

Retraction

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Retraction for “Long-term aggregation of larval fish siblings during dispersal along an open coast,” by Daniel Ottmann, Kirsten Grorud-Colvert, Nicholas M. Sard, Brittany E. Huntington, Michael A. Banks, and Su Sponaugle, which was first published November 21, 2016; 10.1073/pnas.1613440113 (*Proc Natl Acad Sci USA* 113:14067–14072).

The authors wish to note the following: “It has come to our attention that our paper includes findings that should be updated. Along with the publication of the paper, we made the raw data from this study publicly available, which enabled a reanalysis by Drs. Eric Anderson and John Carlos Garza at the National Marine Fisheries Service Southwest Fisheries Science Center. In our study, we used microsatellite genotypes to infer that 57 of 491 new splitnose rockfish (*Sebastes diploproa*) recruits were siblings, suggesting cohesive dispersal over a 4–6 month period. After their examination of the raw data, Drs. Anderson and Garza suggested an alternative hypothesis in which the results derived from the existence of a cryptic species within our sample collection. We supplied them with all of the biological samples to reanalyze using a novel next-generation sequencing approach for species identification. The results from the new approach were confirmed by sequencing the control region of the mitochondrial genome. Together these new analyses reveal that instead of groups of siblings and nonsiblings, our juvenile samples consisted of two different rockfish species: splitnose rockfish and redbanded rockfish (*S. babcocki*). Given these new findings, we conclude that our estimates of relatedness were inflated within dyads containing individuals from the same species. Thus, while it is still possible that siblings may travel together in the pelagic ocean, we currently do not have evidence to support this hypothesis. The application of increasingly advanced molecular techniques to address fundamental ecological questions is of immense benefit to the field of marine ecology. As genetic techniques continue to rapidly evolve, we are firm supporters of open science and the publishing of raw data that allows vetting and collegial collaboration to advance science. We hereby retract the article and regret any inconvenience that it may have caused.”

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Long-term aggregation of larval fish siblings during dispersal along an open coast

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Pelagic dispersal of most benthic marine organisms is a fundamental driver of population distribution and persistence and is thought to lead to highly mixed populations. However, the mechanisms driving dispersal pathways of larvae along open coastlines are largely unknown. To examine the degree to which early stages can remain spatially coherent during dispersal, we measured genetic relatedness within a large pulse of newly recruited splitnose rockfish (*Sebastes diploproa*), a live-bearing fish whose offspring settle along the US Pacific Northwest coast after spending up to a year in the pelagic environment. A total of 11.6% of the recruits in a single recruitment pulse were siblings, providing the first evidence for persistent aggregation throughout a long dispersal period. Such protracted aggregation has profound implications for our understanding of larval dispersal, population connectivity, and gene flow within demersal marine populations.

larval dispersal | kin aggregation | genetic patchiness | marine fish recruitment | population connectivity

Dispersal of offspring from parental sources to distant destinations benefits natural populations by reducing density-dependent mortality and inbreeding, as well as enhancing population persistence in a changing environment (1). These benefits are widely accepted for terrestrial species, where diverse taxa have developed strategies to enhance dispersal, especially of the young (1, 2). Similarly, the early stages of demersal marine taxa are often pelagic, a strategy that connects local populations over a range of ecologically relevant scales (3). The pelagic habitats experienced by these early life stages are highly dynamic, especially along open coasts with complex current systems. Thus, the prevailing thought has been that dispersal of offspring of most marine organisms is highly diffusive and dominated by ocean currents (4). However, recent studies have shown that behavior of pelagic larvae can reduce dispersal distances (5–7), to the extreme case where larvae of some species can recruit to their natal reef after spending days in the pelagic environment (8, 9). Such retentive patterns typically involve vertical migration of larvae to depths with reduced or recirculating currents, larval navigation, and habitat selection at settlement (10).

Although it is currently not possible to test these mechanisms directly via continuous in situ tracking of larvae, modern molecular techniques can provide critical information to indirectly test fine-scale dispersal hypotheses. For instance, parentage analysis has proven useful to determine starting and ending positions of larvae with relatively short dispersal periods (11). However, disentangling the mechanisms that drive dispersal patterns across larger spatial and temporal scales has been more elusive. Evidence of sibling corecruitment (when siblings are detected simultaneously as newly settled recruits in the same local habitat) has only been found in species inhabiting relatively retentive systems (semienclined bays, estuaries, and coral reef lagoons), or in species with relatively short (11–36 d) pelagic larval durations (12–16). In some of these examples, high rates of retention near the natal habitat inherently increase the abundance of related individuals at a particular location.

