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Article *in* Molecular Ecology · February 2019

DOI: 10.1111/mec.15044

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Received: 2 October 2018 | Revised: 28 January 2019 | Accepted: 30 January 2019

DOI: 10.1111/mec.15044

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Dispersal of a nearshore marine fish connects marine reserves and adjacent fished areas along an open coast

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Funding information
Division of Ocean Sciences, Grant/Award Number: 1260693; US National Science Foundation

Abstract

Marine species with pelagic larvae typically exhibit little population structure, suggesting long-distance dispersal and high gene flow. Directly quantifying dispersal of marine fishes is challenging but important, particularly for the design of marine protected areas (MPAs). Here, we studied kelp rockfish (*Sebastes atrovirens*) sampled along ~25 km of coastline in a boundary current-dominated ecosystem and used genetic parentage analysis to identify dispersal events and characterize them, because the distance between sedentary parents and their settled offspring is the lifetime dispersal distance. Large sample sizes and intensive sampling are critical for increasing the likelihood of detecting parent–offspring matches in such systems and we sampled more than 6,000 kelp rockfish and analysed them with a powerful set of 96 microhaplotype markers. We identified eight parent–offspring pairs with high confidence, including two juvenile fish that were born inside MPAs and dispersed to areas outside MPAs, and four fish born in MPAs that dispersed to nearby MPAs. Additionally, we identified 25 full-sibling pairs, which occurred throughout the sampling area and included all possible combinations of inferred dispersal trajectories. Intriguingly, these included two pairs of young-of-the-year siblings with one member each sampled in consecutive years. These sibling pairs suggest monogamy, either intentional or accidental, which has not been previously demonstrated in rockfishes. This study provides the first direct observation of larval dispersal events in a current-dominated ecosystem and direct evidence that larvae produced within MPAs are exported both to neighbouring MPAs and to proximate areas where harvest is allowed.

KEYWORDS
larval dispersal, marine protected areas, microhaplotype, parentage analysis, rockfish, *Sebastes*

1 | INTRODUCTION

The structure, distribution and population dynamics of many marine species rely on the dispersal or retention of planktonic larvae (Cowen & Sponaugle, 2009; Levin, 2006). During the period when larvae drift in the pelagic environment, they can travel hundreds to thousands of kilometres, if they do not encounter oceanic barriers, before settling in suitable habitat (Cowen, 1985). Although organisms with extensive dispersal capabilities are generally presumed to have limited population structure, interactions between geophysical ocean features and biological attributes of dispersing larvae can modify the distribution of organisms and the extent of connectivity

(Kinlan & Gaines, 2003). Studies of larval duration (Shanks, 2009; Shanks, Grantham, & Carr, 2003), behaviour (Metaxas, 2001; Morgan, 2014; Pineda, Porri, Starczak, & Blythe, 2010) and navigational ability (Nanninga & Berumen, 2014) highlight organismal characteristics that contribute to demographic connectivity or independence. However, environmental factors (reviewed by McManus & Woodson, 2012), including habitat patchiness (Pinsky, Palumbi, Andréfouët, & Purkis, 2012), and oceanic (Nickols, Gaylord, & Largier, 2012; Woodson et al., 2012) and geographical features (Drake, Edwards, & Barth, 2011; Mace & Morgan, 2006) also play a role. Yet our ability to understand exactly how population dynamics are affected by dispersal is impeded by the challenge of explicitly measuring it by following multiple larvae from their location at birth to their eventual destinations and fates.

Tracking larval dispersal in the ocean is considered one of the great logistical challenges in marine ecology (Pineda, Hare, & Sponaugle, 2007). Studies that have successfully addressed this challenge have produced intriguing results regarding the prevalence of self-recruitment (Berumen et al., 2012; Jones, Planes, & Thorrold, 2005), connectivity among reefs (Almany et al., 2017; Christie et al., 2010) and the effectiveness of marine reserves (Harrison et al., 2012; Le Port et al., 2017; Planes, Jones, & Thorrold, 2009).

There is a substantial history of using genetic markers to study dispersal in marine species. Historically, marine dispersal was primarily measured using indirect methods, including predictive models (Pinsky et al., 2017) and genetic summary statistics that integrate information across many generations to produce estimates of average dispersal rates and distances (Buonaccorsi et al., 2004). However, these methods are highly dependent upon assumptions about parameter values, such as those regarding population sizes and physical oceanographic properties, and, at best, provide estimates of mean values across populations and generations. Alternatively, traditional tagging approaches have been explored, but these are hampered both by the typically enormous population sizes of the organisms under study, and by the challenge of capturing and recapturing individuals in the marine environment. Genetic assignment, or stock identification, methods have also been used to study dispersal (e.g., Horne, Momigliano, Welch, Newman, & van Herwerden, 2011). These methods use a reference data set of known-origin individuals from distinct populations to determine the origin of individuals of unknown provenance and are often used to identify "recent" migrants, as individuals residing in a specific location that are of nonlocal origin. However, these methods require population-level genetic differences that arise through population structure, which is often absent for marine species.

For marine species with sedentary adults and planktonic juveniles, the study of dispersal with genetic parentage analysis has seen substantial use over the last decade, particularly for species in which structure is absent at fine spatial scales (e.g., Christie et al., 2010; Jones et al., 2005). Furthermore, parentage analysis has been used to test assumptions of marine reserve design: specifically, the ability of reserves to increase the number of individuals within the reserve as well as export individuals beyond reserve boundaries, through either spillover or recruitment subsidies (Botsford et al., 2009; Botsford, Micheli, & Hastings, 2003; Sale et al., 2005). Whether reserves enhance populations in fished areas has been a crucial knowledge gap (Sale et al., 2005), and many studies have attempted to evaluate the extent to which self-recruitment, spillover or recruitment subsidies occur (Almany et al., 2017; Berumen et al., 2012; Christie et al., 2010; Harrison et al., 2012; Le Port et al., 2017).

While the identification of parent–offspring relationships has been the dominant form of relationship inference used in the study of dispersal in the marine realm, Schunter, Pascual, Garza, Raventos, and Macpherson (2014) showed how combining identification of sibling groups with parentage analysis provides a more complete description of dispersal patterns. Such sibship analysis has since seen additional use in the study of marine fishes (e.g., Ottmann et al., 2016), but Baetscher, Clemento, Ng, Anderson, and Garza (2018) have shown that most such analyses have lacked sufficient power to accurately identify sibling groups.

