from. The P values in each panel list the non-parametric probability that the assignment shown occurred by chance. The results of tests of population structure are presented in detail in the "Appendix" and are summarized in Table 3.

Microsatellite loci were examined for deviations from Hardy–Weinberg equilibrium (HWE) using the web version of GENEPOP v3.3 (http://genepop.curtin.edu.au) (Raymond and Rousset 1995). Expected and observed heterozygosities were calculated using Arlequin 2.001 (Schneider et al. 2000). Genetic differentiation among populations of each species was also estimated using Arlequin 2.001. Two measures of genetic differentiation were used for the microsatellite analyses: F_{ST}, which does not explicitly account for a mutational mechanism, and R_{ST}, which does (Slatkin 1995). Assignment tests were also performed to assess how distinct individuals from one population of a species were from individuals from another population (Paetkau et al. 1995). Assignment probabilities were generated using the software program Doh (http://www2.biology.ualberta.ca/jbrzusto/Doh.php). Significance of the assignments was assessed using a 2×2 contingency test.

Table 1 Sample sizes (N), estimates of the population parameter θ_S and haplotype diversity H for the mitochondrial control region in 11 species of *Sebastes*

	MB					OR					SB				
	N	θ_S	H	Hap	Pvt	N	θ_S	H	Hap	Pvt	N	θ_S	H	Hap	Pvt
Shallow-water species															
Blue	22	9.876	0.974	17	15	23	13.005	0.992	21	20	28	13.877	0.979	23	20
Black	24	4.552	0.862	14	12	19	3.433	0.877	12	10					
Olive	30	6.815	0.908	19	10						33	7.885	0.964	12	3
Copper	18	6.396	0.895	13	12	18	7.850	0.987	16	15	9	12.142	0.972	8	8
Gopher	18	12.211	0.994	18	17						26	12.841	0.982	23	22
Brown	23	5.961	0.957	16	9						29	4.329	0.946	18	11
Deep-water species															
Yellowtail	27	4.151	0.926	17	11	18	4.361	0.922	13	11	22	4.664	0.974	17	11
Widow	15	7.996	0.857	11	9						36	13.746	0.929	22	20
Bocaccio	10	3.535	0.867	7	5						14	4.088	0.879	9	7
Starry	27	13.232	0.983	10	4						28	11.307	0.989	20	14
Vermilion	16	3.315	0.817	22	17						47	14.943	0.899	25	20

The number of haplotypes (Hap) and the number of those not found in any other population (private haplotypes; Pvt) are also shown for each population

Results

We collected mtDNA sequence and microsatellite genotype data from 578 individuals of 11 species from three locations along the west coast of North America to discern major patterns of population structure across species and compare these with biogeographic and ecological differences. Because all species do not range across the sampling area, and because some species are rare at their range edges, only three of 11 species were compared across all three sites. One species, black rockfish, is not found in Santa Barbara and was only compared to the north of Monterey. Seven species were rare or unavailable from Oregon and were compared to the south of Monterey. Data were collected for the mitochondrial control region and for 5–7 microsatellites per individual. Samples sizes averaged above 20 individuals per location except for bocaccio and copper rockfish ($N = 12$ and 15 per location, respectively). For these species, we supplement our data in the metadata analysis with published data (Buonaccorsi et al. 2002; Matala et al. 2004). Details are reported in the "Appendix".

Genetic diversity

Haplotype diversity at the mitochondrial control region was high, with average estimates ranging from 0.858 in vermilion rockfish to 0.988 in gopher rockfish. The number of segregating sites within approximately 400 bp of control region sequences within species (θ_S) ranged from 4 to 15. See Table 1 for sample sizes and estimates of diversity by species for the control region data. Neighbor-joining (NJ) trees were constructed for each species using control region sequence from a congener (speckled rockfish, *S. ovalis*) to root the trees. Only in two of the species was there marked clustering of haplotypes by geographic origin. For blue rockfish, the majority of the OR samples of blue rockfish form a clade, which also includes one individual from each of the other populations (Fig. 2a). In yellowtail rockfish, again the tree revealed strong clustering by geographic location (Fig. 2b). Almost all the OR samples form a single clade, which does not include any samples from either of the other populations. One other case of two divergent lineages was evident from the NJ trees: in vermilion rockfish some of our SB samples fall into a deeply divergent mtDNA clade (Fig. 2c). This is discussed further below. Phylogenetic trees for the remaining species showed no strong evidence of clustering by sampling location.

The microsatellite loci showed an average of 9.5 alleles over all loci over all species. Among loci, the number of alleles ranged from 6.4 to 14.0, while among species there were between 4.4 (in widow rockfish) and 13.7 (in vermilion rockfish) alleles per locus. Allelic variation by species and by locus is shown in Table 2. Across species, there was no statistically significant relationship between allelic diversity for microsatellite loci and θ_S values for the control region.

Most microsatellite loci were in concordance with Hardy–Weinberg equilibrium (HWE) in all species except vermilion. In cases where HWE was violated, further analyses

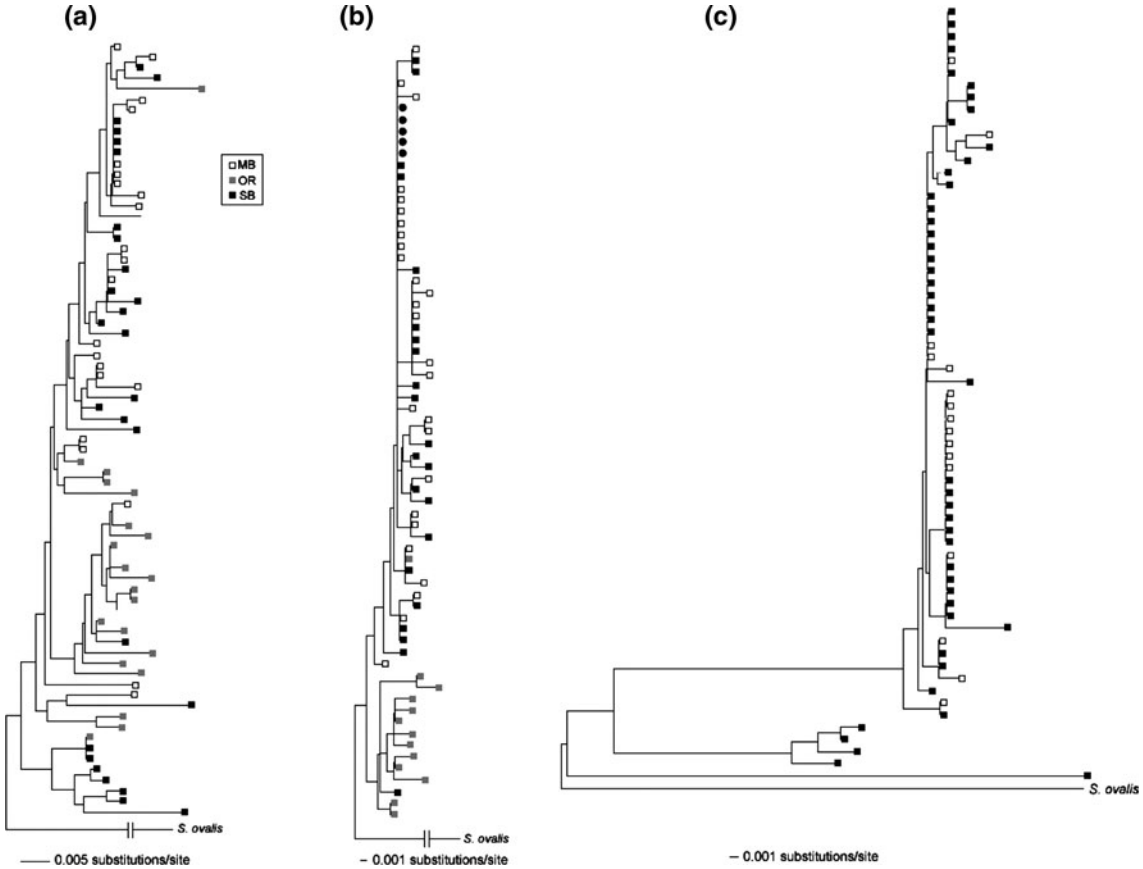


Fig. 2 Neighbor-joining trees of control region sequences for **a** blue, **b** yellowtail and **c** vermilion rockfish

