Seascape habitat patchiness and hydrodynamics explain genetic structuring of kelp populations

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ABSTRACT: Macroalgae underpin most temperate inshore ecosystems, but increasing macroalgal loss, fragmentation and range contractions are eroding connectivity among populations. Understanding loss, and predicting the likelihood of recovery, is dependent on knowledge of population connectivity and how it is mediated by variability in local seascapes. Although many studies of marine macroalgal connectivity have focussed on influences of geographic distance on genetic structure, the contribution of intervening habitat is rarely considered. We tested the extent to which geographic separation, intervening suitable habitat (reef versus sand and open water) and local hydrodynamics (inferred from particle dispersal models) explained structuring of genetic variation at microsatellite loci in the habitat forming macroalga *Lessonia corrugata*. Genetic structuring was best explained by the availability of suitable intervening habitat (rocky reef) rather than by geographic separation, although biologically realistic estimates of dispersal probability also became important at smaller spatial scales. Our results indicate that ecological separation can be more influential than geographic distance on population genetic structuring, and this should be considered during the assessment of connectivity and gene flow in marine species.

KEY WORDS: *Lessonia corrugata* · Dispersal · Macroalgae · Seascape genetics · Microsatellites

INTRODUCTION

Population connectivity is an important aspect of evolutionary, ecological and conservation biology, as it controls the exchange of genetic material among populations. Connectivity maintains genetic variability within populations, potentially conferring population resilience through the maintenance of genetic diversity and hence the ability to respond to change (Reusch et al. 2005, Wernberg et al. in press). Population connectivity allows individuals to recolonise or influence the growth of populations in areas that have previously been negatively affected by anthropogenic disturbance and environmental stressors (Pulliam 1988). Furthermore, connectivity and gene flow can reduce inbreeding depression in a popula-

tion (Saccheri et al. 1998), which may otherwise increase the probability of population extinction (Castorani et al. 2015). However, at the other extreme, high levels of population connectivity will synchronise responses to perturbation (Heino et al. 1997) and reduce among-population distinctiveness, potentially inhibiting local adaptation (Almany et al. 2009). Therefore, knowledge of population connectivity, and the factors that influence it, is important for understanding species loss and population response and recovery to environmental change.

Despite the importance of knowledge regarding population connectivity, studies on temperate marine macroalgal population connectivity are rare and remain a factor that is infrequently integrated into conservation planning (Almany et al. 2009, Magris et al.

2014, Coleman et al. 2017) Furthermore, most effort has gone into testing the effect of life history and raw geographic separation on connectivity (e.g. Coleman & Brawley 2005, Durrant et al. 2014), although recent studies have introduced more refined measures of separation, such as those from particle dispersal models (e.g. Coleman et al. 2011b, Pujolar et al. 2013). Few macroalgal studies have examined the importance of intervening habitat on connectivity, probably due to the greater difficulty in obtaining contextual 'seascape genetics' data (but see Ierodiaconou et al. 2007, Alberto et al. 2010, Johansson et al. 2015), although it has been more commonly assessed for other marine taxa, such as corals (e.g. Davies et al. 2015, Van Wynsberge et al. 2017). Inferences from seascape genetics studies, where the influences of environmental variables such as intervening habitat and sea surface temperature on population genetic structuring are assessed (Johansson et al. 2008, Selkoe et al. 2008, Alberto et al. 2010), are necessary to identify the most important variables influencing population connectivity.

Macroalgae are considered foundation species that provide habitat for a diversity of marine taxa of both economic and ecological significance (Dayton 1985). However, with increasing anthropogenic disturbance, climate change and invasive species, the abundances and geographic ranges of some macroalgal species have decreased, posing a threat to temperate marine biodiversity (Wernberg et al. 2011, Vergés et al. 2014). Recent research has documented the importance of connectivity for population dynamics in marine macroalgae, particularly among small patches (Castorani et al. 2015). Likewise, reduced fitness has been observed under elevated inbreeding (Raimondi et al. 2004). Previous studies have determined how well existing networks of macroalgal populations maintain genetic connectivity (e.g. Coleman et al. 2011a), and the impact of geographic separation on dispersal (e.g. Coleman et al. 2009, Durrant et al. 2014). However, only a handful of studies have used seascape genetics to better understand the drivers of macroalgal population genetic structuring (see Alberto et al. 2011, Brennan et al. 2014, Johansson et al. 2015). Given that the distribution of macroalgal beds has been observed to influence connectivity of other taxa (Selkoe et al. 2010), knowledge of the genetic structuring of macroalgal species themselves has great importance for the conservation of biodiversity.

