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# CURRENT SHIFTS AND KIN AGGREGATION EXPLAIN GENETIC PATCHINESS IN FISH RECRUITS

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*Abstract*. The scales of population structure in marine species depend on the degree to which larvae from different populations are mixed in the plankton. There is an intriguing trend in marine population genetic studies of significant genetic structure for larvae, recruits, or populations at fine scales that is unpatterned across space and changes through time. This "chaotic genetic patchiness" suggests that larval pools are not well mixed in the plankton. However, few studies have been able to distinguish among potential causes of spatial and temporal genetic heterogeneity: changes in larval migration patterns, changes in environmental selection, or stochasticity caused by "sweepstakes" reproductive success of spawners creating detectable family structure. Here we use microsatellite markers to show that significant allele frequency shifts occurred sporadically in space and time for cohorts of recruits of *Paralabrax clathratus* (kelp bass) collected once every two weeks over two years from five sites in the Santa Barbara Channel, California, USA. We found that the pattern of genetic differentiation among cohorts was explained by a combination of (1) family structure in some cohorts, evidenced by half and full siblings, and (2) an indication of changes in larval delivery. It is unlikely but possible that environmental selection also plays a role. Although sampling of potential source populations was incomplete, cohorts arriving during western current flows show most genetic similarity with a population sample collected in the west, and cohorts arriving during current flows from the southeast show similarity with population samples collected in the south and east. Despite the family structure apparent in some cohorts, these "sweepstakes" events occur on too fine a scale to create lasting year class genetic structure. The results corroborate oceanographic models of larval dispersal, which suggest that larval mixing in the plankton is less extensive than previously believed.

*Key words: chaotic genetic patchiness; kinship; larval dispersal; marine connectivity; microsatellites;* Paralabrax clathratus; *recruitment; sweepstakes hypothesis.*

## INTRODUCTION

For coastal marine species, dispersal often occurs during the larval phase when individuals are too minute to track directly. Larvae may drift in the plankton for weeks to months, enabling relatively high connectivity across populations compared to terrestrial systems (Kinlan and Gaines 2003, Shanks et al. 2003). While recent studies have shown that larvae of many marine species are capable swimmers, especially at the end of their pelagic phase, ocean currents still play a central role in larval transport (Sponaugle et al. 2002, Fisher 2005). In theory, larvae released from a given location can spread by diffusion over a large area within a typical months-long dispersal phase, mixing with larvae released from populations elsewhere to form a "well-stirred" larval pool and dampening the genetic differences across populations that lead to population structure (Roughgarden et al. 1988, Eckman 1996, Gaylord and Gaines 2000). However, the dynamics of realized dispersal, the fraction of larvae that successfully recruit into a local population, may not reflect a well-mixed, diffuse larval pool for several reasons. The movement of water packets in coastal systems shows high spatial and temporal autocorrelation, which decreases the total number of independent larval trajectories (Gaines et al. 2003, Siegel et al. 2003). Conditions for larval survival or larval delivery may also be limited in time or space, and environmental selection may be patchy, resulting in few successful spawning events and patchy recruitment despite continuous production (Gaines and Bertness 1992, Morgan et al. 2000, Ellien et al. 2004). Moreover, many marine species have a combination of high fecundity and narrow conditions for spawning success that may lead to wide individual variation in realized reproductive success, such that an annual cohort is the result of only a few spawning events or individuals (Hedgecock and Sly 1990, Hedgecock 1994*a*, *b*). Such "sweepstakes reproductive success" would result in small effective population sizes despite large census sizes and if common,

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imply that fisheries management should conservatively plan for large areas and time spans of reproductive failure (Hedgecock 1994*b*, Larson and Julian 1999).

These three phenomena, limited mixing of larvae from distinct sources, patchy environmental selection in the plankton, and sweepstakes reproductive success, may act in concert to produce the high stochasticity in recruitment levels through time and space often displayed by coastal marine species (reviewed by Eckert 2003). Many genetic studies have found significant changes in allele frequencies of larvae or recruits at marker loci from one sampling time to the next, a type of "chaotic genetic patchiness" that suggests larval pools are heterogeneous at small-to-moderate spatial scales (Johnson and Black 1982, Kordos and Burton 1993, Ruzzante et al. 1996, Li and Hedgecock 1998, Johnson and Wernham 1999, Moberg and Burton 2000, Toonen 2001, Flowers et al. 2002, Planes et al. 2002). Teasing apart the mechanism(s) producing chaotic genetic structure is challenging, and few studies have been able to do so definitively, because it requires (1) sampling larvae or recruits over fine spatial and temporal scales, (2) a study design that allows testing for reproductive variance or sibships among larvae to detect sweepstakes phenomena, (3) powerful tests for selection on genetic markers to detect environmental selection, and (4) the ability to link patterns of genetic heterogeneity to independent data on changes in current patterns and potential natal source populations (Johnson and Black 1984). Intense interest in exploring the prevalence and scale of genetic heterogeneity in larvae and recruits of marine species stems from its broad implications for our understanding of the formation of a genetic deme (Koehn and Hilbish 1987), basic population dynamics (Eckman 1996, Pineda 2000), microevolutionary processes (Lessios et al. 1994), species interactions (Muko and Iwasa 2003, Witman et al. 2003), and resource management (Hedgecock 1994*b*, Larson and Julian 1999) in marine systems (David et al. 1997).

We examined the causes of small-scale chaotic genetic patchiness in the larval pool for a temperate reef fish, *Paralabrax clathratus* (kelp bass), by combining detailed oceanographic data with genetic assessment of early recruits collected once every two weeks from sites in the Santa Barbara Channel, California, USA. Specifically, we examined support for the three potential mechanisms described above by testing for: (1) the influence of selection on the genetic markers (varying environmental selection), (2) detectable family structure in cohorts (sweepstakes reproductive success), and (3) the correlation of genetic changes across cohorts with changes in the direction of larval delivery (water flow), plus genetic differentiation of potential source populations (varying larval source). Kelp bass are popular game fish and common predators in kelp forests and rocky reefs along the Pacific coast between Point Conception, California, USA, and central Baja California, Mexico. The high fecundity of the species (Oda et al. 1993) may allow high reproductive variance, making sweepstakes reproductive success a possibility (Hedrick 2005). The approximately 30-d planktonic larval duration (PLD) makes the results potentially applicable to a variety of species in coastal systems that share a similar larval life history (Grantham et al. 2003, Shanks et al. 2003).

## Methods

Samples of recruits were collected using artificial juvenile fish collectors (standardized monitoring unit for the recruitment of fishes [SMURFs]) in the Santa Barbara Channel (Ammann 2004). At each site, three SMURFs were placed in open water just offshore of adult habitat, where they provide attractive habitat for post-larval fish settling onto the coastal reefs and kelp forests where adults are found (Ammann 2004). All fish were collected from SMURFs biweekly (on the first and third quarter moons) and preserved in 95% ethanol. Based on studies of age at settlement (Cordes and Allen 1997, Findlay and Allen 2002), individuals settle between 25 and 36 d old. Thus, individuals found on the SMURFs after a two-week collection period are assumed to be 25–50 d old and ranged 8–20 mm in standard length (SL). All recruits taken from a single site (three SMURFs combined) after a single biweekly period are deemed a cohort. Monitoring at 13 sites around Santa Cruz and Anacapa Islands and along the adjacent mainland coast occurred from 21 July to 21 November 2000 and from 16 June to 29 October 2001, to capture the peak of the settlement season. At five of these sites, kelp bass recruited to SMURFs in sufficiently high numbers (multiple times with $>30$ fish) to permit genetic analysis, and so only those sites are used here (Fig. 1). Despite similar effort in 2002 and 2003, no kelp bass settled on any SMURFs in the Santa Barbara Channel.