Table 2 The number of alleles at microsatellite loci for 11 species of *Sebastes*

	Sal2	*Sal3*	*Sma2*	*Sma4*	*Sma5*	*Sma10*	*Sra7-2*	*Sra7-7*	Average
Shallow-water species									
Blue	14	7				9	14	12	11.2
Black	7	11	9		12		27	13	13.2
Olive	4	8	12		8	5	15	7	8.4
Copper	9	6	3		4	15			7.4
Gopher	11	13	7		5	20		14	11.7
Brown	4	7	2		6		4		4.6
Deep-water species									
Yellowtail	12	8		14		8	17	13	12.0
Widow	2	5	2		3	11	3	5	4.4
Bocaccio	10	16	7		7	10	9	13	10.3
Starry	3	8	6		6		12		7.0
Vermilion	1	10	10		11	14	18	19	13.7
Average	7.6	9.0	6.4	14.0	6.9	11.5	13.2	12.0	9.5

for those species were conducted both including and excluding the loci that were not in HWE. No linkage disequilibrium was detected between any pair of loci in any of the species.

Strong genetic breaks

Genetic breaks occur in the blue rockfish and the yellowtail rockfish, where strong genetic differentiation (F_{ST} or

Table 3 Summary of population genetic differentiation in 11 species of rockfishes inferred from mitochondrial DNA sequences (Φ_{ST}), microsatellites (F_{ST} and R_{ST}) and assignment tests

	mtDNA	Microsatellites	Assignment test	North	South
Shallow-water species					
Blue (Sebastosomus)	0.19/0.25***	0.11***/	***	Y	N
Black (Sebastosomus)	0.05*/	–	–	Y	n/a
Olive (Sebastosomus)	–	/0.01*	**	n/a	Y
Copper (Pteropodus)	0.021/0.121**	–	–	N	Y
Gopher (Pteropodus)	/0.06*	–	–	n/a	Y
Brown (Pteropodus)	–	/0.02*	**	n/a	Y
Deep-water species					
Yellowtail (Sebastosomus)	0.25/0.01***	0.094/***	***	Y	Y
Widow (Sebastosomus)	–	–	–	n/a	N
Bocaccio	–	–	*	n/a	N
Starry	–	–	–	n/a	N
Vermilion type 2	–	–	–	n/a	N

Values are F_{ST} or Φ_{ST} for northern/southern comparisons, followed by symbols for statistical tests: "***" strong and significant differentiation, "**" moderate differentiation, "*" weak but statistically significant differentiation, "–" no significant differentiation. Only significant values are shown. The geographic location of genetic discontinuities, relative to Monterey Bay, is also shown (north, south: Y = genetic break, N = no break, n/a = comparison not available). Detailed results are presented in "Appendix"

$\Phi_{ST} > 0.1$, $P \ll 0.01$) occurred between Oregon and Monterey. These patterns are clear for both mtDNA and microsatellites in all analyses (Table 3; Fig. 3). Northern mtDNA differences range from 0.19 to 0.25 for these species while microsatellite variation is 0.09–0.11. Between Monterey and Santa Barbara, only the blue rockfish shows strong differences, driven by an mtDNA clade common only in Santa Barbara (Fig. 2). No other strong breaks were recorded among any of the 11 species between Monterey and Santa Barbara.

Weak population structure

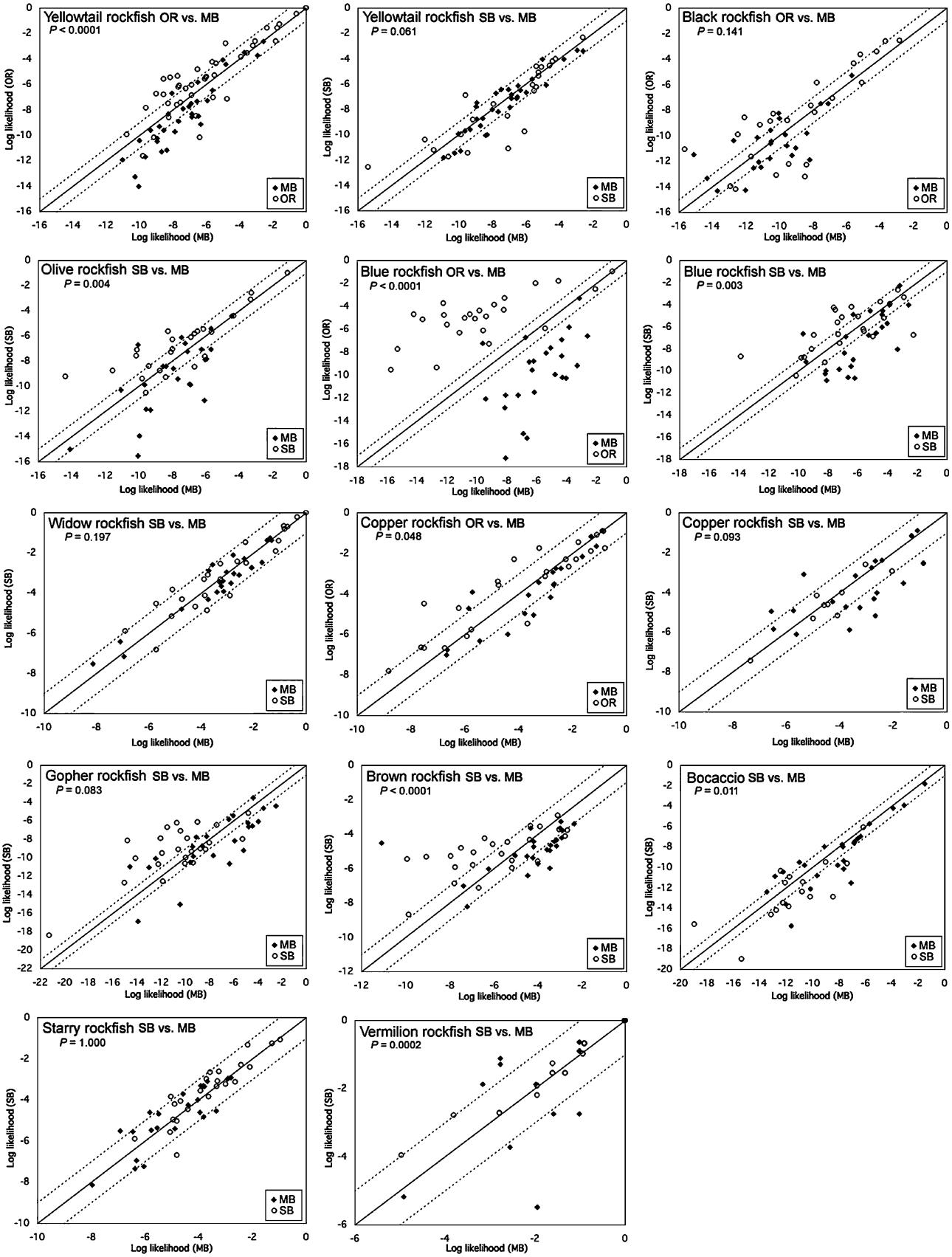
All the shallow *Sebastosomus* species (blue, black and olive) show statistically significant structure in mtDNA, microsatellites or both (Table 3). Among the shallow water *Pteropodus*, copper and gopher rockfish show moderate to slight mtDNA structure but no nuclear structure, and the brown rockfish shows mild nuclear structure without mtDNA differentiation (Table 3).

