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RESEARCH ARTICLE

Genetic heterogeneity in a single year-class from a panmictic population of adult blue rockfish (*Sebastes mystinus*)

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Abstract We used microsatellite genetic markers to investigate adult population structure and the formation of a new year-class in *Sebastes mystinus* (blue rockfish). Since *S. mystinus* may live as long as 45 years and reach reproductive age at approximately 5 years, the adult population may contain as many as eight generations of reproductive adults. We investigated whether the juveniles of the 2000 year-class and the adult population were genetically homogeneous along the California coast. We sampled approximately 100 juveniles from three sites, two sites along the Monterey Peninsula (Carmel and Monterey) in central California and one at Fort Ross in northern California, and approximately 50 adult *S. mystinus* from five sites throughout the population center. The adult sampling spanned approximately 700 km from the northern Channel Islands to Fort Bragg. The juveniles showed significant heterogeneity in allele frequencies among distant locations and genetic homogeneity among adjacent locations. In contrast, the adults showed genetic homogeneity over large distances (San Miguel Island to Fort Bragg), indicating little limitation of gene flow in this region. Allele frequencies of juveniles differed from adult samples and in some cases reduced genetic diversity indicative of sweepstakes recruitment (small sample of the adult reproductive potential). The genetic structure of the 2000 year-class suggests that despite a genetically homogenous adult population, settled juveniles can be genetically heterogeneous along the California coast. The results also suggest that the adults, with several year-classes, are capable of maintaining a panmictic population despite the genetic distinctiveness of individual year-classes.

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Introduction

Understanding the spatial pattern of gene flow and movement of individuals among populations is critical for assessing impacts of fishing on genetic composition and diversity of a stock, for identifying relative contributions of local populations to replenishment of others, and to determine how such spatial patterns vary through time (Allendorf et al. 1987; Bagley et al. 1999). Such knowledge is essential for developing conservation and management strategies for marine populations (Avise 1994; Bagley et al. 1999; Moberg and Burton 2000).

Analyses of the genetic structure of marine organisms with pelagic larvae measure both the level of realized connectivity among populations of the species and evolutionary and ecological time-scale events that shaped the observed genetic signature. While dispersal of larvae may lead to genetic continuity through much of the range (see Waples 1987), oceanographic processes, geographic barriers, ecological factors (e.g., timing of spawning), or a combination of processes could contribute to isolation of populations (see Avise

1994). These processes could lead to genetic differentiation even in species with long pelagic phases and could be important in understanding the persistence of marine populations (Allendorf et al. 1987; Avise 1992; Moberg and Burton 2000).

Currently, there are mixed results on the correlation between dispersal ability and genetic differentiation in marine species (Waples 1987; Hedgecock et al. 1994; Palumbi 1995 and 2003). Resolving the discrepancy between dispersal estimates in the field and population genetic studies is critical for the management of marine species. A complicating factor in evaluating dispersal in marine populations is year-to-year variability in dispersal and survival of the young-of-the-year. Occasional but repeated episodes of long-distance dispersal (Cowen 1985; Pringle 1986; Richardson and Cowen 2004), smaller-scale variation in dispersal (Cowen 1985; Wing et al. 2003), and spatial variation in patterns of survival through the pelagic phase (Lasker 1978; Sakuma and Ralston 1995) mean that sources of young-of-the-year may vary over time. While many marine populations with pelagic larvae may show genetic differences on relatively large geographic scales (e.g., Buonaccorsi et al. 2002, 2004; Cope 2004), understanding year-to-year and smaller spatial-scale variability can only be analyzed by assessing the genetic structure of individual year-classes.

In species like rockfishes (family Scorpaenidae), in which the adult population consists of many generations, the genetic composition of the adult population reflects many year-classes, produced under a variety of conditions that affect the mating of adults and dispersal and survival of larvae. In contrast, the genetic composition of an individual year-class is not integrated over multiple years and indicates the effect of factors acting at the time of year-class formation. Therefore, an analysis of the genetic structure of a particular year-class will be critical for understanding dispersal potential of a given adult population in any particular year. Since young-of-the-year reflect the genetic output of an adult population at a given time, spatial or temporal variation in settling juveniles may reveal oceanographic, behavioral, or life history factors that influence larval dispersal and survival (Moberg and Burton 2000).

Several studies indicate that even marine species with substantial larval dispersal capabilities [long pelagic larval durations (PLDs)] can show population heterogeneity in the northeastern Pacific coast of the United States (Hedgecock 1994a; Hedgecock et al. 1994; Edmands et al. 1996; Moberg and Burton 2000; Flowers et al. 2002). Genetic patchiness among locations could be explained by settlement of individuals that represent just a small portion of the genetic composition of the adult population (via a bottleneck in larval survival or reproductive output among adults), by natural selection that may occur either before or after settlement, or settlement of juveniles comprised of patches from different parts of a genetically divergent adult population. If there is variation within a region and this variation changes between years, processes acting prior to settlement may be responsible for the variation (natural selection—Johnson and Black 1982, 1984; genetic drift or ''sweepstakes'' recruitment—Hedgecock 1994a, b). Alternately, a consistent pattern over years in the genetic variation observed after settlement may suggest the effects of post-settlement selection or local adaptation within the species range (Johannesson et al. 1995). In the case of sweepstakes recruitment (larval or spawner bottleneck), there should be a decrease in genetic variation, genetic heterogeneity, or both when comparing adult and juvenile stages.

Many marine organisms, including most of the nearshore rockfish species, are sedentary as adults and have larvae that are pelagic for weeks to months, allowing the potential for dispersal over long distances. In this paper we characterize and compare the genetic structure of adults and one year-class of juveniles in the blue rockfish, *Sebastes mystinus*. *S. mystinus* resides in rocky subtidal habitats in nearshore areas from northern Baja California to Vancouver Island (Love et al. 2002), and is a very significant member of the sport fishery in California (Leet et al. 2001; Love et al. 2002). In northern California, O'Farrell and Botsford (2005) reported that *S. mystinus* and several other nearshore rockfish declined to 30% of their 1980 stock levels. Several species of rockfish currently suffer from overfishing, and remediation may be required to replenish the depleted stocks. The population center for *S. mystinus*, an area with the largest population numbers, is along the central and northern California coast from the northern Channel Islands to Fort Bragg (Leet et al. 2001; Love et al. 2002). Tagging studies indicate that individual adults of *S. mystinus* move only short distances, if at all (< 1–2 km) (Miller and Geibel 1973). Juveniles are also reported to settle to a given portion of a reef and remain at that location (Miller and Geibel 1973; Leet et al. 2001). After the protracted pelagic phase (4 months), juveniles settle approximately from April through July (Wyllie-Echeverria 1987). *S. mystinus* reaches a maximum age of 45 years and reproductive maturity at approximately 5 years of age (Laidig et al. 2003). Therefore, adult populations of this species may contain as many as eight generations and 40 reproductive year-classes. Due to these life-

history traits, which are common to many other temperate reef fishes, *S. mystinus* is an appropriate subject to address the characteristics of larval dispersal and the contribution of the adult population to a given year-class. Cope (2004) found evidence for large-scale genetic differences of adult *S. mystinus* throughout its range. While we do assess genetic differences among adults in the central portion of the range of *S. mystinus*, we do so primarily as a point of comparison for the genetic composition and diversity of young-of-the-year.

