


RESEARCH ARTICLE

Contrasting patterns of population structure in two habitat-forming kelp species in southeastern Australia

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Abstract

The distribution and connectivity of species around the globe are changing at a rapid pace. Increasing sea temperatures are a driving factor of changes in temperate macroalgal distributions. Southeast Australia is considered a global ocean-warming hotspot, where macroalgal populations are predicted to decline significantly by 2100. We used genotyping by sequencing and Lagrangian particle modeling to compare the genetic population structure and connectivity of two habitat-forming macroalgae, *Macrocystis pyrifera* and *Durvillaea potatorum*, in southeastern Australia. Both species showed regional population structures, although this was greatest in *D. potatorum*, as which populations showed greater dissimilarity than in *M. pyrifera*. Particle modeling suggested that self-recruitment and connectivity among populations were highest in northeast Tasmania for both species, with particles often stranding along the nearby coast. Intriguingly, the southernmost *M. pyrifera* population in Tasmania shared more recent ancestry with a mainland Australia population. Although uncommon, simulations indicated that it is possible for rafts of *M. pyrifera* from mainland Australia to reach far-southern Tasmania. Hindcast simulations indicated those rafts are likely to come from mainland Australia via the Zeehan Current and along the western Tasmanian coast; unsampled western Tasmanian populations might therefore also share close ancestry with western mainland populations. With genetically distinct populations and low connectivity among areas, southeastern Australian kelp populations are vulnerable to losses of genetic diversity. This study provides insights into contemporary population structure and connectivity processes in two kelp species that form important habitats for biodiversity and fisheries on the Great Southern Reef and which are both undergoing range contractions with rapid environmental change.

KEYWORDS

connectivity, dispersal, genetic diversity, genetic isolation, kelp, particle modeling

Abbreviations: bp, base pairs; EAC, East Australian Current; GBS, genotyping by sequencing; GSR, Great Southern Reef; PCA, principal component analysis; PCR, polymerase chain reaction; SNP, single nucleotide polymorphism.

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INTRODUCTION

Climate change is driving changes in species distributions around the globe, altering ecosystem function and impacting human well-being (Pecl et al., 2017; Zarnetske et al., 2012). As the environment changes, species must adapt and move, or they will become extinct (Berg et al., 2010; Román-Palacios & Wiens, 2020). At the leading edges of species distributions, populations are advancing into new areas and could face new challenges; similarly, populations at the retreating edges, where species ranges are contracting, face deteriorating habitat suitability (Hampe & Petit, 2005). Range changes can have significant genetic and evolutionary consequences for populations, such as reduced genetic diversity and stronger population differentiation (Arenas et al., 2012). Species at the retreating edge are often occupying environmental conditions near their tolerance limits, and therefore, changes in environmental conditions are more likely to result in a loss of individuals (Araújo et al., 2013; Britton et al., 2024; Clark et al., 2020). For dominant autogenic ecosystem-engineers, that is, species that alter the environment and resources creating habitat for other species (Jones et al., 1996, 1997), range shifts can have cascading effects on associated species. These range shifts can cause profound ecosystem changes such as an ecosystem shift from kelp forest to coralline turf or to smaller canopy species (Airoldi et al., 2008; Montie & Thomsen, 2023). Moreover, this can result in the loss of genetic diversity as lineages near the retreating edges are lost (Nicastro et al., 2013). High-resolution information on genetic population structure and connectivity are key for understanding changes in species ranges (Peluso et al., 2018; Ramos et al., 2018) and for focusing conservation management (Forbes et al., 2024; Layton & Johnson, 2021).

Southeast Australia is an ocean-warming hotspot, warming faster than 90% of the global ocean (Hobday & Pecl, 2014). Sea surface temperature is one of the dominant predictors for habitat-forming, temperate macroalgal distributions in southern Australia (Martínez et al., 2018). Giant kelp (*Macrocystis pyrifera*; Laminariales) and southern bull kelp (*Durvillaea* spp.; Fucales) are large brown macroalgae that form extensive kelp forests in the mid and shallow subtidal (respectively) on Australia's Great Southern Reef (GSR; Bennett et al., 2015). *Macrocystis pyrifera* is a widely distributed species that also occurs in New Zealand, North and South America, South Africa, and the sub-Antarctic. However, within Australia, it is restricted to the cool temperate waters in the southeast and has also undergone severe declines due to climate change (Butler et al., 2020; Johnson et al., 2011). *Durvillaea potatorum* is one of two species of endemic *Durvillaea* spp. in Australia, the other being *D. amatheiae*. Both *D. potatorum* and *D. amatheiae* are restricted to the cool temperate waters of southeast Australia (Velásquez et al., 2020;

Weber et al., 2017). *Macrocystis pyrifera* and *D. potatorum* are important autogenic ecosystem-engineers (Miller et al., 2018; Perry, 2023; Teagle et al., 2017), contributing to the ecological, recreational and commercial value of the GSR (Bennett et al., 2015; Eger et al., 2023; Forbes et al., 2024; Thomsen & South, 2019).