Except for yellowtail rockfish, deep-water species generally showed little hint of genetic structure. Most other species had no discernable patterns in these tests. An exception is the mild genetic differentiation ($P = 0.011$) in bocaccio seen in our assignment tests (Fig. 3). Other work on this species has also suggested very weak genetic structure along the California coast south of Point Conception (Matala et al. 2004). The vermillion rockfish showed genetic patterns recently revealed to reflect parapartric cryptic species (Hyde and Vetter 2007). We limit our comparison here to vermillion lineage 2, which shows no genetic differentiation between Monterey and Santa Barbara in our small sample. Detailed results for individual species are available in the "Appendix".

Metadata analysis

In addition to the new data on 11 *Sebastes* species collected in this study, data from grass, black-and-yellow, kelp and chilipepper rockfish are available from the literature (Wishard et al. 1980; Buonaccorsi et al. 2004; Narum et al. 2004; Gilbert-Horvath et al. 2006). These data are largely based on microsatellite comparisons of populations along the Washington–Oregon–California coast. To include these data, and in order to summarize our new data from the aforementioned sections, we tabulated comparisons of population differences between Oregon/Washington and Monterey and between Monterey and southern California. We gave each comparison a score of 0, 1 or 2 depending on whether it showed no differentiation, mild differentiation (P values between 0.01 and 0.05) or strong differentiation ($P \ll 0.01$), respectively. We included three kinds of genetic comparisons: mtDNA, microsatellite (F_{ST} or R_{ST})

Fig. 3 Plots of likelihoods of assignment tests showing the likelihoods of individuals belonging to each of populations compared. P values shown on the plots are the probabilities that the observed assignments were the result of chance. The *solid diagonal line* indicates equal probability of being assigned to one population or the other. Points outside the *dotted lines* are assigned to one population with more than ten times the likelihood as the other one ▶


Yellowtail rockfish OR vs. MB
P < 0.0001
Log likelihood (OR)
Log likelihood (MB)
MB
OR
Yellowtail rockfish SB vs. MB
P = 0.061
Log likelihood (SB)
Log likelihood (MB)
MB
SB
Black rockfish OR vs. MB
P = 0.141
Log likelihood (OR)
Log likelihood (MB)
MB
OR
Olive rockfish SB vs. MB
P = 0.004
Log likelihood (SB)
Log likelihood (MB)
MB
SB
Blue rockfish OR vs. MB
P < 0.0001
Log likelihood (OR)
Log likelihood (MB)
MB
OR
Blue rockfish SB vs. MB
P = 0.003
Log likelihood (SB)
Log likelihood (MB)
MB
SB
Widow rockfish SB vs. MB
P = 0.197
Log likelihood (SB)
Log likelihood (MB)
MB
SB
Copper rockfish OR vs. MB
P = 0.048
Log likelihood (OR)
Log likelihood (MB)
MB
OR
Copper rockfish SB vs. MB
P = 0.093
Log likelihood (SB)
Log likelihood (MB)
MB
SB
Gopher rockfish SB vs. MB
P = 0.083
Log likelihood (SB)
Log likelihood (MB)
MB
SB
Brown rockfish SB vs. MB
P < 0.0001
Log likelihood (SB)
Log likelihood (MB)
MB
SB
Bocaccio SB vs. MB
P = 0.011
Log likelihood (SB)
Log likelihood (MB)
MB
SB
Starry rockfish SB vs. MB
P = 1.000
Log likelihood (SB)
Log likelihood (MB)
MB
SB
Vermilion rockfish SB vs. MB
P = 0.0002
Log likelihood (SB)
Log likelihood (MB)

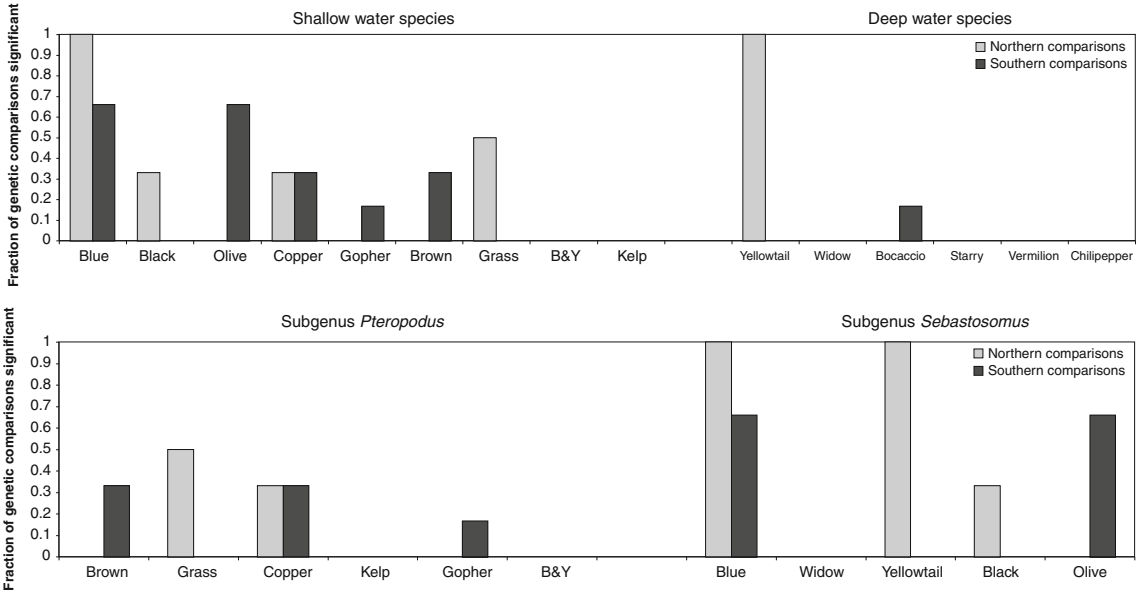


Fig. 4 Prevalence of population substructuring in comparisons to the north and to the south of Monterey Bay among shallow and deep-water species (*top panel*) and among species of the subgenera *Sebastosomus* and *Pteropodus* (*bottom panel*). Results derive from data collected in this study and from the literature. For references to data sources see Table 4

Table 4 Summary of population genetic differentiation in 15 species of rockfishes, using data from this and other studies, inferred from mitochondrial DNA sequences (Φ_{ST}), microsatellites (F_{ST} and R_{ST}) and assignment tests

