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Species' attributes predict the relative magnitude of ecological and genetic recovery following mass mortality

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Abstract

Theoretically, species' characteristics should allow estimation of dispersal potential and, in turn, explain levels of population genetic differentiation. However, a mismatch between traits and genetic patterns is often reported for marine species, and interpreted as evidence that life-history traits do not influence dispersal. Here, we couple ecological and genomic methods to test the hypothesis that species with attributes favouring greater dispersal potential—e.g., longer pelagic duration, higher fecundity and larger population size—have greater realized dispersal overall. We used a natural experiment created by a large-scale and multispecies mortality event which created a "clean slate" on which to study recruitment dynamics, thus simplifying a usually complex problem. We surveyed four species of differing dispersal potential to quantify the abundance and distribution of recruits and to genetically assign these recruits to probable parental sources. Species with higher dispersal potential recolonized a broader extent of the impacted range, did so more quickly and recovered more genetic diversity than species with lower dispersal potential. Moreover, populations of taxa with higher dispersal potential exhibited more immigration (71%–92% of recruits) than taxa with lower dispersal potential (17%–44% of recruits). By linking ecological with genomic perspectives, we demonstrate that a suite of interacting life-history and demographic attributes do influence species' realized dispersal and genetic neighbourhoods. To better understand species' resilience and recovery in this time of global change, integrative eco-evolutionary approaches are needed to more rigorously evaluate the effect of dispersal-linked attributes on realized dispersal and population genetic differentiation.

KEYWORDS
dispersal, dispersal syndrome, genetic recovery, life history, mass mortality, pelagic duration

1 | INTRODUCTION

As mass mortality events (MMEs) increase in frequency and severity (Fey et al., 2015), understanding their causes and predicting their consequences becomes ever more urgent. These consequences are generally divided into two broad phases: a first, during which impacts of the rapid decline in population size "ripple" out into competitors, prey, predators, symbionts or the broader community; and a second, the recovery of the MME-species and interactions with them. Although much effort is being marshalled to document and decipher events leading up to, and including, MMEs (Altieri et al., 2017; Fey et al., 2015; Jurgens et al., 2015; Miner et al., 2018), comparatively little is known about the aftermath of MMEs (Fey et al., 2019). While the sudden loss of a substantial proportion of a population during an MME probably has substantial ecological and evolutionary repercussions over various temporal and spatial scales (Burt et al., 2018; Harvell & Lamb, 2020; Verdura et al., 2019), few empirical data exist on the rate and degree of recovery in natural populations following an MME: of 3194 publications on "mass mortality" ("topic" search of Web of Science, September 27, 2021), ~10% ($n = 336$) address "recovery," often speculatively. Even fewer, 0.5% ($n = 16$), incorporate "genetic" or "genomic" data. This is a patent knowledge gap, which exposes the need for a conceptual framework for understanding the processes that determine recovery.

While there is a general expectation that population structure will reflect spatial patterns of dispersal (e.g., Griffiths et al., 2020), using population parameters to integrate ecological with evolutionary processes (Lowe et al., 2017) and scales and patterns of connectivity (Olds et al., 2018) remains a considerable challenge (Lindsay, 2012). This challenge is especially daunting in marine systems where it is multifaceted and requires an integrated approach (Lindsay, 2012). Although the physical and biological attributes that influence connectivity in coastal marine systems are becoming clearer (e.g., Cowen & Sponaugle, 2009; Morgan, Fisher, Mace, et al., 2009; Pineda et al., 2007), the ways in which they interact to shape patterns of genetic structure remain enigmatic, often attributed to stochasticity (Catalano et al., 2021; Saenz-Agudelo & Harrison, 2021). Reconciling geographical and temporal patterns of genetic structure with underlying mechanisms has proven particularly challenging conceptually and practically. Though Bohonak (1999) identified a positive relationship between dispersal potential and genetic structure across diverse taxa, larval dispersal remains the most important but least understood demographic process in the sea (Swearer et al., 2019). Attempts to link ecological scales to evolutionary scales raise several questions, notably the generality of the expected link between pelagic duration, dispersal potential and population genetic structure within and across species (D'Aloia et al., 2015; Shanks, 2009). Phylogeographical studies, which integrate migration, selection and drift over millennia or more, can provide rigorous comparative evidence of the predicted influence of dispersal potential on population genetic structure (e.g., Dawson, 2012; Dawson et al., 2002, 2014; Schiebelhut & Dawson, 2018). However, their direct relationship to ecological dispersal is temporally remote. On the other hand, spatiotemporal snapshots of patterns of population genetic structure and recruitment dynamics can be misleading due to high variance between years (Catalano et al., 2021; Saenz-Agudelo & Harrison, 2021; Sun & Hedgecock, 2017).

On ecological scales, multiyear studies in marine systems show that recruitment rates vary substantially across space, time and species (Broitman et al., 2008; Toonen & Grosberg, 2011) and that source populations can vary depending on spawning season or variation in ocean currents (Kordos & Burton, 1993). These factors contribute to patterns of recruitment where cohorts of recruits are genetically distinct from both nearby adult populations and other larval cohorts, termed chaotic genetic patchiness (Johnson & Black, 1982, 1984), a common feature of many meroplanktonic species (Eldon et al., 2016). Although chaotic genetic patchiness may be pervasive, it reflects interactions among well-defined processes, such as selection, sweepstakes reproductive success, collective dispersal, temporal shifts in population dynamics at a local scale (Eldon et al., 2016) and stochastic ocean mixing processes (Siegel et al., 2008); in some circumstances it can look less chaotic when relevant hydrodynamic or ecological drivers are measured (Selkoe et al., 2010). Additionally, sweepstakes reproductive success (Hedgecock, 1994) may be common in a variety of marine taxa, elevating the role of genetic drift (Hedgecock & Pudovkin, 2011). Despite the extensive list of interacting physical and biological processes that complicate the interpretation of genetic patterns in coastal marine systems, the lack of short-term concordance between dispersal potential, direct (e.g., genetic assignment tests of recruits) and indirect (e.g., F_{ST} of adult population) measures of connectivity does not preclude a significant long-term relationship (Hedgecock, 2010).

Although empirically measuring the specific trajectory and ultimate fate of dispersing larvae at a particular time is currently intractable, it is necessarily the accumulation of such recruitment events that determines the metapopulation dynamics between locations and the connectivity and genetic similarity of populations (Catalano et al., 2021; Hellberg et al., 2002). As such, an integrated mechanistic eco-evolutionary approach for predicting recruitment is needed, as no single predictor can account for the full dispersal potential of a species (e.g., pelagic duration) (Riginos et al., 2011; Shanks, 2009). Failing to include particular traits, such as fecundity (Castorani et al., 2017), can lead to over- (or under-) estimation of potential connectivity. Dispersal potential itself reflects the interaction among multiple complex traits, potentially in "dispersal syndromes" (Dawson, 2014a). Pelagic duration (*PD*) within species is normally distributed (D'Aloia et al., 2015; Johnson & Black, 1984), suggesting it is influenced by multiple loci. By taking into account multiple life-history traits, such as pelagic duration, population size and fecundity, it is possible for trait-based predictions to bracket genetic estimates of long-term successful larval dispersal and subsequent gene flow (Dawson et al., 2014). Our understanding of recruitment has been advanced by genetic studies of single species (e.g., D'Aloia et al., 2015; Johnson & Black, 1984; Kordos & Burton, 1993; Puritz et al., 2016) and ecological studies across multiple species and years (e.g., Broitman et al., 2008;

Catalano et al., 2021; Morgan, Fisher, Mace, et al., 2009). However, to clarify how dispersal potential translates to realized dispersal and genetic connectivity and determine whether generalities exist, additional genetic studies that incorporate multiple species (D'Aloia et al., 2015), multiple years (Catalano et al., 2021; Hellberg et al., 2002) and multiple approaches (e.g., direct and indirect genetic measures) are needed (Hedgecock, 2010) to bridge the eco-evolutionary gap.