As cold-water species, these kelps are highly susceptible to increasing water temperatures (Le et al., 2022; Tait et al., 2021; Velásquez et al., 2020). Even under a conservative climate change scenario with low emissions and strong mitigation predictions (RCP 2.6, Van Vuuren et al., 2011), *Durvillaea potatorum* and *Macrocystis pyrifera* have both been predicted to experience extremely severe, southerly range contractions by 2100 (Martínez et al., 2018). Although globally, *M. pyrifera* has a more southern distribution than that in Australia, Tasmania has the southernmost distribution of *D. potatorum* (Hurd et al., 2023). Given there is minimal suitable habitat between the GSR and sub-Antarctic Islands and Antarctica, a southern range expansion is unlikely (Jayathilake & Costello, 2020). Furthermore, *D. potatorum* is also non-buoyant, so presumably has more limited dispersal potential via floating rafts than *M. pyrifera* (Kelly et al., 2021). Long distance dispersal for *D. potatorum* may be dependent on anthropogenic transport or, perhaps, entanglement/conjoining with more buoyant species such as *M. pyrifera* (Kelly et al., 2021; Macaya et al., 2016).

To understand patterns of genetic diversity and connectivity in populations of these declining autogenic ecosystem-engineers on the GSR, high-resolution genomic analyses from populations of both *Macrocystis pyrifera* and *Durvillaea potatorum* throughout their contracting ranges in southeastern Australia were conducted. These results were then combined with oceanographic particle dispersal models to assess connectivity potential. Non-buoyant *Durvillaea* spp. were shown by mitochondrial and nuclear genetic markers (Weber et al., 2017) to have been affected by past separation of Australian populations by Pleistocene sea regressions, leading to divergence and speciation. We therefore hypothesized that *D. potatorum* would show strong population structure throughout its range, indicating limited population connectivity. In contrast, we hypothesized that the buoyant *M. pyrifera* would show lower population structure with more similarity among populations, indicating high levels of connectivity. This hypothesis aligns with previous research that describes low spatial diversity for *M. pyrifera* using mitochondrial and chloroplast markers (Durrant et al., 2015).

MATERIALS AND METHODS

Field samples

Between 15 and 49 tissue samples from the blades of *Durvillaea potatorum* and *Macrocystis pyrifera* were