Coral reef environments have dominated dispersal research (Almany et al., 2017; Berumen et al., 2012; Christie et al., 2010; Herrera et al., 2016; Jones et al., 2005; Planes et al., 2009; Saenz-Agudelo, Jones, Thorrold, & Planes, 2009, 2011), while just two studies have directly measured empirical dispersal in temperate marine environments (Le Port et al., 2017; Schunter et al., 2014). The most productive temperate marine regions, those in which coastal upwelling drives ecosystem dynamics, such as the Humboldt, Benguela or California Current ecosystems, are understudied in this respect. The dearth of information about dispersal in such marine ecosystems, particularly in the temperate realm, is due to the challenges of sampling a sufficient number of individuals when larval dispersal is propelled by dominant alongshore currents.

Rockfishes of the genus *Sebastes* are a prominent component of the ichthyofauna in such temperate ecosystems, particularly in the northern Pacific Ocean, where they form a marine species flock that includes over 100 closely related species (Johns & Avise, 1998; Love, Yoklavich, & Thorsteinson, 2002). Although adults can generally be classified to species correctly based on morphology during field collections, many rockfish species are visually indistinguishable as juveniles (Butler, Love, & Laidig, 2012) and generally require genetic analysis for identification (Pearse, Wooninck, Dean, & Garza, 2007).

Kelp rockfish (*Sebastes atrovirens*) are part of this species flock and one of over 50 rockfish species present in the Monterey Bay region of California (Love et al., 2002). Adults and post-recruitment juveniles are associated with rocky reefs and are abundant in kelp beds and in nearshore marine reserves to a depth of ~30 m (Love et al., 2002). Previous work found no population structure across the species range (Gilbert-Horvath, Larson, & Garza, 2006). Kelp rockfish is similar to many other nearshore rockfish species, in that adults have very small home ranges (~3–7 m^2; Van Dykhuzien, 1983) and give birth to thousands to hundreds of thousands of larvae that are planktonic for ~2–4 months, after which they settle into suitable kelp forest habitat (Gilbert-Horvath et al., 2006; Love et al., 2002). In the central California study region, parturition occurs from February to June, with the majority of larvae typically released in May (Love

et al., 2002). Rockfishes are popular in commercial and recreational fisheries, and historical depletion led to protected status for some species and the establishment of networks of marine reserves and Rockfish Conservation Areas along the west coast of North America (Lotterhos, Dick, & Haggarty, 2014).

Here, we apply genetic pedigree reconstruction analysis to study larval dispersal of kelp rockfish along an open coastline in a current-dominated temperate ecosystem and among a network of marine reserves in central California. We describe the first direct measurements of larval dispersal for kelp rockfish and elucidate how these events provide connectivity between reserves, as well as between reserves and areas where harvest is allowed. We also describe the implications of the results for our understanding of the species life history. To have high confidence in inferring relationships, and also confirm species identification of the juveniles in the study, we used the novel microhaplotype marker approach described by Baetscher et al. (2018). This approach provides orders of magnitude more power than the same number of single nucleotide polymorphisms (SNPs) for inferring pedigree relationships with short read next-generation sequencing data.

2 | METHODS

2.1 | Samples

Approximately 25 km of nearshore habitat in Carmel and Monterey bays was intensively sampled from May to September in 2013–2016 (Supporting Information Figure S1). This area contains a network of marine protected areas (MPAs), including State Marine Reserves, where no harvest of marine resources is allowed, and State Marine Conservation Areas, where recreational harvest of fishes is allowed during certain seasons. Adult rockfishes were sampled by one of two methods: hook-and-line capture, in which a small piece of fin tissue was removed before release, or by divers on SCUBA using a nonlethal, underwater biopsy pole (Smith, Malone, Baetscher, & Carr, 2018). Recruiting juvenile rockfishes were captured by one of two methods: by SCUBA divers using Bincke nets (Anderson & Carr, 1998) in the kelp canopy, or following settlement into Standard Monitoring Units for the Recruitment of Fishes (SMURF) collectors (Ammann, 2004). A small piece of fin tissue was removed from juveniles and fish were released alive. Tissue samples for both adults and juveniles were dried on blotting paper, dehydrated for at least 24 hr, and then stored at room temperature until DNA extraction with DNeasy 96 Blood and Tissue kits on a BioRobot 3000 (Qiagen). DNA was eluted into a final volume of 200 µl for adult tissues and 150 µl for juvenile tissues.

2.2 | Genotyping

All fish were genotyped with 96 microhaplotype markers designed for kelp rockfish (Supporting Information Table S1; Baetscher et al., 2018). Each microhaplotype locus is 100–130 bp and contains at least one SNP. Genotyping followed the Genotyping-in-Thousands by sequencing (GT-seq) protocol of Campbell, Harmon, and Narum (2015), with modifications as described by Baetscher et al. (2018). Each sequencing library consisted of 384 individually indexed samples. Sequencing was performed on a MiSeq instrument (Illumina) with 2 × 75 bp paired-end reads.

2.3 | Data analysis

Raw sequencing reads were assigned to individual samples by indexes using the MiSeq Analysis Software (Illumina), and then analysed with the workflow described by Baetscher et al. (2018). Briefly, paired-end reads were combined using FLASH (fast length adjustment of short reads; Magoč & Salzberg, 2011) with a minimum overlap of 10 bp and maximum overlap of 100 bp. Combined reads were mapped to a reference FASTA file, which contained consensus sequences for all 96 loci, using the Burrows–Wheeler Aligner (BWA-MEM). Next, mapped data files were sorted to generate alignments with loci in a consistent order, as defined by the reference file using SAMTOOLS, and FREEBAYES (Garrison & Marth, 2012) was used to generate a reference variant call format (VCF) file for six sequencing runs (three runs contained adult samples from four species of interest and three runs contained juvenile samples from multiple species), which were filtered for minimum base quality (minQ = 30), minimum read depth (minDP = 10) and removal of indels. These six filtered VCF files were merged together using VCFTOOLS. Phased haplotype data were produced using the R (R Core Development Team, 2016) software package MICROHAPLOT (Ng & Anderson, 2016) and associated Shiny app (http://shiny.rstudio.com/). MICROHAPLOT takes aligned SAM files for each sample and a VCF file, which contains variant location information, and outputs the individual base calls for the variants designated in the VCF file. Base calls and read depths for each individual/haplotype were then exported from MICROHAPLOT.

