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RESEARCH PAPER

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Contrasting genetic structure of sympatric congeneric gastropods: Do differences in habitat preference, abundance and distribution matter?

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Abstract

Aim: The relationship of population genetics with the ecology and biogeography of species may be explored by comparing phenotypically similar but ecologically different congeners with overlapping ranges. We compared genetic differentiation between two congeneric rocky intertidal gastropods across a major portion of their sympatric range. We hypothesized that the habitat generalist with high abundance and continuous distribution would exhibit comparatively less genetic differentiation than the habitat specialist with low abundance and a fragmented distribution.

Location: North-east Atlantic from the north-west Iberian Peninsula to southern British coastline.

Taxon: Gastropoda, Trochidae, *Steromphala* (formerly *Gibbula*).

Methods: Field surveys were conducted to assess the presence/absence and the abundance of *Steromphala umbilicalis* (generalist) and *S. pennanti* (specialist) at 23 localities along ~1,800 km coastline. We isolated polymorphic microsatellite markers for both species (seven loci for *S. umbilicalis* and eight for *S. pennanti*) and used these to genotype 187 *S. umbilicalis* and 157 *S. pennanti* individuals. We used standard population genetic analyses to compare patterns of genetic differentiation between species in relation to the field surveys.

Results: *Steromphala pennanti* showed a more fragmented distribution, significantly lower abundance, and greater genetic differentiation than *S. umbilicalis*. One *S. umbilicalis* population towards the north of the range (southern Britain) was genetically distinct from all other sampled populations. *Steromphala pennanti* showed greater genetic differentiation between three southern localities, which may be attributable to its fragmented distribution and lower abundance because of limited availability of its preferred fucoid habitat in this region. We also suggest that oceanographic currents could be associated with regional genetic structure.

Main conclusions: The habitat generalist showed high-local abundances, continuous distribution and low regional genetic differentiation. We found the opposite pattern

for the habitat specialist. Our study highlights the importance of considering ecological (e.g. abundance, habitat preferences) and abiotic variables (e.g. ocean currents and temperature) for understanding differences in genetic structure of sympatrically distributed congeners.

KEYWORDS
abundance, comparative population genetics, habitat specialist, intertidal ecology, Microsatellites, north-east Atlantic, *Steromphala*

1 | INTRODUCTION

A central question of biogeography asks how the population genetic structure of species is affected by environmental, ecological and life history variables and whether there are any associations with patterns of abundance and distribution (Hellberg, Burton, Neigel, & Palumbi, 2002; Riginos, Crandall, Liggins, Bongaerts, & Treml, 2016; Schiebelhut & Dawson, 2018; Selkoe et al., 2016). It has been classically assumed that early life history traits (e.g. duration of a dispersive phase) are good predictors of population genetic structure (Almeida et al., 2017; McInerney, Allcock, Johnson, & Prodöhl, 2012; Rognstad, Wethey, & Hilbish, 2014). However, recent meta-analyses are equivocal and approach generalizations with caution because other factors, such as adult body size, egg type and microhabitat preferences, can also influence genetic structure (Kelly & Palumbi, 2010; Riginos, Douglas, Jin, Shanahan, & Treml, 2011; Selkoe & Toonen, 2011). Likewise, the distribution of physical habitat (e.g. geological substrate) and environmental conditions appear to influence genetic structure for some species, but not others (Almeida et al., 2017; Haye et al., 2014; Marko, 2004; Marko & Hart, 2011; McInerney et al., 2012). Recent biogeographical studies have shifted focus to ask whether demographic and ecological traits, such as abundance or habitat specificity, are related to differences in genetic structure (Engler, Balkenhol, Filz, Habel, & Rödder, 2014; Kierepka, Anderson, Swihart, & Rhodes, 2016; Selkoe et al., 2016).

To explore whether differences in species' abundance and habitat specificity affect population genetic structure, it is useful to compare closely related species. Ideally this comparison would involve co-distributed congeners with the same propagule dispersal type. Such species would experience broadly similar environmental conditions and dispersal potential, but differ in their habitat preferences and overall abundance. This will increase confidence that any population genetic differences between species are related to these targeted ecological or demographic factors, rather than differences in environment or dispersal (Schiebelhut & Dawson, 2018). For example, a habitat generalist species, which should have relatively high abundances and hence, larger population sizes, may exhibit lower population subdivision than a sympatric congener with more restrictive habitat preferences (i.e. more fragmented geographic distribution), and therefore comparatively lower abundances and population sizes. For the high abundance/habitat generalist species, comparatively more offspring are expected to be produced, leading to a greater chance of recruitment, higher gene flow, and ultimately lower population genetic differentiation than for the low abundance/habitat specialist (Scheltema, 1971). Moreover, this species is likely to have shorter dispersal pathways than the habitat specialist among populations due to its more continuous geographic distribution. However, if one or both species have experienced a recent range expansion (e.g. post-glacial), then its genetic signature could mask some of these predicted population genetic patterns (Marko & Hart, 2011).

The relationship between habitat specificity and abundance with genetic population structure has been explored in terrestrial systems, where habitat generalist species exhibited more genetic connectivity than sympatric congeners with more restrictive habitat preferences and therefore a more fragmented geographic distribution (Engler et al., 2014; Kierepka et al., 2016). There are fewer examples in marine systems, but a recent study showed a positive relationship between estimates of local abundance and genetic structure, although this varied between pairs of synchronously diverging co-distributed species (Dawson, Hays, Grosberg, & Raimondi, 2014). In a review of reef community population genetics, all species with "chaotic" genetic structure (highly variable levels of genetic structuring with no obvious spatial patterning) were habitat generalists, whereas habitat specialists showed genetic differentiation between regions (Selkoe, Gaggiotti, Bowen, & Toonen, 2014). Differing habitat preferences and subsequent variation in current and historic distribution in intertidal gastropod congeners have also been associated with population genetic structure (Marko, 2004).