Alternatively, sibling corecruitment after dispersal may result from aggregation of siblings throughout the entire pelagic stage. Although protracted larval aggregation has been suggested as a possible mechanism, clear distinction between this and other processes (larval retention, natal homing) requires the examination of species that occur in open, oceanographically dynamic (i.e., nonretentive) systems, that have relatively long pelagic larval durations (i.e., time to diffuse), and that settle to a site distinct from the natal location (i.e., natal homing does not occur). We tested the hypothesis that persistent larval aggregation occurs in splitnose rockfish (*Sebastes diploproa*) by genetically identifying the occurrence of siblings among members of a large corecruiting pulse. Rockfishes comprise a highly diverse genus with many live-bearing demersal species that are targeted by commercial and recreational fisheries. Although adult splitnose inhabit deep water (commonly 100–350 m), pelagic juveniles frequently settle to shallow (<20 m) nearshore habitats after dispersing for up to a year in the pelagic ocean (17). Given the oceanographically dynamic system that splitnose rockfish inhabit (i.e., the California Current), corecruiting siblings in this species would indicate that individuals remained cohesive throughout their larval period.

Results

In 2013, we collected newly settled splitnose rockfishes recruiting to a nearshore habitat in central Oregon (Fig. 1) after a period of low recruitment from May to August (0–7 fish per sampling interval;

Significance

Larval dispersal in the ocean is thought to be highly diffusive, but the pathways larvae follow during their pelagic stage are largely unknown, as direct tracking of larvae in the open ocean is not yet possible. We provide the first evidence of continuous aggregation of fish larvae over extensive periods in an oceanographically complex environment. This finding has far-reaching implications for our understanding of population genetics and dynamics, as it points to an underestimated layer of complexity in current models of dispersal and connectivity. Consideration of complex larval behavior during dispersal, including the aggregation of related individuals, can improve the accuracy of such models and lead to more effective management and conservation of marine organisms.

Author contributions: K.G.-C. and S.S. designed research; D.O., K.G.-C., N.M.S., and B.E.H. performed research; M.A.B. contributed new reagents/analytic tools; D.O. and N.M.S. analyzed data; and D.O., K.G.-C., and S.S. wrote the paper.

The authors declare no conflict of interest.

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Data deposition: Microsatellite genotype data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b7m47>.

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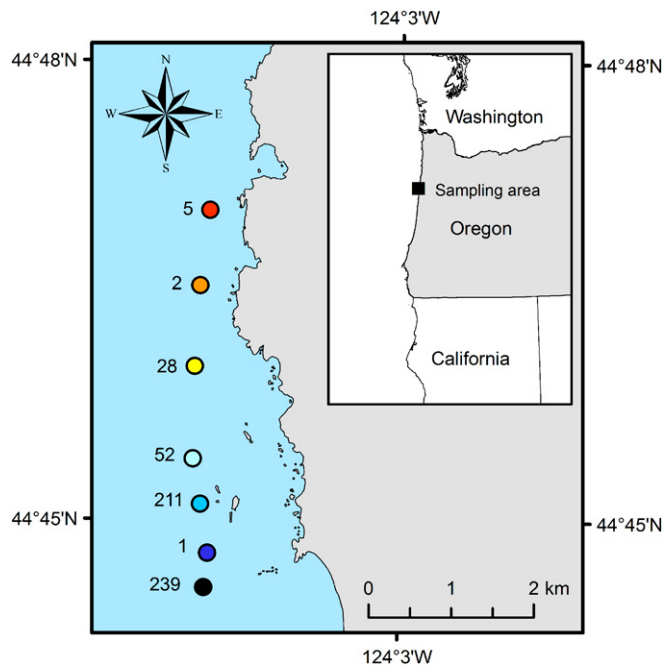


Fig. 1. Sampling locations of fish recruits. Recruits were sampled using seven collectors (colored circles) that were located 425–1,315 m apart in a nearshore rocky reef habitat along the Oregon Coast. Values indicate number of splitnose rockfish (*S. diploproa*) collected in September 2013 after a 15-d sampling interval.