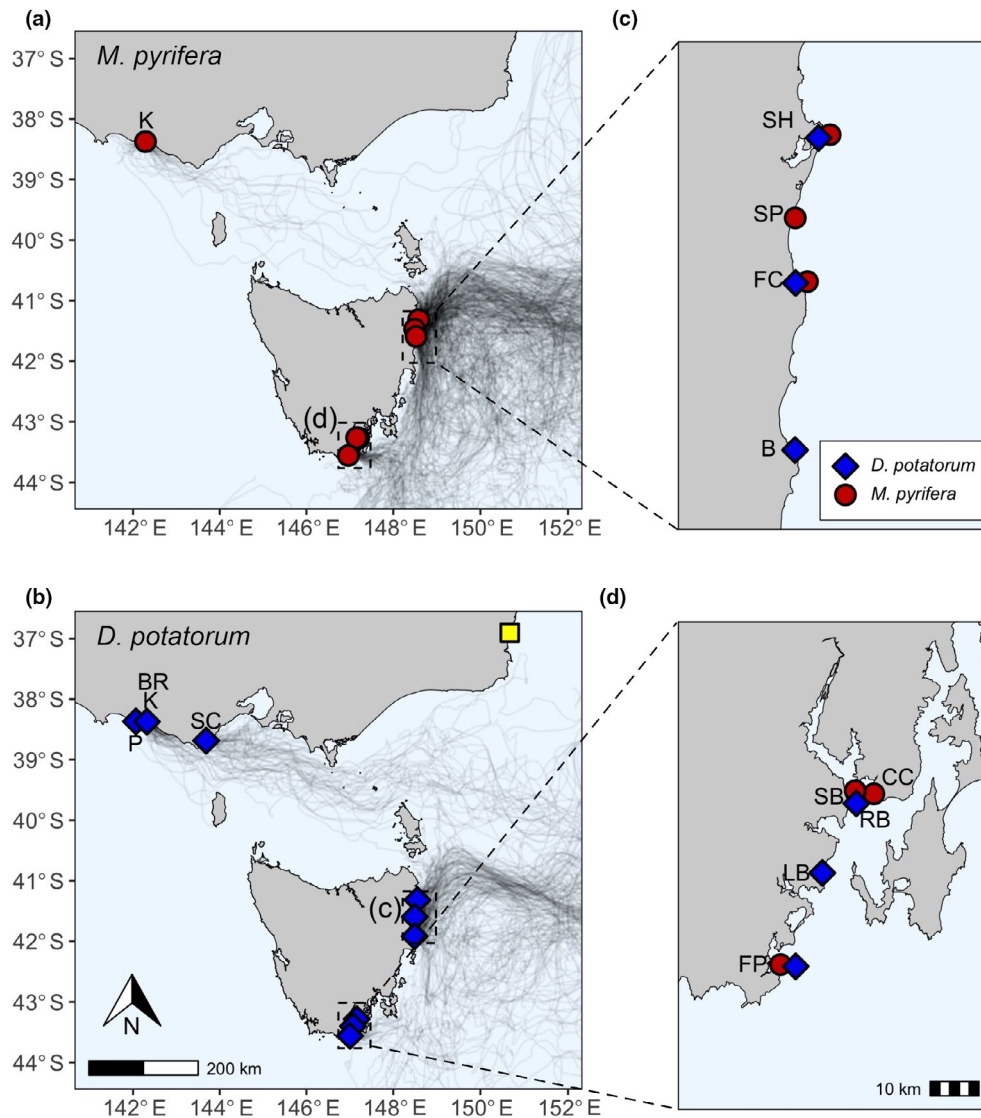


FIGURE 1 Map of sampling sites and a subsample of tracks from the connectivity analysis for (a) *Macrocyctis pyrifera* (red circles) and (b) *Durvillaea potatorum* (blue diamonds) in southeast Australia. Sites in the Victoria region: The Passage (P), Breakwater Reef (BR), Keyhole (K), and Skenes Creek (SC). Sites in northeast Tasmania (inset c): St Helens (SH), Shelly Point (SP), Four Mile Creek (FC), and Bicheno (B). Sites in southeast Tasmania (inset d): Charlottes Cove (CC), Surveyors Bay (SB), Roaring Bay (RB), Lady Bay (LB), and Fishers Point (FP). Subsample of particle tracks is limited to 2000 particles from each species respective reproductive season in 2017. Yellow square in (b) indicates where *Durvillaea amatheiae* samples were collected and where *D. potatorum* does not occur.

collected from 15 sites between July 7 and August 31, 2018 (Figure 1, Table S1). To avoid sampling closely related individuals, replicates were taken at least a 20-m separation. Immediately after being collected, samples were dried with paper towel and stored in 96% ethanol. Following fixation, samples were transferred to silica for desiccation and were stored dry until DNA extraction.

DNA extraction and sequencing

Genomic DNA was extracted from dried specimens using the Qiagen DNeasy PowerPlant Pro kit with minor modifications as previously applied to *Durvillaea* spp. (Peters et al., 2020). Approximately 1 cm² of tissue

was soaked in lysis buffer at 65°C for 24 h. Following soaking, 100 μL of isopropanol was added, and samples were incubated at 65°C for 30 min, vortexing every 10 min. Subsequent steps followed the kit protocol, with the final elution of DNA in 100 μL elution buffer while incubating samples at room temperature for 10–15 min to maximize DNA yield. The extracted DNA was purified using the Qiagen DNeasy PowerClean Pro Cleanup Kit, following the kit protocol, except for adding an extra wash step using 100% ethanol and eluting the DNA in 100 μL of elution buffer.

A standard single digest genotyping by sequencing (GBS) library preparation protocol (Elshire et al., 2011) was followed with modifications previously used for *Durvillaea* spp. (Peters et al., 2020). DNA aliquots were

loaded into GBS adapter plates, which included 2.25 ng of uniquely barcoded PstI adapter stock per well, and dried using a vacuum centrifuge at 45°C. Digestion was carried out using PstI-HF and 10× NEB Cut Smart Buffer, incubating samples at 37°C for 2 h. Adapter ligation was then carried out using T4 DNA Ligase in 10× ligase buffer under following conditions: two cycles of 16°C for 30 min and 37°C for 2 min, followed by 1°C for 30 min, and finally 80°C for 30 min. A Qiagen MinElute 96-well polymerase chain reaction (PCR) purification kit was then used to purify post-ligation DNA, with modifications that included adding one wash step using 30 µL of dH₂O prior to the final elution of DNA using 23 µL of 1 × TE. Ten microliters of the purified product were then added to 40 µL of PCR master mix containing Bioline 2 × Taq Master Mix, GBS PCR Primer 1 and GBS PCR Primer 2. The PCR protocol followed: 72°C for 5 min, 95°C for 60 s, 28 cycles of 95°C for 30 s, 65°C for 30 s, 72°C for 30 s, followed by a final extension step of 75°C for 5 min. PCR products were first visualised using a 1% agarose gel, and subsequently pooled into libraries based on digested DNA molecular weight distribution (aiming for a consistent smear of lower molecular weight DNA), fluorescence intensity, and consistency. Prior to sequencing, pooled libraries were size selected for molecules of between 300 and 600 base pairs (bp). Paired-end sequencing was carried out on three lanes of a mid-output flowcell in an Illumina NextSeq 500 system (75 bp paired-end).