A massive multispecies invertebrate die-off along ~100 km of coast in north central California (Figure 1) in 2011 provided a virtual "blank slate" on which to examine the ecological and genetic consequences of dispersal in multiple taxa. This MME affected intertidal species with a wide range of larval developmental modes and pelagic durations (hence, dispersal potential) (Table 1), including the purple sea urchin (*Strongylocentrotus purpuratus*), ochre sea star (*Pisaster ochraceus*), six-armed sea star (*Leptasterias aequalis*) and dwarf mottled star (*Henricia pumila*) (Jurgens et al., 2015). This natural removal experiment of multiple members of the intertidal community in this region allowed us to explore the relationship between life-history characteristics, dispersal and the distribution of genetic variation in the years immediately following the MME. To test whether species with life-history characteristics favouring greater dispersal potential—e.g., longer pelagic duration and higher fecundity (Table 1)—have greater recovery potential we used (i) the rate of recolonization of the affected region over 3 years (Figure 1) and (ii) genetic assignment tests of new recruits to probable source populations over 2 years.

2 | MATERIALS AND METHODS

For four intertidal marine invertebrates—*Strongylocentrotus purpuratus*, *Pisaster ochraceus*, *Leptasterias aequalis* and *Henricia pumila*—that experienced mortality associated with the 2011 harmful algal bloom in Sonoma County, California, USA (Jurgens et al., 2015), we collated species' attributes influencing dispersal, conducted ecological surveys to quantify population size and abundance of recruits (<1 year old), and gathered genetic samples. We used these data to evaluate the impact of life history and demography on dispersal and recruitment following mass mortality, as follows.

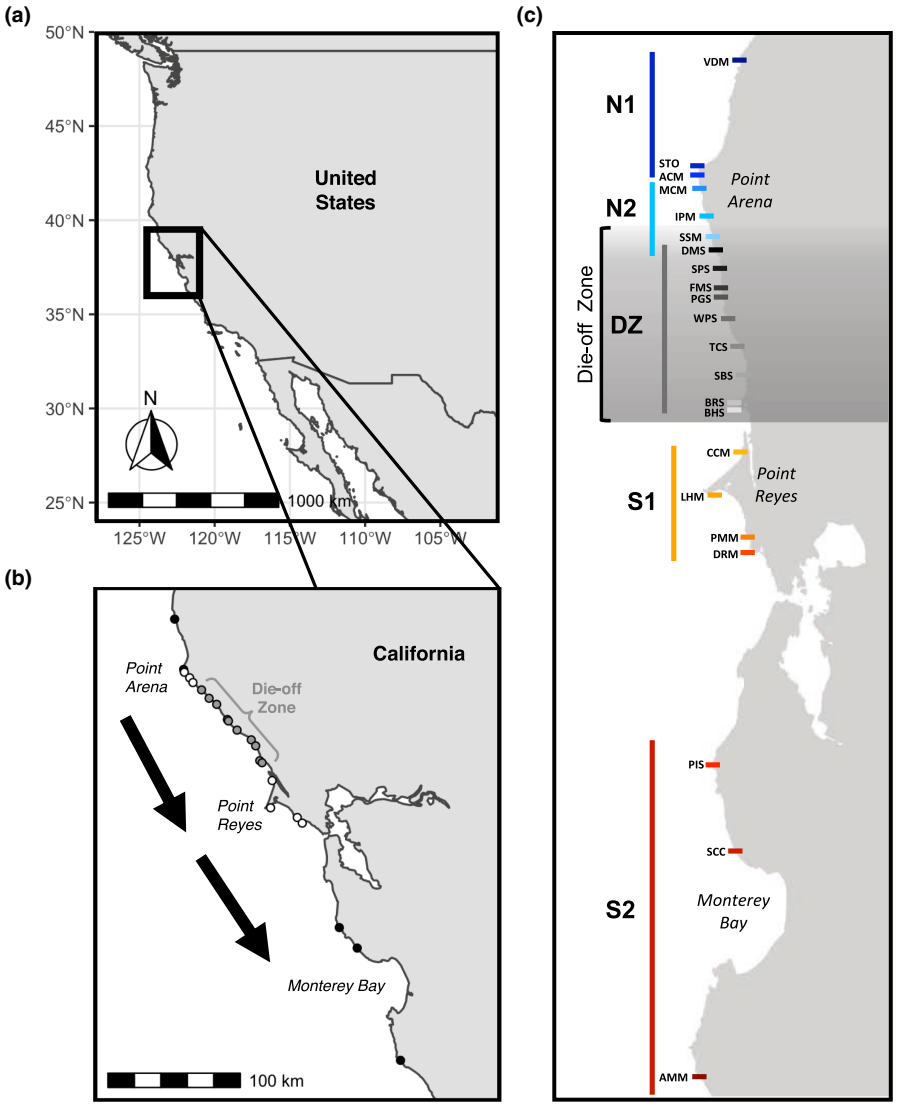

FIGURE 1 Geographical locations of ecological surveys and genetic sampling used in this study in (a) California, USA. (b) Extent of die-off zone with grey circles representing sites experiencing mortality associated with the harmful algal bloom in 2011; white circles are reference sites used to assess recruitment outside the die-off zone; and black circles indicate additional sampling locations for broader population genetic context. Arrows indicate the prevailing current direction during the time at which larvae of the broadcast spawning species in this study would be in the plankton. (c) Detailed view of sampling sites; vertical, coloured bars indicate site groupings for genetic analyses (further broken down by species in Figure S3a); specific site details are given in Table S1.

TABLE 1 Life-history characteristics, population density and theorized relative dispersal potential of the study species

	Strongylocentrotus purpuratus	*Pisaster ochraceus*	*Leptasterias aequalis*	*Henricia pumila*
Density, m^{-2} (N_c proxy)[a]	0.0544	0.0513	0.0011	0.0002
Pelagic duration	9–19 weeks[1]	6–8 weeks[2,3], up to 226 days[4]	0 weeks; brooder[5]	0 weeks; brooder[6]
Annual fecundity	6.8 million[7]	8.0 million[8]	265–1243 (proportional to mother size)[9,b]	>36 (low estimate)[10,b]
Longevity	10–50 years[11]	34.1 years[12]	10.2 years[12]	Unknown
Age at first reproduction	2 years[13]	5 years[12]	2 years[12]	Unknown
Reproductive season	January–March[5]	April–May[5]	November–April[5]	January–April[6]
Relative dispersal potential	Highest 6–1485 × *P. ochraceus*	Next highest $1.7 \times 10^8 - 1.9 \times 10^8$ × *L. aequalis*	Lowest	Predicted similar to *L. aequalis*

Sources: (1) Strathmann (1978); (2) George (1999); (3) Pia et al. (2012); (4) Strathmann (1987); (5) Morris et al. (1980); (6) Eernisse et al. (2010); (7) Leahy et al. (1981); (8) Fraser et al. (1981); (9) Menge (1974); (10) This paper (Figure S1); (11) Ebert (1967); (12) Menge (1975); (13) Conor (1972).

[a]Adult densities were quantified in this study and averaged across sites outside the die-off zone to provide proxies for relative N_c across species. Sites included: MCM, IPM, CCM, LHM, PMM, DRM, PIS, SCC and AMM. Transect data were used for this estimate for consistency.

[b]Egg diameter is comparable in *Leptasterias hexactis* (995 μm) and *H. pumila* (1144 μm) (Strathmann, Staver, & Hoffman, 2002) as is adult size (Schiebelhut & Dawson, unpublished data). We therefore speculate that the observed fecundity of these two brooding species is of similar magnitude.