To compare the recruits to potential source populations, we genotyped samples of older individuals from nine sites in the Southern California Bight (Fig. 1). Samples were taken by angling that targeted $>1$-yr-old individuals. Sampling occurred in 1990 (by L. Allen and colleagues), 2001 (by A. Vogel), and 2004. Most sites were only sampled in one year, but two sites (Naples and San Pedro) were sampled twice. In addition, we compared recruits to a sample from San Miguel Island made up of 39 recruits that settled to SMURFs in 2004. This represents the most northwestern kelp bass sample we could obtain. Unfortunately, no adult populations were successfully sampled farther north or west, because kelp bass become less common and less responsive to angling in the colder water.

Fin and gill samples were frozen or stored in 95% ethanol until DNA extraction. DNA was extracted using a DNeasy kit (QIAGEN, Valencia, California, USA) or a rapid boiling technique (Valsecchi 1998) and genotyped at seven unlinked microsatellite loci: Mbo66, Pam13, Gag010, AV6, AV15, AV17, and AV88. Primer sequences, detailed methods of ploymerase chain reac-

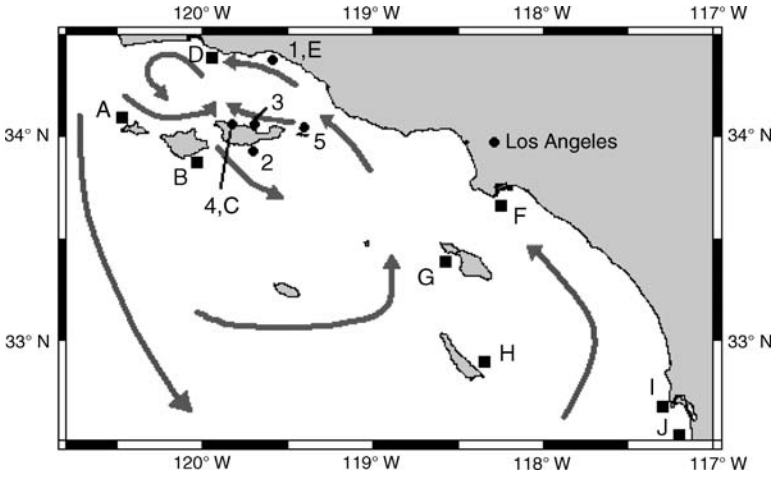


FIG. 1. The Southern California Bight with prevailing currents during summer, after Hickey (1998). Recruits were sampled from: (1) Carpinteria Reef; (2) Willows, (3) Pelican, and (4) Hazards on Santa Cruz Island; (5) Winfield on Anacapa Island. Adult collection sites indicated by letter codes A–J are described in Table 3.

tion (PCR) amplification and results of linkage tests are described in Selkoe et al. (2005), except for Pam13 (GenBank Accession DQ845458; same PCR methods). The PCR products were visualized with an ABI 310 DNA sequencer (Applied Biosystems, Foster City, California, USA), and alleles were grouped into two-base-pair bins that correspond to peaks in allele size frequency.

To test the null hypotheses of genetic homogeneity among cohorts of recruits and also among adult samples, we evaluated whether global and pairwise estimates of $F_{ST}$ were significant using 10 000 permutations in an AMOVA framework (Schneider et al. 2000). $F_{ST}$ is a measure of the degree of genetic differentiation over samples based on differences in their allele frequencies. Because $F_{ST}$ is based on an average across all alleles at a locus, the precision of the estimate increases with allelic diversity, despite the fact that the sample size may be too low to represent the rarer alleles well (Kalinowski 2005). To test whether genetic variability in recruits was partitioned within sites or within years, we used a hierarchical AMOVA with SMURF, sample site, and then year as the group factor. We used a Mantel test in GENEPOP (Raymond and Rousset 1995) to assess whether adult and recruit samples showed patterns of isolation by distance (Slatkin 1993). We also analyzed cohorts and adult samples with global and pairwise Fisher's exact tests implemented with default Markov chain parameters in GENEPOP. We calculated observed and expected heterozygosity (Nei 1987), rarefied allelic richness, $F_{IS}$, and genotypic disequilibrium with FSTAT (Goudet 1995). Because many of the tests above revealed significant genetic heterogeneity across recruit cohorts, we investigated the potential causes of heterogeneity by testing the alternative hypotheses outlined in the introduction with the following approaches.

*Environmental selection*

First, we simply determined whether statistically significant genetic differences among cohorts were attributed to just a single locus, perhaps indicating that patterns are driven by selection at that single locus or a nearby gene. If genetic differentiation is significant at multiple loci (presumably scattered throughout the genome), one expects that it is less likely the differentiation is due solely to selection. Next, we tested for the conformity of allele frequencies at each locus to the Ewens sampling distribution with a Monte Carlo Markov chain (MCMC) simulation approach (Slatkin 1994), using 1000 iterations in the program PYPOP (Lancaster et al. 2003), because selection can cause a locus to deviate from the Ewens sampling distribution. While other factors aside from selection can cause a significant deviation from the Ewens sampling distribution (Slatkin 1994, Schlotterer et al. 2004), if no deviation is found, the result can still be considered in support of neutral dynamics. We also specifically examined whether any allele frequencies correlated with minimum or mean water temperature at each site during the two-week collection period (recorded by thermistors attached to the SMURFs, described in *Methods: Heterogeneity in larval source*). Temperature shows large fluctuation in this region and might be a likely selective force given that kelp bass reproduction and larval development may be compromised below 16°C (Oda et al. 1993). We examined the correlation between the minimum or mean temperature and allele frequency for the four most common alleles at each locus, except in the case of locus Mbo66, for which only the most common allele was examined as it has only two alleles. In total, 29 alleles were tested and significance was adjusted using sequential Bonferroni correction (Rice 1989).

### *Sweepstakes*

Because the sweepstakes hypothesis posits that the recruits in a cohort come from a small number of parents, we evaluated half-sibship and full-sibship relationships (i.e., relatedness coefficient $R_{XY} \geq 0.25$ and $R_{XY} \geq 0.5$, respectively) for every pair of individuals within a cohort with the program KINSHIP (version 1.2; Goodnight and Queller 1999). KINSHIP calculates the $R_{XY}$ value for a pair of individuals in a cohort and evaluates the likelihood of that value both under a specified hypothesized relationship ($H_1$) and under the null hypothesis of no relationship ($H_0$), given the allele frequencies in the cohort. The program uses a simulation approach to determine how large the ratio of the likelihoods ($H_1/H_0$) must be to reject $H_0$ for a given significance level ($\alpha$). Because it is not difficult to get $R_{XY} = 0.25$ by chance with seven-locus genotypes, Type II error ($\alpha_{0.05}$) equals 0.41 for half sibships while it is 0.06 for full sibships. The sibship analysis within each cohort involved between 435 and 3160 pairwise comparisons, so one expects many significant $P$ values by chance. We used a simulation approach to determine how many significant $P$ values could be generated under a null hypothesis of no true relationships. Using MATLAB 7.1, Release 14 (Mathworks, Natick, Massachusetts, USA), we created data sets with the same global allele frequencies and sample sizes as the 20 cohorts, by drawing seven-locus genotypes independently with replacement from a gene pool. We used KINSHIP to evaluate the number of significant half and full sibships at $\alpha_{0.05}$ for the simulated data sets and repeated this 300 times to generate frequency distributions of the number of significant half and full sibships simply due to chance. We considered the number of significant sibship pairs in the real recruit data in excess of the 95th percentile of the simulated data sets as significant evidence for sibships. We also examined whether simulated data sets with large numbers of significant sibships displayed similar $F_{ST}$ values to those real cohorts displaying the most siblings. As a second approach to sweepstakes evaluation, we calculated gametic phase disequilibrium for all pairs of loci in all cohorts with default parameters in LinkDos (Garnier-Gere and Dillmann 1992) because sibships should produce individuals with correlated alleles across loci.