Here, we assessed the extent to which geographic separation, intervening suitable habitat, and hydrodynamics explain population genetic connectivity of the macroalga *Lessonia corrugata* Lucas. *L. corru-*

gata is an important habitat-forming component of nearshore ecosystems in Tasmania, and is one of only 3 kelp species routinely quantified during nearshore surveys within the temperate biodiversity hotspot of southern Australia (Bolton 1994, Wernberg et al. 2010).

MATERIALS AND METHODS

Study species

Lessonia corrugata is a habitat-forming laminarian kelp that occupies shallow subtidal rocky shorelines (< 5 m) with moderate wave exposure. This species is continuously distributed in such areas through space and time (Edgar 1984). *Lessonia* has a typical laminarian life history, with gene flow mediated via sperm (Reed et al. 1992) and spores (Santelices 1990), at putative relative dispersal scales of millimetres and metres, respectively. However, as *Lessonia* sporophytes are negatively buoyant, it has been suggested that they have limited dispersal capabilities through rafting (Dayton 1985, Santelices 1990), and observations from other laminarians have revealed significant genetic structuring at small spatial scales (e.g. Valero et al. 2011, Robuchon et al. 2014) relative to macroalgal species with floating structures that confer the ability to raft (e.g. Coleman & Kelaher 2009, Coleman et al. 2011a).

Study site

To address the effects of external factors on gene flow, it is important to choose a study scale between the extremes at which (1) all populations are genetically homogeneous because gene flow regularly exceeds the spatial scale of the study, even with heterogeneity of gene flow with habitat, and (2) all populations are completely isolated from one another because gene flow is not experienced across these distances, even when connected by habitats most amenable to dispersal. Given expectations of limited dispersal capabilities in *L. corrugata* based on studies of related taxa, we conducted our study at spatial scales of 0.3–10 km. Conclusions applicable at this scale should also be relevant to more dispersive taxa at larger spatial scales.

The lower Derwent Estuary in southern Tasmania provides an ideal opportunity to assess potential factors influencing gene flow of *L. corrugata*. The shorelines of the lower estuary are characterised by

heterogeneous distributions of suitable habitat, i.e. rocky reef, disrupted by intervening stretches of unsuitable habitat comprising sand, along with deep water between adjacent shores (Fig. 1). In the lower reaches, the estuary is fully marine. A high-resolution particle dispersal model also exists for this region (Condie et al. 2005; www.csiro.au/connie2/), which considers factors such as tidal flux, wind forcing, seasonality and depth to generate an informed set of probability statistics for particles dispersing between locations. Additionally, because tides dominate particle dispersal in the estuary on short time scales (i.e. hours to days), any influence they have on individual dispersal will be accurately modelled (Whitehead et al. 2010).

Sample collection, DNA extraction and microsatellite genotyping

L. corrugata thalli were sampled from 14 shallow subtidal locations in the Derwent Estuary, Tasmania, in May 2014 (Fig. 1 and see Table S1 in the Supplement at www.int-res.com/articles/suppl/m587p081_supp.pdf). At most locations, approximately 15 individuals were collected in each of 3 clusters that were separated by a minimum of 30 m (approximately 45 individuals in total per location). Within each cluster, sampled individuals were spread over an area of approximately 10 m radius. Genomic DNA was isolated from silica gel dried tissue, and 7 polymorphic microsatellite loci were amplified and scored for 562 individuals over the 14 sampling locations following Durrant et al. (2015b).

Test of assumptions and descriptive genetic analysis

For each locus, we tested for evidence of null alleles and scoring errors due to PCR stuttering and large allele dropout using Microchecker 2.2.3 (Van Oosterhout et al. 2004). Observed (H_o) and expected (H_e) heterozygosities were calculated using GenAlEx (Peakall & Smouse 2012). Conformance of loci to