2.1 | Estimating dispersal potential

We estimated relative dispersal potential for *S. purpuratus*, *P. ochraceus* and *L. aequalis* by converting quantitative species' attributes—pelagic duration (*PD*), annual fecundity (*F*) and census population size (N_c) (Table 1)—into predicted number of migrants (*Nm*) following Dawson et al. (2014). *PD* was converted to *Nm* by way of the regression $\log(F_{ST}) = -0.043$ (no. of days) $- 0.315$ from Doherty et al. (1995), followed by $Nm = (1/F_{ST} - 1)/4$, as has been implemented previously for diverse nonfish marine species (Dawson et al., 2014). *F* and N_c were each used as proportional estimates of *Nm*. Because fecundity was not documented for *H. pumila* in the literature we estimated this value from a photograph (Figure S1; Table 1). We used the product of relative *Nm* taken from the low and high estimates (if a range was available) for each of *PD*, *F* and N_c for each pair of species to estimate the relative difference in overall dispersal potential between each pair of taxa—*S. purpuratus*–*P. ochraceus*, *P. ochraceus*–*L. aequalis* and *S. purpuratus*–*L. aequalis*—in terms of the lower disperser. Although much less is known about the recently described *H. pumila* (Eernisse et al., 2010), it is a small brooder with low population densities that we would expect to have similar dispersal potential to *L. aequalis*, in stark contrast to *S. purpuratus* and *P. ochraceus* which have planktotrophic larvae.

2.2 | Ecological surveys

We conducted surveys annually starting in 2012—the first recruitment season following the 2011 mortality event—at 10 sites within, and seven outside, the zone affected by the harmful algal bloom (Figure 1). Five additional reference sites to the north and south of the mortality zone were sampled less frequently (Table S1; Figure 1). At each location, we sampled two rocky intertidal areas, usually one on either side of a beach or headland and separated by ~100 m. To estimate abundance, we used quadrats to target juveniles and small sea stars and transects to target larger adult *P. ochraceus* and *S. purpuratus*. Size was recorded per individual: radius (centre to arm tip) for *P. ochraceus* and *H. pumila*, diameter (arm tip to opposite arm tip) for *L. aequalis*, and diameter of the test for *S. purpuratus*. All specimens were georeferenced using a Garmin C60X GPS (±3 m precision) and data reported as the number of individuals per square metre (Jurgens et al., 2015).

2.2.1 | Quadrats

We exhaustively searched 32–40 1-m^2 quadrats (composed of four contiguous 0.5–0.5 m quadrats) per site (i.e., 16–20 per each of two areas, depending on sea conditions and tidal height), recording GPS waypoint, time, percentage cover of major substrate and macrophytes, and abundances and sizes of each target species for each quadrat. Quadrat locations were selected by first finding one of the target habitat types (based on preliminary surveys of recruit

distributions)—surf grass, low-zone red algae, coralline turf, boulder field or urchin pools with pits (either empty or occupied)—selecting a starting point haphazardly, and then using a random numbers table (range of 1–10 steps approximating 0.5 m each) to choose quadrat locations.

2.2.2 | Transects

To provide more thorough estimates of site-specific density for the large, conspicuous *P. ochraceus* and *S. purpuratus*, we conducted timed, GPS-tracked, 2- or 4-m-wide swath transects nested in each of two areas at each site. From a distance, an approximate starting point and orientation (with landmarks) for the starting transect was selected. Transects ran from the most shoreward to the most seaward possible suitable habitat at ~10-m intervals along shore, particularly targeting the low intertidal zone when the tide was maximally receded, with as many transects being done as permitted by the tide. The GPS was set to autorecord a trackpoint every 6 s. To reduce error in estimates of the length and position of transects (commonly ±3 m for civilian GPS), we smoothed tracks by averaging across windows of two consecutive trackpoints, and removed outlying trackpoints that led to a Euclidean distance ≥8 m, since these were probably due to temporary drop-outs in satellite signal. We calculated the total transect search area by multiplying the adjusted transect length by swath width.

2.2.3 | Statistical analyses of recruitment

Given the high number of zeros and right skew in the data, we fourth-root transformed densities (Anderson et al., 2008). We tested for differences in recruitment among species within the die-off zone—at nine sites: SSM, DMS, SPS, FMS, PGS, WPS, TCS, BRS, and BHS (we excluded site SBS from the analysis because it was not surveyed in year 3)—using nonparametric permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001). Analyses were executed using the PERMANOVA+ add-on for PRIMER7 (Anderson et al., 2008). Study design included three factors: species (fixed, four levels—*S. purpuratus*, *P. ochraceus*, *L. aequalis* and *H. pumila*), site within the die-off zone (random, nine levels), and area within site (random, nested in site, 18 levels). The Euclidean distance measure, Type III sums of squares and 999 permutations of the residuals under a reduced model were used to calculate the pseudo-*F* statistic. Significance was assessed at alpha = 0.05. We conducted *a posteriori* pairwise comparisons among species when significant main effects were found.

We also used PERMANOVA to test for differences in recruitment by year for each species. The study design included three factors: year (fixed, three levels—year 1, year 2 and year 3), site within the die-off zone (random, nine levels), and area (random, nested in site, 18 levels). The Euclidean distance measure, Type III sums of squares and 999 permutations were used. Significance was assessed at alpha = 0.05. We conducted *a posteriori* pairwise comparisons among years when significant main effects were found. We corrected for multiple tests using the Benjamini and Hochberg (1995) method.

2.3 | Sample collection and processing for genetic analyses

For genetic analyses, our target sample size for each species was 10 adults per site when present and all recruits sampled in year 1 and year 2 following the mortality event (Table S1). We used as minimally invasive sampling techniques as possible, taking spines for urchins and tube feet or 2–3 mm of arm tip for small sea stars. Samples were immediately preserved in 95% ethanol for subsequent genetic analyses. We extracted DNA using a silica-based filter plate (PALL Corp., Cat#5053; Ivanova et al., 2006) and submitted 50–100 ng of DNA in a total volume of 25 µl for each specimen to the Genomic Sequencing and Analysis Facility at the University of Texas at Austin (GSAF) for quantification, normalization, double-digestion with the *Eco*RI and *Msp*I restriction enzyme pair for double digest restriction-site associated DNA (ddRAD) sequencing following Peterson et al. (2012), size selection for 300 ± 50 bp using custom bead prep, adaptor ligation, purification and 2 × 150 paired-end sequencing on an Illumina HiSeq 4000 device.

We demultiplexed raw sequences using process_radtags from STACKS version 1.35 (Catchen et al., 2011), allowing a maximum of two mismatches in the barcode, and deposited reads in the Sequence Read Archive of NCBI (see data accessibility section). We used DDOCENT version 2.2.13 (Puritz et al., 2014) to trim, assemble (*L. aequalis* and *H. pumila* only) and map demultiplexed reads to available genomes, and genotype single nucleotide polymorphisms (SNPs). *S. purpuratus* and *P. ochraceus* reads were trimmed and then directly mapped to either the *S. purpuratus* (GenBank assembly accession: GCA_000002235.3) or *P. ochraceus* (GCA_010994315.1; Ruiz-Ramos et al., 2020) genome, respectively. For *L. aequalis* and *H. pumila* we generated a de novo assembly using DDOCENT. To construct each de novo assembly, we randomly selected three individuals (with a minimum of 1 million reads each) from each of the 10 total sites, totaling 30 individuals for *L. aequalis* and 29 individuals for *H. pumila*. We used this suite of individuals to test multiple assembly parameter combinations (k1 = 2–8: k2 = 2–8). For the final assembly we used a 90% clustering similarity and selected values of k1 = 2 (the minimum within-individual coverage level to include a read for assembly) and k2 = 3 (the minimum number of individuals a read must be present in to include for assembly) to maximize properly mapped reads and coverage and minimize mismatched reads. Reads from the remaining specimens were then mapped to the de novo reference assembly for *L. aequalis* and *H. pumila*, respectively. For all species, SNPs were genotyped by DDOCENT using FREEBAYES (Garrison & Marth, 2012).