### *Heterogeneity in larval source*

The study region is ideal for investigating the correlation of genetic changes in cohorts with changes in the direction of larval delivery because it encompasses a transition zone between a colder current carrying water from north of Point Conception into the west end of the Santa Barbara Channel and a warmer current carrying water from the Southern California Bight into the east end (Fig. 1). A sharp temperature discontinuity often forms where the two water masses meet (Fig. 2), and regional maps of dynamic height anomaly data show that it corresponds with a frontal boundary of convergent flow (e.g., see 2000 and 2001 data report figures for July California Cooperative Fisheries Investigations [CalCOFI] cruises, *available online*).[4] We hypothesized that the origin of water bathing the study sites (and of the larvae carried in the flow) likely fluctuates as the position of the frontal boundary shifts relative to the sites. Thus, we tested for a positive correlation between shifts in the position of the boundary and difference in genetic composition of the recruit cohorts. To estimate the position of the boundary objectively we used two data sources. First, 1-km resolution sea surface temperature (SST) maps of the Santa Barbara Channel are derived from advanced very high resolution radiometer (AVHRR) satellite images taken several times per day (*available online*).[5] We used the temperature discontinuity to determine the boundary's position relative to the island sampling sites, denoted by the dashed line drawn in Fig. 2A. Second, thermistors attached to the island-site SMURF moorings a few meters below the SMURF recorded temperature every two minutes during the sampling period. Data were subjected to a 36-hour low-pass filter and then subsampled to one point per day centered around 12:00 Pacific Standard Time to minimize tidal influence. With this time series we identified sharp changes in temperature over the sampling period (Fig. 2B). These changes corresponded well to the movement of the temperature front across the study area indicated by the satellite images. Together, these data allowed us to categorize the likely source of the water bathing each site on a daily basis as "east" or "west" of the frontal boundary (done blindly with respect to the genetic data). We then assumed that recruits arriving at a site on a day that the water is predicted to be "eastern" in origin are likely to have distinct sources from recruits arriving when water bathing the sites is "western." At the least, these water mass data are assumed to indicate gross differences in the larval pools potentially available to each site.

Because recruits were allowed to accumulate in the SMURFs over a two-week period before each collection, it was not possible to determine the exact day of settlement for each individual. Therefore, we calculated the fraction of days that a given site was exposed to the western side of the front during each two-week sampling period and call it the Western Larval Pool (WLP) index. For example, if recruits were collected from a site over 10 days during which the frontal boundary sat to the east of the site (exposing it to the western larval pool) for three days, WLP = 0.3 for that recruit sample. Days for which SST or mooring temperature data were missing were left out of the calculation. Given the likelihood of pulsed settlement through time for kelp bass (Findlay and Allen 2002), it is unlikely that recruits in a cohort arrived evenly over the collection period. Uneven settlement over the sample interval would therefore

[4] ⟨http://www.calcofi.org/data⟩
[5] ⟨http://www.icess.ucsb.edu⟩

reduce the accuracy of the WLP index as an estimate of the probability of western origin. Sample intervals with a WLP near the bounds of 0 or 1 should most closely approximate the true probability of western origin since the timing of settlement during the interval should have little consequence.

For those cohorts in which all recruits had extremely small or large body size, it is possible to improve on the precision of the WLP index by excluding the last or first week (respectively) of the two-week collection period from the calculation, as it is unlikely the recruits arrived during that time. According to two age–length regressions (Cordes and Allen 1997, Findlay and Allen 2002), recruits <10.5 mm SL are unlikely to be >34 d old. In cohorts 10, 11, and 17, 75–90% of the fish were <10.5 mm SL, so we calculated the WLP index on just the last eight days prior to collection, as few fish settle at <26 d old (Cordes and Allen 1997, Findlay and Allen 2002). No cohorts with large mean length (e.g., cohorts 19 and 20) had length distributions skewed far enough to the right to warrant a similar refinement of the WLP index.

We tested for a positive linear relationship between pairwise difference in WLP and pairwise $F_{ST}$ values and assessed significance of the slope using a Mantel test implemented in GENEPOP with 10 000 permutations (Raymond and Rousset 1995). We also calculated pairwise $F_{ST}$ between each recruit cohort and each of the adult samples to examine whether WLP predicts the pattern of genetic differentiation (i.e., low WLP cohorts are most differentiated with the western sample and high WLP cohorts are most differentiated with the southern and eastern samples).

### *Synergistic effects*

Lastly, to assess whether temperature, kinship, and/or flow patterns were acting in concert on the genetic structure of the recruit cohorts, we constructed a model in a multiple regression framework with pairwise difference in minimum temperature, total number of excess sibships (summed over the pair), and pairwise WLP difference as independent variables and pairwise $F_{ST}$ as the dependent variable. We also tested models with minimum temperature, excess number of sibships, and WLP against $F_{IS}$ and mean $F_{ST}$. We assessed significance of the model coefficients with 1000 bootstraps in a partial Mantel test.

## Results

### *Locus characteristics*

In total, 1184 recruits were analyzed at seven microsatellite loci, representing 20 biweekly cohorts of 30–80 recruits (Table 1). Several cohorts show $F_{IS} > 0$, although none are significant after Bonferroni correction (Table 1). A significant global $F_{IS} = 0.014$ ($P = 0.008$) indicates some heterozygote deficit driven by loci Mbo66 and AV6 for the recruits but not the adults (Table 2). Mean pairwise relatedness ($R_{XY}$) in cohorts ranged from 0.025 to 0.056 and averaged 0.003 (Table 1). Loci appear to be independent as tests for gametic disequilibrium returned few significant values (18 observed vs. 21 expected), although two cases were highly significant: AV15 and AV88 in cohort 11 and AV6 and G10 in cohort 5.

### *Recruit genetic structure*

The global $F_{ST}$ value of 0.002, while small, was statistically significant ($P = 0.013$), as was a global exact test ($P < 0.0001$), indicating significant genetic differences among cohorts. Three loci gave significant $F_{ST}$ values individually (Table 2). AMOVA revealed no significant variance among SMURFs within a site ($F_{CT} = 0$, $P = 0.62$), sites ($F_{CT} = 0.0003$, $P = 0.13$), or years ($F_{CT} = 0$, $P = 0.54$), nor was there any isolation by distance effect ($R^2 = 0$, Mantel $P = 0.62$). All but five of the significant pairwise $F_{ST}$ tests involve at least one of three cohorts from Hazards (cohorts 11, 16, and 18; Appendix A). These three cohorts also showed large pairwise $F_{ST}$ values (0.012–0.013) when compared among each other. The cohort with the most pairwise differences and highest mean $F_{ST}$ is cohort 16 (Hazards, 26 July 2001).