Hardy-Weinberg equilibrium and linkage disequilibrium were assessed using Genepop (Rousset 2008), with significance adjusted for multiple tests using the false discovery rate (FDR: Benjamini & Yekutieli 2001). Inbreeding coefficients (F_{IS}) were calculated using Genodive (Meirmans & Van Tienderen 2004). Tests for clones within populations were also performed using Genodive, with pairwise distances calculated under the stepwise mutation model, using a clone threshold of 1 step. Tests of clonal structure (the probability that the observed clonal diversity could be expected from random mating without clonal
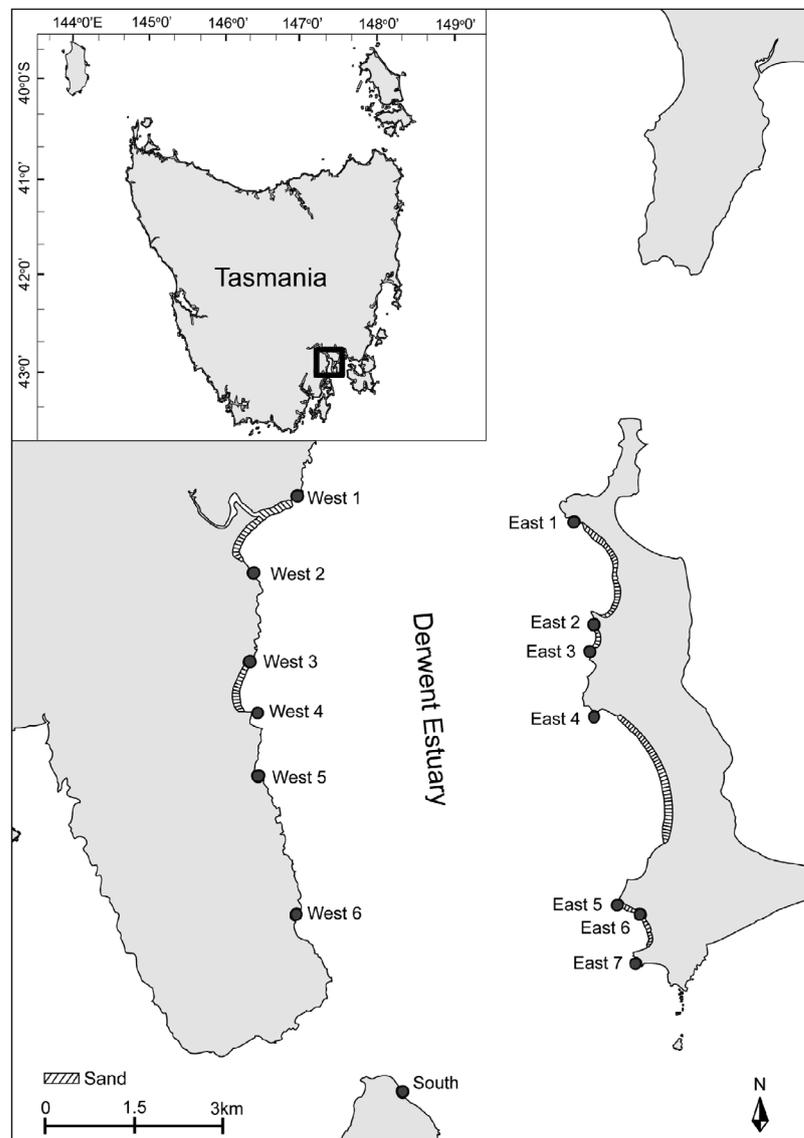

Fig. 1. Sampling locations of *Lessonia corrugata* in the Derwent Estuary, Tasmania, Australia. Shorelines between sampling sites are rocky reef except where otherwise indicated. Geographical coordinates for each site are provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m587p081_supp.pdf

reproduction) were also performed using Nei's (1987) corrected genetic diversity, with randomisation of alleles over individuals within populations.

Tests of population structure

The contribution of spatial autocorrelation to total genetic variation was assessed by redundancy analysis (RDA), with the geographic coordinates of sample sites as the independent variables, and allele frequencies as the dependent variables. This method is favoured over Mantel tests, and was performed following the methodology of Meirmans (2015). Pairwise F_{ST} (Excoffier et al. 1992) values for populations and exact tests of allele frequency homogeneity were calculated using Genodive. Where null alleles were invoked, pairwise F_{ST} values were also corrected using the ENA method of Chapuis & Estoup (2007) and the software FreeNA. Linearised F_{ST} ($F_{ST}/1-F_{ST}$) and particle dispersal probabilities (see below) among sites were also visualised via non-metric multidimensional scaling using R (R Development Core Team 2014). As this analysis accepts dissimilarity matrices only, and cannot accept zeros in matrices, particle dispersal probabilities were converted to (1 − probability). G''_{ST} (Meirmans & Hedrick 2011) was also calculated using Genodive to ensure forward comparability with other studies employing markers with different diversity.

Population structure was assessed under Bayesian clustering with STRUCTURE 2.3.4 (Pritchard et al. 2000) and 100 000 Markov chain steps under the admixture model. The number of potential clusters (K) ranged from 1 to 14, with 20 replicate analyses for each K. Optimal number of clusters was guided using ΔK (Evanno et al. 2005) in Structure Harvester (Earl & vonHoldt 2012), and clumpp (Jakobsson & Rosenberg 2007) was used to collate all runs produced by STRUCTURE for a given value of K. Results were then visualised using Distruct (Rosenberg 2004).