Fig. 2). A pulse of 538 recruits settled to midwater collectors during a 15-d sampling interval (August 20–September 11). This pulse coincided with a strong upwelling relaxation event that triggered an onshore-north flow of surface waters. The spatial pattern of recruitment to our seven collectors during this pulse was highly patchy, spanning a range from 1 to 239 (mean, 79; median, 28) fish per collector (Fig. 1).

Measurements of pairwise levels of relatedness (r) (18) showed that this recruitment pulse contained multiple sibling pairs. We genotyped all 538 recruits and an additional 95 adults collected off the Oregon Coast (used as reference population; Fig. S1) by applying a large panel (20 loci) of polymorphic microsatellite markers. Only 491 fully genotyped recruits and 94 adults genotyped at 10 or more loci were used for the analysis (see explanation in *Materials and Methods*). The genotypes yielded 23 ± 12 (mean $\pm$ SD) alleles per locus in the recruit samples and 17 ± 8 (mean $\pm$ SD) in the reference population (Table S1), providing powerful means to detect siblings. Deviation from Hardy–Weinberg proportions (HWP) and linkage disequilibrium (LD) is expected in samples containing a high proportion of related individuals (19). Indeed, independent tests showed that the recruits had 15 (75%) loci out of HWP, and 31 (16%) pairs of loci in LD, as opposed to one (5%) locus out of HWP, and one (0.5%) pair of loci in LD in the reference population. We note that the analytical power driven by the different sample sizes of the recruits and reference population likely contributes to these differences, but the estimator of r used in this analysis is remarkably robust to departures of HWP and LD (18). Thus, neither of these factors are expected to substantially affect our estimates of r .

On the basis of a power analysis consisting of r measurements of simulated data, we found an optimal and conservative $r = 0.35$ threshold to discriminate siblings from cousins and unrelated pairs (Fig. S2). The simulations predicted 6 ± 2 (mean $\pm$ SD) false-positive pairs (unrelated pairs with an $r \geq 0.35$), yet r estimates among our recruits yielded 74 pairs of related individuals (Fig. 3). We note that 74 pairs of siblings is a conservative estimate, given the proportion of expected false negatives (related pairs with an

$r < 0.35$; 84% half-siblings, 10% full-siblings; Fig. S2). Thus, the real number of sibling pairs is probably greater. Among the 57 different fish that made up the 74 related pairs, 35 were clumped into a large “family” of half- and full-siblings, and the remaining 22 formed independent sibling pairs. The effective number of breeders for all 491 recruits was estimated to be 153 (95% confidence interval [CI], 146–159), which is relatively small, as expected for a cohort containing individuals that share common parents. Furthermore, the effective number of breeders was estimated to be smaller (35; 95% CI, 33–38) when using only the 57 recruits identified as siblings (i.e., sharing common parents), and larger (651; 95% CI, 577–744) when using only the remaining 434 individuals. Related recruits were identified at all but one of the collectors (dark blue collector in Fig. 1), where only one recruit was collected, suggesting that corecruiting siblings arrived within a water mass extending over at least 4 km.

Discussion

Sibling Corecruitment. The finding of at least 57 (11.6%) siblings in a single pulse of corecruiting individuals is the first documentation