The trochids *Steromphala umbilicalis* (da Costa, 1778) and *Steromphala pennanti* (Philippi, 1846) were chosen to explore these patterns because they are phenotypically similar and sympatrically distributed along the rocky intertidal zone of the north-east Atlantic. The recorded range of *S. umbilicalis* extends from north-west Scotland (Mieszkowska, Milligan, Burrows, Freckleton, & Spencer, 2013) to Morocco (Southward, Hawkins, & Burrows, 1995). *Steromphala umbilicalis* is a habitat generalist, found within the mid to low-intertidal zone in rockpools, cracks, above and under boulders/rock ledges/platforms, and the fucoid zone (Mieszkowska et al., 2013; Muñoz-Colmenero et al., 2015). *Steromphala pennanti* is distributed from the Cherbourg peninsula in northern France to Morocco (Southward et al., 1995) on the low-intertidal zone, and is more closely associated with fucoid habitat, such as *Fucus serratus* (Linnaeus, 1753), than *S. umbilicalis* (Bordeyne et al., 2017). *Steromphala pennanti* is therefore a habitat specialist and largely restricted to the fragmented

distribution of fucoids along the Bay of Biscay. Regarding dispersal potential, *Steromphala* species are widely held to produce lecithotrophic larvae and are estimated to have approximately the same maximum larval duration of 7 to 9 days (Keith, Herbert, Norton, Hawkins, & Newton, 2011; Underwood, 1972a,b).

Within the ranges of both species lies 230 km of almost uninterrupted sandy intertidal habitat in south-west France (Castelle et al., 2006). This habitat gap (Figure 1) results in the absence of both species along that shoreline and coincides with the northern range limit of the rocky intertidal gastropods *Patella rustica* (Linnaeus, 1758) (Lima et al., 2007) and *Stramonita haemastoma* (Linnaeus, 1767) (EJGW & PBF, personal observation). However, no studies to date assess whether the habitat gap affects population connectivity of rocky shore species that are found on both sides of the gap.

Here, we explored differences in the abundance, distribution, and population genetic structure of *S. umbilicalis* (habitat generalist) and *S. pennanti* (habitat specialist) within the sympatric portion of their ranges. In order to evaluate their genetic structure, we isolated and genotyped microsatellite loci of both species. We hypothesized that, if more abundant and continuously distributed (resulting in a larger overall population size), the habitat generalist will have lower-genetic differentiation than the habitat specialist. We also ask whether genetic breaks for both species occur in association with large habitat gaps and/or other physical variables.

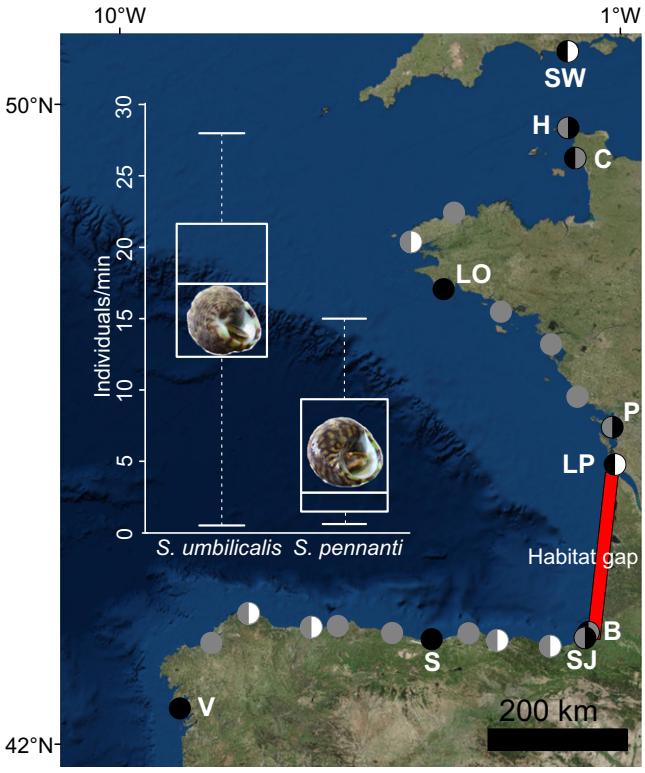

FIGURE 1 Map using World_Aitoff projection in ArcGIS displaying sampling localities on the north-east Atlantic coasts of the Iberian Peninsula, France and the British Isles as circles, and abundance box plots for localities where both species were present (n = 16). Left semi-circles represent *Steromphala umbilicalis*, right semi-circles represent *Steromphala pennanti*: white = absent; grey = present; black = present and used as DNA sample locality. Locality codes correspond with Table 2

2 | MATERIALS AND METHODS

2.1 | Sampling

Abundance estimates were made at 23 localities (Figure 1) at low tide in November 2014, August 2015, April 2016 and August 2016, with multiple visits to several localities. These localities were roughly evenly spaced and equally sampled north and south of the habitat gap (11 north and 12 south). At each locality, four people searched the mid to low shore in varied microhabitats where both species occurred, for 2 to 4 minutes. To prevent sampling overlap, a distance of at least 10 m was kept between each person. Timed searches were part of a wider sampling effort to quantify the presence/absence of rocky shore gastropods at each locality (~3 hr per locality). This additional sampling effort was used to increase confidence of any locality-specific *S. pennanti* absences. For both species, the mean number of individuals found per minute was calculated at each locality where both species were present (n = 16). The normality of abundance distributions was tested using a Shapiro–Wilk test in RSTUDIO 1.1.383, which showed a non-normal abundance distribution in *S. pennanti*. Therefore, a Wilcoxon–Mann–Whitney test was used in RSTUDIO to compare abundances between species over their sympatric range. Abundance measurements were also compared between mean value of localities to the north of the habitat gap in south-west France against the mean value of localities to the south of the habitat gap for both species.

An average of 27 (SE = 1.04) individuals of *S. umbilicalis* and 26 (SE = 2.30) individuals of *S. pennanti* were collected from three localities to the south of the habitat gap and three to the north (Fig. 1 and Table 2) and stored in 95% ethanol. Where it was not possible to collect enough specimens of each species from the same locality, the nearest locality was used instead for the under-sampled species (usually *S. pennanti* due to its fragmented distribution and often low abundances). *Steromphala umbilicalis* was also collected from Swanage (the UK) to investigate whether the English Channel was associated with a genetic break.