	Shallow-water species									Deep-water species					
	Blu	Blk	Olv	Cop	Gop	Brn	Grs	B&Y	Kel	Yel	Wid	Boc	Sta	Ver	Chi
mtDNA															
OR–MB	2	1		0						2					
MB–SB	2		0	1	1	0				0	0	0	0	0	
Microsatellite															
OR–MB	2	0		0	0*[1]	0*[2]	1*[3]	0*[1]		2		0			0*[5]
MB–SB	1		1	0	0	0	0*[3]	0*[1]	0*[4]	0	0	0	0		0*[5]
Assignment															
OR–MB	2	0		1						2					
MB–SB	1		1	0	0	2				0	0	1			
Northern	6/6	1/6		1/6	0/2	0/2	1/2	0/2		6/6		0/2			0/2
Southern	4/6		2/6	1/6	1/6	2/6	0/2	0/2	0/2	0/6	0/6	1/6	0/6	0/2	0/2
Northern comparisons	1	0.33		0.33	0	0	0.5	0		1		0			0
Southern comparisons	0.66		0.66	0.33	0.167	0.33	0	0	0	0	0	0.167	0	0	0

Scores of 2, 1 and 0 imply strong differentiation, moderate differentiation and non-significant differentiation, respectively. Data with asterisks derive from other published studies as follows: 1: Narum et al. (2004); 2: Buonaccorsi et al. (2005); 3: Buonaccorsi et al. (2004); 4: Gilbert-Horvath et al. (2006); 5: Wishard et al. (1980)

Blu blue, *blk* black, *olv* olive, *cop* copper, *brn* brown, *grs* grass, *B&Y* black and yellow, *kel* kelp, *yel* yellowtail, *wid* widow, *boc* bocaccio, *sta* starry, *ver* vermilion, *chi* chilipepper

and assignment tests. We divided the score for each case by the maximum possible given the data available. For example, species for which both geographic comparisons and all three types of genetic tests are available can have a maximum score of six.

Nine of 15 rockfish species show some level of population structure north or south of Monterey (Fig. 4). Six of 14 comparisons between Monterey and Point Conception, and five of nine comparisons north of Monterey are significant. The strongest differences are in blue rockfish and in yellowtail

rockfish, both of which show strong differentiation to the north of Monterey. Deep-water species show less structure (two of six species) than shallow-water species (seven of nine species; Fig. 4 upper panel).

However, the data are also consistent with a phylogenetic difference in structure. Species in the subgenus *Sebastosomus* (blue, widow, yellowtail, black and olive rockfish) show higher structure (5 of 7 comparisons, Fig. 4 lower panel) than species in the subgenus *Pteropodus* (5 of 11 comparisons). These patterns remain visible even among shallow-water species but the number of species compares is currently small. Though further data are warranted, the three shallow water *Sebastosomus* for which we have data show as high or higher structure than the six shallow water *Pteropodus* for which data are available.

Discussion

Among 15 species of the rockfish genus *Sebastes*, we find a wide variety of genetic patterns ranging from sharp genetic breaks in all tests for two species to no differentiation in three. The rest shows moderate to slight variation, about equally distributed across Cape Mendicino and Point Conception. These differences are similar in magnitude to those that have been reported among species with large differences in dispersal potential—often among invertebrates or fish with planktonic feeding larvae compared to non-feeding larval types (McMillan et al. 1992; Bernardi 2000, 2005). Yet these *Sebastes* rockfish species share similar traits, namely internal fertilization with pelagic feeding larvae (Love et al. 2002). This variety of genetic patterns across the same coastline for similar species might be explained by a number of life history and other species-specific traits.

Inference based on coarse geographic sampling

The coarse-grained nature of the geographic sampling scheme employed in this study cannot, by design, provide a detailed appraisal of spatial genetic structure within individual species. Instead, it focuses on asking whether genetic structure exists over large distances, and provides a mechanism to collect comparable data sets for many loci across many species. Though this approach provides no data for intervening locations, species lacking genetic differentiation at this broad spatial scale are unlikely to harbor strong hidden structure at finer scales. Cases of strong genetic differentiation in coastal marine species seldom show a patchwork where strongly differentiated populations are interspersed with genetically indistinguishable ones. Possible exceptions may occur when species occur in different habitats such as open coasts and estuaries (Mulvey et al. 2002) or in specific microhabitats (Schmidt and Rand 2001). In European eels, genetic differentiation at some locations has been traced to differences in genetics of settling cohorts, which creates a mild patchwork of genetic structure (Dannewitz et al. 2005). These mild spatially disjunct patterns of genetic differentiation, which also have been described as chaotic patchiness (Planes and Lenfant 2002), may not be detected by our coarse-grained approach though our examination of mtDNA and multiple nuclear loci increases this likelihood.

At the same time, species that do show differentiation at this scale warrant further investigation at finer spatial scales. Detection of strong genetic differentiation from Monterey to Oregon, for example in blue and yellowtail rockfish, leaves open the possibility that the species show abrupt genetic breaks, wide genetic clines or gradual isolation by distance. In each of these cases, reduced larval gene flow is indicated, though the geography of this reduction is likely to be very different for these different patterns. In such cases, finer scale geographic study is warranted. Recently, Burford and Bernardi (2008) traced the fine scale differentiation of blue rockfish to the region around Cape Mendocino. By contrast, study of the fine scale patterns of genetic differentiation in barnacles has shown a 500-km cline in gene frequencies (Sotka et al. 2004). Isolation by distance patterns in rockfish tend to produce relatively low levels of differentiation—often about 0.01 difference in F_{ST} over 1,000–2,000 km (Buonaccorsi et al. 2004)—and so it is less likely that the large differences we see in yellowtail rockfish are due to this mechanism.

Though coarse-grained sampling has drawbacks, the critical value of such an approach is to generate a highly comparative data set across many species where geography and statistical power are controlled for. In this case, differences between species are more likely to be biological in origin rather than artifacts of sampling. In the past, this approach has provided key insights into the determinants of population genetic structure of fish (e.g. Waples 1987; Doherty et al. 1995; Shulman and Bermingham 1995) even without the spatial scale of sampling that is typically employed in investigations of single species. Because marine communities are made up of so many species with such different potential dispersal patterns (Shanks and Eckert 2005) and because the connectivity of species among locations is a primary part of efforts to understand and manage whole marine ecosystems

(Palumbi 2003), data on genetic structure of many species from within an ecosystem are an important future goal. Coarse-grained genetic surveys may be an efficient first step in collecting such data.

Geographic correlates of differentiation

Although the biogeographic break at Point Conception has received the most attention from population geneticists (e.g. Burton 1998; Dawson 2001; Buonaccorsi et al. 2002, 2004), the coast of California is home to a large number of ecological shifts and oceanographic features that may play a role in genetic differentiation. Between Monterey and Oregon, there is a shift in oceanographic conditions that have a strong impact on coastal marine ecosystems (Fig. 1). In Oregon, intermittent upwelling combines high-nutrient pulses with local water retention nearshore, and allows both high larval growth rates and low larval loss offshore. Recruitment is higher by orders of magnitude for coastal invertebrates such as barnacles and mussels (Connolly et al. 2001; Menge et al. 2004). In California, persistent upwelling throughout the summer reduces larval settlement except when occasional upwelling relaxation events allow local larval retention. Major upwelling centers at Cape Mendocino, Point Arena and Santa Cruz in northern California represent major features of the oceanographic landscape and may affect settling marine species.

A number of oceanographic features make Cape Mendocino a particularly likely candidate to reduce connectivity in marine species. This is the area of maximum upwelling within the California Current System (Parrish et al. 1981) because the southern-flowing California Current shifts offshore at this point. Current drifters released near Oregon often move south and then offshore at this point of the coast (Sotka et al. 2004), and as a result, gene flow across this cape may be difficult for species that settle during upwelling conditions. The vicinity of Cape Mendocino is also the area of the local minimum abundances of rockfishes, which are much more common to the north and the south (Gunderson and Sample 1980; Parrish et al. 1981). In addition, the Mendocino Escarpment, a submarine ridge extending out from Cape Mendocino, might limit the amount of nearshore habitat patches available to rockfishes, and serve as a barrier to gene flow (Williams and Ralston 2002; Cope 2004).