In analyzing genetic structure in juveniles and adults of *S. mystinus* we addressed several specific questions. First we asked whether juveniles of one year-class (the 2000 year-class) were representative of the adult population, or whether they showed reduced genetic diversity and genetic differentiation when compared to the adults as predicted by Hedgecock's sweepstakes hypothesis (Hedgecock 1994a, b). Second, we asked whether the larval pool is well mixed and whether juveniles from distant locations are similar genetically. Finally, we attempted to identify potential sources of juveniles by comparing individual juvenile samples to adult samples. Spatial variation in genetic composition of recruits that does not mirror the types of variation found in adults may help to establish the spatial scale of patchiness in sources of recruits.

Materials and methods

Sampling

We designed the sampling of the adults to include a site south of Point Conception (San Miguel Island) to test for structure across the proposed zoogeographic barrier between the southern Oregonian Province and Californian Province (Horn and Allen 1978). At each of these sites, the nearshore environment is affected by upwelling and relaxation events, and these events may influence the settlement patterns of fish and invertebrates with planktonic larvae such as rockfish (Roughgarden et al. 1991; Larson et al. 1994; Wing et al. 1995a, b). It is possible that different upwelling centers may have inherently different long-term influences in recruitment patterns. Therefore, we chose sites that were evenly distributed between upwelling centers (indicated in italics on Fig. 1). To identify patterns of genetic structure in adult *S. mystinus* throughout the central portion of their range (San Miguel Island to Fort Bragg), we sampled approximately 50 individuals from five sites. The sites included San Miguel Island (SM), Big Creek (BC), Monterey (MB), and Fort Bragg (FB) (Fig. 1). NMFS and port samplers with the CDFG provided adult specimens at some of our sites. We obtained lengths when we collected individuals and only used reproductive size males and females for analysis (over 200 mm SL).

To examine among-site genetic structure and for comparisons to adult patterns, we sampled approximately 50–100 juveniles (young-of-the-year) at Monterey and Carmel along the Monterey Peninsula, and Fort Ross along the Sonoma Coast, during the settlement season (Fig. 1). To examine genetic structure within sites, we sampled juveniles throughout the 2000 settlement season (five collection dates) in Monterey. Divers using scuba and pole spears collected juveniles within the kelp forests, dominated by *Macrocystis pyrifera* in Monterey and Carmel and *Nereocystis luetkeana* in Fort Ross, between May and September 2000. We chose the Monterey and Carmel sites because they are situated between the upwelling centers at Point Sur and Año Nuevo (Fig. 1). We chose the Fort Ross site because it is between the upwelling centers at Point Arena and Point Reyes and therefore the Fort Ross area is part of a different upwelling cell. In addition, settlement of *S. mystinus* reportedly occurs later in the year than in Monterey (T. Laidig, Tom.Laidig@noaa.gov). We positively identified all juveniles using diagnostics including coloration, dorsal fin ray counts, and gill raker counts (Miller and Lea 1972; Laroche and Richardson 1980).

Length and aging of juveniles

We measured the standard length (SL) of all juveniles sampled at each site to the nearest millimeter. We used the lengths of settled juveniles as a proxy for age within a sample to distinguish individuals that may have been born at different times within the reproductive season. Woodbury and Ralston (1991) using otoliths to back-calculate birthdate found a linear relationship between SL and age for several species of rockfish. One species, bocaccio (*Sebastes paucispinis*), showed temporal size modes that represented different birthdates, supporting our assumption that distinct size modes of *S. mystinus* represented different birthdate groups. To examine the possibility of genetic heterogeneity within an apparent temporal pulse of juveniles, we also restricted analyses to individuals near the size modes at each site (which we refer to as the ''main pulse'' of juveniles). We define a cohort as those individuals that settled at the same time and show a similar length increase or growth rate throughout the settlement season.

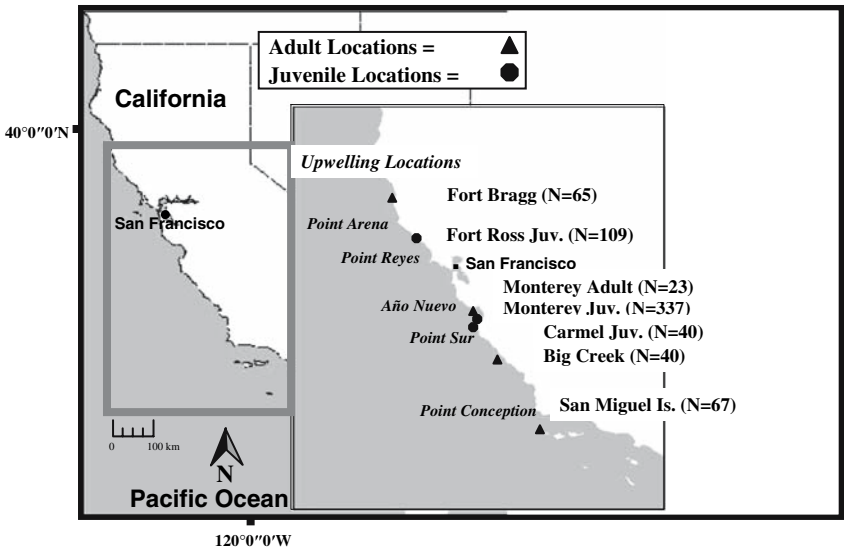

Fig. 1 Collection location on the west coast of the United States in California and samples sizes (N = number of individuals collected)