### *Adult genetic structure*

Adult samples showed a similar level of genetic structure to the recruit cohorts ($F_{ST} = 0.003$, $P = 0.013$; exact test $P \sim 0$) and to a previous allozyme study of kelp bass from six sites (Waples 1987). Two loci gave significant $F_{ST}$ values individually (Table 2). Observed heterozygosity and rarefied allelic richness for the adults are similar to recruit samples, but $F_{IS}$ values tend to be smaller (Table 3). There is no pattern of isolation by distance ($R^2 = 0.02$, Mantel $P = 0.45$), indicating chaotic genetic patchiness on this regional scale. Allele frequencies at Naples showed no significant change between 2001 and 2004 samples ($F_{ST} = 0.003$, $P = 0.08$; exact test $P = 0.17$), and San Pedro also appeared to be genetically stable between 1990 and 2004 samples ($F_{ST} = 0.002$, $P = 0.16$; exact test $P = 0.12$). To estimate how well the 2004 recruits from San Miguel might represent the adult population from the same location, we compared the recruit and adult populations from Santa Cruz Island. When all recruits at Hazards are lumped by year, neither 2000 nor 2001 recruits show allele frequency differences with Santa Cruz Island adults, which were collected around the Hazards site ($F_{ST} < 0$).

### *Is selection driving recruit genetic structure?*

The recruit genetic structure cannot be ascribed to selection acting on a single locus. Three individual loci show significant global $F_{ST}$ values and four loci give significant global exact test values (Table 2). Moreover, no locus violated the Ewens-Watterson sampling distribution, which might indicate selection, except for AV88 in cohorts 13, 14, and 19. However, Table 2 shows that AV88 is not the source of significant genetic structure in

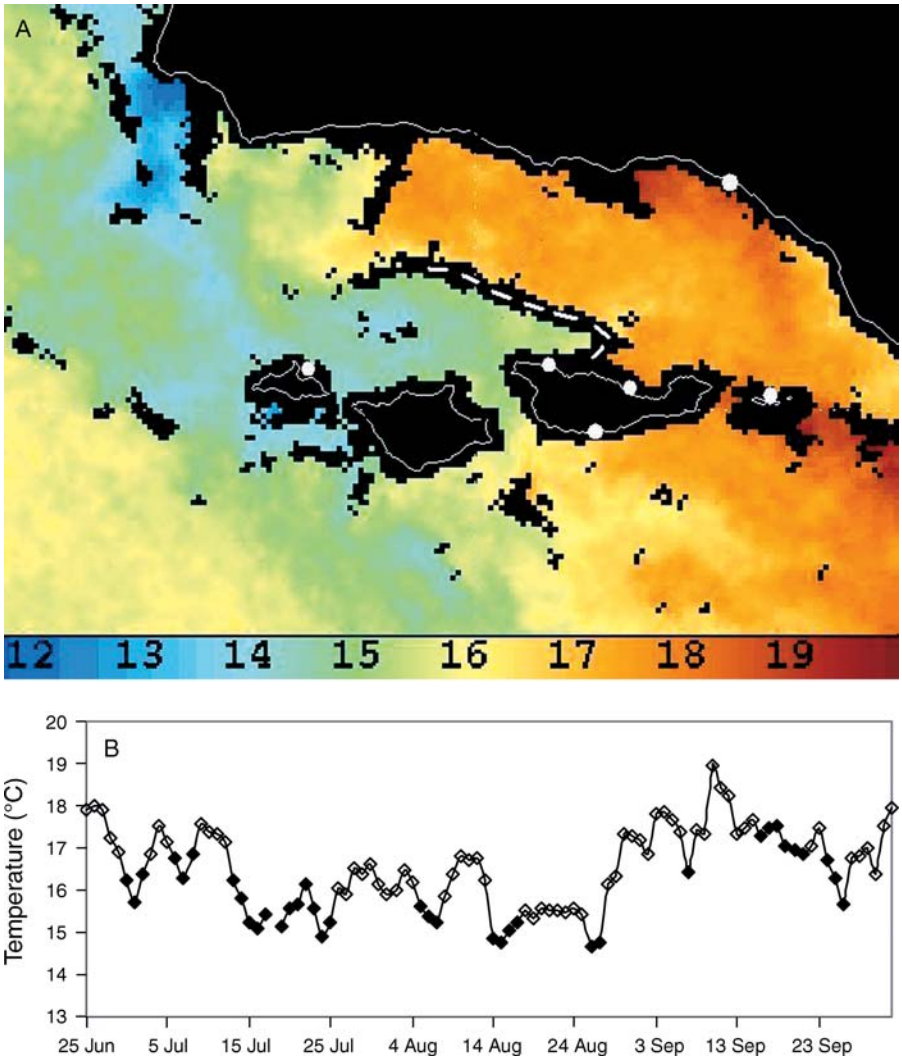


FIG. 2. The dynamic current break. (A) Satellite image of the Santa Barbara Channel exemplifying the boundary (enhanced with a dashed white line) between colder northern-derived water and warmer southern-derived water (image from 25 September 2001). White dots are sampling sites; the color bar indicates temperature (°C). (B) Example of thermistor-derived temperature time series using data from Hazards taken in 2001. Solid symbols indicate days scored as west of the boundary based on the combination of thermistor and satellite data, and open symbols indicate days scored as east of the boundary.

recruits, so if selection truly is acting on AV88, it does not explain the observed genetic differences. Specific examination of allelic correlations with temperature found no significant correlations between minimum or mean temperature during the two-week collection period and allele frequency for the four most frequent alleles at each locus, after Bonferroni correction. Minimum and mean temperature showed no significant correlation with $F_{IS}$ for any individual locus after Bonferroni correction, although locus Gag10 showed some correlation with minimum temperature before correction ($R^2 = 0.28$). Gag10 appears to drive a significant correlation between minimum temperature and the mean of $F_{IS}$ across all loci ($R^2 = 0.34$, $P = 0.007$), as the relationship is not significant when Gag10 is excluded.

*Is family structure driving the recruit genetic structure?*

On average, the 20 cohorts showed significantly more sibships than the 5% expected by chance ($t$ test, half sibs, $t = 2.7$, $P = 0.012$; full sibs, $t = 2.9$, $P = 0.008$). In seven cases the number of either half or full sibships exceeded the number in 95% of the simulated data sets (termed "excess sibships"; Table 4). The probability of getting seven significant tests of 40 by chance is 0.0034, indicating high significance. These seven cases were distributed over five cohorts from four different sites: cohort 20 contained 53 excess sibling pairs and cohorts 1, 9, 11, and 17 contained 5–11 excess sibling pairs. The summed number of excess sibships was unrelated to $F_{IS}$ ($R^2 = 0.03$, $P = 0.81$). In contrast, pairwise $F_{ST}$ significantly increases with the total number of excess

TABLE 1. Sampled recruit cohorts.