Genotypic analysis

The GBS sequence library was first filtered using cutadapt v. 4.4 (Martin, 2011) to remove homopolymers, with an overlap setting of five. These data were subsequently demultiplexed using the process_radtags function in STACKS 2.65 (Rochette et al., 2019), trimming to 68 bp, with the -r, -c, and -q flags included. Reference-based single nucleotide polymorphism (SNP) calling was used to maximize the number and quality of loci to ensure sufficient data for robust filtering (Shafer et al., 2017; Vaux et al., 2023). Reads were first aligned to reference genomes *Macrocystis pyrifera* (Diesel et al., 2023) or *Durvillaea antarctica* (Fraser et al., 2022) using BWA v. 2.2.1 (Li, 2013). Alignments were then assembled into loci using the ref_map (with the -r flag) and populations (with $-p=1$) modules of STACKS. The resultant VCF library was then filtered for each species using SNPFILTER (DeRaad, 2022), with a minimum depth of 5×, maximum depth of 100×, and genotype qualities of 27. A missingness filter of 0.7 was then applied to SNPs such that SNPs missing >70% of data across individuals were removed, a minor allele count of two was applied, and then individuals missing >50% of data were then removed. To this data set,

principal component analysis (PCA) was applied using adegenet (Jombart & Ahmed, 2011).

Durvillaea potatorum samples were genetically distinguished from potentially co-sampled *D. amatheiae* through PCA, with samples clustering with known *D. amatheiae* samples (sourced from Turingal and Tathra; Figure 1b, yellow square) being removed (Figure S1). The SNPs were subsequently recalled for the *D. potatorum* samples.

ADMIXTURE analysis was conducted for *Macrocystis pyrifera* and *Durvillaea potatorum* by first filtering data using PLINK2 to filter for linkage (flags --indep-pairwise 50 100 8). Subsequently, ADMIXTURE analysis (Alexander et al., 2009) was conducted for each value of K from 2 to 20, and the lowest value that minimized the cross validation error was chosen (Figure S2). This resulted in values of K of 3 and 5 for *M. pyrifera* and *D. potatorum*, respectively. Genotypic analysis was visualized in R (version 4.4.3, R Core Team, 2024) using ggplot2 3.5.1 (Wickham, 2016) and mapmixture 1.1.4 (Jenkins, 2024).

Pairwise F_{ST} was calculated using the pairwise.fst.dosage function in hierfstat (v. 0.5–11), developed by Goudet and Weir (2023). Significance of the F_{ST} results was calculated by permutation, randomly shuffling the population labels and recalculating F_{ST} for a total of 1,000 permutations. p -values were then calculated as the proportion of F_{ST} values greater than or equal to the observed F_{ST} . Individual-level heterozygosity was calculated using the gl.report.heterozygosity function in dartR 2.9.7 (Gruber et al., 2018).

Particle modeling

Connectivity among sampling locations was determined using Lagrangian drift particle modeling using OpenDrift (v1.11.12, <https://opendrift.github.io>). Models were run using surface seawater velocity from the Global Ocean Reanalysis (GLORYS12; 10.48670/moi-00021) and wind vector data from the Global Ocean Hourly Reprocessed Sea Wind and Stress Model (10.48670/moi-00185). Three thousand particles were randomly seeded daily within 1.5 km of each sampling location and advected at hourly timepoints for 6 months or until particles were stranded. Three different particle types (1000 particles each) that were the most comparable to a rafting piece of kelp (PIW-1, PIW-5, and PIW-6, defined in the Leeway model <https://opendrift.github.io>) were used to cover a range of different raft geometries (Pearman et al., 2024). The same variety of particles were used for both species, as macroalgal species can become entangled and form one rafting mass (Fraser et al., 2011). Horizontal diffusion was set to $0.1 \text{ m} \cdot \text{s}^{-1}$, and vertical diffusion was set at $0.0 \text{ m} \cdot \text{s}^{-1}$. A particle was considered to reach a sampling site if it had stranded or was within 3 km of

the site at the end of the simulation. Sites within 10 km of each other were combined for analysis. Connectivity between each site was calculated as the mean percent of particles that reached each site from January 1, 2008, to December 31, 2017.

Probable source location was determined using the same methods but by hindcasting particles instead of forecasting them. From January 1, 2017, to January 1, 2018, 3000 particles were randomly seeded daily within 3 km of sampling locations and advected backward at hourly timepoints for 6 months or until particles were stranded. Stranded particles were then used to determine source locations on a 0.2° resolution. Source locations with <1% probability were removed before visualization using ggplot2 (Wickham, 2016). Least-cost distance between each population was calculated in R using marmap 1.0.12 (Pante & Simon-Bouhet, 2013) with a minimum depth of 0 and the costDistance function in the gdistance v.1.6.4 package (Van Etten, 2017). Isolation by distance analyses were conducted using multiple regression of distance matrices, as implemented in the ecodist R package (v.2.1.3) with 1000 permutations (Goslee & Urban, 2007; Legendre & Fortin, 1989).

RESULTS

Species and SNP identification

Species identification analysis of the *Durvillaea* spp. data indicated 27 samples collected from multiple sites across Tasmania were not *D. potatorum*, clustering with known *D. amatheiae* samples (Figure S1). Furthermore, PC1 clearly delineated *D. potatorum* and *D. amatheiae* and explained 41% of the genetic variation within the data.

Following SNP calling, there were a total of 7161 SNPs for *Macrocystis pyrifera* and 2375 SNPs for *Durvillaea potatorum*. Following stringent filtering, 5544 and 1410 SNPs were retained for *M. pyrifera* ($n=97$) and *D. potatorum* ($n=159$), respectively.