DNA extraction and amplification

We extracted genomic DNA of *S. mystinus* from caudal fin and muscle tissue using a salt extraction protocol (Medrano et al. 1990). From the extracted genomic DNA, we amplified seven microsatellite loci designed from *S. rastrelliger* (Westerman et al. 2005; *Sra.6-52* GenBank: AF269057) using the polymerase chain reaction (PCR) (Table 1). The PCR reactions followed the GIBCO BRL PCR reagent protocol (Invitrogen Corp.) using approximately 50–150 ng of template DNA in a 15 μl PCR reaction. We used fluorescently labeled primers (Perkin Elmber; ABI) for the PCR reactions. Cycling conditions included initial denaturation for 2 min 30 s at 95°C, 35 cycles of 45 s at 95°C, 1 min at 57 or 52°C annealing, and 1 min at 72°C and a final extension for 5 min at 72°C. We electrophoresed final PCR products on 6.5% Long-Ranger polyacrylamide gels (FMC BioProducts) on 36 cm plates. Each lane had internal molecular weight size standards. We used an ABI 377 scanner to detect the PCR product and size standards and used GeneScan software (Perkin Elmer, ABI) to analyze the results.

Statistical analyses

We estimated the average number of alleles captured at different sample sizes using Resampling Stats (Simon 1997). For this analysis, we computed averages of 1,000 permutation resamples and combined all five loci for each adult sample. We used this method to assess whether individual samples at a location were sufficient

Table 1 Information on the microsatellite loci used in this study

Locus	Primer sequence	Repeat motif	Size (bp)	Annealing temp. (°C)	*S. mystinus*	
					Size range (bp)	Number of alleles per locus
Sra.7-2	F: GAACATCCCTCCTTCCGACGC R: GTCAAACAACTGCAGAATGTTCG	$(CA)_{17}$	153	57	142–210	19
Sra.7-7	F: GCATGAAAGTGTATGAAAGGC R: CATGTGATTCTGTGTCTAACTGAG	$(CA)_{26}$	209	57	188–216	17
Sra.7-25	F: GACCTTTCCCTGAACACACTCG R: CAAGAGGCGGTGGTGCTGATGG	$(CA)_{21}$	187	57	164–264	45
Sra.15-8	F: GGAGATGTGCGTGGCTCGTCTGG R: GGGTTTACTCATTGTAGAC	$(CTAT)_{16}$	328	52	290–342	14
Sra.6-52	F: ATCGGGTGTCCTTCAGTCAG R: CGCTTTAATTTCCCGTTGAA	$(GT)_{16}$	127	52	123–144	11
Sra.5-9	F: CTTGCTACTGCAGAGTGACTAC R: CCTCATAATAGAGCTTGTAATAACG	$(CA)_8$	102	57	96	1
Sra.11-103	F: CTTGCAGGTAACGGGAAGG R: GGCTGATGACATTGCAACCTTG	$(CAA)_8$	269	57	277	1
Averages for loci used in data analyses			201		54	21.2

to capture most of the allelic diversity in the population. To analyze each locus for scoring errors due to null alleles, large allele dropout, or stutter, we used Micro-Checker (Van Oosterhout et al. 2004). We measured genetic diversity (H_E; Nei 1987, Eq. 7.39) or unbiased expected heterozygosity, which is the probability of finding two distinct alleles at random within a population or sample, for both the adult samples and juvenile samples at each location, including all juveniles and the main pulse of juveniles at each site. We generated estimates of H_E using GDA version 1.0 (Lewis and Zaykin 2001). In addition, we conducted an allelic richness measure implemented in FSTAT (Goudet 1995) to analyze the allelic richness at equivalent sample sizes. This test uses the rarefaction index of Hurlbert (1971). As larger sample sizes have greater genetic diversity and allelic richness, this test corrects for that bias by comparing the probabilities of capturing a given allele at a given locus for each sample of similar size. We used a two-tailed paired *t* test to test for differences in genetic diversity between juveniles and adults within and among sites (Sokal and Rohlf 1995) using both genetic diversity and allelic richness measures.

We analyzed within-sample deviations from Hardy–Weinberg (HW) expectations using an exact test of HW proportions for multiple alleles (Guo and Thompson 1992) as implemented in GENEPOP version 3.2 (Raymond and Rousset 1995a). For this test and following exact tests, we generated significance probabilities using the Markov chain method as described in Guo and Thompson (1992) and implemented in GENEPOP (using 50,000 iterations). Using Fisher's method of combining probabilities of exact tests (see Sokal and Rohlf 1995; Raymond and Rousset 1995a, b), we obtained multi-locus significance values in GENEPOP. We further examined conformance to HW expectations by generating unbiased estimates of F_{IS}, the local inbreeding coefficient (Weir and Cockerham 1984; using GDA). F_{IS} is a measure of the degree of conformance to HW proportions using genotype frequencies. When a local population is in HW equilibrium $F_{IS} = 0$.

To analyze the independence of the microsatellite loci, we used an exact test for linkage equilibrium in GENEPOP. We used the test on the adult and juvenile samples separately and then together.

To assess genetic divergence among individual adult sample locations or individual juvenile sample locations, we conducted tests of differences in both allele and genotype frequencies using an exact test as described by Raymond and Rousset (1995a) and a goodness of fit log likelihood test (G-tests) as described by Goudet et al. (1996) and implemented in FSTAT using 10,000 randomizations (Goudet 1995). We used the exact genotypic G-test, as recommended by Goudet et al. (1996), to test for genetic differentiation when HW equilibrium within samples could not be assumed. However, there were no differences between the main results of the exact tests and the G-tests even in instances where there was violation of HW expectations within a sample; therefore, we only report the results from the exact test. To further examine population differentiation, we used an unbiased estimate of F_{ST} (θ, Weir and Cockerham 1984) to measure inter-population divergence as implemented by FSTAT (Goudet 1995) and used 10,000 permutations to generate *P* values. This statistic quantifies variance in allele frequencies among samples relative to the overall population variance and is used for analyzing the genetic divergence among subpopulations (Hartl and Clark 1997). We obtained means and variances of F_{ST} across loci by jackknifing, and confidence intervals (CI) across loci by bootstrapping using FSTAT (Goudet 1995). Finally, to test for isolation by distance in the adult sample, we conducted a MANTEL test using linear pairwise F_{ST} values and pairwise distance among adult samples as implemented in GENEPOP (10,000 permutations).