We performed SNP filtering using a modified pipeline from Puritz et al. (2016), using VCFTOOLS version 0.1.15 (https://vcftools.github.io/index.html; Danecek et al., 2011) and custom scripts

(https://github.com/jpuritz/dDocent/tree/master/scripts; Puritz et al., 2016). Final filtered variant call format (VCF) files for all species had a 90% genotype call rate across all individuals, minor allele frequency of at least 0.01, minimum read depth of 20, only included biallelic SNPs and retained only one SNP per 500 bp (i.e., one SNP per RAD locus). To achieve this level of coverage, a subset of individuals with low read depth had to be excluded from subsequent genetic analyses. For downstream analyses, VCF files were either recoded to plink format using VCFTOOLS version 0.1.15 (Danecek et al., 2011), recoded to genepop format using STACKS *populations* version 1.46 (Catchen et al., 2013), or directly imported to R using VCFR (Knaus & Grünwald, 2017).

2.4 | Population genetic analyses

We quantified and visualized the distribution of genetic variation in adult populations of *S. purpuratus*, *P. ochraceus*, *L. aequalis* and *H. pumila* using F_{ST} and minimum spanning trees. Global F_{ST} and 95% confidence intervals were calculated across all loci for each species using diffCalc in the DIVERSITY package version 1.9.90 (Keenan et al., 2013) in R (R Core Team, 2016). F_{ST} was then converted to *Nm* using $Nm = (1/F_{ST} - 1)/4$ for comparison with estimated dispersal potential. Although there is some concern regarding the effects of nonequilibrium dynamics on estimation of *Nm* from F_{ST}, we consider it a useful first approximation (Meirmans & Hedrick, 2011). We constructed minimum spanning trees (MSTs) using the Kruskal algorithm in the R package NETVIEW version 1.0 (Neuditschko et al., 2012) with a mutual k-nearest neighbours (mk-NN) value of 15 for *S. purpuratus* and *P. ochraceus* and 10 for *L. aequalis* and *H. pumila* (Figure S2)—to balance fine- and large-scale structure in the network (Steinig et al., 2016)—and genetic distance matrices calculated using biallelic SNPs in PLINK version 1.07 (Purcell et al., 2007).

For species with recruitment in the die-off zone, we compared the genetic diversity (observed heterozygosity, H_O) of annual cohorts of new recruits to adult populations using biallelic SNPs in HIERFSTAT version 0.5-7 (Goudet, 2005) in R. Where sample sizes allowed, we randomly subsampled 50 individuals from each group five times to calculate a mean and 95% confidence interval. In cases with fewer than 50 individuals we used all individuals (Table S2). Estimates of H_O will be biased because we are only using variable sites (SNPs) from our reduced representation sequencing.

2.5 | Genetic assignment of recruits and rafting *L. aequalis*

Using all biallelic SNPs, we determined the probable source of new recruits for each species with a discriminant analysis of principal components (DAPC). We implemented the DAPC first on the adult populations using dapc in the ADEGENET version 2.1.3 package in R (Jombart & Ahmed, 2011). Geographical location was used for discrimination *a priori*. We conducted cross-validation tests to evaluate the performance of adult assignments as a function of principal components (Table S3). We further validated our ability to genetically distinguish geographical regions in the species with limited population genetic differentiation (*S. purpuratus* and *P. ochraceus*) by conducting a principal components analysis (PCA) on SNPs with the top 5% of loadings from the first discriminant function in the DAPC using the prcomp function in the STATS package in R. We replaced missing data with the mean allele frequency and centred and scaled allele frequencies using scaleGen in ADEGENET version 2.1.3. After performing the DAPC on the adults, we assigned recruits by transformation using the centring and scaling of the adult data and projected them onto the predicted position using the same discriminant coefficients as the adults (Jombart & Collins, 2015). Recruit assignment was evaluated using posterior membership probabilities generated with the predict.dapc function in ADEGENET version 2.1.3. We visualized membership assignment by constructing stacked bar graphs of posterior membership probabilities for all recruits.

We incorporated three additional *L. aequalis* individuals found on beachcast kelp holdfasts by J. Sones at the Bodega Marine Reserve in our analysis using the assignment test described for the recruits above, as well as a separate PCA using the prcomp function in the STATS package in R. For the PCA, we used a reduced set of SNPs with fewer missing data (i.e., 1088 SNPs that were represented in at least 98% of the 84 individuals), replaced missing data with the mean allele frequency and centred and scaled allele frequencies using scaleGen in ADEGENET version 2.1.3.

3 | RESULTS

3.1 | Estimates of dispersal potential

Quantitative species attributes including life-history traits (Table 1) converted to *Nm* reveal *Strongylocentrotus purpuratus* has the greatest dispersal potential, followed by *Pisaster ochraceus*, and then *Leptasterias aequalis* and *Henricia pumila*. For relative *Nm* estimated from *PD*, *S. purpuratus* has 7–1682 times higher *Nm* than *P. ochraceus* and 898–832,712 times higher *Nm* than *L. aequalis* while *P. ochraceus* has 123–495 times higher *Nm* than *L. aequalis*. For relative annual *F*, *P. ochraceus* was 1.18 times greater than *S. purpuratus*, *P. ochraceus* was 6436–30,189 times greater than *L. aequalis* and *S. purpuratus* was 5471–25,660 times greater than *L. aequalis*. For relative N_c, *S. purpuratus* was 1.06 times greater than *P. ochraceus*, *P. ochraceus* was 51.30 times greater than *L. aequalis* and *S. purpuratus* was 47.44 times greater than *L. aequalis*. Therefore, the ranges of overall (i.e., the composite of *PD*, *F* and *Nc*) relative differences in *Nm* estimated from species attributes were, for each pair of taxa: *S. purpuratus* was 7–1517 times greater than *P. ochraceus*, *P. ochraceus* was 1.6×10^8–1.9×10^8 times greater than *L. aequalis* and *S. purpuratus* was 1.1×10^9–2.2×10^{11} times greater than *L. aequalis*. *H. pumila* is predicted to be approximately similar to *L. aequalis*.

3.2 | Ecological pattern of recruitment

The taxa with higher dispersal potential—*S. purpuratus* and *P. ochraceus*—had higher recruitment in the die-off zone relative to the taxa with lower dispersal potential, *L. aequalis* and *H. pumila*. By the second year following the mortality event, new *S. purpuratus* recruits were detected at all surveyed sites in the die-off zone, and *P. ochraceus* was detected at all surveyed sites by year 3 (Figure 2). PERMANOVAs revealed significant differences in recruitment among all species (except between *L. aequalis* and *H. pumila*, which had similar predicted dispersal potential) and between the three collection years (Table S4; Figure 2). Interactions revealed significant variability in recruitment between areas (nested within sites) by species in all years studied and variability between sites by species in years 2 and 3 ($p < .05$, Table S4a). Recruitment differed significantly among species in all three years ($p < .01$, Table S4a); pairwise tests revealed significant differences ($p < .05$) in recruitment between species by year as follows: Yr 1 & Yr 2, *S. purpuratus* > *P. ochraceus*, *L. aequalis* and *H. pumila*; and Yr 3, *S. purpuratus* and *P. ochraceus* recruitment was not significantly different from one another, but both had higher recruitment than *L. aequalis* and *H. pumila* ($p < .05$).