Genotypes were filtered for retention by imposing a minimum of 10 sequencing reads for the first allele and six reads for the second allele (in heterozygotes), as well as a minimum of 20 total reads per individual–locus combination as a read depth threshold for both homozygotes and heterozygotes. Haplotypes that had a read depth ratio of <0.4 were removed. The read depth ratio is calculated as the number of reads for each haplotype divided by the number of reads of the most common haplotype in that individual at that locus. This read depth ratio criterion is intended to remove spurious haplotypes caused by index switching and genotyping error, which may not be identified by the read depth threshold alone (Baetscher et al., 2018). Additionally, the presence of more than two haplotypes in an individual at multiple loci after filtering provided an opportunity to identify potentially contaminated DNA extracts. Samples that produced retained genotypes at <90% of the 78 retained loci (see below) were re-genotyped in an attempt to recover a sufficiently complete genotype. Samples that did not meet this missing data criterion following two genotyping attempts were excluded from further analysis.

A number of loci exhibited signatures of null alleles, as evidenced by significant deviations between the expected and observed

frequencies of heterozygous genotypes (Chakraborty, De Andrade, Daiger, & Budowle, 1992). In parentage studies, the presence of null alleles may cause a true parent to be excluded (Dakin & Avise, 2004), and both the frequency of a null allele and the number of null alleles present in the data set cause an increased likelihood of false exclusion. Because of this concern, loci with such heterozygote deficits (*z*-statistic of observed heterozygote frequency vs. that expected under Hardy–Weinberg equilibrium <−3) were removed.

Because kelp, copper (*Sebastes caurinus*), black-and-yellow (*S. chrysomelas*) and gopher (*S. carnatus*) rockfishes recruit to the kelp forest canopy together and are often visually indistinguishable as juveniles, after filtering the data and before pedigree analyses, the species affiliation of each genotype was verified using a genetic identification technique. Genotypes from potential source species were used to estimate allele frequencies that compose a reference against which data from individuals of unknown species were assessed (Clemento, Crandall, Garza, & Anderson, 2014; Pella & Milner, 1987), with maximum-likelihood or Bayesian methods (Pella & Masuda, 2001; Smouse, Waples, & Tworek, 1990). Here, genotypes from adults of these four species (kelp, copper, black-and-yellow and gopher rockfishes) were included in the genetic stock identification (GSI) baseline and each adult rockfish genotype was assigned a likelihood of being from each of these species using the self-assignment function in the software GSI_SIM (Anderson, Waples, & Kalinowski, 2008; Moran & Anderson, 2018). Adult rockfishes are typically identifiable by colour and morphology, and the GSI_SIM assignments confirmed field identifications and detected any misidentified fish. Adult samples that did not assign to one of these four species with a likelihood, scaled to sum to 1.0 across the four species, of >0.99 were excluded from further analyses. Juvenile samples that did not assign to any of the four species in the baseline with a scaled likelihood >0.99 were similarly removed from the data set.

Following species identification, duplicate samples were identified as those with mismatching genotypes at three or fewer loci and different sample identification numbers. In this case, the highest read depth genotype at each locus was retained. This eliminated the potential for spurious relationship inference caused by sampling or genotyping the same fish multiple times.

Next, internal heterozygosities were computed for each individual in the data set, because contaminated samples often exhibit elevated internal heterozygosity, and low heterozygosity could indicate genotypes from nontarget species. The range of expected values for internal heterozygosity in kelp rockfish provided a check for samples involved in pedigree relationships.

2.4 | Parent–offspring and full-sibling analyses

Parent–offspring analysis was performed in the software program CKMRSIM (Anderson, 2016), implemented in R. This program uses Monte Carlo simulation and an importance-sampling algorithm, similar to that described by Anderson and Garza (2006), tailored to pairwise relationship inference using multiallelic markers, and generates expected log-likelihood ratio distributions for parent–offspring and full-sibling relationships. CKMRSIM then calculates the log-likelihood ratios for pairwise comparisons between all adult samples compared to all juvenile samples, which allowed comparison of observed likelihood ratio values of parent–offspring relationships with the distribution of simulated pairwise values. The same approach was implemented to identify full siblings in a combined data set of both adult and juvenile genotypes.

To validate CKMRSIM analyses, the computer software CERVUS (version 3.0.7; Kalinowski, Taper, & Marshall, 2007) was used for parent–offspring pairs, and COLONY (version 2.0.0.1; Jones & Wang, 2010) was used for full-sibling relationships. CERVUS simulated parentage using allele frequency data and 10,000 offspring and 2,000 adults, a minimum of 75 successfully genotyped loci, estimated genotyping error of 1%, and with multiple estimates of the proportion of the adult population sampled (0.01, 0.05, 0.10), to account for uncertain population size estimates in the study region. Pairs were assigned at 80% (low) and 95% (high) confidence. Full-sibling validation in COLONY used the pair-likelihood method, and assumed monogamy and no prior or any information about sex or putative parents present in the data set.

2.5 | Relationship validation with microsatellites

Relationships inferred with the microhaplotype data were further evaluated by genotyping putative parents, offspring and siblings at 25 microsatellite loci (Supporting Information Table S2). Twenty-four of these loci were previously used in population genetic studies of *S. oculatus* (Venerus et al., 2013) and *S. levis* (Hess et al., 2014), and a subset of these loci were used previously to infer paternity of kelp rockfish larvae (Sogard et al., 2008). The microsatellite genotyping protocols were adapted from Venerus et al. (2013) for fragment analysis on an ABI 3730 capillary sequencer and with allele calling in GENEMAPPER version 4.0 (Applied Biosystems). The goal of this analysis was to use an independent data set to check for incompatibilities among the inferred family relationships found using the microhaplotype data. In addition to the individuals involved in pedigree relationships, 26 fish were genotyped that were potentially involved in either full-sibling or parent–offspring relationships, but that were statistically just below the log-likelihood ratio threshold for retention (<16 for full siblings and <15 for parent–offspring pairs). These individuals were genotyped to evaluate whether the microsatellite loci might help to clarify true relationships. Finally, 96 unrelated adult kelp rockfish were genotyped to estimate allele frequencies and serve as a control to assess potential false positives.