2.2 | Microsatellite identification and primer development

Microsatellite markers for *S. umbilicalis* were developed from the transcriptome sequence generated from a single individual collected at Southsea, Hampshire, the UK. Details of the transcriptome sequencing and assembly for *S. umbilicalis* are given in Appendix S1 in the Supporting Information. The assembled transcriptome of *S. umbilicalis* was mined for microsatellites using MISA (http://pgrc.ipk-gatersleben.de/misa/) with the minimum number of repeats being: dinucleotide ≥8x, trinucleotide ≥6x and tetranucleotide ≥4x. Loci without >20 bp of sequence flanking the microsatellite were removed and longer microsatellites were preferred for primer design.

TABLE 1 Microsatellite loci, primer and PCR information. Locus = locus associated primer names, marked "U" for *Steromphala umbilicalis*, or "PEN" for *Steromphala pennanti*; Forward = forward primer sequence; Reverse = reverse primer sequence; SSR = simple sequence repeat; Mix (label) = multiplex mixes (fluorescent label); T = annealing temperature of PCR reaction (°C); A = number of alleles recorded for each locus; R = range length for variation observed among alleles

Locus	Forward	Reverse	SSR	Mix	T	A	R
U26231	GCAGGGCTGGTTTGAAGATC	GCATGGATTCAGCGCGTTAT	$(ATA)_6$	D(FAM)	55.7	22	209–332
U23195	GCAGGCAGGTAGAGCTAGAG	TTCGGGCATAAACAGGTCCT	$(GCAG)_4$	A(FAM)	60	11	156–208
U34184	GCACAGGCCCTCAGATCATT	AACCCTCTCATGTCCACAGC	$(AT)_8$	A(HEX)	60	12	199–233
U36148	GGCCACCCTGAAGAGATAGG	AGGGGTGGCTCAACTTTCAT	$(ACAG)_5$	A(NED)	60	11	174–214
U15541	GTATTGGCTTGCTGTCCGTC	TGCCTCCATGATAAGCTTACCA	$(AATG)_4$	B(FAM)	58.1	14	217–257
U34428	ATAGTATTGGGCAGCGTCCG	TGAGATATCCCGCTGACAAGG	$(TACG)_4$	C(FAM)	58.1	9	213–249
U62438	TTGAACCCCAAACTCAACGC	TTGTCAAAACTGGTGCTGGC	$(ACA)_8$	C(NED)	58.1	10	136–178
PEN79	CACGTTTGAGTCCTGTCGAA	CGTTGCATCAGTTTGACGAT	$(AG)_6$	1(FAM)	55.7	3	115–119
PEN86	TTTTGAGCGATGCTTTATGC	TGCATTTGACTGTTCAATTCAT	$(ATGT)_7$	1(HEX)	55.7	18	122–214
PEN146	TCTCTTGTAGCCCTTTTGCG	AAATCCCATGTTTCCGTTCA	$(TC)_5$	1(NED)	55.7	23	172–230
PEN65	CCAGTTCTGCAAGTGAACCA	CAGGATCACCTCTCGCTTCT	$(CAG)_7$	2(FAM)	58.1	5	92–104
PEN138	ATCATTGCACTTCCTCTCGG	CAGGCAGATAGGGTAGCAGC	$(AG)_5$	2(HEX)	58.1	5	165–173
PEN104	TCGTCTCTGCTCATTGTTACC	AGAGATGACGCTCCCTCGTA	$(CT)_5$	2(NED)	58.1	6	133–143
PEN168	CCCAATGTAAGTCCGCTGTT	TTCGATGTGCAGAAGGAATG	$(TTTG)_6$	3(FAM)	58.1	7	207–231
PEN145	GCCATTAGCAGAGTGACCTTG	ATAGAGAAGGCCGAGCAGC	$(GA)_5$	3(NED)	58.1	10	169–193

Microsatellite primers were designed using different methods for each species. For *S. umbilicalis*, the selected sequences of transcripts containing simple sequence repeats (SSRs) were entered into Primer3 4.0.0 (Koressaar & Remm, 2007; Untergasser et al., 2012) one by one with the SSRs highlighted using default settings. For each locus where primers could be designed, the highest ranking primer pair based on default settings was retained. We removed any primers with: (a) non-zero values for self-complementarity score (any_th), (b) the 3' self-complementarity (3'_th), (c) the value of the melting temperature of the most stable hairpin structure of the primer (hairpin) or (d) low (<60°C) annealing temperatures. Remaining loci were BLAST searched against the mt genome of *S. umbilicalis* in Geneious 8.1.5 (Kearse et al., 2012), and any loci potentially belonging to the mt genome were excluded (Wort, Fenberg, & Williams, 2017). Any primers that contained an SSR-like repeat were excluded, or in some cases a new primer pair designed with the above conditions.

For *S. pennanti*, DNA extractions from 10 specimens from San Vicente de la Barquera and Vilagarcía de Arousa (referred to for the remainder of the text as Vilagarcía) were diluted to approximately equal concentrations as measured by a NanoDrop, mixed to achieve ≥1 μg of DNA and sent to Genoscreen (Lille, France) to develop microsatellite primers. Generation of multiplex-enriched libraries and sequencing was carried out as reported in Malausa et al. (2011). Briefly, genomic DNA was mechanically fragmented, enriched in microsatellite loci with eight probes (TG, TC, AAC, AGG, ACG, AAG, ACAT and ACTC) before amplification by PCR with a High Fidelity Taq. PCR products were purified, quantified and GsFLX libraries were then carried out following the manufacturer protocols and sequenced on 1/32 of a 454 GS-FLX PTP. The bioinformatics program QDD 3 (Meglécz et al., 2009) was used to analyse *S. pennanti* DNA sequences to obtain PCR primers. Among 5,945 sequences containing a microsatellite motif, 189 primer sets bioinformatically validated were designed which had "perfect" characteristics. After excluding primer pairs that failed to amplify in the majority of samples and those that were monomorphic, seven remained that amplified all *S. umbilicalis* individuals, and eight from an initial nine trialled in *S. pennanti* (Table 1).