Quantifying intervening habitat

The proportion of habitats intervening sampling locations and the minimum marine distance between sites were quantified along 1-dimensional vectors using ArcGIS v10.3 and habitat data from Seamap Tasmania (http://seamap.imas.utas.edu.au/) and Google Earth 7.1. Reef was quantified as the length of coast with shallow subtidal (<5 m) reef habitat where the line of minimum marine distance between sites was no more than 500 m offshore. Similarly, open water was quantified as the length of the line of minimum marine distance between sites that was more than 500 m offshore. Intervening habitat was quantified as proportions instead of absolute distances to avoid correlation with minimum marine distance between sites, which was also employed as a predictor. When calculating proportions, total distance between sites comprised reef and open water, as quantified above, plus sandy shore, which was quantified in the same manner as reef but for sections of coast lacking reef within 5 m of the sea surface.

Particle dispersal modelling

The probability of particle dispersal between sites was determined with a pre-release of the Aus-Connie2 model for the Derwent Estuary (Condie et al. 2005). Propagules were released at each sampling location at a depth of 2 m, with a dispersal period of 2 d. Individuals are frequently observed at these depths within the estuary, and dispersal period was based on results from the literature that suggest macroalgal spores, including *Lessonia*, remain viable and buoyant for a matter of hours to days before settlement (Santelices 1990, Tellier et al. 2009). We then determined the probability of each location acting as a source for all other locations. At the time of analysis, this model had a resolution of 500 m^2 and a data range from 18 January to 31 March 2010. Runs were only able to function for a maximum period of 19 d, and therefore we ran 3 non-overlapping 19 d intervals during this period, and summed the final probabilities of particle arrival after 2 d of drifting. Cells of 500 m^2 representing sample locations were chosen based on their proximity to the sample locations and the requirement that they did not overlap any land. Given the short dispersal times of spores (Santelices 1990, Reed et al. 1992), it is likely that tidal fluxes mostly influence spore dispersal, which does not differ considerably between seasons. Furthermore, as Aus-Connie releases particles every day the model is run, particles will experience different tidal cycles (ebb, flow, slack water) at the time of release across our modelling period (57 d). The estuary at the study sites is also greater than 4 km wide and purely marine, such that strong rainfall events not captured by the modelling period are unlikely to influence particle dispersal. Therefore, the 57 d period was considered sufficient to capture potential influences of particle dispersal on genetic structure. Dispersal of propagules between some locations was bidirec-

tional; in this situation, the total probability of dispersal between 2 locations was used in subsequent analyses. We also tested the effects of a 3 d dispersal period, but the results were highly correlated with those assuming 2 d dispersal (r = 0.977)

Seascape genetic analysis

We used a linear mixed effects (LME) modelling approach estimated via maximum likelihood population effects (Clarke et al. 2002) in our seascape genetic analysis. This method has provided accurate inferences about influential habitat types and population genetic variation (Van Strien et al. 2012), and was employed as an alternative to other landscape genetics methods that have known limitations when assessing multiple explanatory variables and multiple tests simultaneously (Balkenhol et al. 2009, Legendre & Fortin 2010). The proportion of reef and open water, minimum marine distance, and the probability of particle dispersal were fixed effects, and the non-independence of pairwise distances was the random effect. Predictor variables were centred prior to analysis (Van Strien et al. 2012). We used R^2_β (Edwards et al. 2008) rather than traditional R^2 values to provide a more realistic measure of model fit, as it compensates for the number of predictor variables included in a model. The use of AIC values is inappropriate for LME model selection in landscape genetics, as these values can be influenced by the non-independence of predictor variables (Clarke et al. 2002), and therefore R^2_β has been used to compare models (Van Strien et al. 2012). Analyses were performed using the lme4 and pbkrtest packages in R.

While methods exist for estimating recent gene flow that lack population genetic equilibrium assumptions and may not be influenced by differences in effective population size (i.e. do not rely on F_{ST}), when such methods were trialled on this dataset they were either inappropriate with respect to assumptions regarding levels of gene flow and sample size (Bayesass; Meirmans 2014) or failed to converge (BIMr; Faubet & Gaggiotti 2008). Therefore, linearised F_{ST} was employed as the response variable. This metric approaches equilibrium more rapidly than others (Epps & Keyghobadi 2015).