Other ecological alterations—some associated with oceanographic differences—occur north of Monterey and cannot be ruled out as correlates of genetic change. The dominant kelp species switches from the perennial *Macrocystis pyrifera* to the annual species *Nereocytis luetkana* (Foster and Schiel 1985), altering the understory algal species, and perhaps changing the nature of nearshore kelp beds where rockfish larvae often recruit. Braby and Somero (2006) described a parallel cline in the dominance of species of bay mussels: *Mytilus gallo-provincialis* is common south of Monterey, and grades into populations dominated by *M. trossulus* to the north. Sotka et al. (2004) described a strong genetic cline in barnacles in this region that is bounded on the north by Cape Mendocino. Overall, the ecological community of California invertebrates shows a marked shift north of Monterey (Blanchette et al. 2008). Our data suggest that tests of geographic concordance of genetic patterns along the west coast of North America expand focus to include Cape Mendicino as a potential barrier to larval dispersal.

Genetic breaks and speciation

One strong genetic pattern south of Monterey was the distinction in mtDNA between populations of vermillion rockfish. A recent study (Hyde et al. 2008) reported the existence of a cryptic species within *S. miniatus*, and our sampling appears to consist of a mixture of the two types. We sequenced a portion of the cytochrome *b* gene in order to assign our samples to the types described by Hyde et al. (2008). The divergent SB samples correspond to their "Type 1", while all other samples correspond to their "Type 2". Consistent with their study, Type 1 samples were only found from our site south of Point Conception (SB), while Type 2 was found at both sites. Confining our genetic comparison to the Type 2 'species', we saw no significant difference between Monterey and Santa Barbara.

However, there are unexplained patterns of microsatellite variation in our samples. Most microsatellite loci were out of Hardy–Weinberg equilibrium, showing a strong deficit of heterozygotes even in Monterey where the Type 2 'species' is thought to be allopatric. Analysis with STRUCTURE did not suggest that the nuclear data could be separated into two gene pools, as might be expected if there were two species in Monterey. Dividing the Santa Barbara sympatric population into two on the basis mtDNA lineages did not restore HWE in that location. Both these results suggest that there may be genetically distinct sub-populations of vermillion rockfish left to be discovered, that hybrid genotypes may be strongly selected against, or that mtDNA lineages may not be a perfect indication of species status.

Across Cape Mendicino, a combination of species range summaries, and genetic patterns suggest a similar generation of new species. This geographic feature not only divides species phylogeographically but also marks the shift in numerical dominance among sister species.

Yellowtail rockfish (*S. flavidus*) are commonly found from Alaska to southern California (Love et al. 2002), whereas its sister species pair, black and olive rockfishes tends to divide the latitudinal range: olive rockfish (*S. serranoides*) occur most commonly between Cape Mendocino and Santa Barbara, while black rockfish (*S. melanops*) are common from Alaska south to northern California, becoming increasingly uncommon further south (Love et al. 2002) (Fig. 5). The part of the coast where these two sister species still overlap coincides with the major biogeographic break in yellowtail rockfish as well as the closely related blue rockfish (*S. mystinus*; Fig. 5). It is possible that olive and black rockfish represent a more advanced stage in the speciation process than seen within blue rockfish or within yellowtail rockfish, and that in each of these cases, the same geographic factors are at work to limit intraspecific gene flow and spark species differentiation.

Links between species traits and genetic structure

Our data show a wide variety of genetic patterns among similar species across a similar geographic range. This basic result suggests a wide range of realized dispersal distances among species with similar life histories, and allows an examination of the relationship between species traits and genetic structure.

Cladogenesis rates

Unlike the situation for other marine species, in which rapid speciation is associated with high-population structure (Hansen 1982; Jablonski and Lutz 1983; Duda and Palumbi 1999), we see no such correlation here. Based on the phylogeny and levels of genetic differentiation summarized in (Hyde and Vetter 2007), the rapidly diversifying *Sebastosomus* clade includes many species with intense-to-moderate-population structure (blue, yellowtail, black, olive), but the *Pteropodus* clade, diversifying at least as quickly, tends to have low structure (gopher, kelp rockfish, black-and-yellow). Boccacio in its monotypic clade has little structure, but so too does the starry rockfish within its quickly diversifying group. There are numerous reasons why speciation rate and population structure may not correlate: (1) species may be so recent that they extend over small ranges and have little structure yet, (2) recent range expansions after the last glacial maximum may have obscured structure (e.g. Hellberg et al. 2001), (3) species may not form by exclusively allopatric mechanisms, and so the link between dispersal rate and species divergence that drives correlations in other taxa may be broken.

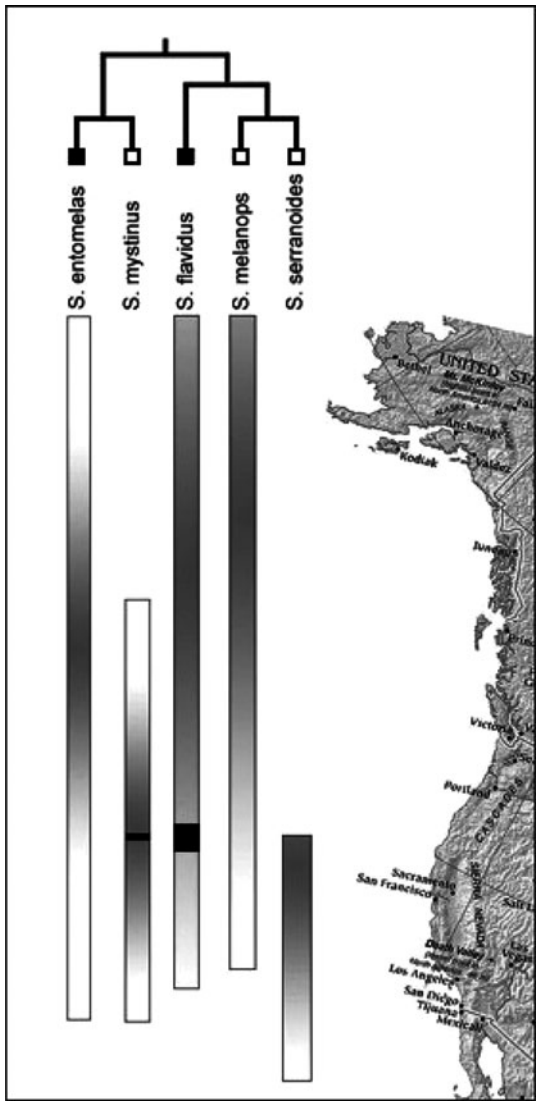


Fig. 5 The biogeography of rockfish in the subgenus *Sebastosomus* (*filled black squares* for deep-water species, *open squares* for shallow-water species) in northern California shows genetic breaks and sister species separation at Cape Mendocino. *Vertical bars* mark the latitudinal range of five species—*shading* is an approximate index of density from highest (*darkest*) to lowest (*white*). *Black* areas within ranges represent genetic breaks; their widths are determined by the extent of geographic resolution of exact breakpoints that are available from current studies. The phylogeny is based on mitochondrial cytochrome *b* (Hyde and Vetter 2007) and control region sequences