PCR was performed in 25 μl reactions containing 1 μl of forward and reverse primers of each microsatellite locus at 10 μM concentration, 12.5 μl of GoTaq G2 Green Master Mix (Promega, Madison, WI), 2 μl of DNA solution between 50 and 500 ng/μl concentration measured using a Nanodrop, and sterile distilled water. Thermal cycling was performed with initial denaturation for 5 minutes at 95°C, 40 cycles of 60 s at 95°C, 60 s at the given annealing temperature (Table 1), 90 s at 72°C, and a final elongation step of 15 min at 72°C. PCR product was then diluted to 1:50 volume with sterile distilled water and sent to DBS Genomics (Durham University, the UK) for fragment length analysis (FLA) using a 3,730 DNA Analyser (Applied Biosystems) with the filter set DS-30, and ROX500 as the size standard. Primers were initially trialled with two samples from three localities using a temperature gradient PCR for annealing temperatures from 52°C to 62°C, and subsequent FLA. Where amplification of polymorphic loci was unsuccessful regardless of temperature or samples, the primers were excluded.

2.3 | Peak scoring and analysis

Peak scoring was carried out using Peak Scanner 2.0 (Applied Biosystems). The observed (H_o) and expected (H_e) heterozygosities, and the number of alleles (Â) per locus and locality were calculated with GenAlex 6 (Peakall & Smouse, 2006) (Tables 2 and Tables S2.1 and

S2.2). Heterozygote deficiency both by locus and by locality were also tested in GENEPOP ON THE WEB 4.2 (Rousset, 1995, 2008) with 10,000 dememorization steps, 1,000 batches and 10,000 permutations per batch (Fenberg, Hellberg, Mullen, & Roy, 2010) (Table S2.3). GENEPOP ON THE WEB 4.2 (Rousset, 1995, 2008) was used to obtain pairwise and global F_{ST} (Weir & Cockerham, 1984) and subsequent *P*-values with default settings and significance (α = 0.05) determined following the sequential Bonferroni correction. Nei's pairwise F_{ST} (Nei, 1973) was calculated using the "hierfstat" package (Goudet, 2005) in "adegenet" 2.0.1 (Jombart, 2008) in RSTUDIO and used to generate a discriminant analysis of principal components (DAPC) using the package "adegenet" 2.0.1 (Jombart, 2008; Jombart, Devillard, & Balloux, 2010) in RSTUDIO.

Structure 2.3.4 (Pritchard, Stephens, & Donnelly, 2000) was used with an admixture model on microsatellite data with and without prior populations input to the model. Ten runs were carried out for each of the potential number of populations (*k*) (1–6 for *S. pennanti*, 1–7 for *S. umbilicalis*) with a burn-in of 30,000 steps followed by 100,000 Markov Chain Monte Carlo (MCMC) iterations to estimate mean and variance of posterior probabilities and log likelihoods of the number of assumed populations. The best estimate of *k* was determined in STRUCTURE HARVESTER (Earl, 2012) using the peak in the delta *k* value. Subsequent visualisation of the data as bar graphs was carried out in CLUMPAK (Kopelman, Mayzel, Jakobsson, Rosenberg, & Mayrose, 2015) for the best assumed *k* value. The population structure was also assessed with R-package GENELAND 4.0 (Guillot, Mortier, & Estoup, 2005) using the spatial model and uncorrelated frequencies. One million iterations, 100 iterations of thinning and a final burn-in of 10% of the saved iterations were used to test for the best *k* between one and the maximum number of samples in each species.

AMOVAs (Excoffier, Smouse, & Quattro, 1992) were carried out in RSTUDIO using the "poppr" package 2.5.0 (Kamvar, Tabima, & Grünwald, 2014) on each species between two groups for *S. pennanti* (north and south of the habitat gap), and for *S. umbilicalis* among three groups (Swanage, north and south of the habitat gap), between sites within those groups, and all individuals. Significance of results was tested using MC tests with 10,000 repeats. The number of migrants per generation was estimated in GENEPOP ON THE WEB using the private alleles method (Barton & Slatkin, 1986) between localities north and south of the habitat gap. Genetic effective sizes (N_E) were calculated with the Linkage Disequilibrium Method implemented in NEESTIMATOR 2.01 (Do et al., 2014).

TABLE 2 Descriptive statistics from seven *Steromphala umbilicalis* and eight *Steromphala pennanti* microsatellite loci: locality, number of samples (*N*), the expected (H_e) and observed heterozygosities (H_o) and the number of alleles (Â) with standard deviation (*SD*) found per locus at each locality from north to south, with SW France habitat gap shown as thicker line

Code	Locality	*N*	H_e	H_o	Â ± *SD*
S. umbilicalis					
SW	Swanage	22	0.703	0.234	6.86 ± 1.57
C	Cap de Carteret	27	0.626	0.481	6.43 ± 1.99
LO	Loctudy	29	0.651	0.437	7.29 ± 2.06
LP	Les Pierrieres	29	0.598	0.452	6.86 ± 1.86
B	Biarritz	29	0.589	0.433	7.14 ± 3.48
S	San Vicente de la Barquera	24	0.582	0.379	6.43 ± 3.21
V	Vilagarcía de Arousa	27	0.614	0.381	6.71 ± 2.56
S. pennanti					
H	Cap de la Hague	33	0.566	0.245	6.75 ± 4.92
LO	Loctudy	30	0.558	0.259	6.38 ± 4.57
P	Point du Chay	20	0.547	0.270	4.88 ± 2.17
SJ	St Jean de Luz	19	0.649	0.270	5.50 ± 1.69
S	San Vicente de la Barquera	26	0.501	0.296	5.75 ± 4.06
V	Vilagarcía de Arousa	29	0.535	0.291	6.00 ± 3.66