The microsatellite data set included genotypes from 114 adults and 105 juveniles. Parent–offspring relationships were inferred from the microsatellite genotypes with CERVUS and parentage simulated using allele frequency data with 100 offspring and 100 adults; 80% of loci were typed and 1% mistyped. The approximate proportion of adult genotypes from the total data set (10%) that were re-genotyped with microsatellite loci was used as an estimate of the proportion of the adult-population-sampled parameter. Full-sibling

TABLE 1 Field identification of *Sebastes* rockfishes collected in Carmel and Monterey bays, California

Life stage	Species	Number of samples
Adult	*atrovirens*	1,925
Adult	*carnatus*	67
Adult	*caurinus*	26
Adult	*chrysomelas*	396
Total		2,414
Juvenile	*atrovirens*	3,869
Juvenile	*caurinus*	30
Juvenile	*carnatus* or *chrysomelas*	1,626
Juvenile	*carnatus*, *chrysomelas* or *atrovirens*	1,522
Juvenile	*carnatus*, *chrysomelas*, *atrovirens* or *caurinus*	4,637
Juvenile	Unknown	5
Total		11,689

relationships were inferred from the microsatellite genotypes using COLONY. Simulation parameters corresponded to those used in sibship assignments from the microhaplotype data, as described above.

3 | RESULTS

3.1 | Genotyping and data analysis

A total of 14,592 rockfish samples (2,586 adults; 12,006 juveniles) were genotyped in 40 sequencing runs with an average of 26.9 million reads per run (range 16.2–39.6 million) and an average of 23.3 million reads passing initial quality filters (range 15.4–30 million; ~87%). From these data, genotypes from 2,304 samples were used to generate a VCF file that included 1,524 filtered variant sites across the 96 loci. Comparison of the expected versus observed frequencies of heterozygous genotypes at each locus revealed evidence (z-statistic < −3) for null alleles, or other non-Mendelian inheritance, at 18 of the 96 loci, and these loci were removed from further analyses (Supporting Information Table S1). After application of read depth, allele balance and missing data (>10% of the 78 retained loci) criteria, 14,105 samples remained for subsequent analyses. In these data, average read depth per individual and locus was 397 (range 43–1,694).

3.2 | Species identification

The reference baseline for species identification was composed of genotypes from 2,414 visually identified adults, including 1,925 kelp, 67 gopher, 396 black-and-yellow and 26 copper rockfishes. The data set for identification included 11,689 genotypes from juvenile rockfish (Table 1). Following this analysis, genotypes for 1,912 adult and 4,250 juvenile genetically identified (likelihood > 0.99) kelp rockfish were retained (Table 2). Juvenile and adult kelp rockfish were sampled in similar proportions throughout the study area (Supporting Information Figure S1). Finally, a small number of fish (n = 72) were sampled and genotyped multiple times and the data were used to generate a per-genotype discordance rate (0.0022). A subset of 12 of these repeatedly sampled fish were adults that were recaptured on different days (range 29–637 days) and were appropriate for estimating movement of adults during the study period. The median distance between location of captures for an individual was 53 m (range 22–1,020 m), and the precision of location estimates was 50–100 m, depending upon sampling method, confirming the assumption of small adult home ranges for kelp rockfish. After removing one of each duplicate sample from the data set, the remaining 6,091 samples (1,847 adults; 4,244 juveniles) were analysed to identify parent–offspring and full-sibling pairs.

TABLE 2 Genetic species identification results for adult and juvenile *Sebastes* rockfishes

Species	Juveniles, scaled likelihood >0.99 (total)	Adults, scaled likelihood >0.99 (total)
atrovirens	4,250 (4,250)	1,912 (1,912)
carnatus	1,363 (2,906)	24 (62)
caurinus	2,075 (2,075)	27 (27)
chrysomelas	1,093 (2,458)	328 (413)

In parentheses is the total number of samples assigned with scaled likelihood >0.50 to that species

3.3 | Parent–offspring pair identification

The kelp rockfish data set contained 993 alleles (haplotypes) in the 78 retained loci and between three and 27 haplotypes per locus (Supporting Information Table S1; mean = 12.7 alleles per locus, SD = 5.25). Simulation analysis showed the distribution of log-likelihood ratios for parent–offspring pairs ranged from ~10 to 50, while the distribution for unrelated individuals was centred at −65 (range = −125 to −20; Figure 1a).

Based on these distributions, a log-likelihood ratio threshold >15 was used, corresponding to a calculated per-pair false positive rate of 2.7×10^{-9} at an expected false negative rate of 0.015. At this threshold, eight single-parent–offspring pairs were identified