| Site | Cohort ID | Collection date | No. collected | Sample size | Mean length | $H_O$ | $A$ | $F_{IS}$ | Mean $F_{ST}$ | Mean $R_{XY}$ | WLP value | Min. temp. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Carpinteria | 1 | 5 Sep 2001 | 120 | 65 | 11.40 | 0.73 | 11.87 | −0.028 | 0.0010 | −0.001 | 0 | 16.5 |
| | 2 | 24 Sep 2001 | 55 | 51 | 13.06 | 0.71 | 12.04 | −0.038 | 0.0013 | 0.030 | 0 | 17.5 |
| Willows | 3 | 17 Aug 2000 | 41 | 41 | 11.46 | 0.72 | 11.63 | 0.006 | 0.0010 | 0.015 | 0.13 | 16.8 |
| | 4 | 10 Aug 2001 | 84 | 60 | 11.72 | 0.73 | 11.74 | 0.034 | 0.0000 | −0.002 | 0.06 | 16.1 |
| Pelican | 5 | 28 Sep 2000 | 37 | 37 | 13.92 | 0.74 | 11.95 | 0.028 | 0.0005 | −0.012 | 0.13 | 15.6 |
| | 6 | 13 Jul 2001 | 129 | 72 | 11.33 | 0.75 | 12.81 | −0.009 | 0.0003 | −0.025 | 0.19 | 16.5 |
| | 7 | 26 Jul 2001 | 88 | 57 | 10.14 | 0.73 | 11.58 | −0.007 | −0.0008 | −0.003 | 0.5 | 15.5 |
| | 8 | 10 Aug 2001 | 144 | 68 | 10.39 | 0.73 | 12.19 | −0.025 | 0.0013 | 0.004 | 0 | 16.0 |
| | 9 | 28 Sep 2001 | 99 | 78 | 13.99 | 0.72 | 11.30 | 0 | 0.0010 | 0.017 | 0.24 | 16.8 |
| Hazards | 10 | 21 Jul 2000 | 209 | 65 | 9.30 | 0.72 | 12.09 | 0.061 | −0.0008 | 0.008 | 0.14 | 14.2 |
| | 11 | 2 Aug 2000 | 244 | 70 | 9.43 | 0.72 | 11.45 | 0.041 | 0.0038 | 0.017 | 0.75 | 14.7 |
| | 12 | 30 Aug 2000 | 618 | 30 | 12.39 | 0.74 | 11.86 | 0.022 | 0.0006 | −0.009 | 0.07 | 17.4 |
| | 13 | 28 Sep 2000 | 447 | 68 | 12.38 | 0.73 | 11.97 | 0.02 | 0.0012 | −0.004 | 0.44 | 15.8 |
| | 14 | 8 Oct 2000 | 61 | 61 | 10.70 | 0.73 | 12.08 | 0.018 | 0.0004 | −0.003 | 0.36 | 16.3 |
| | 15 | 13 Jul 2001 | 117 | 80 | 10.16 | 0.73 | 12.20 | −0.009 | 0.0003 | −0.006 | 0.38 | 15.7 |
| | 16 | 26 Jul 2001 | 49 | 49 | 10.50 | 0.75 | 12.18 | 0.047 | 0.0077 | −0.009 | 1 | 14.9 |
| | 17 | 10 Aug 2001 | 64 | 64 | 9.16 | 0.73 | 11.96 | 0.042 | 0.0002 | 0.002 | 0.25 | 15.3 |
| | 18 | 28 Sep 2001 | 77 | 42 | 13.32 | 0.73 | 11.38 | 0.023 | 0.0050 | 0.005 | 0.53 | 15.7 |
| Winfield | 19 | 29 Sep 2000 | 225 | 62 | 15.20 | 0.75 | 12.28 | 0.022 | 0.0000 | −0.024 | 0.3 | 17.0 |
| | 20 | 9 Aug 2001 | 78 | 64 | 17.72 | 0.70 | 11.70 | 0.026 | 0.0036 | 0.056 | 0 | 16.8 |

*Notes:* The "No. collected" column reports the total number of recruits taken from three standardized monitoring units for the recruitment of fishes (SMURFs) on that sample date; sample size is the subset analyzed for this study. Samples were taken in the Santa Barbara Channel, California, USA. $H_O$ is observed heterozygosity, $A$ is rarefied allelic richness, $F_{IS}$ is a measure of heterozygote deficit, mean $F_{ST}$ measures the mean genetic differentiation from other cohorts, mean $R_{XY}$ is the mean relatedness coefficient for all pairs of individuals, WLP is an independent measure of the fraction of days over the two-week collection period that the site was exposed to the western side of the frontal boundary, and Min. temp. is the minimum water temperature (°C) recorded at the site during the collection period.

sibships in the pair ($R^2 = 0.11$, Mantel $P = 0.015$). The association of high numbers of sibships with high pairwise $F_{ST}$ is unlikely to be a sampling effect producing random clustering of genotypes, as substituting the observed cohorts with simulated cohorts containing identical numbers of significant sibships generated no positive $F_{ST}$ values with the other cohorts (data not shown). Another measure of relatedness, gametic phase disequilibrium, was more widespread than expected by chance for the recruits (97 observed vs. 21 expected cases), but this is the same percentage as seen for the adults (56 observed vs. 13 expected cases) and the number of cases per cohort did not correlate with number of excess sibships ($R^2 = 0.002$, $P = 0.91$) or mean $F_{ST}$ ($R^2 = 0.16$, Mantel $P = 0.20$).

### *Are changes in larval delivery driving the recruit genetic structure?*

The 20 recruit cohorts ranged from 0 to 1 in WLP values, indicating the potential for differences in the direction of larval delivery across cohorts. Only two cohorts, 11 and 16 from Hazards, however, have high WLP values (>0.7; Table 1). The WLP values are uncorrelated with mean $F_{IS}$ ($R^2 = 0.17$, $P = 0.07$). Pairwise $F_{ST}$ values for the 20 cohorts are significantly correlated with the pairwise difference in WLP value ($R^2 = 0.28$, Mantel $P = 0.001$). Pairwise $F_{ST}$ values show no correlation with pairwise difference in minimum temperature ($R^2 = 0.007$, Mantel $P = 0.32$), despite the fact that WLP is partly derived from temperature. Pairwise $F_{ST}$ for just the Gag10 locus

TABLE 2. Locus characteristics: genetic variation within ($H_E$) and among ($F_{ST}$) samples for all seven loci.

| | Recruit cohorts, $N = 1184$ | | | | | | Adult samples, $N = 726$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | No. alleles | $H_O$ | $H_E$ | $F_{IS}$ $P$ value | $F_{ST}$ | Exact test $P$ | No. alleles | $H_O$ | $H_E$ | $F_{IS}$ $P$ value | $F_{ST}$ | Exact test $P$ |
| Mbo66 | 2 | 0.374 | 0.407 | 0.001 | 0.009* | 0.015 | 3 | 0.390 | 0.418 | 0.056 | 0 | 0.142 |
| Pam13 | 18 | 0.537 | 0.544 | 0.437 | 0 | 0.021 | 16 | 0.553 | 0.554 | 0.567 | 0 | 0.259 |
| Gag010 | 18 | 0.765 | 0.764 | 0.575 | 0.002* | 0.032 | 17 | 0.759 | 0.76 | 0.693 | 0 | 0.355 |
| AV6 | 54 | 0.923 | 0.924 | 0.001 | 0.001 | 0.000 | 53 | 0.933 | 0.949 | 0.003 | 0.003* | 0.000 |
| AV17 | 21 | 0.601 | 0.596 | 0.857 | 0.003* | 0.055 | 15 | 0.621 | 0.577 | 0.995 | 0.013* | 0.055 |
| AV15 | 45 | 0.926 | 0.918 | 0.627 | 0.001 | 0.246 | 43 | 0.921 | 0.919 | 0.301 | 0 | 0.474 |
| AV88 | 30 | 0.923 | 0.927 | 0.212 | −0.001 | 0.897 | 31 | 0.926 | 0.924 | 0.426 | 0.001 | 0.256 |
| All | 188 | 0.721 | 0.73 | 0.004 | 0.002* | <0.0001 | 178 | 0.729 | 0.729 | 0.387 | 0.002* | <0.0001 |

*Notes:* Significance of genetic structuring is indicated by asterisks for $F_{ST}$ values, and by the $P$ values listed for a Fisher's exact test.