Additional species-specific PERMANOVAs revealed significant differences in annual recruitment (Table S4; Figure 2) and interactions revealed significant variability in recruitment between areas (nested within sites) or sites by year for *S. purpuratus* and *P. ochraceus* ($p < .05$, Table S4a). Recruitment differed significantly among years for *S. purpuratus* and *P. ochraceus* ($p < .05$, Table S4b). Pairwise tests revealed significant differences ($p < .05$) in recruitment between years as follows: *S. purpuratus* recruitment was greater in Yr 2 and Yr 3 relative to Yr 1, *P. ochraceus* recruitment was greater in Yr 3 relative to Yr 1 and Yr 2, and *L. aequalis* and *H. pumila* had no recruitment detected by surveys in all three years. Overall, recruitment increased in each subsequent year for *S. purpuratus* and *P. ochraceus*.

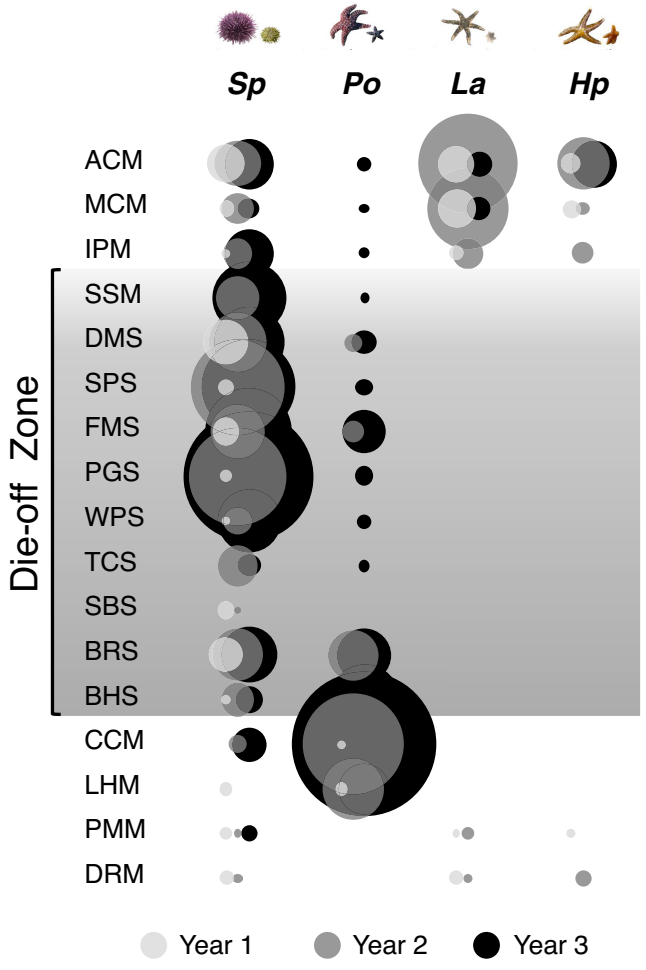

FIGURE 2 Recruitment dynamics. Bubble plot showing new recruit densities by year over the 3 years following the harmful algal bloom (HAB) in 2011. Year 1 refers to the surveys conducted beginning ~1 year after the mortality event. *Sp* = *Strongylocentrotus purpuratus*, *Po* = *Pisaster ochraceus*, *La* = *Leptasterias aequalis*, *Hp* = *Henricia pumila*. Circle area is proportional to density and relative to the highest density circle (7.61 recruits·m^{-2}). The grey shaded region indicates the sites impacted by the HAB. Site names correspond to the map in Figure 1c. Note, site SBS was not surveyed in Year 3.

3.3 | Samples for genetic analyses

A total of 1220 samples—564 *S. purpuratus*, 296 *P. ochraceus*, 285 *L. aequalis* and 75 *H. pumila* (Table S1)—were retained after bioinformatic filtering. *S. purpuratus* had a final set of 2839 biallelic SNPs, *P. ochraceus* had 4025, *L. aequalis* had 1616 and *H. pumila* 3691.

3.4 | Patterns of population diversity and genetic differentiation

The species with the highest dispersal potentials showed well-mixed gene pools over broad geographical scales: *S. purpuratus* F_{ST} = −0.0015 (95% confidence interval [CI] −0.0228 to 0.0213) and *P. ochraceus* F_{ST} = 0.0019 (−0.0097 to 0.0154) (Figure 3). The two brooders showed greater population genetic differentiation: *L. aequalis* F_{ST} = 0.1965 (95% CI 0.1568–0.2438) and *H. pumila* F_{ST} = 0.1374 (0.0381–0.2470) (Figure 3). These results are largely congruent with the relative dispersal potentials outlined in section 3.1, but the time to the most recent ancestor (tMRCA) was not estimated for these taxa and, if different, could contribute to differences in population genetic differentiation. Empirically estimated *Nm* converted from F_{ST}, using the equation $Nm = (1/F_{ST} - 1)/4$, is 131 for *P. ochraceus*, 1.0 for *L. aequalis* and 1.6 for *H. pumila*. There is an average difference of 106× between *P. ochraceus* and the brooding species, which tends toward predictions based solely on species' attributes (albeit is six orders of magnitude less than expected; see dispersal potential in Table 1). *S. purpuratus* F_{ST} was effectively zero and therefore could not be converted to *Nm*.

Comparisons of genetic diversity between adults and recruits show that heterozygosity of recruits in the die-off zone is nondifferentiable from adults for *S. purpuratus* and was ~91% of that of adults for *P. ochraceus* within 2 years following the MME (Figure 4).

3.5 | Genetic assignment of recruits and rafting *L. aequalis*

New recruits in taxa with higher dispersal potential—*S. purpuratus* and *P. ochraceus*—showed signals of dispersal to more distant non-natal sites than shown by recruits in the species with low dispersal, *L. aequalis* and *H. pumila* (Figure 5). By exploring recruitment patterns beyond the die-off zone, genetic assignment tests revealed *L. aequalis* and *H. pumila* had high local recruitment at subregional levels, 83% (of 201 recruits, four regions) and 56% (of 43, four regions), respectively (Figure S3c). *L. aequalis* also had high local recruitment even at the site-specific level, 72% (of 201, 10 sites). However, the site-specific assignment of *H. pumila* had less confidence, particularly at sites north of the die-off zone, because the northerly sites were poorly resolved in the DAPC (Figure S3b), probably due to small sample sizes of adults (Table S1). Nonetheless, *H. pumila* still showed at least 21% local recruitment (of 43, seven sites) (Figure S3). Despite limited population genetic differentiation in *S. purpuratus* and *P. ochraceus* (Figure 3), a subset of high-loading SNPs from the DAPC distinguish major geographical regions (Figure S4), revealing low local recruitment at the subregion level in *P. ochraceus* (29% of 103, three regions) and *S. purpuratus* (8% of 485, four regions), with most recruits having dispersed from other subregions, predominantly from north to south (Figure 5; Figure S3). However, it is important to note that using differing assignment groups was necessitated by the differing genetic structure among species, which precludes direct comparisons of local recruitment among species for particular regions.

The three *L. aequalis* individuals found rafting on kelp holdfasts in Bodega were genetically distinct from one another (Figure S5). One assigned with high confidence to adults sampled north of the die-off zone, while the other two were more genetically similar to southern groups (Figure S5).