3 | RESULTS

3.1 | Abundance distribution

Steromphala umbilicalis was significantly more abundant (Wilcoxon–Mann–Whitney test, W = 219, *p* = 0.0006) than *S. pennanti* at localities where both species were present (*n* = 16), with mean abundance of 16.38 (*SE* = 2.03) individuals per minute search time for *S. umbilicalis* compared to 5.44 (*SE* = 1.22) individuals per minute for *S. pennanti* (Fig. 1). *Steromphala pennanti* was absent from six localities within our sampling range, four of which were south of the habitat gap where fucoids were not present, whereas *S. umbilicalis* was present at every locality. Thus, the habitat generalist, *S. umbilicalis*, was more abundant and more continuously distributed than *S. pennanti* within their sympatric range. *Steromphala pennanti* was less abundant south of the habitat gap [mean abundance = 3.34 (*SE* = 1.08) individuals per minute, *n* = 8] than north of the habitat gap [mean abundance = 7.19 (*SE* = 1.98) individuals per minute, *n* = 8], albeit not significantly due to the small sample size (W = 45, *p* = 0.1949). *Steromphala umbilicalis* showed the opposite pattern, with a mean abundance of 19.12 (*SE* = 2.01) individuals per minute south of the habitat gap (*n* = 13) and 12.17 (*SE* = 2.55) individuals per minute north of the habitat gap (*n* = 9) (W = 16.5, *p* = 0.1149).

3.2 | Microsatellite population genetics

Microsatellite data were obtained for 187 *S. umbilicalis* and 157 *S. pennanti* individuals (Table 2). A larger number of between locality measures of differentiation (pairwise F_{ST}) were significant for *S. pennanti* than *S. umbilicalis* (Table 3). The only significant pairwise differences for *S. umbilicalis* were found when one population under consideration was the British locality (Swanage). By contrast, *S. pennanti* showed significant differentiation between San Vicente de la Barquera (on the central north coast of the Iberian Peninsula) and all other localities, and Vilagarcía (NW Iberian Peninsula) with Cap de la Hague (Cherbourg Peninsula, France). The habitat gap did not

TABLE 3 Pairwise comparisons of microsatellite genotypic differentiation (*P*-value) and F-statistics: localities north of the habitat gap in bold, sites ordered from south (top) to north (bottom); significant *P*-value following sequential Bonferroni correction marked with asterisk (*); F_{ST} WC = F_{ST} calculated according to Weir and Cockerham (1984); F_{ST} WC C = corrected F_{ST} WC values; species = U for *Steromphala umbilicalis* and P for *S. pennanti*. Where calculations gave negative F_{ST} values, these were reported as 0. Locality codes correspond with Table 2.

Localities	*P*-value	F_{ST} WC	F_{ST} WC C	Species
V & S	0.074	0.011	0.023	U
V & B	0.004	0.023	0.023	U
V & **LP**	0.046	0.007	0.007	U
V & **LO**	0.126	0.004	0.005	U
V & **C**	0.072	0.004	0.011	U
S & B	0.178	0.000	0.010	U
S & **LP**	0.629	0	0.006	U
S & **LO**	0.189	0.009	0.017	U
S & **C**	0.374	0	0.001	U
B & **LP**	0.079	0.005	0.010	U
B & **LO**	0.342	0.009	0.011	U
B & **C**	0.613	0	0.009	U
LP & **LO**	0.011	0.008	0.009	**U**
LP & **C**	0.388	0	0.005	**U**
LO & **C**	0.854	0	0.003	**U**
SW & V	<0.001*	0.066	0.052	U
SW & S	<0.001*	0.082	0.104	U
SW & B	<0.001*	0.066	0.074	U
SW & **LP**	<0.001*	0.075	0.074	U
SW & **LO**	<0.001*	0.064	0.061	U
SW & **C**	<0.001*	0.067	0.082	U
V & S	0.003*	0.014	0.016	P
V & SJ	0.005	0.028	0.035	P
V & **P**	0.124	0.023	0.017	P
V & **LO**	0.078	0.014	0.017	P
V & **H**	0.001*	0.047	0.035	P
S & SJ	<0.001*	0.052	0.071	P
S & **P**	0.001*	0.044	0.042	P
S & **LO**	<0.001*	0.043	0.043	P
S & **H**	<0.001*	0.060	0.057	P
SJ & **P**	0.474	0.000	0.012	P
SJ & **LO**	0.021	0.019	0.029	P
SJ & **H**	0.021	0.029	0.037	P
P & **LO**	0.051	0.017	0.014	P
P & **H**	0.189	0.016	0.012	P
LO & **H**	0.055	0.007	0.008	P

coincide with significant genetic differentiation in either species between the two localities immediately north or south, or when tested using AMOVA (Table 4). Analysis of the number of migrants per generation between groups north and south of the habitat gap showed that *S. pennanti* had 6.91 migrants per generation, whereas *S. umbilicalis* had 10.87 migrants per generation (excluding Swanage for *S. umbilicalis*). Using all populations of the data set (excluding Swanage for *S. umbilicalis*), the number of migrants per generation was 2.71 for *S. pennanti* and 5.43 for *S. umbilicalis*. Because the number of migrants per generation is greater than 1 for both species (and between groups), then we can discard random genetic drift as a cause of genetic differentiation among samples (Wright, 1931).

For both species, the optimum *k* was determined to be 3 based on the peak in Δk, with or without prior population information. However, GENELAND analyses estimated that *S. pennanti* constituted a single genetic unit ($k = 1$) while two different units were found in *S. umbilicalis*: the first was represented by the Swanage population, and the second by the continental populations. It is possible that STRUCTURE is less useful (Appendix S3) due to high gene flow (Waples & Gaggiotti, 2006). The DAPCs for *S. umbilicalis* showed substantial overlap of genetic similarity for most populations (Fig. 2a), but Swanage (and to a lesser extent, Vilagarcía) is a clear outlier population. By contrast, the DAPC for *S. pennanti* showed less overlap between populations (Fig. 2b). N_E and their 95% confidence interval were calculated by groups within species. The northern group of *S. pennanti* showed a N_E of 268 (95% CI = 130–3,813) while for the southern group it was 103 (95% CI = 66–197). Estimates in *S. umbilicalis* were 198 (95% CI = 114–558) in the northern group (Swanage not included) and 835 (95% CI = 198–∞) in the southern group. Additional microsatellite analyses and results including Mantel tests are available in Appendix S4.