* $P < 0.05$.

TABLE 3. Characteristics of adult samples and San Miguel 2004 recruits.

| Sample code | Location | Year | Sample size | $H_O$ | $A$ | $F_{IS}$ |
|---|---|---|---|---|---|---|
| A | San Miguel recruits | 2004 | 39 | 0.69 | 12.16 | 0.01 |
| B | Santa Rosa Island | 2004 | 43 | 0.75 | 11.30 | −0.023 |
| C | Santa Cruz Island | 2004 | 76 | 0.71 | 12.13 | 0.021 |
| D | Naples Reef | 2001 | 64 | 0.75 | 12.52 | −0.016 |
| | | 2004 | 40 | 0.72 | 11.41 | −0.024 |
| E | Carpinteria | 2004 | 59 | 0.76 | 12.23 | −0.013 |
| F | San Pedro | 1990 | 60 | 0.73 | 12.06 | −0.008 |
| | | 2004 | 64 | 0.74 | 11.52 | 0.007 |
| G | Catalina Island | 2001 | 43 | 0.73 | 12.12 | 0.013 |
| H | San Clemente Island | 2001 | 83 | 0.72 | 12.15 | 0.022 |
| I | San Diego | 2001 | 84 | 0.72 | 11.91 | 0.007 |
| J | Coronado Island | 2001 | 71 | 0.71 | 12.20 | 0.004 |

*Notes:* See Table 1 for explanations of abbreviations $H_O$, $A$, and $F_{IS}$; see Fig. 1 for map of sample locations.

(which showed some correlation between $F_{IS}$ and minimum temperature) also shows no such correlation ($R^2 = 0$, Mantel $P = 0.98$).

### *Do cohort–adult relationships corroborate the presumed direction of larval delivery?*

Although the results above suggest recruits arriving from the west tend to be genetically distinct, the idea requires that populations to the west/north are genetically differentiated from populations to the east/south. The sample farthest to the northwest (2004 recruits from San Miguel Island) indeed shows significant differentiation with many of the other adult sites (e.g., $F_{ST} =$ 0.004–0.009), while the rest of the adult samples show few differences among them (Appendix B). Samples from Santa Rosa Island and Naples are similar to the other southern sites, as expected from their frequent exposure to flow originating from the south. The San Miguel sample shows strong differentiation with recruit cohorts with low WLP values, but similarity to those with high WLP values (Table 5), suggesting that high WLP may indicate a similar source as the San Miguel sample. Cohort 11 has a high WLP value but differs genetically from the San Miguel recruits, indicating either a distinct source or that its high number of sibships inflates the $F_{ST}$ value. The rest of the adult samples show the opposite trend, but again cohort 20, which has many sibships, is distinct from adults despite low WLP (Table 5). These results suggest that cohorts with low WLP are more likely to resemble populations

TABLE 4. Half and full sibship results from KINSHIP and significance testing.

| Cohort ID | Pairwise comparisons | Sig. pairs exp. for $\alpha_{0.05}$ | 95% cutoff (half, full) | Observed half sibs | Observed full sibs | Summed excess pairs |
|---|---|---|---|---|---|---|
| 1 | 2080 | 104 | 117, 125 | **118** | **133** | **9** |
| 2 | 1275 | 64 | 74, 78 | 69 | 81 | −2 |
| 3 | 820 | 41 | 50, 52 | 47 | 52 | −3 |
| 4 | 1770 | 89 | 100, 107 | 91 | 91 | −25 |
| 5 | 666 | 33 | 42, 43 | 39 | 34 | −12 |
| 6 | 2556 | 128 | 142, 153 | 125 | 113 | −57 |
| 7 | 1596 | 80 | 91, 97 | 73 | 76 | −39 |
| 8 | 2278 | 114 | 127, 136 | 122 | 130 | −12 |
| 9 | 3003 | 150 | 166, 178 | 164 | **189** | **9** |
| 10 | 2080 | 104 | 117, 125 | 99 | 118 | −25 |
| 11 | 2415 | 121 | 135, 144 | 133 | **155** | **9** |
| 12 | 435 | 22 | 30, 29 | 21 | 21 | −17 |
| 13 | 2278 | 114 | 127, 136 | 116 | 110 | −38 |
| 14 | 1830 | 92 | 104, 110 | 93 | 91 | −30 |
| 15 | 3160 | 158 | 174, 188 | 150 | 176 | −36 |
| 16 | 1176 | 59 | 69, 72 | 62 | 65 | −14 |
| 17 | 2016 | 101 | 113, 122 | **118** | 107 | −10 |
| 18 | 861 | 43 | 52, 54 | 48 | 44 | −14 |
| 19 | 1891 | 95 | 107, 114 | 100 | 106 | −15 |
| 20 | 2016 | 101 | 113, 122 | **118** | **170** | **53** |

*Note:* Pairwise comparisons indicate the number of multiple tests per cohort per relationship tested. The number of significant pairs expected for $\alpha_{0.05}$ is 5% of the number of pairwise comparisons. The 95% cutoff indicates the number of significant pairs created by chance in the 95th percentile of the simulated data sets (see *Methods*). Observed full and half sibs indicate the number of significant pairs for $\alpha_{0.05}$ in the cohorts; boldface type indicates those with numbers in excess of the 95% cutoff. Values in the summed excess pairs column represent observed minus the 95% cutoff values summed for half and full sibs; these values were used for regressions.

TABLE 5. Pairwise $F_{ST}$ values between recruit cohorts and adult samples, sorted by Western Larval Pool (WLP) value.

| Cohort | WLP | San Miguel recruits | Santa Rosa Island | Santa Cruz Island | Naples 2001 | Naples 2004 |
|---|---|---|---|---|---|---|
| 1 | 0 | 0.0051* | −0.0007 | −0.0015 | 0.0017 | 0.0035 |
| 2 | 0 | 0.0057* | −0.001 | −0.0027 | −0.0001 | 0.0005 |
| 8 | 0 | 0.0061* | −0.002 | −0.0007 | 0.0045 | 0.0026 |
| 20 | 0 | 0.0088** | 0.0014 | 0.0007 | 0.0038 | 0.0041 |
| 4 | 0.06 | 0.0029 | −0.0018 | −0.0022 | 0.0002 | −0.0005 |
| 12 | 0.07 | −0.0016 | 0.0017 | −0.0022 | −0.0008 | −0.0012 |
| 3 | 0.13 | 0.0019 | −0.0022 | −0.002 | 0.0021 | 0.0031 |
| 5 | 0.13 | 0.003 | −0.0009 | −0.0011 | 0.0033 | 0.0031 |
| 10 | 0.14 | 0.0052 | −0.0044 | 0.0017 | −0.0001 | 0.0017 |
| 6 | 0.19 | 0.0038 | −0.0016 | −0.0003 | 0.0038 | 0.0015 |
| 9 | 0.24 | 0.007* | −0.0016 | −0.0008 | 0.0066* | 0.0029 |
| 17 | 0.25 | 0.0033 | −0.0002 | −0.0016 | 0.0001 | 0.0017 |
| 19 | 0.3 | 0.0031 | −0.0031 | −0.0022 | 0.0003 | −0.0019 |
| 14 | 0.36 | 0.0036 | −0.0017 | −0.001 | 0.0004 | 0.0008 |
| 15 | 0.38 | 0.0043 | −0.0017 | −0.0023 | 0.0022 | −0.0018 |
| 13 | 0.44 | 0.0075* | −0.0014 | −0.0012 | 0.0033 | 0.0012 |
| 7 | 0.5 | 0.0033 | −0.0021 | −0.004 | 0.0005 | −0.0006 |
| 18 | 0.53 | 0.0045 | 0.0058* | 0.0029 | −0.0005 | 0.0012 |
| 11 | 0.75 | 0.0118** | 0.0005 | 0.0005 | 0.0103** | 0.0047 |
| 16 | 1 | 0.0043 | 0.006* | 0.0059* | 0.0074* | 0.0106** |