4 | DISCUSSION

Although some phylogeographical and seascape genetics studies have called into question the relationship between pelagic duration and population genetic structure (e.g., Bowen et al., 2006; Selkoe et al., 2010), others have found a significant relationship when pelagic duration is considered more holistically with a suite of other dispersal-relevant attributes—e.g., fecundity and census population size—in appropriate analytical frameworks (Dawson, 2014a; Dawson et al., 2014; Riginos et al., 2014; Treml et al., 2012). Using a large-scale natural experiment created by a multispecies mortality event that generated a largely "clean slate" on which to study recruitment dynamics, simplifying this usually complex problem, we similarly found concordance between theoretical predictions and empirical measurements. Moreover, our study addressed concordance across a broader range of scales than prior studies, showing predictable directionality in recruitment between years within species—aligned with prior evidence that dispersal pathways are correlated within decadal scales ($r = .21 \pm .67$ SD) (Catalano et al., 2021). Furthermore, recruitment rates and genetic diversity in recruits reliably reflect predictions based on life-history differences among species. The dispersal differences predicted by species' attributes (and empirically measured using surveys) also align with estimates of population genetic differentiation within each species. While dispersal potential is clearly a determining influence on recruitment, genetic recovery, population structure and among-species differences in gene flow, additional considerations indicate its effect is not homogeneous through time or across space.

4.1 | Directionality in recruitment: seasonal timing of larval transport corresponds with southward flow

The predominant direction of flow in this study system is from north to south during the upwelling season (Figure 1; García-Reyes & Largier, 2012). Our genetic analyses commensurately revealed a dominance of upcurrent populations of adults contributing to downcurrent recruitment in the broadcast spawning species *Strongylocentrotus purpuratus* and *Pisaster ochraceus* (Figure 5; Figure S3). However, the relative importance of southward flow varied regionally. Though substantial *P. ochraceus* mortality was observed in the die-off zone, densities did not differ significantly from surveys conducted before the mortality event (Jurgens et al., 2015). Consequently, the analysis assigned the vast majority (66%) of *P. ochraceus* recruits in region S1 (Point Reyes) to adult survivors in the upcurrent die-off zone, whereas it assigned only 22% of recruits to adults north of the die-off zone, and as many as 12% to adults south of the die-off zone (Figure S3). This spatial variation in *P. ochraceus* recruitment across the study region is broadly consistent with the physics of mesoscale mixing processes and variation in oceanographic patterns during times of seasonal reproduction and larval transport during the upwelling season (Table 1; Largier et al., 1993; Wing et al., 1995). While southward flow predominates, waters immediately downcurrent and upcurrent of Point Reyes are known to persist during upwelling events, potentially restricting advection offshore (Largier et al., 2006); the highest *P. ochraceus* recruitment thus corresponds to this region (Figure 2). Thus, transient oceanographic features coupled with the timing of phenological events can have significant impacts on dispersal and/or settlement rates.

4.2 | Variation in contrasts between predicted and empirical dispersal

Rank dispersal potential estimated using a suite of quantitative attributes including life-history characteristics accounted for the observed rank differences in empirical estimates of dispersal: *S. purpuratus* had the highest dispersal potential, followed by *P. ochraceus* and then *Leptasterias aequalis* and *Henricia pumila*. Moreover, these

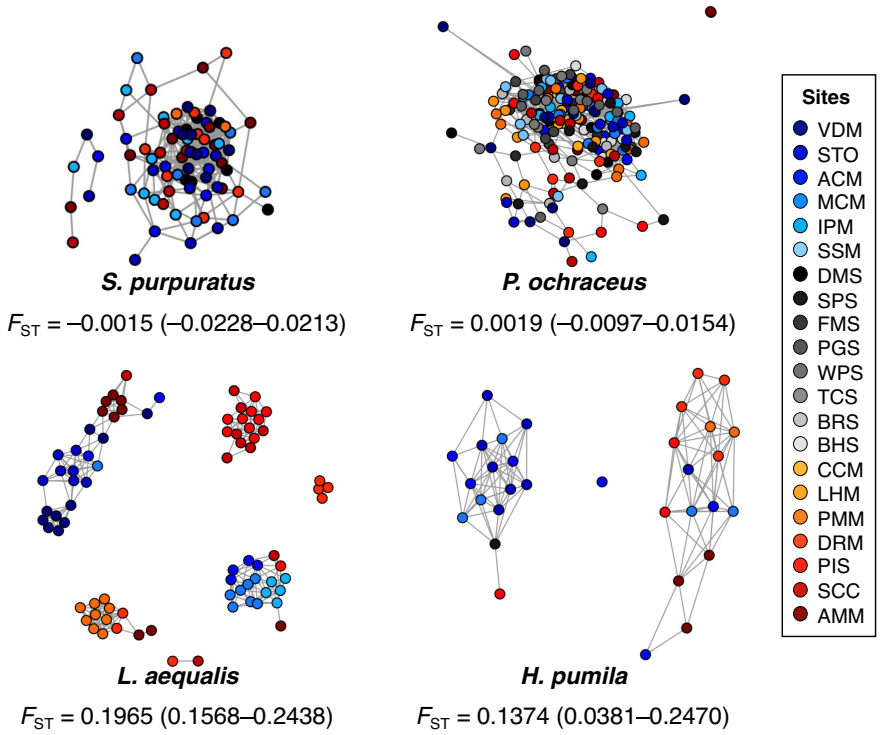

FIGURE 3 Minimum spanning trees and F_{ST} (and 95% confidence intervals) across all loci for adults from each species. Each circle represents an individual. Colours correspond to geographical locations in Figure 1. Cool colours are sites north of the die-off zone, greyscale are sites in the die-off zone and warm colours are south of the die-off zone. Sample sizes are provided in Table S1. Graphical representation in this figure space may contain superimposed individuals.

observed empirical differences were consistent across ecological, ecological–genetic and population genetic measures of recruitment in the die-off zone (Figure 2; Figure 5), as seen in the genetic assignment of recruits (Figure 5; Figure S3) and adult population genetic structure (Figure 3). However, whereas contrasts in predicted *Nm* (Table 1) differ by eight orders of magnitude between *L. aequalis* and *P. ochraceus*, empirical contrasts in *Nm* estimated via F_{ST} differ by less—six orders of magnitude between *L. aequalis* and *P. ochraceus*—suggesting mechanisms other than dispersal (e.g., drift, selection) also have effects.

The analytical landscape for inferring gene flow is thus complex (Marko & Hart, 2011). Population genetic structure can be influenced by the capacity of life-history traits to influence dispersal, by abiotic and biotic factors, and by eco-evolutionary interactions. Different coalescent ages among species can contribute to noise in estimates of *Nm* taken from F_{ST} of adults (Dawson, 2014b), but whether differences in the tMRCA between *P. ochraceus* (which had a population expansion ~50,000 years ago; Marko et al., 2010) and *L. aequalis* (with coalescents during the Pleistocene; Foltz et al., 2008; Melroy & Cohen, 2021) can explain six orders of magnitude difference in *Nm* taken from F_{ST} between *P. ochraceus* and *L. aequalis* is unclear. Other possible explanations include estimates of predicted *Nm* failing to account for important dispersal-relevant life-history characteristics or other factors. For example, phoretic dispersal can be particularly hard to predict but is highly influential in some circumstances. Despite no detection of *L. aequalis* in quadrat and transect surveys in the die-off zone, independent observations captured three *L. aequalis* rafting in kelp holdfasts washed up on shore (J. Sones, personal observation). Furthermore, the presence of two distinct genetic clusters of adults across sites north of the die-off zone as well as adults collected from subregion S1 clustering with adults from N1 and N2 (Figure 3) suggest that long-distance dispersal via rafting may play an important role in recolonization of *L. aequalis* (and *H. pumila*) in the die-off zone. While *PD*, *F* and N_c might reasonably account for differences in taxa with a pelagic larval phase (Dawson et al., 2014), existing frameworks may fall short in taxa for which pelagic dispersal is accomplished via phoretic dispersal of adults. Although the frequency of dispersal via rafting is unknown, documentation of such events in this study and in previous work on *Leptasterias* sp. (e.g., Highsmith, 1985) finding multiple individuals on a single kelp holdfast suggests phoretic dispersal is not uncommon.