4 | DISCUSSION

Until recently, studies infrequently accounted for the potential of differing abundance and distribution patterns to help explain the contrasting patterns of genetic structure between species. Our study joins a small, but growing literature that combines such field data with population genetics for marine species [e.g. Dawson et al. (2014)]. By integrating field data on abundance and distribution with knowledge of their respective ecologies, we are able to more clearly isolate the ecological and physical mechanisms behind differences in genetic structure of the studied species. Our results are in accordance with recent studies of rocky shore invertebrates and fish (Dawson et al., 2014; Selkoe et al., 2014), as well as butterflies and mammals (Engler et al., 2014; Kierepka et al., 2016), showing that specialist species (which are often less abundant with fragmented distributions) exhibit more genetic differentiation compared to generalist species (which are often more abundant with more continuous distributions).

Within the same region, a habitat generalist species with high-local abundance and a continuously spread distribution should yield greater reproductive output than a phenotypically similar habitat specialist congener with lower abundance and a more fragmented distribution. Assuming juvenile mobility is similar, then this will result in shorter dispersal pathways among populations and more emigrant

TABLE 4 AMOVA results for: (a) *Steromphala umbilicalis* with loci U34184 and U36148 removed from calculations as greater than 5% values missing; (b) *Steromphala pennanti* with loci HEX1, NED1 and FAM3 removed from calculations as greater than 5% values missing

Comparison between:	*df*	Sum of squares	σ	% variation	φ	*P*-value
a)						
Gap groups	2	15.417	0.088	3.251	φ_{CT} = 0.033	0.058
Localities within gap groups	4	11.313	0.008	0.300	φ_{SC} = 0.003	0.179
Samples within localities	180	469.048	2.606	96.449	φ_{ST} = 0.036	0.000
b)						
Gap groups	1	3.888	−0.008	−0.401	φ_{CT} = −0.004	0.395
Localities within gap groups	4	17.610	0.096	4.723	φ_{SC} = 0.047	0.000
Samples within localities	151	292.955	1.940	95.678	φ_{ST} = 0.043	0.000

offspring for the habitat generalist species, leading to increased gene flow and therefore reduced genetic variation between populations compared to the habitat specialist (Dawson et al., 2014). Other factors such as differences in larval dispersal could also be important [e.g. in congeneric chthamalid barnacles, Pannacciulli, Bishop, and Hawkins (1997)], but remain largely unexplored in rocky intertidal invertebrates. Here we present that the widespread and common *S. umbilicalis* shows lower genetic differentiation among localities compared to the habitat specialist, *S. pennanti*, which is characterized by low abundances and a more fragmented distribution (Figure 1; Table 3). Furthermore, *S. umbilicalis* shows a greater number of migrants between the groups north and south of the Biscayan habitat gap than *S. pennanti*. The greatest number of significant pairwise differences for *S. umbilicalis* were found between the British Isles locality of Swanage and the continental localities, while the absence of significant genetic differentiation throughout the Bay of Biscay suggests a largely panmictic population (Table 3). Thus, the English Channel (which *S. pennanti* does not cross) appears to be a larger barrier to gene flow than the Biscayan habitat gap for *S. umbilicalis*, as described in both the GENELAND and STRUCTURE analyses. In *S. pennanti*, the greatest number of significant pairwise differences are found between San Vicente de la Barquera and all other localities (Table 3). San Vicente de la Barquera (central north Iberian coast) coincides with the most fragmented part of its geographic range that we sampled (Figure 1). In addition, this region (south of the habitat gap) is associated with the lowest abundances (albeit not significant due to the small sample size) and estimates of genetic effective population size in *S. pennanti*. In contrast, this region coincides with highest abundances and estimates of genetic effective population size for *S. umbilicalis*. Below we will further discuss the biological and physical factors that may explain the differences and commonalities of genetic structure between the two species.

4.1 | Differences between species

Steromphala umbilicalis is continuously distributed within the Bay of Biscay and shows high-overall field (census population size) and genetic population sizes (i.e. effective population size). Thus, a panmictic metapopulation fits with predictions for a generalist species such as *S. umbilicalis* (Dawson et al., 2014; Engler et al., 2014; Kierepka et al., 2016). By contrast, *S. pennanti* has a fragmented geographic distribution, lower overall abundance both in field observations and genetic estimations, and is associated with fucoids largely on more sheltered shores (Bordeyne et al., 2017). Given these clear differences between the studied species, we can look more closely at locality specific patterns of genetic differentiation with the abundance and distribution data. For example, we find significant genetic differentiation between San Vicente de la Barquera (central north Iberian coast) and all other localities in *S. pennanti*. Our surveys show that *S. pennanti* and *Fucus* were largely absent within the intervening section of coastline separating St Jean de Luz (SW France) and San Vicente de la Barquera (225 km). The absence of several fucoid species in this region of the Iberian Peninsula has been attributed to its relatively high sea surface temperature (SST) (Duarte et al., 2013; Southward et al., 1995; Zardi et al., 2015). Fucoids act as a bioengineer once established (Pocklington et al., 2017; Seed & O'Connor, 1981) and are thought to facilitate the recruitment of certain gastropods, including *S. pennanti* (Bordeyne et al., 2017). Conversely, there is no such genetic differentiation between any of the mainland sampled *S. umbilicalis* populations. This may be largely attributable to the presence of *S. umbilicalis* at every sampling locality, reducing isolation among populations. *Steromphala pennanti* is also absent from two of five localities between Vilagarcia (NW Iberian coast) and San Vicente de la Barquera (Fig. 1). This may explain the significant genetic differentiation between the two localities. Interestingly, while *S. umbilicalis* shows no significant genetic difference between these two localities, there is a relatively high F_{ST} value (0.011) and Vilagarcia appears as an outlier population in the DACP (Fig. 2).