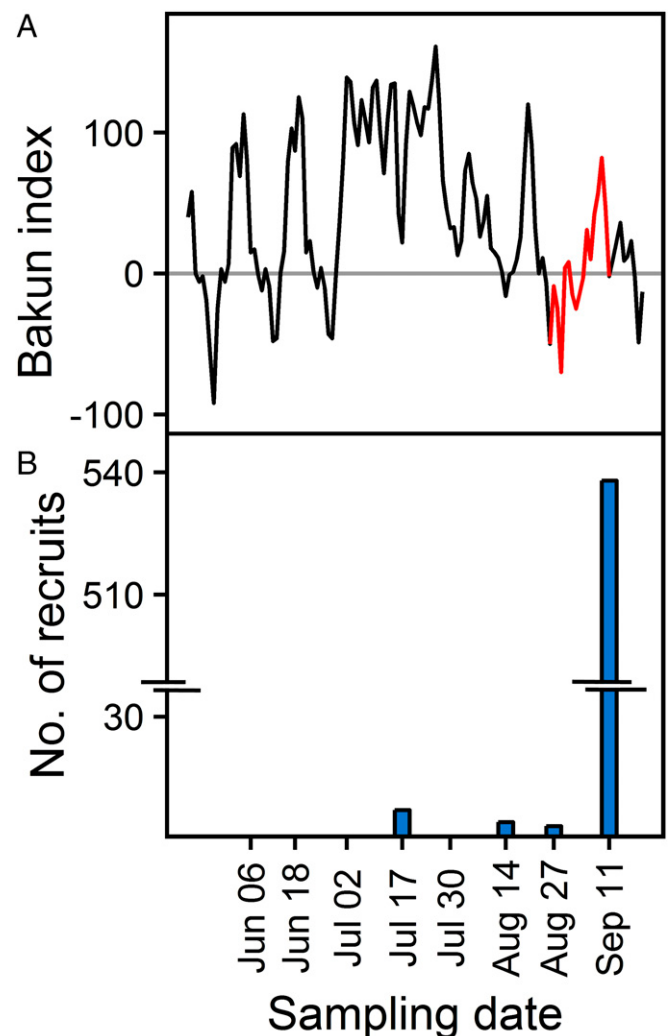


Fig. 2. Upwelling strength and number of collected recruits. Fish collectors were sampled approximately every 2 wk from May 20 through September 11, 2013. (A) The sampling region was characterized by upwelling (Bakun index > 0) interrupted by relaxation periods (Bakun index < 0) associated with onshore flow of surface currents. A strong relaxation event coincided with the sampling interval (red) when (B) 538 splitnose rockfish (*S. diploproa*) recruited to the collectors. Daily Bakun index source: NOAA-PFEL; 45°N, 125°W.

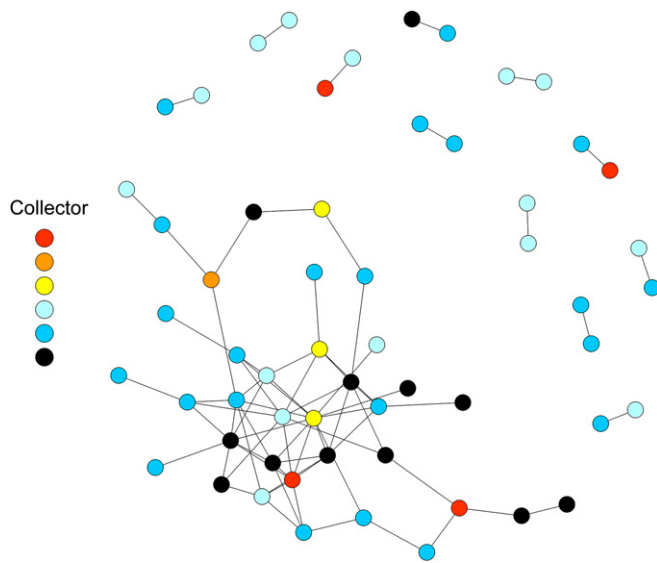


Fig. 3. Recruitment of related splitnose rockfish (*S. diploproa*) to a series of nearshore collectors along the Oregon Coast. Relatedness (r) was determined by analysis of 20 polymorphic microsatellites. Of 491 recruits, 120,295 pairwise comparisons yielded 57 related individuals (circles), of which 35 were grouped into a single ‘family’ of half- and full-siblings (bottom-left web) and 22 formed independent sibling pairs. Collection location of each fish is color-coded to correspond with collector locations in Fig. 1. Related pairs ($r > 0.35$; $n = 74$) are indicated by connected circles. Arrangement and length of connecting lines optimized for display purposes only. Some missing connections are expected as a result of false-negative sibling relationships.