RESULTS

Mean number of alleles per locus at a location ranged from 2.00–2.71, and observed and expected heterozygosities ranged from 0.152–0.487 (mean 0.379) and 0.145–0.483 (mean 0.397), respectively (Table 1). Despite this low level of variation at the molecular level, significant differences in allele frequencies were detected at fine geographic scales (see below). While identical multilocus genotypes were observed among individuals within some populations, we could not reject the possibility that this was the product of random mating in the absence of clonal reproduction in all populations (smallest observed population p = 0.026; FDR threshold for 14 populations = 0.010), with the exception of site East 7 (p = 0.001; see Fig. 1 for site locations); the latter also became non-significant following the removal of a single individual lacking data at the majority of loci (p = 0.102). Most loci were within Hardy-Weinberg equilibrium, with the exception of *Lco102* at West 3 and *Lco217* at South, West 2 and East 7 (p < 0.010), with no evidence of linkage disequilibrium (smallest p = 0.037, FDR threshold for 21 locus comparisons p = 0.014). However, F_{IS} values were significantly positive at some locations, consistent with null alleles or the Wahlund effect (Table 1). Microchecker suggested null alleles were present at loci *Lco102*, *Lco217*, *Lco146*, *Lco199* and *Lco154*; however, inferences were inconsistent across populations, and all loci were retained in subsequent analyses with and without ENA correction for the presence of null alleles. The correlation coefficient of null allele corrected and uncorrected F_{ST} matrices was 0.999. Null alleles were typically only at a high frequency (>0.10) at a single population for a given locus (see Table S2 in the Supplement).

Table 1. Genetic variation of 14 populations of *Lessonia corrugata*. n = number of individuals genotyped, N_A = mean ± SE number of alleles per locus, H_o = observed heterozygosity, H_e = expected heterozygosity, and F_{IS} = multi-locus inbreeding coefficient. Significance is indicated as *p < 0.01 and **p < 0.005

Site	n	N_A	H_o	H_e	F_{IS}
West 1	35	2.57 ± 0.429	0.435	0.431	0.006
West 2	42	2.43 ± 0.297	0.447	0.453	0.024
West 3	40	2.57 ± 0.297	0.428	0.468	0.097*
West 4	45	2.57 ± 0.429	0.437	0.454	0.047
West 5	47	2.71 ± 0.421	0.455	0.476	0.062
West 6	45	2.57 ± 0.429	0.461	0.473	0.037
East 1	43	2.57 ± 0.297	0.368	0.365	0.004
East 2	43	2.29 ± 0.184	0.280	0.350	0.212**
East 3	44	2.00 ± 0.309	0.152	0.145	−0.042
East 4	37	2.14 ± 0.261	0.207	0.233	0.124
East 5	41	2.57 ± 0.297	0.327	0.351	0.081
East 6	15	2.14 ± 0.143	0.382	0.397	0.072
East 7	41	2.43 ± 0.202	0.450	0.474	0.063
South	45	2.71 ± 0.421	0.487	0.483	0.004**

The vast majority of localities could be distinguished genetically (Table S2), even at distances of as little as 380 m (i.e. East 5–East 6). The RDA showed that 34.45 % of among-population variation was spatially constrained (p = 0.001), which equates to an F_{ST} of 0.056, relative to the total F_{ST} (Nei 1987) of 0.164. G''_{ST} was 0.274 (p < 0.001). Pairwise F_{ST} estimates between locations on the western shoreline were smaller in comparison to those on the eastern shoreline (Fig. 2, Table S3). All western sites also displayed lower pairwise F_{ST} values with the southern site compared to pairwise comparisons between eastern sites and the southern site (Fig. 2, Table S3). STRUCTURE showed that the data were best explained under a K value of 2, whereby all western and southern individuals were predominantly assigned to the same group, separate from eastern individuals (Fig. 3 and see Fig. S1 in the Supplement). When $K = 3$, further structuring can be observed in locations situated along the eastern shoreline (Fig. S2).