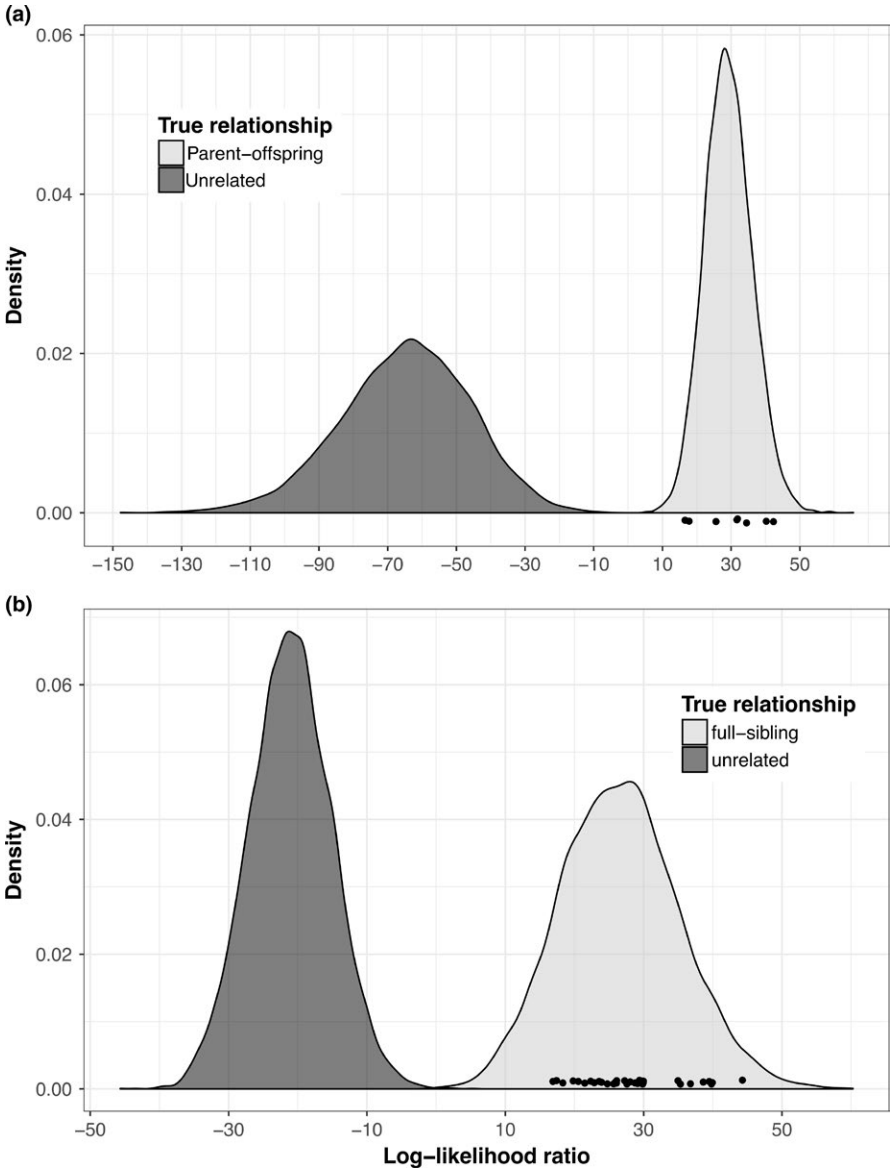

FIGURE 1 Log-likelihood ratio distributions generated by Monte Carlo simulation in CKMRsim for unrelated and true parent-offspring pairs (a) and full-sibling pairs (b). Dots indicate the log-likelihood ratio for retained pairs above a threshold of 15 for parent-offspring (a) and between 14–50 for full siblings (b)

(Figure 2; Supporting Information Table S3). When these putative parent–offspring pairs were further evaluated using CERVUS, the eight pairs identified with CKMRSIM were the top-ranked matches, and all eight pairs assigned above a 95% confidence threshold. Since the confidence level for a true relationship in CERVUS is sensitive to the value assumed for the parameter "proportion of the parent population sampled" and a precise estimate for the number of adult kelp rockfish in the study area was not available, this parameter was varied from 1% to 10%. This did not decrease the confidence level of the eight parent–offspring pairs, which remained top-ranked, as in the CKMRSIM analysis.

3.4 | Full-sibling identification

There were 25 pairs of full siblings identified by CKMRSIM with a log-likelihood ratio between 14 and 50 (Figure 1b) and heterozygote deficiency *z*-statistic between −2 and 2. These siblings included one pair of adults and also two pairs of juveniles that had one individual sampled in each of two consecutive years. COLONY recovered all 25 full-sibling pairs identified by CKMRSIM with a probability of 1 and also identified an additional 1,954 dyads in the microhaplotype data set (probability > 0.95).

3.5 | Validation of microsatellite relationships

Of the 217 rockfish genotyped with microsatellites, 201 (104 adults and 97 juveniles) yielded usable genotypes. Eight of the 96 adult kelp rockfish genotyped as a reference were excluded from further analyses due to insufficient or ambiguous data, as were eight fish from the putative full-sibling pairs. Five of the 25 loci amplified poorly in most samples and were excluded, with the remaining 20 loci used for analyses.

Because only a small fraction of samples were genotyped with microsatellites, these data were used primarily to check for incompatibilities not detected by microhaplotypes and not for de novo inference of relationships. Parentage analysis with the microsatellite

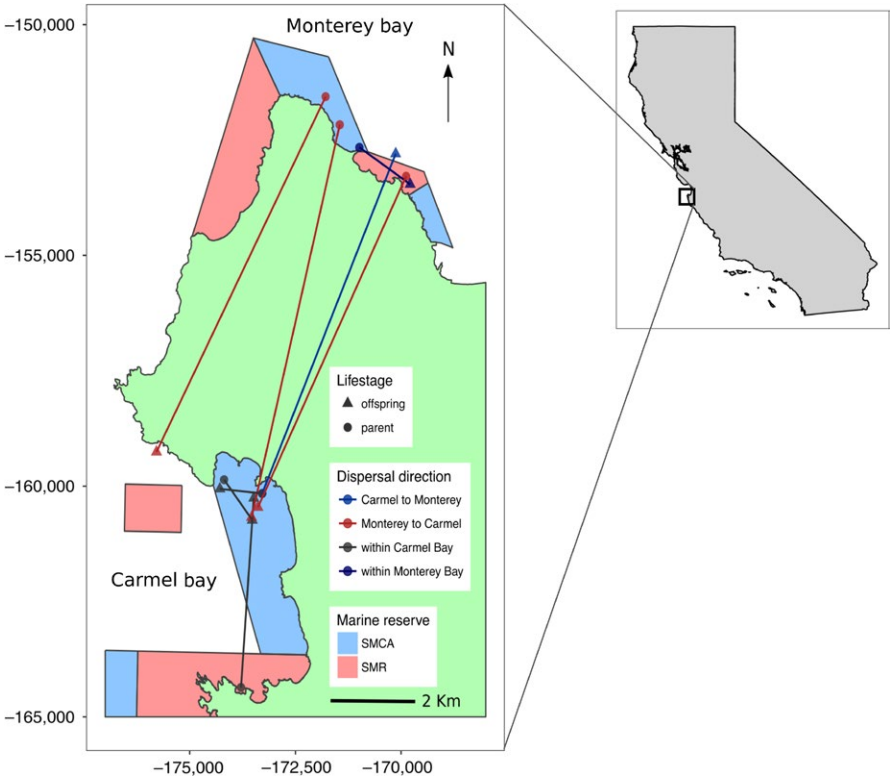

FIGURE 2 Location of eight high-confidence parent-offspring pairs identified by CKMRsim in southern Monterey Bay and Carmel Bay, CA. Parental locations are indicated by circles and offspring by triangles. Colour indicates direction of dispersal from parent-to-offspring. Marine reserves in the area include State Marine Conservation Areas (SMCA), which allow some fishing, and State Marine Reserves (SMR), which do not permit fishing inside reserves

data and CERVUS found all eight of the parent–offspring pairs identified by microhaplotypes as concordant at a 95% confidence threshold. In addition, COLONY analysis of the microsatellite data recovered 19 of the 25 full-sibling pairs found with microhaplotypes with a probability threshold greater than 0.95. In addition to those concordant full-sibling pairs, COLONY identified 73 more dyads that exceeded the probability threshold for full siblings, emphasizing the difficulty in identifying siblings from large samples of mostly unrelated individuals, particularly with limited genetic data.