of high relatedness among recruits of a species with a long pelagic period spent along an open coast. Given that larvae were released by adults residing in deep waters ≥ 20 km away from the nearshore area where the recruits were collected, such a high co-occurrence of siblings cannot be attributed to offspring returning to a natal location. Three possible explanations remain: (i) related larvae diverged after being released into the water column and somehow regrouped shortly before settling to a suitable habitat as juveniles. This scenario is unlikely because once separated, particles in such a dynamic environment have a very low probability of re-encountering each other at the end of a long (120–180 d) period (20). (ii) Because of maternal effects, large splitnose females may produce more eggs and higher-condition larvae than smaller and younger females, contributing more to total recruitment (21). Although maternal effects have not yet been demonstrated in splitnose rockfish, other rockfish species show variable degrees of maternal effects (22). However, we found that $\sim 7\%$ of corecruiting splitnose comprised a single ‘family’ that shared common parents. Considering that the splitnose population produces ~ 10 billion larvae, maternal advantage alone is highly unlikely to account for the large contribution of so few parents (23). The remaining alternative is that (iii) offspring sharing at least one parent experienced greater pelagic survival relative to offspring of other parents and remained aggregated throughout the entire dispersal period. The first part of alternative (iii) relates to the hypothesis of sweepstakes reproductive success (24), whereby a small fraction of the adult population contributes disproportionately to recruits as a result of differential survival of offspring in variable oceanographic conditions. As a consequence, the likelihood of detecting corecruiting siblings at a given location is greater under sweepstakes reproductive success than if all of the adults contribute equally to the genetic pool of the recruits. However, the likelihood of detecting corecruiting siblings diminishes in species with long pelagic stages unless larvae and pelagic juveniles remain aggregated during dispersal. If dispersal is diffusive,

differences in larval survival will be homogenized because larvae released simultaneously will randomly diffuse to high- and low-quality habitats, regardless of their original location. Thus, the genetic signal of sweepstakes reproductive success will be diluted. Furthermore, models of larval dispersal (20) show that passive larvae dispersing over 4–6 mo. experience high rates of mixing over scales of hundreds of kilometers, which would further dilute the genetic signal of sweepstakes reproductive success (25, 26). Because the splitnose recruits in this study spent ≥ 4 mo in an oceanographically dynamic environment, corecruitment of such a large proportion (11.6%) of siblings is only expected if they dispersed together.

Sibling Aggregation Throughout Dispersal. It is generally assumed that eggs and early larvae diffuse at the onset of dispersal, and that larvae may only actively aggregate with conspecifics as their swimming capabilities improve. Our results challenge this hypothesis by suggesting that larval behavior, starting at the onset of dispersal and continuing throughout the pelagic juvenile stage, can counteract early diffusive forces and maintain patch cohesiveness throughout the entire pelagic stage. Elsewhere in regions with currents that favor larval retention, larvae of fish species with relatively short pelagic larval durations can share common dispersal paths for up to 30 d before settlement (27, 28). However, large-scale current movement along the Oregon Coast makes the finding of larval aggregation striking and surprising. Recruitment to our collectors was spatially patchy, and siblings from the same family settled to multiple collectors, indicating that they formed loose cohesive patches with other related and unrelated pelagic juveniles in the same water mass. Larval and pelagic juvenile fish likely co-occurred offshore in this water mass until the upwelling relaxation event transported them nearshore (29) in patches that encountered our collectors.

Most surprising is the finding that siblings maintained this cohesiveness for 4–6 mo, despite the potentially immense diffusion and advective mixing that larvae and pelagic juveniles experience in the open ocean. Although previous studies have found evidence of siblings among recruits and postrecruits of species with shorter dispersal phases (12–16), or suggested larval aggregation over periods up to 30 d before settlement (27, 28), no study has demonstrated that larvae can remain cohesive for extended periods of time (120–180 d) in an open, dynamic system. Such long-term cohesive dispersal may underlie unexpected levels of relatedness found within adult subpopulations of some benthic organisms with high dispersal potential, such as the California spiny lobster, *Panulirus interruptus* (30). However, the extent to which aggregation during dispersal is a widespread trait among marine organisms will remain an intriguing question until studies of this kind are conducted with other species that have long dispersal phases.

Our results reinforce the shifting paradigm that larval dispersal is not driven purely by physical forces in the marine environment but is, rather, a product of biophysical interactions (5, 10). Potential physical mechanisms fostering cohesion of larval and pelagic juvenile patches over extensive periods include coherent physical features such as mesoscale eddies and current filaments (31, 32). However, along the open coast of Oregon, these physical features are not present over sufficient spatial or temporal scales to sustain the cohesiveness observed in this study. For species such as splitnose rockfish, long-term cohesive dispersal may be enhanced by larval and pelagic juvenile aggregation to floating debris, such as kelp mats. Furthermore, as live bearers, splitnose rockfish release larvae capable of having early swimming behaviors that may enhance their capacity to remain cohesive. Interactions among group members both early and later in larval life may play a role: Evidence suggests that successful larval/pelagic juvenile navigation to nearshore settlement sites may be enhanced by remaining in small groups (33).