Larval duration

Genetic structure is higher in the subgenus *Sebastosomus*, with a longer pelagic larval duration than in species within the subgenus *Pteropodus* which have shorter larval durations (Carr and Syms 2006). This counter-intuitive result might suggest that current information on larval

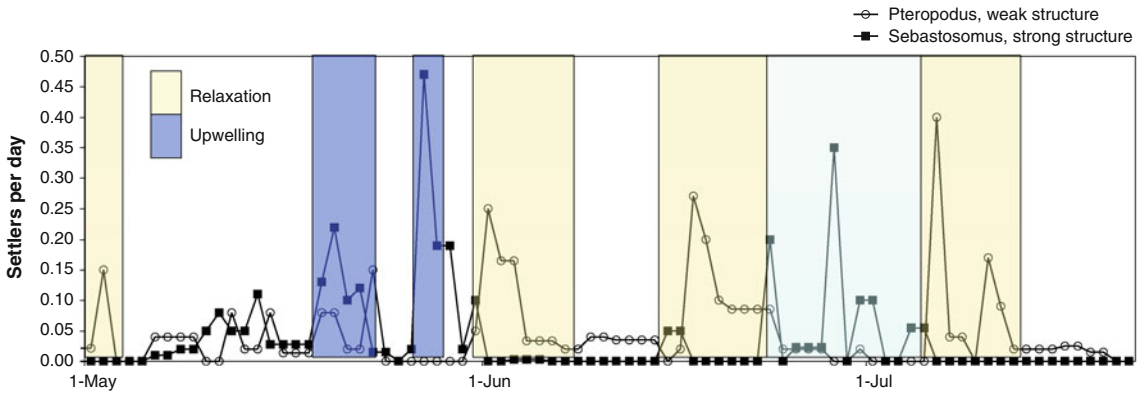


Fig. 6 Settlement patterns of the Sebastosomus clade with strong coastal population structure versus the Pteropodus clade with weak population structure. Species with weak structure appear to settle during warm water periods when upwelling has stopped, perhaps indicating that these larvae are brought into shore by relaxation of offshore current structures, and hence have high dispersal. Species with strong structure appear to settle in the midst of strong upwelling, indicating poorer ability to cross from one upwelling center to another

durations could reward reexamination. Data on larval duration often compares spawning seasons with settlement seasons (Love et al. 2002; Carr and Syms 2006) rather than being based on direct measurement of larval pelagic phase (but see Miller and Shanks 2004). It is possible that refined measurements of pelagic duration will explain the patterns we present.

Settlement behavior

For three species of *Sebastosomus* with moderate to strong structure, yellowtail, olive and black rockfish, larvae are known to recruit during cool water regimes associated with strong upwelling (Lenarz et al. 1995; McManus et al., in preparation; Carr and Syms 2006). By contrast, three closely related species of *Pteropodus* with zero or low genetic structure—kelp, black-and-yellow, and gopher—settle best under the opposite oceanographic conditions, during times of upwelling relaxation when coastal waters warm substantially (Fig. 6). These data are somewhat surprising because they suggest that larvae adapted to settle during conditions of strong upwelling tend not to travel far along the coast, even though upwelling is usually associated with strong larval movement.

One possible explanation is that the intense and consistent upwelling at Cape Mendocino may result in movement of larvae far offshore where they have little chance of return to the coast. Moderate upwelling, by contrast, allows the formation of thin layers of relatively slow-moving water that lie at the interface of surface outgoing and deep incoming water. Phytoplankton and zooplankton tend to accumulate in these areas (McManus et al. 2005), which may be a microhabitat of abundant food. Movement of plankton in these layers has been modeled to be up to ten times slower than just outside these layers (McManus et al. 2005), and so larval behavior mechanisms may play a major role in controlling rockfish settlement patterns. We know of no exploration of species identities of rockfish larval in thin layers, but such a study may allow a test of these ideas.

For species that settle during relaxation conditions, when warmer water persists near shore, two hypotheses have been presented about the origin of larvae. In some cases, these larvae may move from far offshore, being brought back toward the coast when the offshore pressure from upwelled water ceases. In these cases, the larvae have probably come from parents far away. In other cases, the larvae that settle may be local larvae that have not been pushed offshore by upwelling. These 'lucky' local larvae may be the ones to survive and settle, coming from nearby adult populations. The association in our data between settlement during relaxation and low-population structure suggests the lucky local larval hypothesis is not correct for these species and that relaxation events bring in larvae from far away. Buonaccorsi et al. (2004) estimated this dispersal distance as 13 km or less for grass and copper rockfish based on Rousset's (1997) stepping stone model. This value, however, is highly sensitive to the ratio of total population size to effective population size. Whether this pattern exists in other species that settle during relaxation conditions is not known.

Conclusions and caveats

Findings from broad-ranging, coarse-grained multispecies studies such as this one come with caveats. First, when comparing several species, as we have done, using the same battery of molecular markers, there is a distinct possibility of ascertainment bias-population structure or the lack thereof could arise as an artifact of using markers developed in one species to study another species. Second, variation between markers can be important. The extent of population structure inferred from a molecular marker can

be influenced by heterozygosity at that marker {Hedrick, 2005 #600}. Third, in some cases sample sizes can be limited, mainly by practical considerations. Despite these caveats, some patterns stand out, and given the geographic coarseness and the phylogenetic breadth of our sampling, we believe these represent real trends.

In conclusion, very different population structures among very similar fish species provide a strong suggestion that simple models of movement of ocean populations based on planktonic period may not be valid. Instead the link between fish biology and movement patterns comes from the combination of fish settlement monitoring in Monterey Bay and the tracking of ocean upwelling. Data from these sources show an unexpected difference between genetically divergent and genetically homogeneous fish species. The genetic results show that not all rockfish species disperse the same way across the same seascape. The oceanographic and settlement results point to strong hypotheses about why these species are so different, and suggest ways of extending the insight from genetics to others species for which genetic data are unavailable. Without the combination of genetics, ecology and oceanography, our efforts to measure dispersal would result in a complex list of very different results. Combining these approaches delivers us a potential mechanistic explanation of the genetic results, and allows us to make predictions that can lead to greater understanding of the role of marine-protected areas of different size or spacing.

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Appendix: Results for individual species

(1) Population structure in shallow-water species

Blue rockfish S. mystinus

The large estimates for Φ_{ST} between OR and MB populations of blue rockfish (0.2468; $P < 0.05$) and between OR and SB populations (0.1862; $P < 0.05$), but not between MB and SB (0.0235; not significant) reflect the clustering evident in the phylogenetic tree. In concordance with the results from control region data, microsatellite data revealed strong genetic differentiation between OR and the other populations of blue rockfish at every individual locus. Assignment tests further corroborated these patterns. Differentiation between OR and MB was extremely strong and highly significant ($P < 0.0001$), and present but less marked between SB and MB ($P < 0.003$).

Black rockfish S. melanops

For black rockfish, there was a small but significant genetic differentiation between MB and OR ($\Phi_{ST} = 0.045$; $P < 0.05$). A single microsatellite locus, *Sra7-7*, showed significant differentiation between MB and OR populations of black rockfish ($F_{ST} = 0.029$; $P < 0.05$). None of the other loci revealed significant differentiation between the populations, and nor did joint analysis of all loci. Assignment tests corroborated these patterns, with genotype assignment not significantly different from random ($P = 0.141$).