We conducted assignment tests to examine the robustness of genetic divergence for juveniles and adults using Doh (J. Brzustowski: http://www.biology.ualberta.ca/jbrzusto/doh.php). The assignment test calculated a reference frequency for each location while excluding the individual in question, calculated the likelihood that this individual genotype, drawn from the total population (all locations), belonged to one of the reference locations, and then assigned it to the reference location with which it had the greatest affinity (Paetkau et al. 1995; Buonaccorsi et al. 2002). The *P* value represented the percentage of observations from the null distribution with assignment frequencies greater than or equal to the observed frequency. When there were frequencies of zero in the data, we used a correction factor based on Titterington et al. (1981).

Results

Length and aging

Using size frequency distributions, we were able to identify the main settlement pulses (cohorts) at each site (Fig. 2). For the genetic analyses, we used both the

entire sample and the main pulse alone in the Fort Ross and Carmel samples. In the Monterey sample, where there were five collections, we divided juveniles into a ''main pulse'' and an inferred second pulse (''pulse 1''), based on the bimodal distribution of size frequencies (Fig. 2). For this sample, our genetic analyses included the entire sample and the two inferred temporal pulses. We assumed that the mode of larger fish was a pulse of survivors that settled early in the season (pulse 1; Fig. 2) and the mode consisting of smaller fish were a pulse of survivors from later in the season (''main pulse''; Fig. 2). The main cohort can be traced from the first collection to the final collection in August of 2000.

In Monterey, we were able to follow the main cohort through time and used this to determine relative growth rate and approximate time of settlement. Using the mean size of individuals in the cohort on each

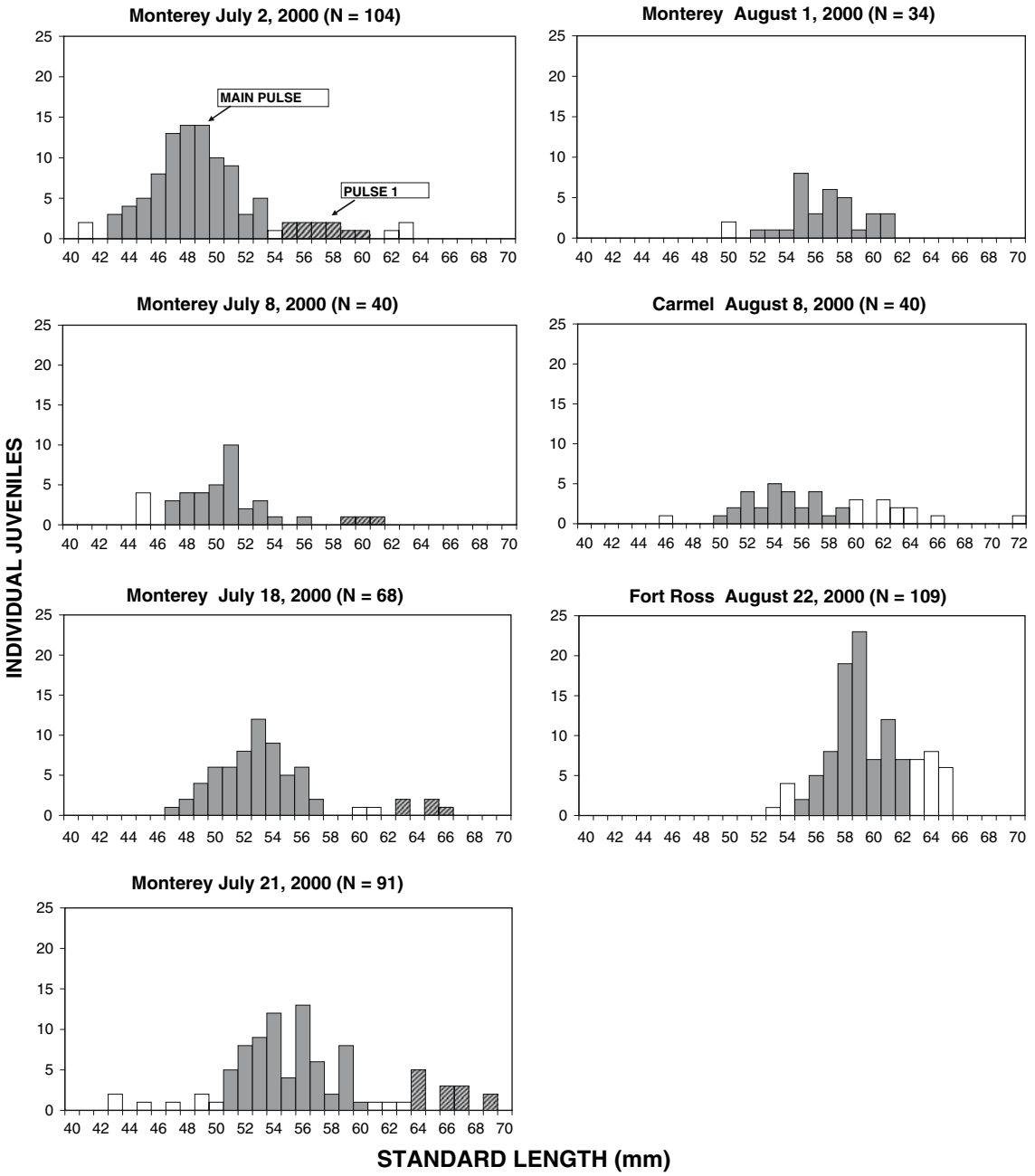

Fig. 2 Length frequency data for collections of juvenile *Sebastes mystinus*. These graphs represent single collection days. There were five collection days and two temporal pulses in Monterey and a single collection day for Carmel and Fort Ross. *Shaded columns* are the main temporal pulse, the *crosshatched columns* are Monterey pulse 1

sampling day, we estimated growth rates of juveniles in Monterey. A linear regression of length versus sampling day produced an estimate of growth rate (slope) of 0.32 mm/day ($y = 0.3179x - 10.211$; $R^2 = 0.9364$). McDonough (1997) estimated the growth rate of settled juvenile *S. mystinus* to be between 0.31 and 0.33 mm/day. Miller and Geibel (1973) indicated that juvenile *S. mystinus* settle in April at approximately 40–50 mm total length. Based on juvenile length at settlement provided in these previous studies, and the juvenile coloration when sampled, the juveniles collected on July 2, 2000 (Monterey) in the smaller size mode were approximately 4- to 5-month-old and appeared to be recently settled fish.