Implications for Larval Ecology and Management and Conservation. Our ongoing understanding of larval behavior during dispersal in the ocean, including the aggregation of related individuals, underscores knowledge gaps that are key for effective conservation and management of marine species. In recent years, efforts have focused on quantifying population connectivity of structured populations (3), often with the goal of designing networks of marine reserves (11, 34, 35) or developing more effective fisheries management of stocks across genetic or geopolitical boundaries (36). However, these approaches seldom consider the effect of fine-scale processes that are influenced by stochastic and patchy dispersal, such as high spatial coherence in the genetic structure of recruits. Such genetic patchiness can translate into cascading effects on local genetic diversity and population regulation (37, 38). By demonstrating that larval aggregation can shape dispersal processes to a greater degree than previously thought, our results highlight the need to better understand the fine-scale physical and biological processes occurring in the pelagic ocean that affect the growth, survival, and dispersal of larvae. Successful recruitment of young individuals is critical to the population dynamics of most marine species, and thus also to their effective management and conservation.

Materials and Methods

Study System. Oceanographic conditions off the Oregon Coast in the US Pacific Northwest are characterized by an offshore, southward-flowing current (California Current) and an inshore, northward-flowing current (California Undercurrent) that has seasonal flow inversions in the top 50 m of water (39). Seasonal wind-driven upwelling occurs throughout spring and summer, with intermittent periods of relaxation that are often accompanied by an inshore flow of surface currents, and large recruitment events of intertidal and nearshore organisms (29, 40, 41). We obtained Bakun index values of daily upwelling at 45°N, 125°W from the Pacific Fisheries Environmental Laboratory division of the National Oceanic and Atmospheric Administration (NOAA-PFEL). This index represents daily averages of wind-driven cross-shore transports computed from Fleet Numerical Meteorology and Oceanography Center 6-hourly surface pressure analysis. Positive values indicate offshore transport in units of cubic meters per second along each 100 m of coastline.

Study Species. Splitnose rockfish (*Sebastes diploproa*) occur from Alaska to Baja California, and adults are most abundant at depths of 100–350 m. They live up to 103 y and have a relatively late (6–10 y) age of maturity, and females can produce up to 255,000 eggs per brood (42). Similar to other rockfish species, female splitnose are live-bearing: eggs hatch in the maternal ovary several days before extrusion, and larvae are capable of swimming on release (43). Females can store sperm from multiple males for several months before fertilizing the eggs, thereby releasing offspring with multiple paternity (44). Larvae and early juveniles can remain in the pelagic environment for up to 1 y before settling to a benthic habitat at a size of 30–50 mm (42). Pelagic juveniles frequently aggregate to drifting kelp mats (45), and the transition to benthic habitats occurs later in northern than southern latitudes, peaking in May–June in Southern California and in August–September in Oregon and Washington. The long pelagic duration of benthic species similar to splitnose rockfish is thought to enable larvae and pelagic juveniles to disperse large distances from the parental source (7). The reproductive output of the splitnose population is estimated to be ~10 billion larvae per year, and there is no evidence of spatial population structure, likely because of their long pelagic larval duration and longevity (46).

Recruits. We collected newly settled splitnose rockfish recruits near Depoe Bay, central Oregon, using standardized monitoring units for the recruitment of fishes (47). These collectors are made of black polyvinyl chloride mesh folded inside garden fencing that is shaped in a long cylinder (100 × 30 cm). This creates a 3D structure that simulates natural recruitment substrates such as a kelp canopy. We deployed seven replicate collectors at 1 m below the surface at sites where the depth was ~15 m. Collectors were located 390–1,170 m offshore and were 425–1,315 m apart (Fig. 1). From April 20 to September 11, 2013, we collected newly recruited fish approximately every 2 weeks, using hinged butterfly-style nets to enclose each standardized monitoring unit and collect the recruited fishes. Collected fish were killed with MS-222, measured with calipers to the nearest millimeter, and stored at –80 °C. An exceptionally large ($n = 538$) pulse of splitnose recruits was

collected on September 11 (Fig. 2). A fin-clip of each recruit was stored in 95% (vol/vol) ethanol for the kinship analysis. According to a size-at-age regression of juvenile splitnose rockfish (48), these recruits ranged in age from 120 to 180 d.