Population genetics

For both *Macrocystis pyrifera* and *Durvillaea potatorum*, regional population structure was observed, with mainland, northeast Tasmania, and southeast

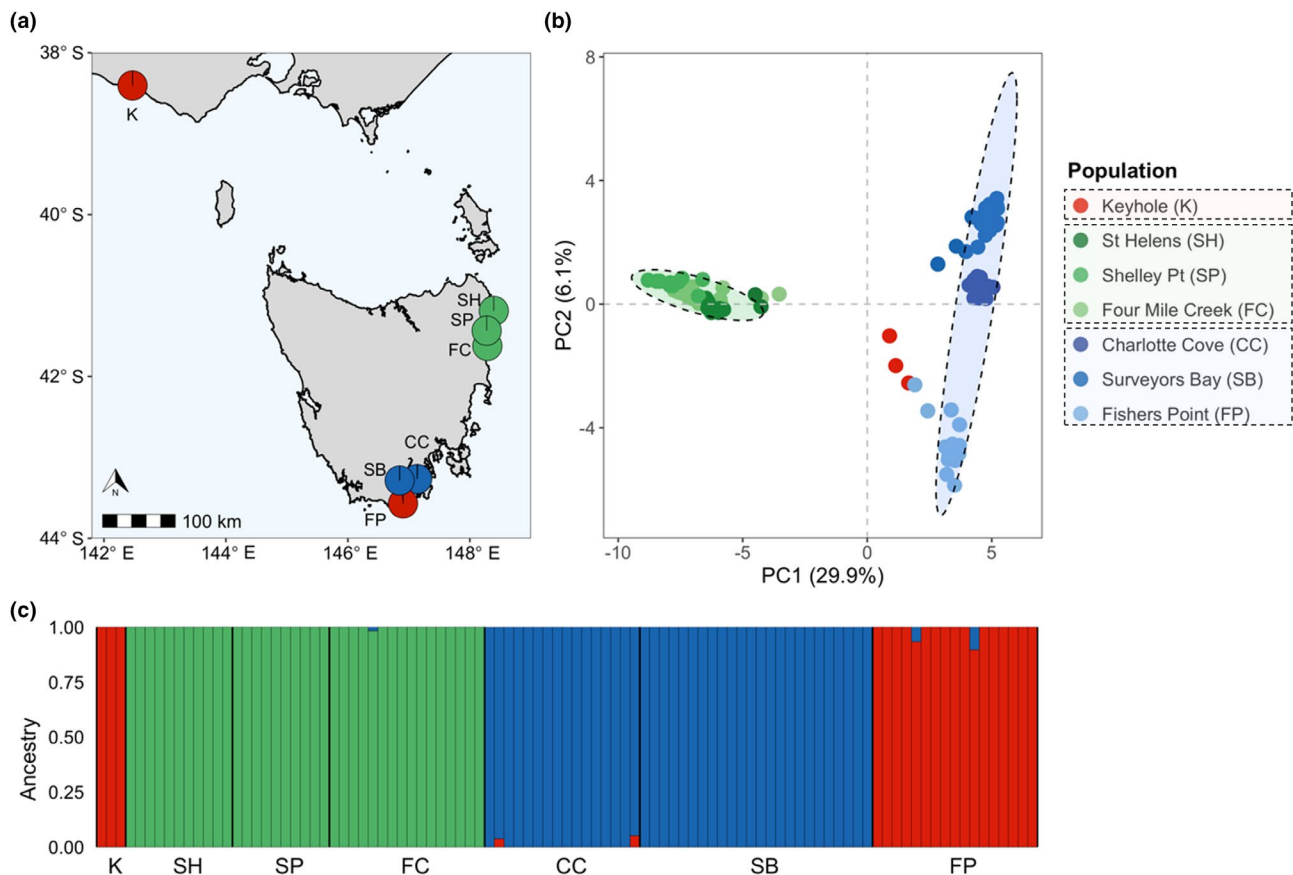


FIGURE 2 Genetic admixture and principal component analysis results for *Macrocystis pyrifera*. (a) Admixture map with pie charts showing membership to each of three genetic clusters identified using 5,544 SNPs. Each pie chart represents a population with color denoted by K cluster, as per admixture plot shown in (c). (b) PCA plot of genetic variation using 7161 SNPs. Ellipses indicate sampling regions: Victoria (red), northeast Tasmania (green), and southeast Tasmania (blue). (c) Admixture plot for *M. pyrifera*, $K=3$. The sample groups are labeled north to south, with colors matching the pie charts shown in (a). Color in legend is for PCA plot only.