Genetic analysis

After initially screening seven microsatellite loci in ten individuals for levels of polymorphism, we analyzed five microsatellite loci (Table 1). We dropped two loci from further analyses, *Sra.5-9* and *Sra.11-103*, which were monomorphic for the ten individuals. The five remaining loci we used were easy to score and showed moderate allelic variation (Table 1). For one population (Monterey adults) and one locus *Sra.6-52*, we dropped four individuals that had aberrant homozygous allele scores.

The allele discovery curve (Fig. 3) indicates that sample sizes of 20–25 individuals ($2N$ = 40–50) capture most of the allele diversity. Therefore, the sample size for each of the locations for both adults and juveniles was sufficient.

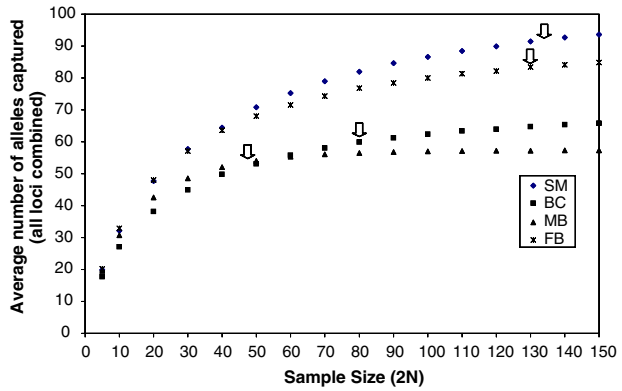

Fig. 3 Allele discovery curve for adult collections of *Sebastes mystinus*. These *curves* represent average number of alleles captured at $2N$ (two times the number of individuals for the diploid microsatellite markers) for all five microsatellite loci combined. *Arrows* indicated the actual sample size for that location. *SM* San Miguel Island; *BC* Big Creek; *MB* Monterey; *FB* Fort Bragg

Genotypic frequencies for both juveniles and adults did not violate linkage equilibrium expectations at any of the five loci (Exact test, $P > 0.1$ for all combinations). This was true for the pooled sample of adults at all five loci. Therefore, we considered these five loci independent in both the juvenile and adult samples. With this test and all subsequent multiple pairwise tests, we controlled for type I error using the sequential Bonferroni method. We also checked all loci for null alleles and scoring errors, using Micro-Checker (Van Oosterhout et al. 2004). We found no evidence for score error due to stutter, large allele drop out, or null alleles for all five microsatellite loci using the adult data. One locus (*Sra.7-7*) at two adult locations (Monterey and Fort Bragg) appeared to have an excess of homozygotes, but the probability of observed versus expected homozygosity was only significant at Fort Bragg ($P > 0.05$) suggestive of a null allele at this location. We believe that the lack of genetic differentiation in the adult population was not affected by a potential null allele at this location.

Diversity

The highest level of genetic diversity among juveniles occurred at Fort Ross ($H_E = 0.804$) and the lowest at Monterey ($H_E = 0.780$) (Table 2a, b). Separating juveniles into main pulses at Fort Ross and Carmel and into two pulses at Monterey did not significantly change genetic diversity measures.

Our sample of adult and juvenile *S. mystinus* had high levels of average genetic diversity ($H_E = 0.78$; Table 2c). When we compared all juveniles and all adults, the juvenile population had slightly greater genetic diversity (overall $H_E = 0.792$) than the adults (overall $H_E = 0.760$), but the results of the two-tailed paired t test showed that the difference was not significant (paired t test, $P = 0.053$). Alternatively, using Hulbert's (1971) rarefaction technique to compare individual juvenile samples to the pooled adult samples with equal sample sizes, we found that the allelic richness of one of the two juvenile samples in the Monterey peninsula (Monterey = 53.98 and Carmel = 49.50) was significantly lower than that of the pooled adult sample (pooled adults = 57.15) (paired t test, $P = 0.059$ and $P = 0.041$ respectively). We found the same result when we compared the main pulse at Monterey with the pooled adult sample (Monterey = 47.47; paired t test, $P = 0.038$). We pooled the adults because there was no significant genetic structure in the adult sample, as outlined below.

Table 2 Summary statistics for adult and juvenile *Sebastes mystinus*

	H_E	H_o	P value	F_{IS}	N	No. of alleles
(a) Descriptive statistics for juveniles						
Carmel	0.793	0.810	0.7280	0.000	40	10
Monterey	0.780	0.748	0.003*	0.042	337	17
Fort Ross	0.804	0.703	0.000***	0.127	109	18
Overall	0.792	0.752	0.000***	0.051	162	15
(b) Descriptive statistics for four juvenile main pulses						
Carmel Main	0.791	0.787	0.269	0.006	28	10
Monerey Main	0.777	0.753	0.174	0.031	278	16
Monterey Pulse 2	0.791	0.728	0.180	0.081	31	11
Fort Ross Main	0.803	0.708	<0.001***	0.120	77	16
Overall	0.791	0.744	<0.001***	0.060	104	13
(c) Descriptive statistics for adults						
San Miguel Island	0.783	0.798	0.316	0.000	65	14
Big Creek	0.735	0.721	0.123	0.020	39	10
Monterey	0.782	0.686	0.055	0.125	23	9
Fort Bragg	0.742	0.672	0.047	0.095	64	12
Overall	0.760	0.719	0.011	0.060	48	11
(d) Descriptive statistics for individual loci averaged over all locations						
Sra.7-2	0.893	0.854	<0.001***	0.044	649	19
Sra.7-7	0.753	0.701	<0.001***	0.070	652	17
Sra.7-25	0.761	0.731	0.002*	0.039	632	45
Sra.15-8	0.736	0.714	0.304	0.030	600	14
Sra.6-52	0.740	0.680	<0.001***	0.083	636	11
Overall	0.777	0.736	<0.001***	0.053	634	21

H_E from Nei (1987) equation 7.39 expected genetic diversity; P values from HW Exact test generated using 50,000 iterations, after corrections for multiple comparisons

*$P < 0.05$

Hardy–Weinberg expectation

Juvenile population

Juveniles at Fort Ross and Monterey showed deviation from HW expectations (Table 2a, b). The results of the exact test for all juveniles at Fort Ross revealed significant non-conformance to HW expectations ($P < 0.05$) at three of five loci. For Monterey juveniles, deviations from HW frequencies were significant at one locus after corrections for multiple comparisons. All of these deviations were due to heterozygote deficiencies. Carmel juveniles did not deviate significantly from HW expectations at any of the five loci. An analysis of the main pulse at Fort Ross with the exact test revealed only one locus of five with a significant deviation from HW expectations after corrections. After dividing the Monterey juveniles into two pulses (main pulse and pulse 1) and correcting for multiple comparisons, the exact test showed that all loci in each pulse conformed to HW expectations (Table 2).