3.6 | Geographical distribution of related individuals

The eight parent–offspring pairs (Figure 2) and 25 full-sibling pairs (Figure 3) identified with the genetic data were used to characterize patterns of larval dispersal in kelp rockfish. For the parent–offspring pairs, multiple combinations of geographical location were found: in three of the pairs, both parent and offspring were in Carmel Bay; one pair had both members in Monterey Bay; three parents sampled in Monterey Bay produced offspring found in Carmel Bay; and one parent sampled in Carmel Bay had a juvenile found in Monterey Bay. Furthermore, 50% of these parent–offspring matches represent two types of "spillover," where the offspring of parents located inside reserves disperse to fished areas. In two instances (25% of total matches), larvae dispersed from parents inside no-take marine reserves to areas where some fishing is permitted, and in two additional pairs, offspring of adults located in conservation areas were found outside the reserve network (Figure 2). For full-sibling pairs, three (12%) included both fish sampled in Monterey Bay, and 11 full-sibling pairs were identified in Carmel Bay (44%), including one pair of adult full-siblings. Finally, 11 full-sibling pairs had one member sampled in Monterey and the other sampled in Carmel Bay (44%), indicating dispersal trajectories that separated the two siblings on opposite sides of the Monterey Peninsula (Figure 3). Note that sibling identification does not provide information on the directionality of dispersal. Two of the 24 juvenile full-sibling pairs had one member each sampled in consecutive years (2014 and 2015), evidence that these siblings must have been born 1 year apart. In both cases, the full siblings were found in geographically distant locations (Figure 3a).

4 | DISCUSSION

Here we provide the first direct observation of patterns of larval dispersal in an abundant nearshore marine fish from a temperate, open-coast ecosystem. We use powerful new genetic markers to first discriminate individuals of the focal species from among several closely related and morphologically similar congeners, and then to identify pedigree relationships. The links between sedentary parents (home ranges of 3–7 m^2; Van Dykhuzien, 1983) and their recruiting offspring identified dispersal events that included all types of major potential trajectories, from recruitment to the same habitat patch to transport to the opposite end of the study area. Pairs of full siblings were similarly found to represent all dispersal trajectories, emphasizing both extremely local retention and apparent panmixia at a local scale. The study area encompasses a network of no-take marine reserves and areas where recreational harvest is allowed, and we describe the implications of our connectivity results for marine

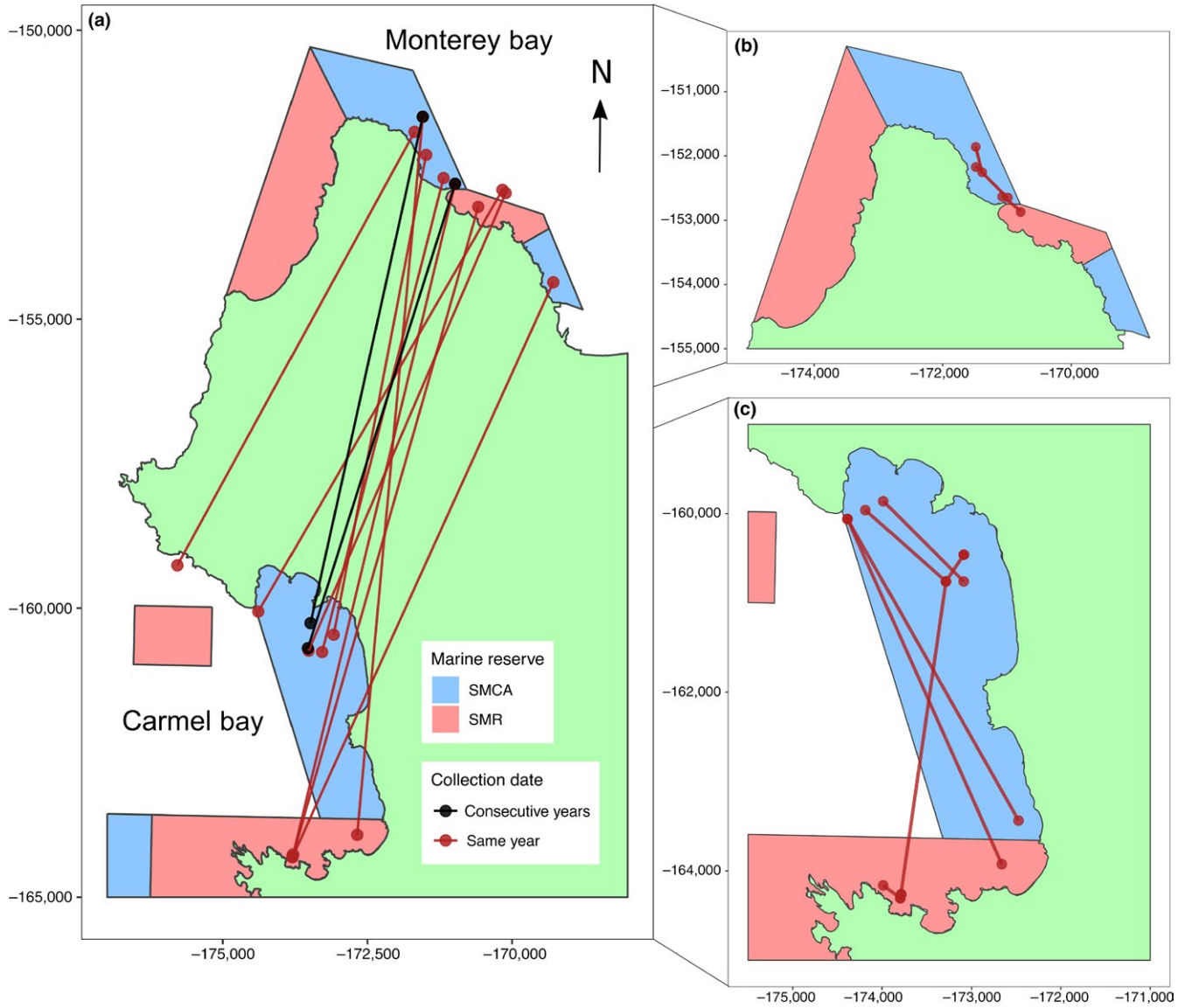

FIGURE 3 Location of 25 full-sibling pairs identified by CKMRsim in southern Monterey Bay and Carmel Bay, CA. Juvenile full-siblings sampled across consecutive years are indicated by black dots and siblings sampled in the same year are displayed in red. Locations include pairs located with one sibling in southern Monterey and one in Carmel Bay (a), both siblings in southern Monterey Bay (b), and both siblings in Carmel Bay (c). Marine reserves include State Marine Conservation Areas (SMCA) and State Marine Reserves (SMR)

spatial planning and reserve design. We also found two pairs of juvenile full siblings with one member each produced in consecutive years, providing the first evidence for monogamy—either by "intention" or by accident—in rockfishes.