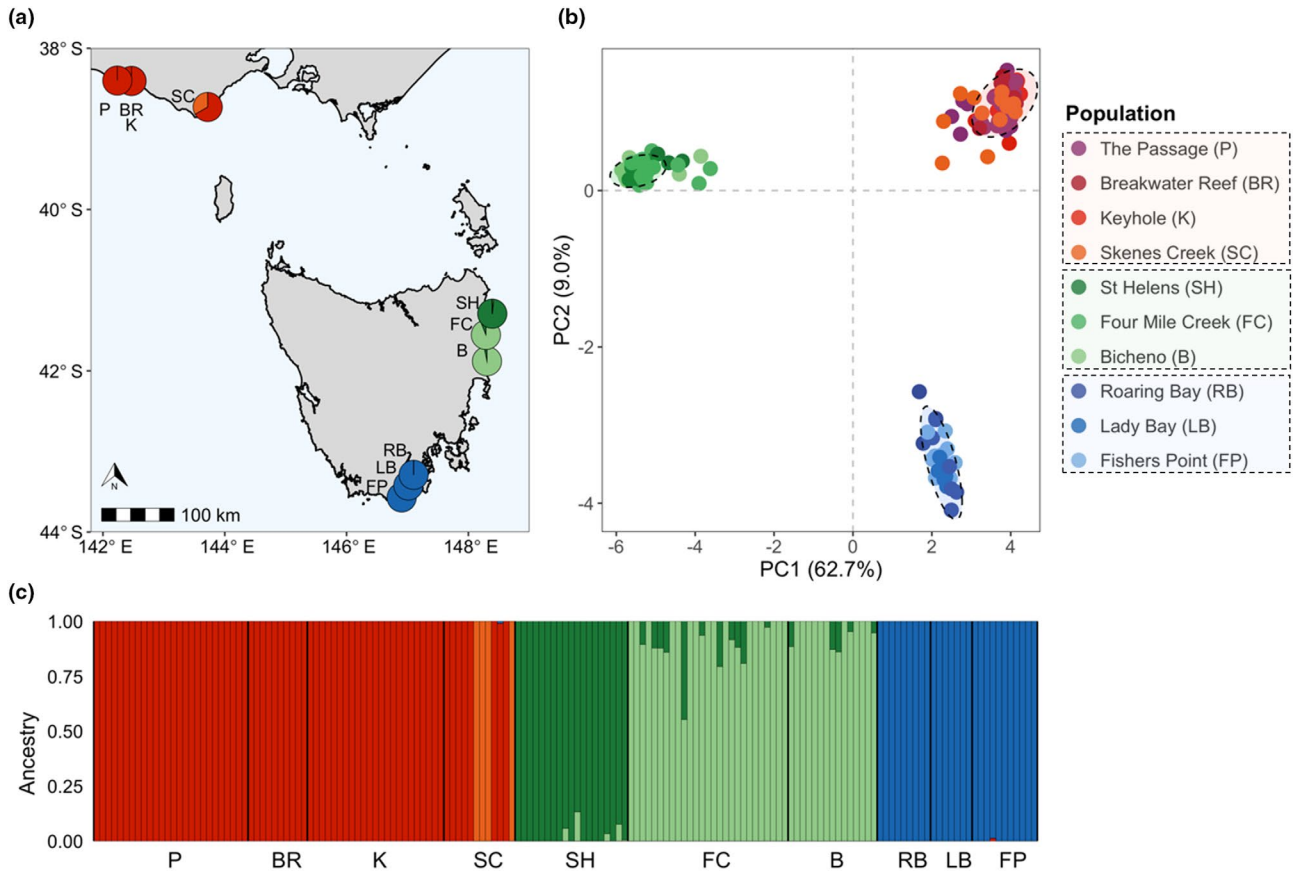


FIGURE 3 Genetic admixture and principal component analysis results for *Durvillaea potatorum*. (a) Admixture map with pie charts showing membership to each of three genetic clusters identified using 1410 SNPs. Each pie chart represents a population with color denoted by K cluster, as per admixture plot shown in (c). (b) PCA plot of genetic variation using 2375 SNPs. Ellipses indicate sampling regions: Victoria (red), northeast Tasmania (green), and southeast Tasmania (blue). (c) Admixture plot for *D. potatorum* $K=5$. The sample groups are labeled north to south, with colors matching the pie charts shown in (a). Color in legend is for PCA plot only.

Tasmania samples tend to cluster together (Figures 2 and 3). *Durvillaea potatorum* exhibited much stronger population structure, with both higher values of K (*D. potatorum*, $K=5$; *M. pyrifera*, $K=3$) and populations delineated as genetically distinct based on ADMIXTURE and PCA (Figure 3). Conversely, connectivity between *M. pyrifera* populations was notably higher, with more proximal populations tending to cluster together (Figure 2). For both species, site-specific ancestry tended to be dominated by one cluster, rather than representing highly admixed populations (ancestry proportion = 0.67–0.99, Tables S2 and S3). Pairwise F_{ST} analysis and permutation significance testing (1000 permutations) showed similar patterns to the PCA and ADMIXTURE analysis, with stronger regional separation for *D. potatorum* than for *M. pyrifera* (Figure 4). Overall, *D. potatorum* tended to have higher F_{ST} values than *M. pyrifera* (Figure 4).