Adult population

In the exact test of HW proportions, all individual loci and individual sample locations were in conformance with HW expectations after corrections were made for multiple tests. These results were consistent when we combined all loci using Fisher's method.

Population differentiation

Juvenile population

Statistical analysis showed genetic differentiation among juvenile samples. Significant allele frequency differences among the juvenile samples were consistent across all loci, both for comparisons involving all juveniles and comparisons among main settlement pulses. The exact test (allele frequencies) was significant for all five loci ($P < 0.001$) and also significant over all loci (Table 3a, b). Pairwise comparisons between the three juvenile samples and main pulses showed similar results (Table 4a, b, $P < 0.001$). Pairwise comparisons showed no significant difference, in any arrangement of juveniles, between Carmel and Monterey or between the two temporal pulses at Monterey; however, both the Monterey and Carmel samples differed significantly from the Fort Ross sample.

We used assignment tests to analyze the robustness of the above patterns. The two assignment tests used (1) all juveniles sampled at all three locations (Fig. 4a), and (2) main pulses at Fort Ross and Carmel and the two pulses at Monterey (Fig. 4b). When we ran the

Table 3 Population divergence for juvenile and adult *Sebastes mystinus*

Locus	Exact test[a]		F_{ST}[b]
	P value	SE	
(a) All juveniles			
Sra.7-2	<0.001***	0.000	0.017*
Sra.7-7	<0.001***	0.000	0.008*
Sra.7-25	<0.001***	0.000	0.012*
Sra.15-8	0.004*	0.001	0.009*
Sra.6-52	<0.001***	0.000	0.008*
Overall	<0.001***		0.011**
(b) Juvenile main pulses			
Sra.7-2	<0.001***	0.000	0.014*
Sra.7-7	<0.001***	0.000	0.014*
Sra.7-25	<0.001***	0.000	0.012*
Sra.15-8	0.025	0.003	0.007
Sra.6-52	<0.001***	0.000	0.007
Overall	<0.001***		0.011*
(c) All adults			
Sra.7-2	0.303	0.021	0.001
Sra.7-7	0.274	0.021	0.000
Sra.7-25	0.079	0.015	0.000
Sra.15-8	0.319	0.019	0.004
Sra.6-52	0.096	0.010	0.001
Overall	0.074		0.000

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

[a] *P* values generated using 50,000 iterations and after corrections for multiple comparisons

[b] F_{ST} *P* values: *$P < 0.05$ generated using 10,000 permutations and after corrections for multiple comparisons

Table 4 Exact test and F_{ST} *P* values (above and below diagonal, respectively) for pairwise comparisons of *Sebastes mystinus*

Location	Fort Ross	Monterey	Carmel Bay	
(a) All juveniles				
Fort Ross		0.017*	0.017*	
Monterey	<0.001***		0.883	
Carmel	<0.001***	0.649		
Location	Fort Ross Main	Monterey Main	Monterey Pulse1	Carmel Main
(b) Juvenile main pulses				
Fort Ross Main		0.008*	0.017*	0.008*
Monterey Main	<0.001***		0.15833	0.80833
Monterey Pulse1	0.009	0.063		0.56667
Carmel Main	0.001**	0.289	0.219	
Location	San Miguel Is.	Big Creek	Monterey	Fort Bragg
(c) All adults				
San Miguel Is.		0.300	0.117	0.225
Big Creek	0.512		0.350	0.625
Monterey	0.094	0.389		0.392
Fort Bragg	0.143	0.455	0.029	

Exact and F_{ST} tests used allele frequency data

P values generated using 50,000 iterations for the exact test and 10,000 permutations for F_{ST} and after corrections for multiple comparisons

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

assignment of all juveniles, Fort Ross juveniles were significantly more likely to re-assign to the Fort Ross location than the other locations (61%, $P < 0.001$). Juveniles sampled from Monterey assigned to the Monterey location at a higher frequency (49%) than to Fort Ross (19%) or Carmel (33%), but this was not significant ($P > 0.05$). Similarly, when we ran the assignment of main pulses, juveniles from Fort Ross re-assigned to the Fort Ross location (56%, $P < 0.001$) and juveniles from Monterey main pulse assigned back into Monterey main pulse (49%, $P < 0.01$). Carmel main pulse and Monterey pulse 1 assigned evenly among all reference locations.

Adult population

Statistical analysis of genetic differentiation suggested no genetic structure in adult *S. mystinus*. The exact test, when combined over all loci using Fisher's method, did not show significant heterogeneity in allele frequencies ($P = 0.075$, Table 3c). The estimate of F_{ST} obtained by combining all four adult sample locations and all five loci was 0.0001 ($P > 0.05$; 95% CI: –0.004 to 0.003). At individual loci, F_{ST} was relatively low (0–0.004). As with the tests of overall differentiation, estimates of F_{ST} indicated that there was no significant genetic structure within the entire adult sample (Table 3c). Pairwise comparisons using the exact test of allele frequencies showed no significant pairwise differences between adult samples (Table 4c). The results of the pairwise exact test and estimates of F_{ST} indicated that the adult samples were not isolated by distance and appear to be panmictic. The insignificant results from the Mantel test (one-tailed $P = 0.58$; two-tailed $P = 0.50$) corroborated the findings from the F_{ST} and exact tests.

Comparisons between juveniles and adults

To investigate the cause of genetic heterogeneity among juveniles from different locations, we conducted three assignment tests, each of which examined the assignment of one juvenile sample to all adult samples and to the juvenile sample itself. We used these tests to examine the affinity of Fort Ross, Monterey, and Carmel juveniles to the adult samples. We found even distribution of the Fort Ross juveniles back

into the juvenile reference location (31%) and into both Big Creek (26%) and Fort Bragg (20%) adult reference locations. However, none of these assignments were statistically significant. Unlike Fort Ross juveniles, juveniles from both Monterey and Carmel samples assigned back into their juvenile reference location, and this was statistically significant (56 and 48%, respectively, $P < 0.01$).

Using an exact test, we conducted independent comparisons of allele frequencies at individual juvenile samples to each of the adult samples to see if there was any relationship between juvenile and adult samples (Table 5). Pairwise comparisons of Monterey juveniles with adult samples showed significant divergence between Monterey juveniles and individual adult samples, with the exception of San Miguel Island (Table 5a). The result of the comparison of Carmel juveniles to adult locations was similar to that of Monterey juveniles (Table 5c). In the pairwise comparisons of juveniles from Fort Ross with the individual adult samples, there were significant differences between Fort Ross juveniles and adult samples only at Fort Bragg and San Miguel Island (Table 5b). The pairwise exact test produced similar results to the assignment tests.