Another major difference between species is the presence of *S. umbilicalis* on the British Isles. As *Steromphala* is thought to have originated south of the British Isles (Southward et al., 1995), two possible explanations for extremely rare but successful recruitment of *S. umbilicalis* from mainland to British shores and the absence of *S. pennanti* on British shores are: (a) its greater abundance (compared with *S. pennanti*) increases the number of larvae released, thereby increasing the probability of propagules reaching Britain; or (b) *S. umbilicalis* has a longer larval duration than *S. pennanti*, allowing

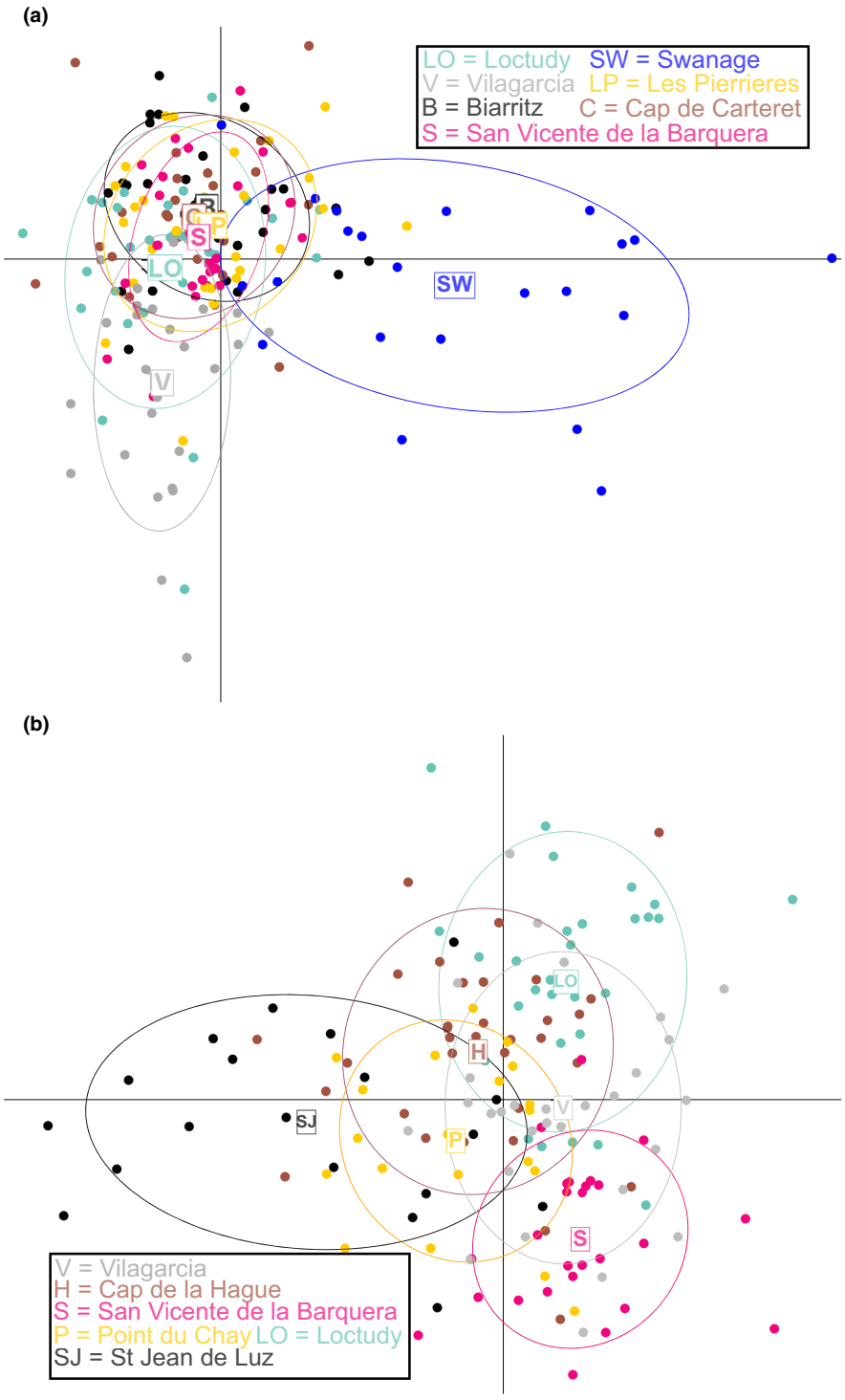

FIGURE 2 Plots of the first two axes obtained by discriminant analysis of principal components (DAPC) visualising genetic distance between samples and localities on the north-east Atlantic coasts of the Iberian Peninsula, France and the British Isles for *Seromphala umbilicalis* (a) and *S. pennanti* (b). Locality codes are indicated at the centre of each group and the ellipses represent 95% inertia.

larvae to disperse further. The significant genetic differentiation between Swanage (Britain) and all other populations (F_{ST} = 0.064 to 0.082, $p \leq 0.001$ for all pairwise comparisons), suggests diminished recruitment across the Channel for *S. umbilicalis* which was not attributable to distance (see Mantel test in Appendix S3.1). This low connectivity in *S. umbilicalis* may be attributable to the Channel acting as a habitat gap, where tidal currents dominate the transport (Pingree & Maddock, 1977). These currents are not driven in a uniform direction, unlike the long shore currents along the sandy habitat gap in south-west France (Castelle et al., 2006; Lazure, Garnier, Dumas, Herry, & Chifflet, 2009), although the currents can be of a comparable order of magnitude (Pingree & Maddock, 1977).