Interestingly, for *Macrocystis pyrifera*, the southernmost Tasmanian population, Fishers Point, clustered most closely with southwest Victorian samples from Keyhole (Figure 2). This unusual clustering was not observed in *Durvillaea potatorum*, which formed three

distinct clusters based on region (Figure 3). Although the northeast Tasmania *D. potatorum* populations clustered together within the PCA, the ADMIXTURE analysis revealed that *D. potatorum* at St Helens appeared to be genetically distinct (Figure 3). Mainland populations of *D. potatorum* showed almost no genetic differentiation with very low F_{ST} values ($F_{ST} < 0.06$, permutation test, 1000 permutations, $p > 0.1$). Mainland populations of *D. potatorum* also showed more genetic similarity to southeastern Tasmanian populations (F_{ST} 0.41–0.63) than northeastern Tasmanian populations (F_{ST} 0.77–0.83). However, all Tasmanian populations were significantly diverged from mainland populations based on F_{ST} (permutation test, 1000 permutations, $p < 0.05$). *Macrocystis pyrifera* populations showed more similar allele frequencies among sampling regions with a max F_{ST} of 0.46. The only two populations for which no significant differences in F_{ST} were observed for *M. pyrifera* were in northeastern Tasmania, between Four Mile Creek and Shelly Point (permutation test, 1000 permutations, $p = 0.06$). Analysis of observed heterozygosity across all populations and both species revealed that *M. pyrifera* tended to have higher heterozygosity than

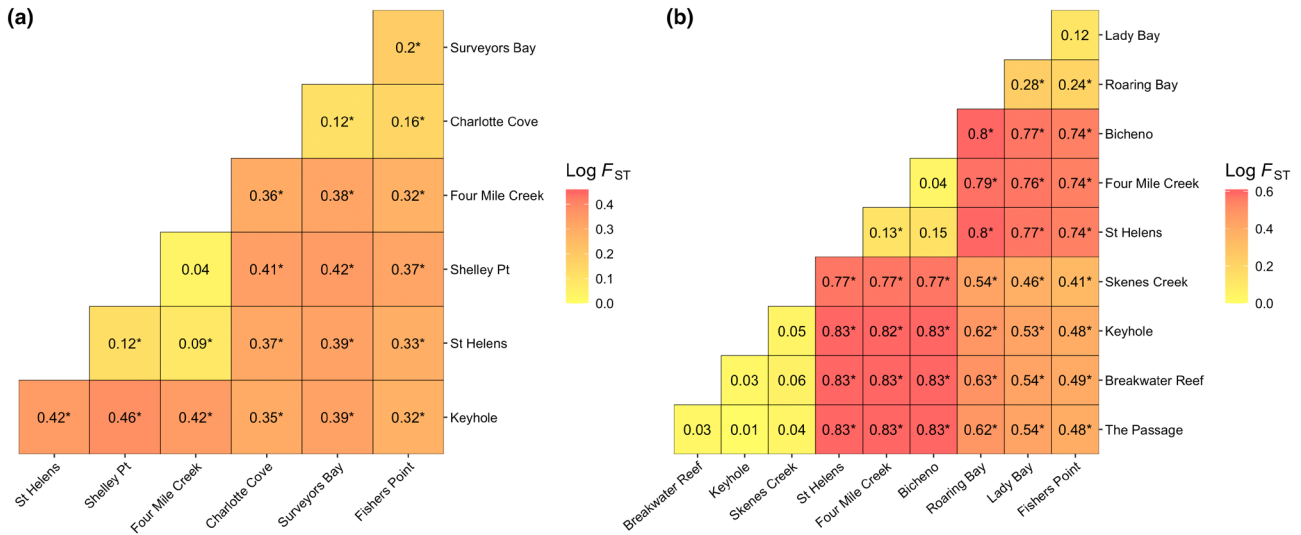


FIGURE 4 F_{ST} pairwise comparisons for (a) *Macrocystis pyrifera* and (b) *Durvillaea potatorum*. * indicates a significant difference at $\alpha=0.05$.