*$P < 0.05$; **$P < 0.01$. $P$ values are uncorrected for multiple tests.

to the east or south and cohorts with high WLP are more likely to resemble populations to the west or north; however, these data are not able to directly test for larval source.

### *Are genetic differences best explained by multiple hypotheses?*

A multiple linear regression model fitting pairwise $F_{ST}$ to two explanatory variables, pairwise difference in WLP value and total number of excess sibships in the pair, explained a substantial amount of the variance ($R^2 = 0.34$), larger than either of these variables used alone. The partial Mantel test showed that the coefficients of both variables are significant (sibships slope $= 3 \times 10^{-5} \pm 7 \times 10^{-6}$, $P = 0.004$; WLP slope $= 0.007 \pm 0.0009$, $P = 0.016$). Adding in pairwise difference in minimum temperature does not increase the fit and is not significant ($R^2 = 0.33$, $P = 0.67$), and running the model with only temperature and sibships produces $R^2 = 0.10$. Although WLP and minimum temperature are correlated ($R^2 = 0.63$), it is not enough to have a substantial impact on the precision of the coefficient estimates when both are included (Fox 1997). A similar analysis for mean $F_{ST}$ instead of pairwise $F_{ST}$ using number of excess sibships, WLP, and minimum temperature produced $R^2 = 0.64$, and again only the sibship and WLP variables are significant (Mantel $P = 0$ and $P = 0.033$, respectively). The better fit for mean $F_{ST}$ results from the dampened variance of taking mean values compared to pairwise $F_{ST}$. The linear relationship with WLP (instead of hump-shaped) results because only a few samples have large WLP values. A similar multiple regression analysis of $F_{IS}$ against number of excess sibships, WLP, and minimum temperature produces $R^2 = 0.38$ but only temperature is significant (partial Mantel $P = 0.002$), confirming the correlation presented above driven by locus Gag10.

## DISCUSSION

The major findings of this study are that kelp bass recruits sampled from sites in the Santa Barbara Channel show evidence of "chaotic genetic patchiness" and that sibships within cohorts of recruits and changes in larval delivery are dual drivers of this genetic differentiation. While the sampling design was not ideal for determining the geographic locations of the sources contributing to the eastern and western larval pools, the wider geographical sampling of kelp bass suggests that cohorts from the western larval pool arriving at the Hazards site tend to be most genetically similar to individuals at San Miguel Island, the site farthest to the northwest, and most different from populations to the south and east.

Investigation of selection due to temperature, as measured by the minimum or mean temperature during the two-week collection period, failed to reveal a significant response by any individual microsatellite allele, and temperature appears not to drive the correlation between difference in WLP and pairwise $F_{ST}$ despite the correlation between WLP and temperature. However, $F_{IS}$ correlates with minimum temperature, perhaps indicating some selection against heterozygotes at least at one of the loci. Note that this temperature variable reflects temperature post-settlement and may be a poor proxy for temperature during the dispersal phase. It is impossible to rule out other potential selective agents that we were unable to measure directly (e.g., temperature during the pelagic phase, nutrition of larvae, etc.) that might contribute to the patterns of genetic structure, although allele frequencies generally conformed to neutral expectations. Thus, it is possible that the correlation of $F_{ST}$ with WLP (driven by cohorts at the Hazards site only) is due to environmental selection during the pelagic larval phase

TABLE 5. Extended.

| Carpinteria | San Pedro 1990 | San Pedro 2004 | Catalina Island | San Clemente Island | San Diego | Coronado Island |
|---|---|---|---|---|---|---|
| 0.0039 | 0.0002 | 0.0028 | 0.0017 | −0.0001 | 0.0035 | 0.001 |
| 0.0033 | 0.0003 | 0.0047 | 0.0049 | 0.0019 | 0.0011 | −0.0012 |
| 0.0004 | 0.003 | 0.0024 | 0.0035 | −0.001 | 0.0014 | 0.0021 |
| 0.0095** | 0.005 | 0.0105** | 0.0109** | 0.0028 | 0.001 | 0.0006 |
| 0.0022 | 0.0015 | 0.0004 | 0.0018 | −0.0023 | 0.0004 | −0.0005 |
| 0.003 | −0.0005 | −0.0007 | 0.0019 | 0.0004 | 0.0004 | 0 |
| 0.0021 | −0.0014 | 0.0025 | 0.0048* | 0.0018 | 0.0029 | 0.0005 |
| −0.0006 | 0.0005 | −0.0016 | −0.0012 | 0.001 | 0.0008 | 0.0014 |
| 0.001 | 0.0005 | −0.0004 | 0.0019 | −0.002 | −0.0009 | −0.0021 |
| 0.0005 | 0.0015 | −0.0001 | 0.0001 | −0.0004 | 0.0022 | 0.0007 |
| 0.0026 | 0.0026 | 0.0018 | 0.006* | 0.0018 | 0.0008 | −0.0001 |
| 0.0033 | −0.0011 | −0.0005 | 0.0001 | 0.0001 | 0.001 | −0.0003 |
| −0.0011 | 0.0012 | 0.0002 | −0.0002 | −0.0006 | −0.0013 | 0.0001 |
| 0.0011 | −0.0003 | 0.0004 | −0.0013 | 0.0003 | 0.003 | 0.0016 |
| 0.0021 | 0.0021 | 0.0018 | 0.0012 | −0.0008 | −0.0002 | −0.0009 |
| 0.0027 | 0.0026 | 0.0024 | 0.0007 | −0.0007 | 0.0005 | 0 |
| 0.003 | 0.0008 | 0.0005 | 0.0018 | −0.0019 | 0.0006 | −0.0006 |
| 0.0098** | 0.0036 | 0.0067* | 0.0063* | 0.0062* | 0.0039 | 0.0049* |
| 0.0023 | 0.0025 | 0.0036 | 0.0054 | 0.0048* | 0.0043 | 0.0017 |
| 0.0065* | 0.0054* | 0.0007 | −0.0002 | 0.0067** | 0.012** | 0.0117** |

instead of, or in addition to, origin from genetically distinct source populations.