4.2 | Patterns associated with both species

According to our hypothesis, there should be low-genetic differentiation among localities in regions where both species are relatively abundant with continuous distributions. As such, we find that on the northern mainland coast (Figure 1) there is no significant genetic differentiation between localities in either species. This cooler region

has a sustained and well-established fucoid habitat (Southward et al., 1995; Zardi et al., 2015), which is mirrored by the relatively consistent presence and higher abundances of *S. pennanti* in this region relative to south of the habitat gap (albeit a non-significant difference due to low sample number) (Figure 1). However, we acknowledge that potential range expansion dynamics (e.g. post-glacial retreat) could also have contributed to the lack of significant population differences within the northern range of *S. pennanti* (Figure 1). Furthermore, the genetic differentiation between southern Britain (Swanage) and mainland European localities of *S. umbilicalis* may be associated with population divergence associated with glacial cycles (Marko, 2004). Future studies should explore these possibilities using a combination of mtDNA and nuclear markers (Marko & Hart, 2011).

We found that both *Steromphala* species exhibit no significant genetic differentiation between the sampled localities directly north and south of the habitat gap (F_{ST} = 0.005, p = 0.079 for *S. umbilicalis* and F_{ST} = 0.000, p = 0.474 for *S. pennanti*), which has also been found for similar scale sandy habitat gaps for some rocky intertidal species (Ayre, Minchinton, & Perrin, 2009). One possible scenario is southward transport of larvae of both species along the surface water layer of this region during late summer (Lazure et al., 2009). Larval transport spanning this gap of ~230 km would require a mean long-shore current of approximately 0.4 m/s, which would be possible considering the estimated larval duration of ≤7 days for *S. umbilicalis* (Keith et al., 2011) and, we assume, *S. pennanti*. Southward-long shore current velocities measured and modelled on this sandy coast mostly range between 0.1 m/s and 0.5 m/s, sometimes reaching 1 m/s (Castelle et al., 2006). These currents may therefore enable southward larval transport over the habitat gap during the spawning season, resulting in genetic connectivity. As such, our results suggest that currents, larval duration and spawning season are more important than absolute distances, when considering genetic differentiation across habitat gaps.

The role of coastal currents and oceanographic fronts in influencing population genetics has been assessed for several species in and around our study region, particularly around Brittany in northern France (Almeida et al., 2017; Couceiro, Robuchon, Destombe, & Valero, 2013). These and other studies highlight the interaction between currents as well as timing of propagule release/spawning (Dong et al., 2012). Spawning of *S. umbilicalis* peaks from August to November/December and October/November on the north and west coasts of the Iberian Peninsula respectively (both south of the habitat gap) (Bode, Lombas, & Anadon, 1986; Gaudèncio & Guerra, 1986; Lewis, 1986). Assuming a similar spawning season for *S. pennanti*, November and December ocean currents around the western Iberian Peninsula are wind driven from the south-west, which would enable autumn and winter dispersal of larvae north towards the centre of the Bay of Biscay (Puillat, Lazure, Jegou, Lampert, & Miller, 2004; Varela, Rosón, Herrera, Torres-López, & Fernández-Romero, 2005). These currents could drive surface water containing larvae away from the suitable habitat on the north coast of the Iberian Peninsula. The remainder of the year, the western Iberian Peninsula is dominated by a north-west oceanic swell (Zardi et al., 2015), possibly resulting in southwards transport of larvae (Ribeiro, Branco, Hawkins, & Santos, 2010). This would reduce recruitment between the north and west coast of the Iberian Peninsula, potentially contributing to Vilagarcía (NW Iberian coast) being an outlier for both species.

5 | CONCLUSIONS

Our study supports the hypothesis that, over their sympatric range, a habitat generalist with a continuous distribution and high abundances will exhibit lower-genetic differentiation compared to a congener habitat specialist with a fragmented distribution and lower abundances. These genetic differences are likely a function of contrasting population sizes and population isolation, which have long been known to influence genetic differentiation in a broad sense (Frankham, 1996; Riginos & Nachman, 2001). However, our study goes further by providing field data supporting the ecological mechanisms that likely drive the observed differences in population genetics. Compared to the largely panmictic and continuously distributed *S. umbilicalis*, higher genetic differentiation in *S. pennanti* is suggested to be caused by an association between habitat availability (fucoid presence/abundance), which is spatially fragmented on the N. Iberian Peninsula where genetic differentiation is highest in this species. Our research broadly supports recent studies that suggest how distribution and abundance data can help the interpretation of comparative population genetic studies (Dawson et al., 2014; Engler et al., 2014; Kierepka et al., 2016). We therefore recommend incorporating a measure of abundance, distribution, and knowledge of the ecology and life history of species in population genetics studies. This can be combined with information on the spatial distribution of habitat availability and environmental variables to inform subsequent interpretation, particularly through targeted sampling of sympatric congeners.

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BIOSKETCH

Edward Wort is interested in the biogeography of rocky intertidal species in the Bay of Biscay. This work represents a component of his SPITFIRE PhD at University of Southampton and the Natural History Museum on the effect of habitat and oceanography on species ecology over historic timescales.

Author contributions: E.J.G.W., S.J.H., M.R. and P.B.F. conceived the ideas; E.J.G.W. and P.B.F. carried out fieldwork and led the writing; E.J.G.W., M.A.C., A.P., L.H. and S.T.W. obtained and analysed the genetic data.

DATA ACCESSIBILITY

The *S. umbilicalis* and *S. pennanti* microsatellite and abundance data are available as files on the Dryad Digital Repository: (doi:10.5061/dryad.t4kv200) https://emea01.safelinks.protection.outlook.com/?url=https%3A%2F%2Fdoi.org%2F10.5061%2Fdryad.t4kv200&data=01%7C01%7Cew6 g09%40soton.ac.uk%7C53bd55f6813c4f626e8a08d649ab2f18%7C4a5378f929f44d3ebe89669d03ada9d8%7C1&sdata=%2FFR4sHVZ8wl8Mh2%2FDW46pUWB3IDZbAOAbkuZVNVGf%2BU%3D&reserved=0.

SUPPORTING INFORMATION

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

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