Discussion

The main results of this study are as follows: (1) allele frequencies of Fort Ross juveniles differed significantly from those of Monterey and Carmel juveniles, both for all juveniles sampled and the main temporal pulses, showing that there was significant genetic heterogeneity among juveniles. (2) The separation of the two temporal pulses in Monterey resolved a significant deviation from HW expectations for Monterey juveniles and lowered the inbreeding coefficient for the main juvenile pulse (Monterey main pulse), suggesting that there may be admixture of genetically heterogeneous pulses of juveniles in *S. mystinus*. (3) The adult population was homogeneous in allele frequencies, showing that genetic heterogeneity among juveniles was not due to reproduction by genetically heterogeneous populations of adults. (4) At two of three locations, juveniles had significantly lower genetic diversity than adults, in agreement with Hedgecock's (1994b) sweepstakes hypothesis. (5) The Monterey and Carmel juveniles were genetically distinct from each of the adult populations, and from the adult sample as a whole, and the Fort Ross juveniles were genetically distinct from adults at two locations. These results

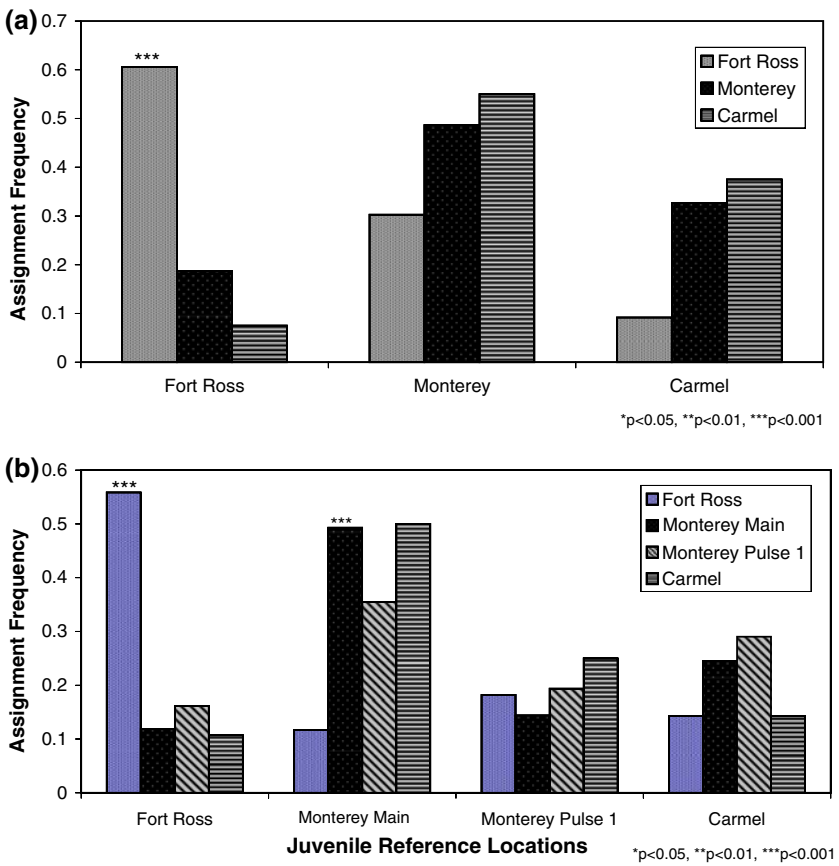

Fig. 4 Assignment tests **a** for all juvenile *Sebastes mystinus* at each location and **b** for juvenile *Sebastes mystinus* main pulses and two pulses from Monterey. *Columns* represent individuals from a given location (indicated in the legend) that assigned to reference locations along the *x*-axis

Table 5 Exact test pairwise comparisons of Juvenile and adult *Sebastes mystinus*

Location	Big Creek	Monterey	Fort Bragg	San Miguel Is.	Monterey Juv.
(a) Monterey juveniles and all adults pairwise comparison results					
Big Creek					
Monterey	0.001*				
Fort Bragg	0.424	0.000***			
San Miguel Is.	0.525	0.006	0.124		
Monterey Juvenile	0.000***	0.000***	0.000***	0.128	
Location	Big Creek	Monterey	Fort Bragg	San Miguel Is.	Fort Ross Juv.
(b) Fort Ross juveniles and all adults pairwise comparison results					
Big Creek					
Monterey	0.0014*				
Fort Bragg	0.415	0.000***			
San Miguel Is.	0.536	0.008	0.1402		
Fort Ross Juvenile	0.008	0.000***	0.0004*	0.000***	
Location	Big Creek	Monterey	Fort Bragg	San Miguel Is.	Camel Juv.
(c) Carmel and all adults pairwise comparison results					
Big Creek					
Monterey	0.001*				
Fort Bragg	0.417	0.000***			
San Miguel Is.	0.527	0.007	0.124		
Carmel Juvenile	0.000***	0.000***	0.000***	0.233	

Exact test used allele frequency data. *P* values generated using 50,000 iterations and after corrections for multiple comparisons

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

further indicate that the recruits of the 2000 year-class were not genetically representative of the adult population.

The lack of genetic differentiation among the adult samples is consistent with the extended pelagic stage in this species (PLD = 4 months), if one assumes that extensive dispersal occurs in every year-class. The lack of genetic structure of adults within California is similar to the findings of Cope (2004), who found genetic structure in populations of *S. mystinus* only at larger spatial scales. There was also no indication of isolation by distance in the adults of *S. mystinus*. Given the results presented here and in Cope (2004), the genetic composition of adults suggests that the population of *S. mystinus* is panmictic within the population center (San Miguel Island to Fort Bragg). Overall, these conclusions support previous studies correlating long pelagic phase with low genetic differentiation (Waples 1987) and differ from recent studies suggesting that larval retention and low realized dispersal can occur in marine organisms (Edmands et al. 1996; Moberg and Burton 2000; Flowers et al. 2002; Palumbi 2003).