To our knowledge, this is the first study to find specific evidence of full and half siblings in cohorts of recruits for a marine fish. A new study recently presented similar results for an intertidal barnacle (Velig et al. 2006). Also, a recent study of the catadromous European eel found high relatedness in some waves of arriving recruits (Pujolar et al. 2006). In addition, Planes et al. (2002) used 25 allozymes to demonstrate that cohorts of incoming larvae of a reef fish in Moorea had high mean relatedness values ($R_{XY} = 0.05$–$0.33$), but the authors did not identify sibships per se. An allozyme study that tracked cohorts of recruits of sea bream over two years ascribed a decline in $F_{IS}$ through time to increased mixing through migration, but did not test for relatedness directly (Planes and Lenfant 2002). In contrast, a past study of kelp bass recruits failed to find support for the sweepstakes hypothesis using a different genetic approach and just three sampled recruit cohorts, one of which was a sample of recruits from cohort 12 in this study, for which we also found no siblings (Luzier and Wilson 2004).

The results here suggest that most cohorts do not contain many sibling pairs, but on occasion they do. Determining the exact number and identity of true siblings in the cohorts given the huge number of pairwise tests is inherently problematic, because one expects many significant pairs due to chance with the number of loci used. The simulation approach confirmed that the observed numbers were highly unlikely by chance, but that the number of true sibships is probably low. Using more loci would reduce the number of false positives so that the significant pairs identified contain a larger fraction of true sibships.

It is not surprising to us that a few larvae produced in the same spawning event (i.e., siblings) can remain together throughout the planktonic period and settle at the same site; if many sibling larvae are released, there is a good probability that at least a few will remain in the same packet of water (Siegel et al. 2003). Nevertheless, it is possible that the small fractions of siblings found in the samples used here may represent much larger numbers recruiting together onto the same reef, because the SMURF collections represent only a small fraction of recruits to the reef. In the case of cohort 20 (with the most significant sibships), sibships between fish on different SMURFs were almost as common as sibships on the same SMURF, indicating the families are diffused over at least a 100-$m^2$ area.

The amount of genetic drift resulting from the observed frequency of sibships is not likely substantial enough to have a strong impact on adult genetic structure, as it is averaged out across multiple cohorts that are subsumed into the year class of an entire recruitment season. None of the variance in genetic differentiation was found to be partitioned by site or by year. Temporal replicates of adult samples taken three and 14 years apart showed no significant allele frequency differences (although a small amount may have been detectable with larger samples sizes), which would be expected if the sweepstakes phenomenon acted at a larger scale (e.g., entire year classes showing family structure). Moreover, preliminary results from a large study investigating year class structure in kelp bass for which thousands of adult samples were aged by their otoliths showed no broad-scale signature of genetic variance partitioned by year class (although as in this study, there are some suggestive patterns on a small scale; A. Vogel, *unpublished data*). That study used many of the same sites, some of the same adult samples as this study, and used the same microsatellite markers plus a mitochondrial d-loop marker.

Despite lack of evidence for a large-scale impact of this small-scale sweepstakes phenomenon, adult populations in the Southern California Bight show no geographical organization to their genetic structure, instead showing chaotic genetic patchiness. The degree of differentiation is no greater than that shown by the recruits. The circuitous flow of the Southern California Eddy and the high frequency of small-scale flow anomalies in the SCB (Bray et al. 1999, DiGiacomo and Holt 2001) likely decouples geographic distance and dispersal distance, and thus isolation by distance would not be expected. For instance, larvae released in the northern Channel Islands may be transported to San Diego in the California Current within a 30-day larval period (Winant et al. 1999).

While the degree of genetic differentiation reported for both the recruits and adults only amounts to slight differences in allele frequencies that may not have substantial biological effects (Waples 1998), they nonetheless signal changes in composition that may be a useful tool for understanding better the connectivity patterns and recruitment dynamics of marine species (Knutsen et al. 2003). This study differs from two previous studies that matched oceanographic flow patterns with variation in larval delivery from heterogeneous sources, in that those studies used single allozyme loci specifically chosen because they exhibited strong clines indicative of environmental selection (Drouin et al. 2002, Gilg and Hilbish 2003). Here we demonstrate that given highly variable neutral markers, slight genetic differences among populations are enough to allow detection of fine-scale spatial and temporal variation in cohorts of recruits. However, the power of this study may have been enhanced by the choice of an oceanographic convergence zone as the study site. Simulations of convergent gene flow demonstrate that genetically distinct source populations at the edges of a linear array can contribute to recruitment in the middle without becoming genetically homogenous (B. Kinlan, K. A. Selkoe, and S. D. Gaines, *unpublished data*).

The success of using a thermal discontinuity to estimate the position of the boundary between larval pools has implications for understanding the dispersal dynamics of many important species in the Santa Barbara Channel. Applying this method to infer the direction of larval delivery over the entire recruitment period from July to October in 2000 and 2001 suggests that the Hazards site on Santa Cruz Island was exposed to the west side of the frontal boundary ~10 times each recruitment season, with each event lasting an average of four days. This pattern matches an independent estimate of the periodicity of flow patterns in the Santa Barbara Channel (Harms and Winant 1998). These events total nearly 50% of the entire kelp bass recruitment season for Hazards and 10–20% of the season for the other three island sites, suggesting there is ample opportunity to receive larvae from the western larval pool. The four-day periodicity suggests that allowing the recruits to accumulate for two weeks made it unlikely to get a "cohort" made up of entirely western or entirely eastern recruits. Only one cohort in this analysis was found to be entirely western, and it indeed showed the strongest differences with all other cohorts. Collecting recruits at higher temporal frequencies or determining the exact day of settlement for each fish using possible settlement marks on the otoliths would be one way to improve the WLP approach for future studies.

The current break at Point Conception has long been thought to isolate populations to the north and south. Point Conception marks the northern range boundary for many species with planktonic larvae but few with crawl-away larvae, a disparity that implies the current break can limit planktonic dispersal that would allow persistent range extension (Gaylord and Gaines 2000, Wares et al. 2001). Nevertheless, studies that have examined the impact of this potential current break on the phylogeographic structure of coastal populations have found no mark of reduced dispersal other than a signature of southward-biased gene flow (Burton 1998, Dawson 2001, Wares et al. 2001). Our focus here on small-scale shifts in the position of the temperature front in the Channel provides a model of how this subtle movement counteracts the effect of the current break as a barrier to gene flow: spatial shifts in the break's location facilitate episodic dispersal across it.

The results of this study point to the importance of considering spatial and temporal variability in both connectivity and reproductive output in managing marine species. The intentional placement of the Channel Islands marine reserves in the northern, southern, and the middle transition zone was based upon biogeographic patterns of species distributions (Airame et al. 2003). This study suggests these divisions may also protect a diversity of potential source populations for kelp bass and other species with pelagic larvae. However, it remains unclear how many kelp bass larvae are imported from elsewhere and from how far away. Genotype assignment methods to match recruits to sources typically require larger $F_{ST}$ values ($>0.01$) than commonly observed for marine fishes and cannot account for genetic drift induced by sweepstakes effects. Otolith microchemistry or tagging approaches may be a fruitful alternative to address questions of source (Swearer et al. 2002). Although this study suggests the likely mechanisms behind chaotic genetic patchiness in kelp bass recruits, for now, the "intractable plankton" (Johnson and Black 1982) still limits our ability to link fish recruits to their sources.

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## APPENDIX A

Pairwise values of $F_{ST}$ for all 20 cohorts (*Ecological Archives* E087-186-A1).

## APPENDIX B

Pairwise values of $F_{ST}$ for adult samples and San Miguel recruits (*Ecological Archives* E087-186-A2).