Particle dispersal simulations indicated no dispersal between eastern and western shorelines (Table S4, Fig. S3) when a dispersal time of 2 d was used. All locations situated along the western shoreline acted as a source for all other western locations, albeit at low probabilities. Dispersal between locations on the eastern shoreline appeared to be more restricted than that of western locations (Fig. 2; Table S4, Fig. S3). Greater dispersal was observed between western populations and the southern location, compared to eastern locations and the southern location (Fig. 2; Table S4, Fig. S3).
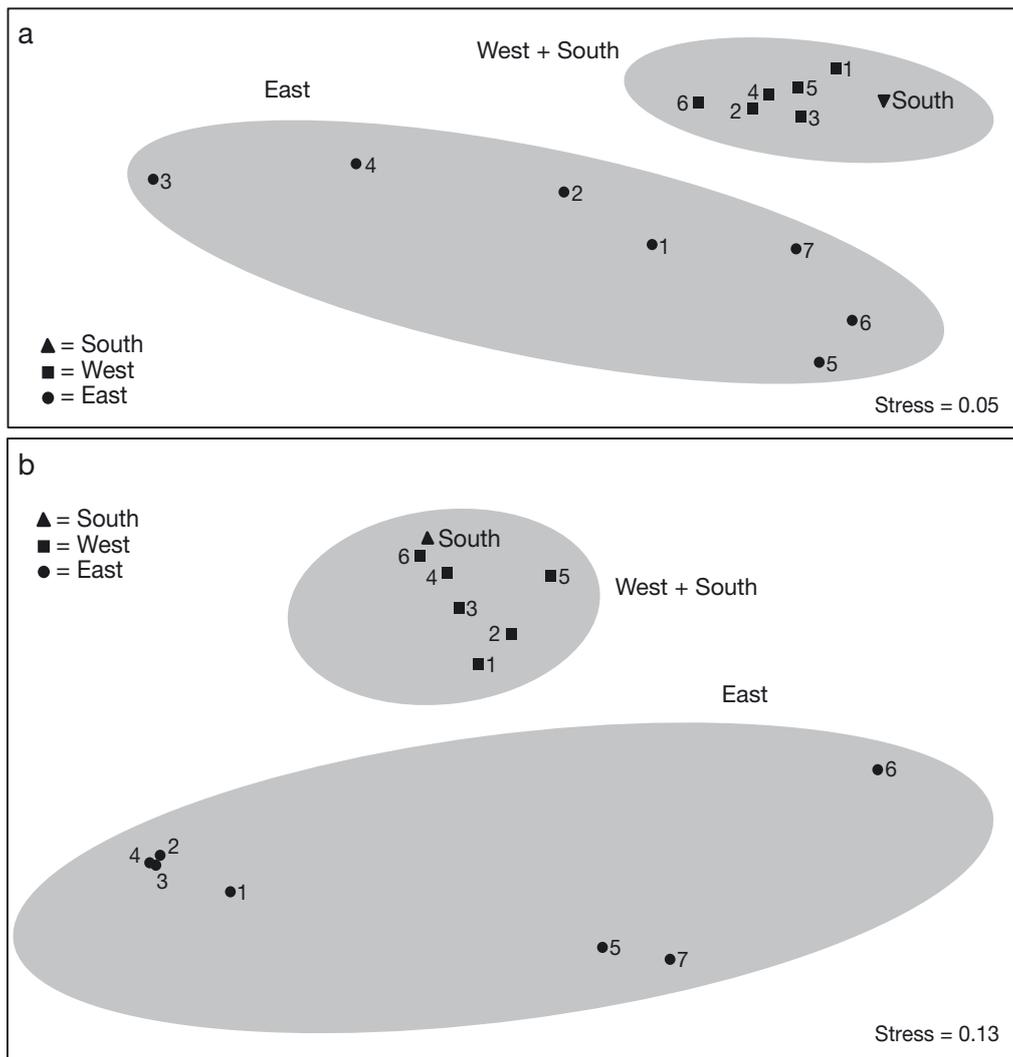

Fig. 2. Non-metric multidimensional scaling plots of *Lessonia corrugata* using (a) an F_{ST} matrix and (b) a particle dispersal matrix. Groupings show distinction between eastern and western shorelines, with the southern sampling location grouping with the western shore locations. Numbers correspond to site locations in Fig. 1
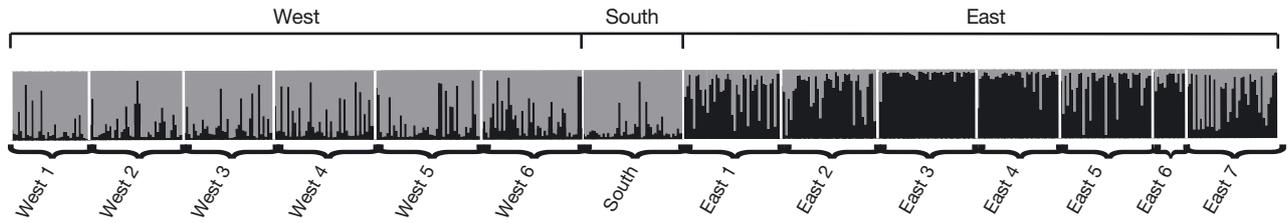
Fig. 3. Results from STRUCTURE analysis, showing *K* = 2 clusters. Each bar represents an individual *Lessonia corrugata* within a location, with each shade representing the co-ancestry coefficient of that individual belonging to a particular cluster

Correlation coefficients between predictor variables were all between −0.47 and 0.31. All variables were significant predictors of F_{ST} when analysed individually, or in combination with other predictors (Table 2). Analysis of pairwise F_{ST} corrected for the presence of null alleles produced almost identical results (Table 2). The proportion of reef between sites consistently had a negative and significant relationship with F_{ST}, and fit of models containing this variable was high relative to those lacking reef. Although minimum distance between sites and probability of particle dispersal had significant relationships with F_{ST}, positive and negative, respectively, the addition of reef to the other predictors resulted in a 78% increase in the proportion of explained variance (R^2_{β}). Therefore, the proportion of reef habitat between sites appears to best explain genetic divergence among all sites. Given that strong genetic structure exists between eastern and western shores, and these are isolated by both unsuitable habi-

tat (open water) and currents, we repeated the analyses using only genetic divergences within shores (grouping south and western sites, given their hydrodynamic connectivity). The results were qualitatively similar with respect to the significance and direction of relationships between predictors and F_{ST} (Table 2). Proportion of reef still made the largest contribution to explained variance (25%), but particle dispersal probability was similarly important (22%). The relationships of each of the predictors to linearised F_{ST} are shown in Fig. S4.