Reference Population. Unbiased measures of genetic relatedness require a reference population of unrelated and noninbred individuals (49, 50). This assumption is violated when the focus population (i.e., fish recruits of the same cohort) is used as a reference population (50). Therefore, we used adult splitnose from nine different locations off the Oregon Coast as a reference population (Fig. S1). Tissue samples from 144 adult splitnose rockfish were collected during the 2015 NOAA West Coast Groundfish Bottom Trawl Survey in Aberdeen net trawls (15 min at ~2.2 m·hr⁻¹) at depths of 117–225 m and stored in 95% (vol/vol) ethanol.

Microsatellite Genotyping. We genetically analyzed 513 splitnose recruits and 95 individuals from the reference population. The remaining 25 recruit samples were suspected of cross-contamination in the laboratory processing, and therefore removed from the analysis. The 95 reference population samples represent all nine sampling locations (Fig. S1). Within location, samples were randomly selected for the analysis. DNA was extracted following a standard silica-based method for all samples (51).

We optimized PCR conditions of 35 microsatellite markers isolated from congeneric species, and screened the loci using 16 of our splitnose recruits. We successfully amplified 24 markers that had multiple alleles per locus. We then selected the 20 most polymorphic markers (Table S1) to genotype all of the remaining samples. PCR products were visualized using an ABI 3730xl DNA Analyzer, and alleles were sized using GENEMAPPER SOFTWARE 5 (Applied Biosystems).

We adopted a conservative approach and removed all of the recruit samples that had any missing loci, leaving 491 (96%) fully genotyped recruits (at 20 loci) to conduct the kinship analysis. One sample from the reference population that was missing >10 loci was also removed, leaving 94 total samples (99%). We regenotyped 95 (19%) randomly selected recruits, and calculated the genotyping error rate by dividing the number of discordant alleles by the total number of scored alleles. The genotyping error rate across all 20 loci was 2% ± 2% (mean ± SD; Table S1). HWP and LD were tested independently for the recruit and reference samples, using GENEPOP 4.2 (52). Significance ($P < 0.05$) of HWP and LD was tested after Bonferroni adjustments (53). We evaluated the effect of the sample size affecting the power to detect departures from HWP by applying a paired t test on the coefficient of inbreeding (F_{IS}). The mean F_{IS} was not significantly different between the reference population and the recruits ($t_{19} = -1.22$; $P = 0.24$), indicating that the power to detect loci out of HWP is greater in the recruits. However, F_{IS} was positive in both cases, indicating that both recruits and reference population have deficient heterozygosity. Presence of null alleles is frequently associated with this condition. Using MICRO-CHECKER (54), we detected the presence of null alleles in nine loci of the recruits and three loci of the reference population (Table S1). Thus, presence of null alleles may contribute to a deficiency of heterozygosity in the recruits. However, null alleles alone are unlikely to account for similar deficiencies in the reference population. To test whether the deficiency of heterozygosity in the reference population was the result of a Wahlund effect, adult genotypes were grouped into northern ($n = 46$) and southern ($n = 48$) sample sites, respective to 44°N (Fig. S2), and we calculated the index of fixation (F_{ST}) between the groups using FSTAT v2.9.3.2 (55). After 1,000 permutations, we found evidence of a small but significant amount of genetic differentiation ($F_{ST} = 0.002$; $P = 0.042$) that, along with the presence of null alleles, likely contributed to the heterozygote deficiency.

Data Analysis. Pairwise relatedness (r) was measured with the Triadic IBD estimator of relatedness, using COANCESTRY 1.0.1.5 (18, 56), which applies a maximum likelihood method that estimates pairwise relatedness using the genotype of a third individual as a control. This estimator measures relatedness effectively (16, 18, 57, 58) and is robust to minor error rates, null alleles, deviation of HWP, and LD, as well as small amounts of genetic structure (18). Allele frequencies of the adult population were used as reference in COANCESTRY (50). The number of missing alleles in the reference population relative to the recruits ranged from 0 to 15 (Table S1). This was expected because the sample size of the reference population was smaller than the sample size of the recruits (59). Thus, we assigned a low (≤ 0.005) frequency value to all missing alleles in the reference population. Although this approach might introduce marginal bias for r estimates, it is likely a conservative bias, as most of the assigned frequencies were higher than those observed in the recruits, thus underestimating r (18).