To identify dispersal events of the kelp rockfish from juveniles originating within marine reserves along ~25 km of coastline in central California, we genotyped over 14,500 adult and juvenile rockfishes with 96 multiallelic microhaplotype loci, assigned fish to species based on allele frequencies from a reference database of adult rockfishes, and then identified parent–offspring and full-sibling relationships using pedigree reconstruction or "close-kin mark recapture" (CKMR) with novel software. We verified pedigree relationships with microsatellite genotypes and the likelihood-based software programs CERVUS and COLONY. All of these methods concurred in the identification of eight high-confidence parent–offspring pairs, where each pair represents an empirical observation of larval dispersal from the sampling location of the adult to that of its recruiting progeny. Twenty-five full-sibling pairs were also identified with high confidence, providing additional information about kelp rockfish dispersal.

Parent–offspring pairs in this study demonstrate direct connectivity between no-take reserves from the network of MPAs surrounding the Monterey Peninsula, as well as between these conservation areas and adjacent areas where recreational fishing is allowed. This second phenomenon confirms the "spillover effect" or "recruitment cross-subsidy" (Le Port et al., 2017), whereby reproduction within reserves replenishes fished populations, as larvae born inside protected areas disperse. Connectivity of habitat patches at a

local scale reinforces the benefit of marine reserve "networks" that conserve characteristic environments, particularly productive, nearshore, temperate rocky reefs.

Full-sibling analyses illustrate a variety of dispersal trajectories for larvae originating at the same location. Pairs clustered within both Carmel Bay and Monterey Bay, and pairs were also split across the peninsula, with one member in each bay. This last type of pattern suggests the potential involvement of behavioural mechanisms, which could influence larval trajectories if local oceanographic conditions act consistently on larvae born synchronously from the same mother in the same location. However, modelling studies emphasize the variability of oceanographic conditions along this portion of coast, and if larval release proceeds over a few hours, the individual larvae might experience radically different physical forcings (Lowe, Drake, & Edwards, 2016).

We found groups of no more than two siblings within our sampling area, in contrast to studies that identified aggregations of full siblings in coral reef systems (e.g., Selwyn et al., 2016; Veliz, Duchesne, Bourget, & Bernatchez, 2006). This suggests that physical dynamics driving aggregation might be weaker along the open coastline of California, or that our statistical power to accurately identify them is higher than that used in previous studies.

Intriguingly, two sibling pairs consisted of juveniles sampled in consecutive years (Figure 3a), suggesting that in two separate instances, the same female and male mated in at least two breeding seasons. In species where breeding pairs are known to occur, such a finding would not be surprising. However, while mate choice has been posited as a mechanism for speciation in rockfishes (Buonaccorsi et al., 2011), to our knowledge multiyear breeding pairs have not been documented in the genus *Sebastes*. There are several mechanisms that could produce full siblings in consecutive years. The first is true monogamy, where a male and female pairbond for more than one reproductive season. The second is that the same female and male mated by chance in consecutive years due to proximity and low adult mobility in the species. To distinguish between chance mating and pair bonding, we would expect to identify full siblings across more than two consecutive years, but given the short time scale of our study (4 years of sampling) and overall small number of full siblings identified, we would not necessarily anticipate such a pattern in our data set. A third possible explanation for this pattern of multiyear full siblings is sperm storage from at least one annual reproductive season to another. Experimental data show that female kelp rockfish can store sperm for at least 1–2 months (Sogard et al., 2008), while some other rockfishes are known to store sperm for several months (Moser, 1967; Nichol & Pikitch, 1994; Takahashi, Takano, & Takemura, 1991), but none of these studies suggests that sperm storage can occur from one season to the next in rockfishes. In the marine sculpin *Alcichthys alcicornis*, which like *Sebastes* is in the order Scorpaeniformes, tight junctures between the epithelia cells of the ovary prevent the female's immune system from attacking sperm during the breeding and spawning season, but after spawning, macrophages enter the ovarian cavity and engulf any remaining spermatozoa (Koya, Munehara, & Takano, 1997). Outside of breeding and spawning, the female immune system eliminates foreign cells within the ovary, including sperm, which disappear from the ovary during nonspawning months (Koya et al., 1997). If the mechanism in rockfishes is similar, then sperm storage would be unlikely to produce the multiyear full siblings in our data set. It is also possible that kelp rockfish females are not monogamous, but polyandrous, and coincidentally mated with the same male in multiple years as part of larger mating aggregations, as multiple paternity of some kelp rockfish broods has been demonstrated (Sogard et al., 2008). Additional experimental and observational data could help discriminate between behavioural and physiological mechanisms as explanations for these sibling results.

The pedigree-derived dispersal data we present supplement a growing body of research describing marine dispersal at an exceptionally fine scale. Parentage analysis has gained popularity for measuring connectivity in marine organisms, given the ease with which molecular markers can be developed and genotyped at decreasing cost, as well as the massive reduction in the scope of the mark–recapture problem provided by intergenerational analyses in high-fecundity species. Furthermore, the analytical framework for identifying high-confidence matches among single parents and offspring, as well as other relationships, has continued to improve and become increasingly sophisticated (e.g., Bravington, Skaug, & Anderson, 2016). For example, the ~1,000 additional full-sibling matches identified in our data set using COLONY are probably an artefact caused by a mismatch between the characteristics of our data and the capabilities of this methodology, specifically the behaviour of unpenalized maximum likelihood with very large samples (Almudevar & Anderson, 2012). Genetic results indicating high levels of self-retention should always be coupled with a complete explanation of the methods used to generate those results (Harrison, Saenz-Agudelo, Planes, Jones, & Berumen, 2013a, 2013b; Saenz-Agudelo, Jones, Thorrold, & Planes, 2009), because the ability to accurately identify true relationships hinges on the statistical power of a given panel of genetic markers, and uncertainty involved in genetic and parentage analyses can lead to uncertainty in estimates of dispersal (Kaplan et al., 2016). Note that it is exceedingly difficult to discriminate full and half siblings, as well as other categories of related individuals, with genetic data (Baetscher et al., 2018). We used a conservative set of criteria for retention of siblings, and thus probably excluded some true sibling pairs from the final set. Conversely, we cannot rule out that some of the sibling pairs identified are actually individuals with other relationships (e.g., half siblings or first cousins). However, this would not diminish the dispersal results, but would rather mean that some of the inferred dispersal distances were achieved over several generations, rather than one.