Other potential sources of variation are introduced by differences in recruit survivorship and imprecision of quantified life-history traits. For species with similar survivorship curves, *Nm* contrasts based on mean annual fecundity are largely comparable; for example, *S. purpuratus* and *P. ochraceus* both have Type III survivorship (i.e., many offspring are produced and the vast majority die). However, comparing these to *L. aequalis*, which has five orders of magnitude higher juvenile survivorship than *P. ochraceus*, that is Type II survivorship (i.e., fewer offspring are produced and mortality is similar throughout life stages; Menge, 1975), clearly illustrates that the relative proportion of offspring recruiting back to shore is not directly proportional to fecundity. Indeed, adjusting the six orders of magnitude difference in fecundity for the five orders of magnitude difference in survivorship brings the estimated predictions of now one order-of-magnitude difference in recruitment far more in line with the observed 128-fold difference between *P.*

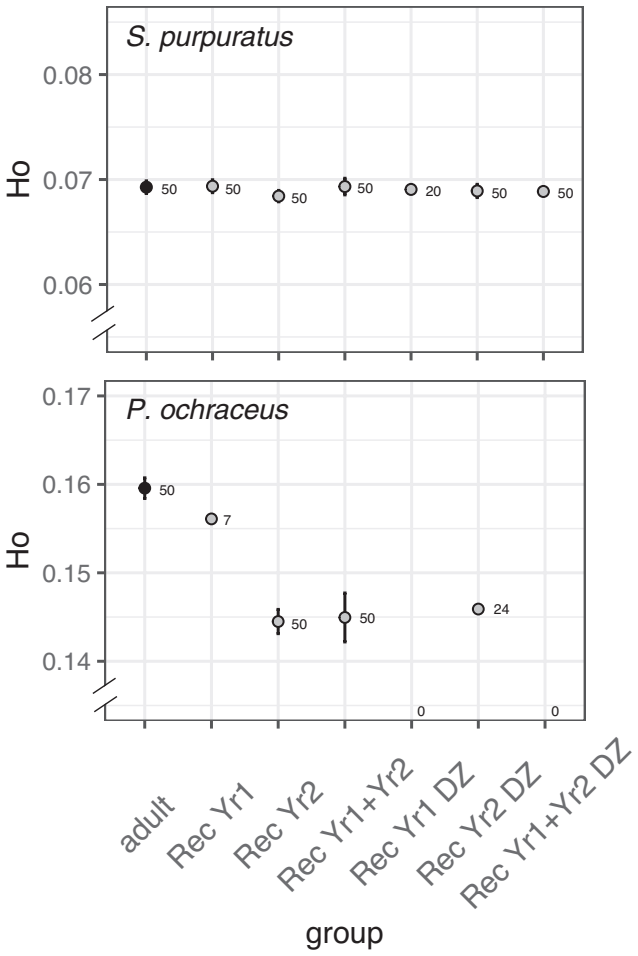

FIGURE 4 Observed heterozygosity of recruits (grey) and adults (black) for *Strongylocentrotus purpuratus* (top) and *Pisaster ochraceus* (bottom). For each group, if the sample size was larger than 50, five replicates of 50 individuals were randomly subsampled and used to calculate the mean and 95% confidence interval. Groups include adults, study-wide recruits from year 1 and year 2 (separately and combined), and die-off zone recruits in year 1 and year 2 (separately and combined) (Table S2). *P. ochraceus* did not have any recruitment in the die-off zone in year 1. Sample sizes are reported next to each point. Note, the vertical axes do not begin at zero.

ochraceus and *L. aequalis*. An additional consideration is that quantitative estimates of individual life-history characteristics used to estimate dispersal potential can be imprecise if they are based on snapshots of a single year or over only a few sites. In principle, measures of population genetic structure in stable populations should reflect mean annual fecundity (if other factors are equal—tMRCA, dispersal ability, etc.); however, other unmeasured factors often differ and bias estimates of differentiation. Fecundity, for example, can itself be highly variable, fluctuating with mean body mass of reproductive adults, food availability or other environmental factors and ignoring this variation can lead to over- or under-estimation of genetic connectivity (Castorani et al., 2017). There also can be considerable between-individual variation in dispersal (D'Aloia et al., 2015) which could be trait-based. Such deviations may add complexity to outcomes.

4.3 | Contrasting demographic and genetic recovery potential in species with low vs. high dispersal potential

Given the low (and/or rare) dispersal potential of *L. aequalis*, recovery in the die-off zone would seem to depend largely on incremental expansion at the edges from adjacent populations to the north and south. That substantial recruitment across the 100 km of the die-off zone has not been seen (despite adult populations at adjacent sites), therefore, is not surprising, and is a pattern documented by other research groups (Jaffe et al., 2019). Conversely, high dispersal taxa (*S. purpuratus* and *P. ochraceus*) already are showing the start of a demographic rebound, with *S. purpuratus* dispersing to all sites and *P. ochraceus* dispersing to nine of 10 sites across the die-off zone within 3 years (Figure 2).

Whether recovery of genetic diversity proceeds at the same rate as demographic recovery has important implications for the adaptive potential of the standing genetic variation at the time of the next perturbation. However, the degree to which genetic recovery follows demographic recovery is not known for most taxa, but should theoretically be driven by the confluence of life-history traits, demography, mechanisms of evolution, and biotic and abiotic factors. Here we find that, within 2 years of recruitment, genetic diversity (observed heterozygosity) of *S. purpuratus* recruits in the die-off zone are nondifferentiable from reference adult populations outside the die-off zone and *P. ochraceus* recruits in the die-off zone have reached ~91% of the reference adult heterozygosity (Figure 4). These two species represent the highest and second highest dispersal abilities in this study, respectively. In contrast, during this time period, the two brooding sea stars, *L. aequalis* and *H. pumila*, failed to detectably recruit to the die-off zone altogether, inevitably meaning zero recovery of genetic diversity over the same period.

Nonetheless, highlighted by the few *L. aequalis* observed on kelp rafts (Figure S5), dispersal, colonization and genetic trajectory may prove more stochastic in nature given colonization of isolated sections of coast may depend on one gravid or few individuals. Moreover, the likelihood of long-distance dispersal events is dependent on the availability of suitable substrate on which successful rafting may occur. Given the decimation of kelp forests in north-central California (Rogers-Bennett & Catton, 2019), these opportunities are probably rarer than in previous years. Thus, genetic recovery in low dispersal species may be constrained by small population size, increasing the potential for inbreeding and genetic drift. Even with demographic recovery, genetic recovery may not follow. For example, two forest-forming seaweeds lost 30%–65% of their genetic diversity following a marine heat wave, with some sites becoming monocultures of a single haplotype, limiting adaptive capacity to ongoing multiple stressors (Gurgel et al., 2020).