DISCUSSION

Habitat and hydrodynamics explain genetic structure

While geographic distance between populations of marine species is an important predictor of pop-

Table 2. Results from linear mixed effects models for the effects of the proportion of suitable habitat (reef) and minimum distance between sites, as well as the probability of particle dispersal, with respect to genetic distance (linearised F_{ST}) in *Lessonia corrugata*. Values in parentheses reflect results from data corrected for the presence of null alleles. R^2_{β} (Edwards et al. 2008) was used, which provides a more realistic measure of model fit (than R^2), as it compensates for the number of predictor variables included in the model. '−' indicates that this variable was excluded from the model. Significance is indicated as *p < 0.05 and **p < 0.01

Model	R^2_{β}	Proportion of reef	Minimum distance	Particle dispersal probability
All site comparisons				
Full	0.438 (0.428)	−0.088** (−0.081**)	0.007** (0.007**)	−0.300** (−0.292**)
Model 1	0.426 (0.417)	−0.113** (−0.106**)	0.010** (0.009**)	−
Model 2	0.443 (0.433)	−0.110** (−0.103**)	−	−0.328** (−0.319**)
Model 3	0.097 (0.094)	−	0.013** (0.012**)	−0.364** (−0.352**)
Model 4	0.435 (0.426)	−0.148** (−0.140**)	−	−
Model 5	0.090 (0.088)	−	0.018** (0.017**)	−
Model 6	0.030 (0.029)	−	−	−0.466** (−0.448**)
Comparisons only within shores				
Full	0.255 (0.241)	−0.131** (−0.134**)	0.010** (0.010**)	−0.399** (−0.391**)
Model 1	0.198 (0.193)	−0.226** (−0.228**)	0.019** (0.019**)	−
Model 2	0.246 (0.232)	−0.081 (−0.082)	−	−0.473** (−0.467**)
Model 3	0.190 (0.171)	−	0.006 (0.006)	−0.458** (−0.452**)
Model 4	0.144 (0.142)	−0.164* (−0.164*)	−	−
Model 5	0.036 (0.033)	−	0.014* (0.014*)	−
Model 6	0.199 (0.180)	−	−	−0.495** (−0.489**)

ulation genetic structure (e.g. Durrant et al. 2014, Wright et al. 2015), and was significant herein, the most important finding of this study was that intervening habitat (proportion of suitable habitat, i.e. reef) and probability of particle dispersal best explained variation in F_{ST}. Habitat was the most important at the scale of the entire study, whereas particle dispersal probability was similarly important during comparisons within shores, where fewer site comparisons had a high proportion of unsuitable intervening habitat.

The negative sign of the correlation coefficient for F_{ST} and reef (and conversely, positive correlation with unsuitable habitat) is consistent with expectations for *Lessonia corrugata* given its obligate association with rocky reef, and likelihood of greater gene flow between sites connected by suitable habitat. The importance of reef is also consistent with observations for other laminarians in which high meiospore densities are required for male and female gametophytes to recruit in sufficient proximity for subsequent egg fertilization and sporophyte development (Reed 1990). Therefore, genes will disperse more readily through regions where adults (and hence spores) are at higher densities. Although the largest genetic divergence we observed was associated with comparisons between sites on opposing shores (east, west), which concomitantly had minimal reef between them, these divergences are unlikely to reflect a deeper geological history of population isolation, as phylogeographic structuring is lacking in this species throughout southeast Tasmania (Durrant et al. 2015a).

Other studies have indicated a more important relationship between intervening habitat and genetic structure than raw geographic distance. For example, Riginos & Nachman (2001) found that genetic structure in the obligate rocky reef fish *Axoclinus nigricaudus* increased when sand dominated intervening habitat in comparison to rocky reef. Moreover, studies of several marine invertebrate species indicate that the influence of habitat on genetic structure is affected by whether a species is a habitat generalist or specialist, and that habitat generalists are more likely to traverse potential barriers to gene flow than habitat specialists (Ayre et al. 2009). This relationship between habitat and genetic structure has also been observed in terrestrial studies (e.g. Hokit et al. 2010, Zhu et al. 2016). However, alternative situations may exist where connectivity may actually be greater across regions comprising unsuitable habitat, as a species may continue to move across these regions rather than settle and unsuccessfully recruit (e.g. Spear et al. 2010, Simpson et al. 2014).