Testing the estimator performance on simulated data is a critical process to predict true relatedness based on measures of r (18, 58, 60). We therefore tested our analytical power by measuring r in simulated datasets composed of individuals with defined relationships. A dataset of 1,000 half-sibling pairs and 1,000 full-sibling pairs (sharing one and both parents, respectively) was used to calculate the expected r estimates among individuals and provide criteria that could be used to distinguish related individuals from unrelated individuals. To predict the number of expected false-positive siblings at a given r threshold, we calculated r in 100 datasets composed of $n = 491$ unrelated individuals (120,295 pairwise comparisons) and averaged the number of false pairs falling above alternate thresholds. The number of simulated unrelated fish was selected to match the sample size of analyzed recruits. We additionally simulated 1,000 first-order cousin pairs to estimate the number of false-positive siblings that might be attributed to cousin relationship. All these simulations were conducted with COANCESTRY, using the allele frequencies of the 491 completely genotyped splitnose recruits. We found that $r = 0.35$ was an optimal cutoff that minimized the number of false-positive pairs (unrelated individuals with an $r \geq 0.35$) while still preserving power to identify true sibling pairs (Fig. S2). The 100 simulations of $n = 491$ unrelated individuals yielded $\sim 6 \pm 2$ (mean $\pm$ SD) false-positive pairs, which is a low proportion (4.6×10^{-5}) considering the 120,295 possible pairwise comparisons of each dataset. Using the same threshold ($r \geq 0.35$), at least 16% of the simulated half-siblings and 90% of the simulated full-siblings were detected, whereas less than 1% of the simulated cousin pairs fell above the threshold. Thus, we concluded that most of the pairs observed above a cutoff of $r = 0.35$ are likely to be siblings and not cousins. A lower r cutoff ($r = 0.3$) resulted in a higher proportion of false positives (36 ± 7 ; mean $\pm$ SD), hampering the discrimination of real siblings from false positives. A higher r cutoff ($r = 0.4$) reduced the detection of real siblings (5% half-siblings; 78% full-siblings), resulting in an increased number of false negatives. We performed a similar power analysis with six other commonly used r estimators implemented in COANCESTRY (56), and found that the Triadic IBD estimator was the most precise and conservative. We tested the performance of COLONY (61) and ML-Relate (62) on simulated data as alternative methods of sibling identification. COLONY produced ~ 750 false-positive siblings and only identified 37% of the 1,000 simulated full-sibling pairs correctly; 58% were incorrectly identified as half-siblings, and the

remaining 5% were classified as unrelated. ML-Relate performed slightly better, detecting 88% and 85% of 1,000 simulated full- and half-sibling pairs, but producing 15 false full-sibling pairs and $\sim 6,300$ false half-sibling pairs. Consistent with these results, only 27 of the 695 sibling pairs identified by COLONY among the recruits coincided with the siblings identified with the Triadic IBD estimator, whereas all of the 74 sibling pairs identified by the Triadic IBD estimator were found within the 9,198 sibling pairs identified with ML-Relate (Fig. S3). On the basis of these simulations, using the Triadic IBD estimator appeared to be the most conservative approach.

As a consequence of siblings sharing common parents, a relatively small effective number of breeders would be expected in a recruitment cohort containing siblings. Using LDNE v2.0 (63), a program that estimates the effective population size based on linkage disequilibrium information, we estimated the effective number of breeders for the entire sample collection ($n = 491$), the putative siblings ($n = 57$), and the collection minus the putative siblings ($n = 434$). The effective number of breeders is expected to be larger in the 434-recruit group than in the entire collection because we removed most of the linkage disequilibrium signature induced by siblings sharing common parents.

All analyses were performed in R v3.2.1 (64), using packages 'plyr' v1.8.3 (65) and 'reshape2' v1.4.1 (66). Figures were created using ARCGIS 10.2 (ESRI 2014), and R packages 'ggplot2' v2.0.0 (67) and 'venneuler' v1.1-0 (68). The network visualization was created with R package 'igraph' v1.0.1 (69), which distributes each node (i.e., fish) maximizing the occupied space of the figure while minimizing crossing-over of connected nodes.

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