5 | CONCLUSION

The greatest promise in describing the relationship between dispersal, recruitment and genetic structure lies in the integration of

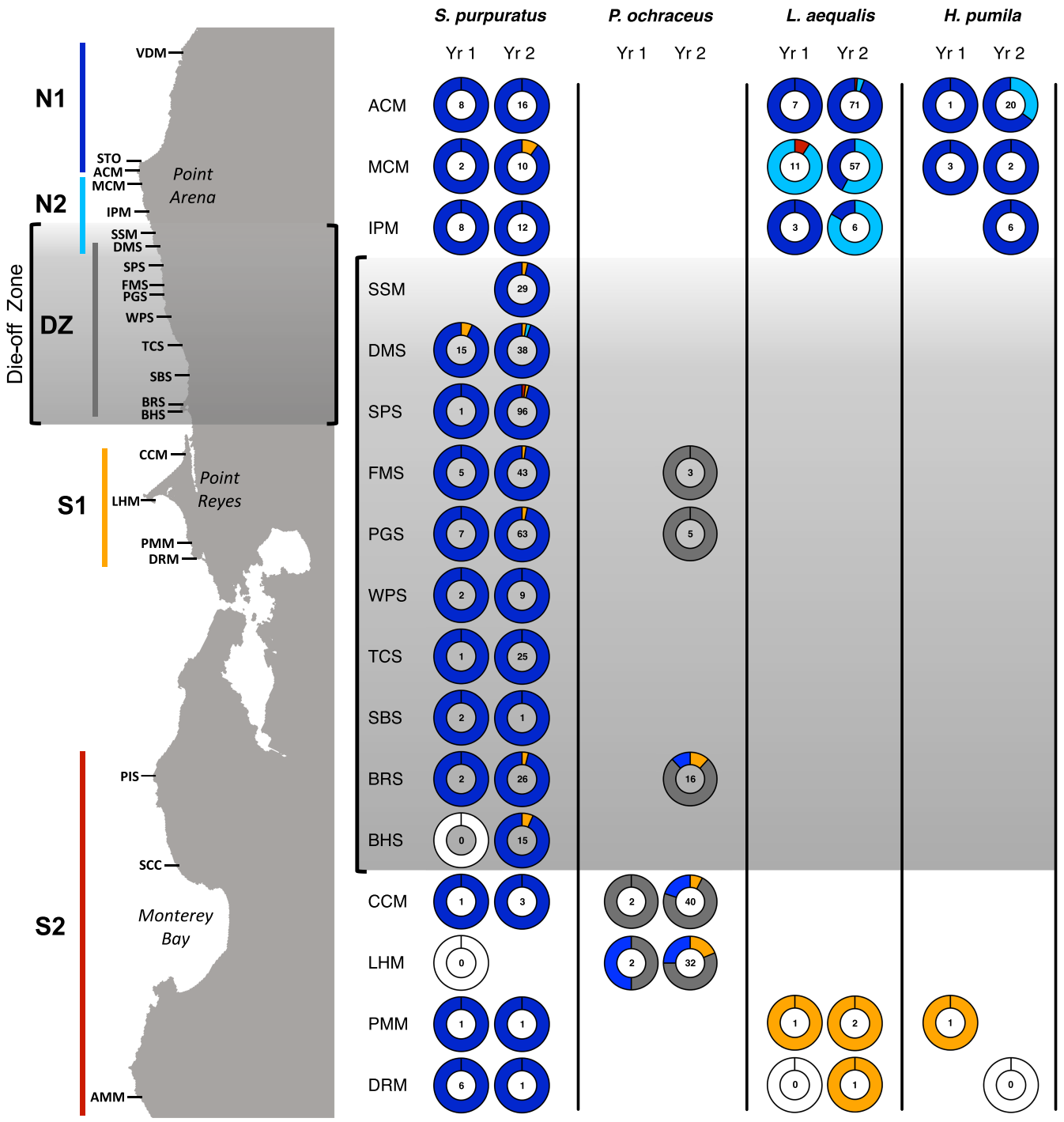

FIGURE 5 Proportion of recruits assigned to likely source populations, indicating immigration predominantly from north to south in *Strongylocentrotus purpuratus* and *Pisaster ochraceus*, and local recruitment in *Leptasterias aequalis* and *Henricia pumila*. The map shows sample sites. By row, doughnut plots show the site from which recruits were collected; the colour slices of doughnuts indicate to which regions (defined by adult genetic diversity) the recruits are genetically assigned. Only recruits collected from within and adjacent to the die-off zone were analysed, with sites farther north and south reserved for sampling putative adult source populations. The first column for each species represents the first wave of recruitment in the winter of 2012/13 following the die-off and the second column represents the subsequent year 2013/14. White doughnuts represent cases where recruits were observed at a site, but did not have sufficient sequencing depth to be included in the analysis. Absence of a plot means no recruits were detected in quadrat surveys at that site. The number of recruits included in the analysis at each site by year is in the centre of each doughnut. Posterior probabilities of recruit assignments to potential adult sources are given in Figure S3c. Recruit density by site is given in Figure 2. In two cases recruits found outside of the quadrat surveys, which therefore do not appear in Figure 2, were used in genetic analyses (i.e., *S. purpuratus* at TCS and CCM in year 1).

a variety of ecological data including functional life-history traits, genetic analyses on comparable scales, along with oceanographic modelling (Dawson et al., 2014; Selkoe et al., 2010). Although we cannot yet predict a particular recruitment event, we should be able to predict general outcomes after the accumulation of multiple events with similar tendencies, and to forecast the relative probabilities of outcomes for different taxa based on differing life-history characteristics. Reflecting on the search for the ecological significance among a number of interacting factors, Dawson et al. (2010) recast chaotic genetic patchiness instead as "eurymixis," trying to re-emphasize the importance of purposefully seeking to understand the mechanisms and interactions determining short- to long-term relationships. Recontextualizing "chaotic patchiness" as complex but explainable variation is even more essential now, in the age of marine genomics, when SNPs and structural variants allow us to extract signals of environmental variation in genomic variation (Dorant et al., 2020). Limitations that must be overcome to obtain better estimates of dispersal potential include the paucity of life-history data for many species, understanding of behaviour (Gaylord et al., 2013; Morgan, Fisher, Miller, et al., 2009) and near-shore oceanography (Largier, 2003; Largier et al., 2006; Nickols et al., 2012; Sponaugle et al., 2002).

In a time when MMEs are on the rise in a variety of taxa (Fey et al., 2015) and there is increased emphasis on networks of marine protected areas and their efficacy in a changing world (Ballantine, 2014; Burgess et al., 2014; Devillers et al., 2015; Toonen et al., 2013), understanding marine connectivity remains an essential goal and "Grand Challenge" *sensu* Lindsay (2012). Further developing the theory and quantitative relationships for forecasting species' potential for recovery using a suite of attributes including life-history characteristics, possibly in part based on "dispersal syndromes" (Dawson, 2014a), would be valuable for conservation and management purposes. The ability to quickly triage impacted species using known traits, attributes and variables would facilitate the application of conservation actions where they are most needed. This goal may not seem out of reach, given the emerging relationship between relative dispersal potential and empirical estimates of connectivity (Haye et al., 2014; Weber et al., 2015; Young et al., 2015).

AUTHOR CONTRIBUTIONS

All authors designed and performed research. LMS analysed the data. LMS wrote the initial paper with contributions from all authors.

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CONFLICT OF INTEREST

The authors have declared no conflict of interest for this article.

OPEN RESEARCH BADGES

This article has earned an Open Data Badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at [provided Raw sequence reads are deposited in the National Center for Biotechnology Information sequence read archive (SRA) under BioProjects PRJNA445895, PRJNA871810 and PRJNA879758. SNP data and metadata for individuals used in genetic analyses are available on Dryad (https://doi.org/10.6071/M3FD4R). Ecological data are archived in the Biological and Chemical Oceanography Data Management Office (BCO-DMO) (Dawson et al., 2015; doi:10.26008/1912/bco-dmo.562467.1).

DATA AVAILABILITY STATEMENT

Raw sequence reads are deposited in the National Center for Biotechnology Information sequence read archive (SRA) under BioProjects PRJNA445895, PRJNA871810 and PRJNA879758. SNP data and metadata for individuals used in genetic analyses are available on Dryad (https://doi.org/10.6071/M3FD4R). Ecological data are archived in the Biological and Chemical Oceanography Data Management Office (BCO-DMO) (Dawson et al., 2015; doi:10.26008/1912/bco-dmo.562467.1).

BENEFIT-SHARING STATEMENT

Benefits Generated: Benefits from this research accrue from the sharing of our data and results on public databases as described above.

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