In contrast, the genetic structure of the 2000 year-class of *S. mystinus* indicates that panmixis does not occur at the time-scale of individual year-classes (i.e., ecological time-scales). Despite the genetic uniformity of the adult population across the same range as the samples of juveniles and the long PLD, the Fort Ross juveniles differed genetically from the Carmel and Monterey juveniles. Furthermore, the juvenile samples did not match either the genetic composition of the entire or individual samples of adults and the Monterey and Carmel juveniles were genetically less diverse than the total adult sample. Finally, there was evidence of admixture in the Monterey juveniles, such that the two temporal pulses treated together showed significant heterozygote deficiency, but when separated each conformed to HW expectations. Therefore, the genetic structure of the adult population, with multiple generations, does not necessarily reflect the level of genetic structure found in an individual year-class.

Our results suggest that the larval pool of *S. mystinus* was made up of genetically distinct patches. Other studies have produced similar results. For example, Moberg and Burton (2000) concluded that recruitment of juvenile *Strongylocentrotus franciscanus* in California was the result of a heterogeneous larval pool that differed genetically among locations and years. Their results were surprising, since the long planktonic phase of *S. franciscanus* (51–152 days) should allow for substantial dispersal and gene flow. As in our study, but at a larger temporal and spatial scale, Moberg and Burton (2000) noted that genetic divergence in recruits within and among years and locations was equal to or greater than that found in adults. Ruzzante et al. (1996) found temporal and spatial variation in a pool of *Gadus morhua* larvae. They suggested that the groupings of larvae were the result of several spawning events. Similar to our findings, Ruzzante et al. (1996) argued that the heterozygote deficiencies, departures from

HW expectation, and heterogeneity of allele frequencies caused population admixture. However, unlike our study, Ruzzante et al. (1996) could, at least in one instance, trace the larval cohort to an adult source.

In addition to the finding of genetic patchiness, our results provide some support for predictions of Hedgecock's sweepstakes recruitment hypothesis (Hedgecock 1994b). We found some indication of a decrease in genetic diversity of juveniles at the two Monterey Peninsula locations and there was strong genetic divergence between the individual juvenile and adult samples at all three juvenile locations. In fact each of the juvenile locations was genetically divergent from either all or most of the adult locations. Julian (1996) found a decrease in genetic diversity within a pulse of late-stage pelagic juveniles of *Sebastes jordani* near Point Reyes. He also found that larvae were as genetically diverse as the adults, indicating that sweepstakes recruitment or random survival of larvae occurred during the transition from larvae to late-stage pelagic juveniles. The combined results of the genetic diversity and genetic divergence of the juvenile samples are suggestive of sweepstake recruitment, at least in the Monterey Bay region (Monterey and Carmel locations). The lack of a similar decrease in genetic diversity at the Fort Ross location indicates that if sweepstakes recruitment is present it may explain patterns at only a subset of juvenile settlement sites. Alternatively, it is possible that sweepstakes recruitment occurred at all the sites; however, the strength could vary among the sites and at low sites may be difficult to detect with genetic diversity or allelic richness measures.

The adult population contains multiple year-classes, and while the 2000 year-class indicates that there is spatial genetic variation among locations, we believe that this pattern could itself be variable. The admixture of several year-classes in the reproductive adult population could erode the distinctiveness of spatial genetic signature of individual year-classes, if there was fluctuation year-to-year in this spatial component. As indicated earlier, this was a moderate year-class for *S. mystinus*. Larger year-classes may contribute disproportionately to the adult population based on their sheer abundance or may allow for more widespread realized dispersal or both. Indeed, during these good years, greater adult contribution and widespread dispersal among locations may serve to homogenize the population and this genetic signature may dominate the adult population gene pool for many years in the future. The results of Bobko and Berkeley's (2004) study on *Sebastes melanops* (black rockfish) provided another explanation for the occurrence of genetic structure in an individual year-class. They found that older and larger females may contribute disproportionately greater to new year-classes than younger and smaller females. In addition, they found that older and larger females spawned earlier in the season and larvae produced by these females had higher growth and survival rates (Berkeley et al. 2004; Bobko and Berkeley 2004). Furthermore, as VenTresca et al. (1995) showed a decline in gonadal condition of both male and female *S. mystinus* during adverse oceanographic conditions, such as El Nino events, which could further lower the contributions from younger and smaller individuals to new year-classes. Alternatively, in years where oceanographic conditions are favorable for spawning and survival for longer periods of time, older female contributions may be less pervasive. This will dissolve any genetic structure established in previous or subsequent years. If the phenomena we observed in the 2000 year-class occur consistently in *S. mystinus*, such that a subset of adult population contributes to new generations, but the juvenile locations that are distinct vary year to year, the admixture of many year-classes in the adult population could also explain the discrepancy between the genetic heterogeneity of individual year-classes and the genetic homogenous adult population.

Our results suggest that a long pelagic phase does not consistently produce genetic homogeneity, at least within one year-class. While several studies (Moberg and Burton 2000; Edmands et al. 1996; Flowers et al. 2002) addressed this question with invertebrate species, there are few examples of the violation of this assumption using a continuously distributed marine fish with a high dispersal potential (e.g., PLD = 4 months). Miller and Shanks (2004) showed that larval dispersal distances in *S. melanops*, which has a long (3–6 months) PLD, were shorter (<120 km) than expected based on passive dispersal models. These results, in conjunction with the results in our study, indicate that a high dispersal potential may not always be realized in all marine species or in every year-class.

An analysis of the genetic structure of juveniles may reveal much more about the movement of larvae and constraints on the reproductive output of the adult population than similar spatial studies of adults alone. Information gained from studies on the genetic structure of new year-classes will facilitate our understanding of how population genetics, ecology, and oceanography affect juvenile settlement (Hedgecock 1994a). The distinctiveness of genetic composition in

settled juveniles of *S. mystinus*, indications of sweepstakes recruitment, and potential multiple sources for each location do not support the establishment of a few large harvest refugia as management strategy to preserve declining rockfish populations. Hilborn et al. (2003) suggested that the preservation of an adult stock, with multiple year-classes produced in a variety of conditions, will be critical for the continued sustainability of the population during significant environmental change. We feel that this applies to the smaller-scale genetic differences observed among juvenile *S. mystinus*, and suggest that further protection of spawning potential throughout the geographic range of the species, at several spatial scales, is important for conservation as suggested by Larson and Julian (1999). Overfished rockfish species may need to be conserved throughout their ranges if there is genetic variation in the spatial or temporal scale of settlement and variation in the portions of the adult population that contribute to a given year-class. Our results support maintaining a healthy adult population, including many year-classes produced in a variety of conditions, to preserve both the inherent genetic diversity and genetic continuity of these continuously distributed reef fishes.

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