Ours is the first study, to our knowledge, to explicitly address the presence of potentially confounding species in our analysis of larval dispersal, which, although not necessarily crucial for parentage assignment, is a minimum requirement for accurate sibship analysis. Although this analytical challenge may not affect some studies, the presence of marine species complexes in both tropical and temperate ecosystems deserves attention, as sibship analysis

with a data set containing genotypes from two or more species that have been misidentified as a single species can lead to the spurious identification of visually indistinguishable, but nontarget, conspecifics as siblings (Ottmann et al., 2016, 2017). Choosing a genetic marker set with the capacity to differentiate species allowed us to include samples from juvenile fish that were not morphologically identified in the field, as well as to definitively identify the samples that were misidentified or mislabelled during field sampling.

Although studying larval dispersal in the marine environment continues to pose significant challenges, accumulating evidence suggests that dispersal trajectories are highly variable, and self-retention occurs at smaller spatial scales than previously predicted from population genetic structure or biophysical models. The contribution of complex nearshore processes and their interaction with larval behaviour remain some of the most crucial gaps in our understanding of dispersal (Nickols et al., 2012). However, our work demonstrates that a network of closely spaced marine reserves, even on the open coast of a boundary current, allows for connectivity among patches of suitable habitat within and outside of the reserves.

Similar to other dispersal and parentage studies, our results could be explored with a biophysical model (e.g., Le Port et al., 2017) to test for concordance with local oceanography. Indeed, dominant springtime flow patterns in the Monterey Bay region are alongshore to the south and offshore, consistent with wind-driven Ekman transport, while connectivity matrices suggest that larvae released in winter or spring and with a 30- to 60-day pelagic duration, such as the kelp rockfish, are most likely to settle closest to their release location (Drake et al., 2011). However, regional ocean models struggle to resolve the complex nearshore processes that affect larvae released at shallow depths (Drake et al., 2011), and even comparatively high-resolution models are limited to >50 m depth (Galindo et al., 2010), where vertical current shifts over small depth ranges can substantially alter horizontal velocity and direction of flow. The variety of dispersal directions captured by the parent–offspring pairs provides challenging data for model comparisons.

Heterogeneity in the spatial distribution of relatives (i.e., situations in which the spatial location of one member of a kin pair is not well predicted by the location of the other pair member) is a characteristic of panmixia (Palsbøll, Peery, & Bérubé, 2010). These results indicate that kelp rockfish around the Monterey Peninsula exhibit panmixia at this local scale, and that knowing the location of a parent provides essentially no predictive power to determine where its offspring might disperse and recruit. The absence of dispersal directionality is intriguing in a current-dominated ecosystem, where the southward-flowing California Current could be expected to dominate larval movement. However, it appears that nearshore oceanographic processes, or possibly behavioural mechanisms, influence the dispersal and distribution of kelp rockfish larvae more so than the California Current, which probably dominates farther offshore (Griggs, 1974).

These results agree with previous work highlighting the absence of genetic population structure throughout the kelp rockfish range (Gilbert-Horvath et al., 2006). When population structure is absent, relationship inference methods can examine individual genotypes to identify relatives and dispersal patterns. Such dispersal data can then help to distinguish whether the absence of population structure, as detected by traditional (i.e., F_{ST}) methods, represents historical gene flow rather than current connectivity (Palsbøll et al., 2010).

Modelling suggests that marine reserve size should mimic average dispersal distance (Botsford, Hastings, & Gaines, 2001), but a network of appropriately spaced reserves can serve a similar purpose, while allowing interspersed public access to coastal fishing and recreation areas (Carr et al., 2017). The variety of dispersal magnitudes and directions identified here is small, but suggest that management of coastal oceans might be effectively served through a patchwork of closely spaced reserves that are representative and inclusive of critical habitats for targeted species and ecosystems.

The relationships among kelp rockfish that we describe here represent a first step toward understanding patterns of dispersal for a common nearshore fish species along an open coastline in a temperate, current-dominated ecosystem. Our study focused on dispersal and retention at a relatively local scale. A full understanding of dispersal in the species will require the identification of long-distance dispersal events to facilitate eventual estimation of the dispersal kernel for kelp rockfish (Bode, Williamson, Harrison, Outram, & Jones, 2018).

The sampling and genotyping effort for this study generated a substantial database of georeferenced genetic information which can be used in the future. Given the long lifespan of the kelp rockfish (Love et al., 2002), juvenile and adult kelp rockfish samples collected along the coast of California can continue to be added to and compared with the existing database for the foreseeable future. Future sampling in the kelp forest habitats of northern Monterey Bay and south along the coast of the Big Sur region will conceivably enable us to identify larvae originating near the Monterey Peninsula, and provide a complete picture of dispersal for the ecologically and economically important kelp rockfish.

ACKNOWLEDGEMENTS

We thank C. Columbus, E. Campbell and E. Correa for laboratory assistance. A. Clemento, C. Edwards, A. Lowe and T. Ng contributed to discussions of analytical techniques and oceanography, and provided helpful comments on the manuscript. This work was supported by a grant from the National Science Foundation (Award number 1260693; principal investigators M.H.C., E.C.A., C. Edwards and J.C.G.).

AUTHOR CONTRIBUTIONS

All authors contributed to study design. D.S.B. and E.G.H. conducted laboratory analyses. D.S.B., J.C.G. and E.C.A. analysed and interpreted data. E.T.S., D.P.M. and M.H.C. coordinated field

sampling. D.S.B. and J.C.G. wrote the manuscript with input from all authors.

DATA ACCESSIBILITY

Genotype data and the variant call format (VCF) file used to generate genotypes for all kelp rockfish are deposited in Dryad, https://doi.org/10.5061/dryad.6cp14g8, and analyses are documented in an R Notebook in the same repository.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Baetscher DS, Anderson EC, Gilbert-Horvath EA, et al. Dispersal of a nearshore marine fish connects marine reserves and adjacent fished areas along an open coast. *Mol Ecol*. 2019;28:1611–1623. https://doi.org/10.1111/mec.15044