Olive rockfish S. serranoides

For olive rockfish samples from MB and SB, there was little evidence of mtDNA differentiation ($\Phi_{ST} = 0.010$; not significant). As with black rockfish, the microsatellite locus, *Sra7-7,* also showed a statistically significant estimate of genetic differentiation between MB and SB populations. When all loci were jointly analyzed for this species, however, there was weak, but statistically significant differentiation ($F_{ST} = 0.010$; $P < 0.05$) between populations. Assignment of genotypes to populations in this species was significantly non-random ($P = 0.004$).

Copper rockfish S. caurinus

The OR and MB populations were both genetically differentiated from the SB populations for mtDNA ($\Phi_{ST} = 0.072$ and 0.121, respectively, $P < 0.05$), but the MB and OR populations could not be distinguished from each other ($\Phi_{ST} = 0.021$). Microsatellite data from copper rockfish from three locations did not reveal the genetic differentiation: one locus was significantly different between OR and SB (*Sma10*; $F_{ST} = 0.065$; $P < 0.05$), but joint analyses did not support this, or any other pairwise differentiation. The assignment tests, however, showed a slight differentiation between OR and MB populations, but not between MB and SB. Though our sample sizes are low for this species, similarly low genetic differentiation was reported by Buonaccorsi et al. (2002), who found only slight differentiation among populations from northern to southern California ($F_{ST} = 0.009$, $P < 0.003$).

Gopher rockfish S. carnatus

There was evidence for mild genetic differentiation in Gopher rockfish mtDNA ($\Phi_{ST} = 0.064$; $P < 0.05$). However, joint analysis of all microsatellite loci did not reveal any significant differentiation between these populations nor did genotype assignments differ significantly from random expectations ($P = 0.083$).

Brown rockfish S. auriculatus

In the third species in this subgroup, there was no significant mtDNA differentiation. Populations of brown rockfish from MB and SB were significantly differentiated at the microsatellite locus *Sma5* ($F_{ST} = 0.092$; $P < 0.05$), but not at any of the other loci. When the five loci were combined, however, there was a significant genetic difference between populations ($F_{ST} = 0.022$; $P < 0.05$). There was also a highly significant difference between populations as assessed by the assignment test ($P < 0.0001$).

(2) Population structure in deep-water species

Only the yellowtail rockfish showed structure in our survey of five deep-water species, and this structure was very high. However, vermillion rockfish showed a striking pattern of deviation from Hardy–Weinberg equilibrium, and the presence of strikingly different mtDNA clade in Santa Barbara that suggests multiple gene pools in these collections.

Yellowtail rockfish S. flavidus

The differentiation of mtDNA of yellowtail rockfish from OR and the other populations is borne out by the large estimates for Φ_{ST} between OR and MB (0.2542; $P < 0.05$) and between OR and SB (0.1909; $P < 0.05$), but not between MB and SB (−0.0141, not significant). As with control region data, microsatellite data from yellowtail rockfish again revealed strong evidence of genetic differentiation between MB and OR samples. There was significant differentiation between these two populations at three of the loci considered individually (*Sal2*, *Sra7-2* and *Sma4*), and when all loci were considered jointly, excluding one locus that was not in HWE, there was high and significant differentiation whether measured as R_{ST} (0.028; $P < 0.05$) or F_{ST} (0.094; $P < 0.05$). The same three loci also showed some differentiation between SB and OR, but joint analysis of all loci did not yield any significant differentiation between these populations. Between MB and SB, a single locus (*Sal2*) had a significant R_{ST} value. Results from the assignment tests revealed the same patterns. Differentiation between OR and MB was marked and highly significant ($P < 0.0001$), while MB and SB were not significantly differentiated ($P = 0.061$).

Widow rockfish S. entomelas

The widow rockfish showed no patterns of genetic differentiation. There was no evidence for mtDNA differentiation between the populations ($\Phi_{ST} = -0.024$). Microsatellite loci also failed to reveal any differentiation among populations either. A single locus, *Sma10*, differed slightly between populations ($F_{ST} = 0.087$; $P < 0.05$). Joint analysis of all loci failed to reveal differentiation between the populations, whether examined by F_{ST} and R_{ST} or by assignment tests ($P = 0.197$).

Bocaccio S. paucispinis

Bocaccio had lower haplotype diversity than most other species, and there was no evidence for mtDNA differentiation between MB and SB ($\Phi_{ST} = -0.019$). With microsatellites, bocaccio from MB and SB showed only slight differences between populations. While joint analysis of microsatellite loci failed to reveal genetic differentiation using *F*-statistics, a single locus differed between populations ($F_{ST} = 0.081$; $R_{ST} = 0.109$; $P < 0.05$). Genotype assignment tests, however, were significantly non-random in assigning individuals to their populations of origin ($P = 0.011$). Matala et al. (2004) used microsatellites to show low but significant differentiation of bocaccio along the California coast…

Starry rockfish S. constellatus

Starry rockfish exhibited high haplotype diversity ($H = 0.986$) with only two haplotypes shared between the populations, as opposed to 17 (in MB) and 20 (SB) private haplotypes. One of the MB haplotypes, which occurs twice in those samples, was highly divergent from all others. There was also no evidence of genetic differentiation between the populations ($\Phi_{ST} = 0.000$). Starry rockfish was the only species which failed to reveal any evidence of population substructuring, whether microsatellite loci were considered individually or jointly. The same was true of the assignment tests, where genotype assignments occurred exactly as expected by chance ($P = 1.000$).

Vermilion rockfish S. miniatus

A number of unusual patterns emerged for vermilion rockfish (Table 5).

Table 5 Pairwise measures of population differentiation in *Sebastes* spp

Blue		MB vs OR	MB vs SB	OR vs SB	N (MB)	N (OR)	N (SB)
Sal2	F_{ST}	***0.1249***	***0.0341***	*0.0271*	23	18	23
	R_{ST}	**0.6164**	**0.2162**	**0.246**	0.913	0.5	0.565
Sal3		***0.1129***	***0.0475***	*0.0131*	15	20	17
		0.0006	0.0577	-0.0142	0.933	0.7	0.706
Sma10		***0.1703***	*0.0238*	***0.1791***	18	20	20
		0.1306	-0.0265	**0.14**	0.667	0.75	0.619
Sra7-2		***0.2124***	*0.0098*	***0.1301***	14	15	17
		-0.0149	0.0212	**0.1247**	0.786	0.533	0.882
Sra7-7		***0.0861***	*-0.0058*	***0.0953***	16	14	17
		-0.032	-0.0174	-0.0287	0.875	0.625	0.857
All loci		***0.084***	*0.003*	*-0.0193*			
		0.459	**0.1828**	**0.0901**			
Loci in HWE		***0.1468***	***0.0216***	***0.1076***			
		0.0098	0.0005	**0.0629**			
Control region	F_{ST}	**0.2468**	0.0235	**0.1862**	22	23	28

Black	MB vs OR	N (MB)	N (OR)
Sal2	*-0.0055*	23	20
	-0.0239	0.348	0.15
Sal3	*0.0088*	21	17
	-0.0272	0.952	0.706
Sma2	*0.0023*	20	22
	-0.0163	0.75	0.909
Sma5	*0.0035*	23	23
	-0.007	0.783	0.957
Sra7-2	*-0.0126*	24	16
	-0.0159	1	1
Sra7-7	***0.0287***	23	20
	0.0251	0.826	0.9
All loci	*-0.0161*		
	0.0109		
Control region	**0.0451**	24	19