Our observation that particle dispersal probability explained genetic divergence among populations during within-shore comparisons is consistent with previous studies on other macroalgae using similar methods (Alberto et al. 2011, Coleman 2013, Brennan et al. 2014). While other macroalgal studies to date have focussed on species with well-developed rafting capabilities, the Aus-Connie model appeared to encapsulate processes important for spore dispersal in *L. corrugata*, and indicates that success of such approaches does not necessarily relate to the presence of rafting sporophytes in a species' life history. Similarly, studies of other taxa where dispersal is mediated by passive, microscopic propagules have revealed the ability of particle dispersal models to predict population genetic structuring (e.g. Davies et al. 2015). The comparatively small contribution of particle dispersal probability to the explained variance in genetic structuring among all sites could reflect occasional gene flow events between shores that were not encapsulated within the time interval of the particle dispersal model.

Unsuitable habitat

The unsuitable habitat between sites in this study comprised regions of deep open water (deeper than the euphotic zone) and sandy shorelines. Deep open water restricts dispersal in marine species such as corals (Ayre & Hughes 2004), fish (Riginos & Nachman 2001) and gastropods (Hoffman et al. 2011). Open water might be expected to be a greater inhibitor of gene flow given that sandy shorelines may at least retain dispersing individuals within a depth stratum more suitable for colonisation on a rocky shore, and movement along a sandy shore should generally result in the encountering of a rocky shore more quickly than movement in open water. The proportions of different habitat types between sites is commonly strongly correlated, owing to the constraint that they all sum to 1.0, and this precluded their segregation and analysis in this study. However, the divergence of the south site from the west sites, relative to that among west sites, suggests that open water is not an appreciably greater inhibitor of gene flow than sandy shore (Fig. 2).

Fine-scale structuring in *L. corrugata*

The fine geographic scales of genetic structuring in *L. corrugata* (<800 m) are consistent with prior sug-

gestions that *Lessonia* species have limited dispersal capabilities (Dayton 1985, Santelices 1990), and with observations from other laminarian kelps (e.g. Robuchon et al. 2014). There were also some significantly positive F_{IS} values at sample sites that may relate to the Wahlund effect, although at the majority of sites local mixing or incompatibility mechanisms appeared sufficient to maintain genotype frequencies consistent with random mating. Another laminarian that shows particularly fine (down to 5 m) spatial genetic structuring is the shallow subtidal *Postelsia palmaeformis*, an observation explained by poor dispersal capabilities of both spores and rafting adult plants (lacking floatation structures) (Kusumo et al. 2006). Similarly, *L. corrugata* is unlikely to disperse widely as drifting adults, and produces spores with poor dispersal capabilities (Norton 1992).

Intraspecific density-dependent barrier effects (competitive exclusion of potential immigrants) could also inhibit gene flow in this species, given their high densities and likely competition for substrate, as has been suggested for populations of other algae that were oceanographically connected (Neiva et al. 2012). Although *L. corrugata* shows limited dispersal in comparison to species whose life history characteristics appear more amenable to long distance dispersal (e.g. *Macrocystis pyrifera*; Dayton 1985), this difference in genetic structuring could also reflect differences in habitat (e.g. depth) rather than species life history or competition. Analyses of additional macroalgal species from a range of habitats and life histories are required to establish whether this is a general trend (e.g. Tellier et al. 2009, Coleman et al. 2011a, Robuchon et al. 2014).

CONCLUSIONS

Our study contributes important knowledge on the factors influencing population genetic structuring in the marine environment. Principally, we found that population genetic structuring was best explained by the amount of intervening habitat (suitable/unsuitable) between sites and the probability of particle dispersal, rather than raw geographic distances. A larger proportion of variance could also be explained by using an alternative method to represent effects of habitat on gene flow between sites, such as resistance surfaces (McRae & Beier 2007). While our results were observed at fine spatial scales (<10 km), they may be important at larger spatial scales for species with higher dispersal capabilities, as has already been observed in other macroalgae (e.g. Alberto et

al. 2010), and the possible scaling of genetic structure with dispersal capability deserves investigation. The influence of intervening habitat and particle dispersal probability should be considered when attempting to understand genetic structure, and likewise during the consideration of population connectivity based on spatial data, such as during the formulation of recommendations for marine reserve spacing (Sala et al. 2002, Shanks et al. 2003, Palumbi 2004, Almany et al. 2009, Magris et al. 2014, Coleman et al. 2017). Further research is needed to improve understanding of the relevant life history characteristics of marine macroalgae that influence dispersal capacity and their interaction with habitat, and these can be readily assessed through detailed seascape genetic analyses of new and existing population genetic datasets.

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