Olive	MB vs SB	N (MB)	N (SB)
Sal2	*0.0066*	20	19
	0.0063	0.65	0.842
Sal3	*-0.0019*	23	19
	0.0188	0.87	0.895
Sma2	*0.0082*	23	22
	-0.0037	0.957	0.864
Sma5	*0.0227*	23	21
	-0.0143	0.696	0.429
Sma10	*-0.0181*	23	22
	-0.0227	0.739	0.909
Sra7-2	*0.0069*	19	18
	0.0074	0.947	0.778
Sra7-7	***0.0542***	21	19
	-0.0116	0.571	0.778
All loci	***0.0101***		
	0.0153		
Loci in HWE	***0.0196***		
	0.0142		
Control region	0.0104	30	33

Table 5 continued

Copper	MB vs OR	MB vs SB	OR vs SB	N (MB)	N (OR)	N (SB)
Sal2	*-0.0264*	*0.0353*	*0.0629*	15	16	9
	-0.0222	0.0419	-0.0263	0.667	0.563	0.889
Sal3	*0.0332*	*-0.0288*	*0.0292*	16	16	9
	-0.0287	-0.0399	-0.0329	0.875	0.625	1
Sma2	*-0.0111*	*-0.0201*	*0.0099*	17	17	9
	0.0152	-0.0442	-0.0076	0.176	0.118	0.333
Sma5	*0.0147*	*-0.0023*	*-0.0319*	17	17	9
	-0.027	-0.0023	-0.0156	0.294	0.176	0.111
Sma10	*0.0055*	*0.0107*	***0.0651***	23	21	9
	-0.0179	0.0874	0.1319	0.957	0.905	0.778
All loci	*0.0068*	*-0.0137*	*0.034*			
	-0.056	-0.0459	-0.0236			
Control region	0.0209	**0.1214**	**0.0719**	18	18	9

Gopher	MB vs SB	N (MB)	N (SB)
Sal2	*-0.001*	24	23
	0.1238	0.667	0.696
Sal3	***0.041***	23	24
	0.0134	0.783	0.75
Sma2	*0.0022*	21	20
	-0.0121	0.524	0.55
Sma5	***0.091***	22	21
	0.0491	0.636	0.381
Sma10	*0.0143*	12	21
	-0.0333	0.917	0.857
Sra7-7	***0.0303***	16	23
	0.2569	0.625	0.913
All loci	*0.006*		
	-0.0612		
Control region	**0.0642**	18	26

Brown	MB vs SB	N (MB)	N (SB)
Sal2	*0.0378*	24	23
	-0.0148	0.375	0.391
Sal3	*0.0237*	23	24
	-0.0136	0.696	0.917
Sma2	*-0.0212*	23	19
	-0.0212	0.435	0.579
Sma5	***0.0924***	23	19
	-0.0245	0.478	0.579
Sra7-2	*0.005*	18	21
	-0.0255	0.5	0.667
All loci	***0.0221***		
	-0.0202		
Control region	0.0055	23	29

Yellowtail	MB vs OR	MB vs SB	OR vs SB	N (MB)	N (OR)	N (SB)
Sal2	***0.0689***	*-0.0086*	***0.0356***	25	29	22
	0.1712	**0.0584**	0.0241	0.92	0.724	0.864
Sal3	*-0.0016*	*-0.0116*	*-0.0109*	32	32	21
	-0.007	-0.0183	-0.0028	0.719	0.75	0.619
Sra7-2	*0.0191*	*0.015*	*0.0273*	26	6	16
	0.2256	-0.0246	0.2163	0.654	0.767	0.875
Sra7-7	*-0.0036*	*0.0242*	***0.0734***	30	34	23
	0.042	0.0279	**0.1742**	0.852	0.862	1
Sma4	***0.0373***	*-0.0073*	***0.0417***	26	30	16
	-0.0166	0.0293	0.0091	0.654	0.5	0.688
Sma10	*0.016*	*-0.014*	*0.0045*	27	29	15
	-0.0172	-0.0199	-0.0233	0.5	0.529	0.435

Table 5 continued

All loci	*-0.0456*	*-0.0083*	*-0.03*			
	0.0449	0.0227	-0.0006			
Loci in HWE	***0.0275***	*-0.0213*	*0.0058*			
	0.0944	0.0321	0.0241			
Control region	**0.2542**	-0.0141	**0.1909**	27	18	22
Widow	MB vs SB	N (MB)	N (SB)			
Sal2	*0.026*	22	21			
	0.026	mono	0.09524			
Sal3	*0.0045*	20	19			
	0.012	0.65	0.84211			
Sma2	*0.0102*	22	16			
	0.0102	mono	0.0625			
Sma5	*0.0059*	22	20			
	0.0255	0	0.05			
Sma10	***0.0865***	22	19			
	-0.0245	0.68182	0.57895			
Sra7-2	*-0.0134*	24	16			
	-0.0205	0.45833	0.1875			
Sra7-7	*-0.0072*	22	14			
	-0.029	0.54545	0.64286			
All loci	*0.0127*					
	-0.0265					
Control region	-0.0238	15	36			
Bocaccio	MB vs SB	N (MB)	N (SB)			
Sal2	*0.0056*	20	15			
	-0.0181	0.95	0.8			
Sal3	*0.0087*	17	12			
	-0.0209	0.588	0.583			
Sma2	*-0.0095*	24	16			
	-0.0239	0.917	0.625			
Sma5	*-0.0033*	24	16			
	0.0254	0.625	0.625			
Sma10	***0.0805***	19	16			
	0.1085	0.684	0.875			
Sra7-2	*-0.0183*	20	14			
	-0.0172	0.9	0.929			
Sra7-7	*-0.017*	20	13			
	-0.0105	0.75	1			
All loci	*-0.0013*					
	-0.0008					
HWE loci	*-0.0036*					
	0.0089					
Control region	-0.0189	10	14			
Starry	MB vs SB	N (MB)	N (SB)			
Sal2	*0.0411*	22	18			
	0.0238	0.182	0.5			
Sal3	*-0.0142*	24	17			
	-0.0245	0.708	0.588			
Sma2	*0.0014*	23	20			
	-0.0231	0.435	0.4			
Sma5	*-0.0166*	24	21			
	-0.0128	0.583	0.571			
Sra7-2	*0.0039*	20	17			
	-0.0235	0.7	0.765			
All loci	*-0.0183*					
	-0.0286					
Control region	0.0002	27	28			

Table 5 continued

Vermilion	MB vs SB	N (MB)	N (SB)
Sal2	*0*	16	27
	0	mono	mono
Sal3	***0.1723***	14	24
	0.237	0.571	0.708
Sma2	*-0.0122*	14	30
	-0.0242	0.643	0.567
Sma5	*0.0137*	14	27
	0.0275	0.429	0.741
Sma10	*0.0098*	15	19
	0.0893	0.733	0.737
Sra7-2	*0.0406*	13	17
	-0.009	0.615	0.824
Sra7-7	*0.0087*	9	26
	-0.0386	0.556	0.769
All loci	*0.0049*		
	0.0456		
Loci in HWE	*0.0098*		
	0.0893		
Control region	0.0068	16	47

For each pairwise comparison, measures of F_{ST} (in italics) and R_{ST} are given for individual microsatellite loci, as well as joint analysis of all loci. In instances where loci were not in HWE, results are presented with and without those loci included in the analyses. The last line of each section shows pairwise Φ_{ST} for control region sequences. Values in bold indicate statistical significance ($P < 0.05$). The columns following the pairwise comparisons list sample sizes for each locus for each population (first row) and observed heterozygosity at that locus for that population (second row). Gray shading indicates non-conformance with HWE for that locus in that population. None of the comparisons based on individual microsatellite loci is significant after Bonferroni correction for multiple comparisons

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