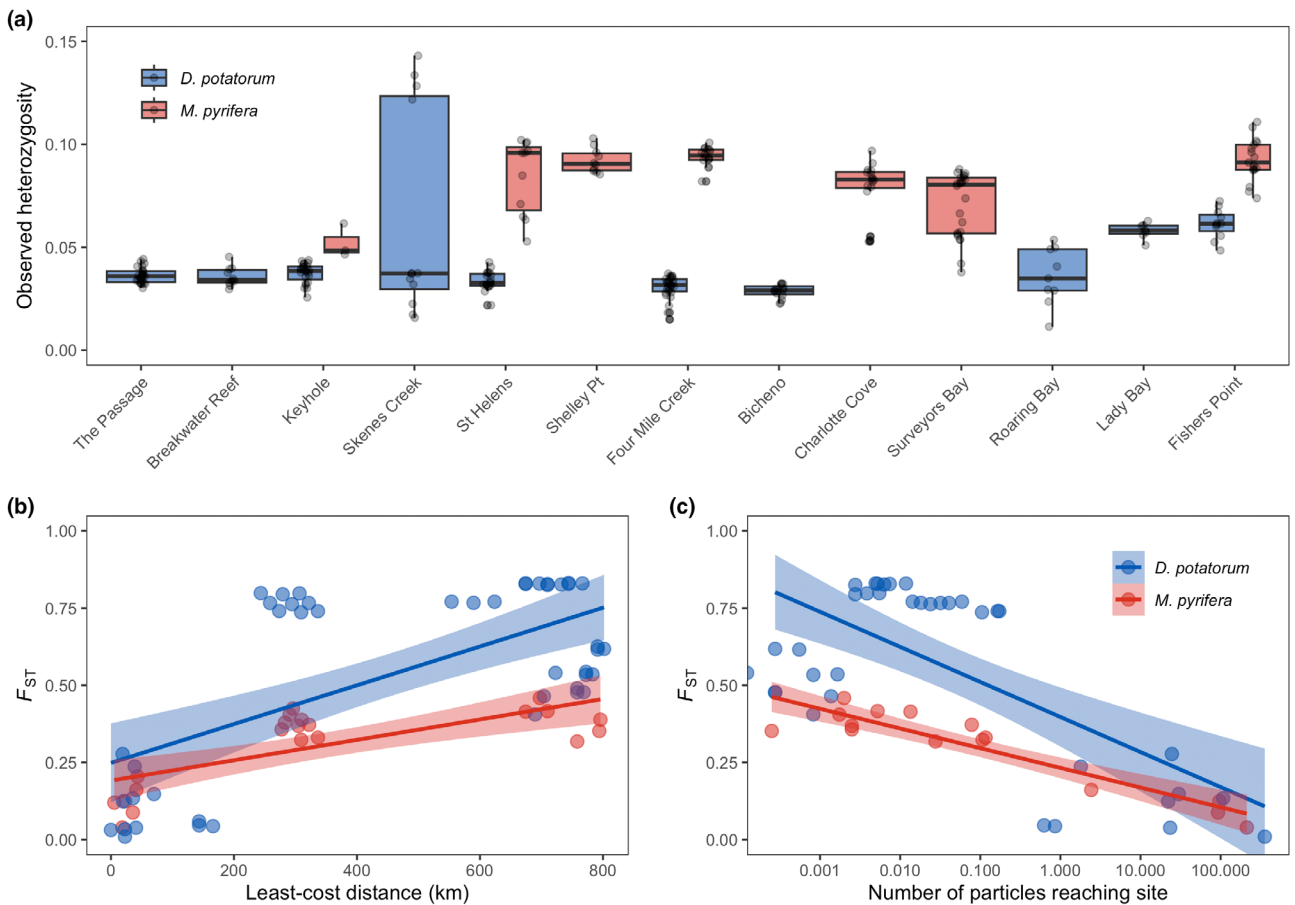


FIGURE 5 (a) Observed heterozygosity for *Durvillaea potatorum* (blue) and *Macrocystis pyrifera* (red). (b) F_{ST} and least-cost-distance. (c) F_{ST} and number of particles reaching each site (log scale).

D. potatorum (Figure 5a). An exception was *D. potatorum* from the mainland population at Skenes Creek, which had a much greater range of heterozygosity values than all sites (Figure 5a).

Population connectivity

Modeled oceanographic connectivity was highest among the northeast Tasmanian populations and lowest

	Mainland		Northeast Tasmania			Southeast Tasmania	
	K		SH	SP	FC	CC+SB	FP
K	31.81		<0.01	<0.01	<0.01	<0.01	<0.01
SH			27.91	0.29	0.65	<0.01	<0.01
SP			2.92	28.47	3.06	<0.01	<0.01
FC			2.440	4.011	32.49	<0.01	<0.01
CC+SB			<0.01	<0.01	<0.01	42.31	<0.01
FP			<0.01	<0.01	<0.01	0.07	17.23

Note: Bold values indicate local retention of particles.

	Mainland			Northeast Tasmania			Southeast Tasmania		
	P	K+BR	SC	SH	FC	B	RB	LB	FP
P	34.20	8.80	0.03	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
K+BR	3.06	36.29	0.02	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
SC	<0.01	<0.01	33.80	<0.01	<0.01	<0.01		<0.01	<0.01
SH				48.67	0.36	0.08	<0.01	<0.01	<0.01
FC				3.23	39.03	0.16	<0.01	<0.01	<0.01
B			<0.01	0.92	0.63	31.04	<0.01	<0.01	<0.01
RB				<0.01	<0.01	<0.01	24.43	0.26	0.01
LB				<0.01	<0.01	<0.01	0.56	28.73	0.05
FP				<0.01	<0.01	<0.01	0.049	0.69	16.17

Note: Bold values indicate local retention of particles.

in the southeast Tasmania populations (Tables 1 and 2). No population was completely isolated for either species (Tables 1 and 2). For *Durvillaea potatorum*, St Helens in northeast Tasmania had the highest self-recruitment (48.7%), whereas the southernmost sampled site, Fishers Point, had the lowest self-recruitment (16.2%). Fishers Point also had the lowest self-recruitment for *Macrocystis pyrifera* (17.2%); however, the combined sites of Charlotte Cove and Surveyors Bay in southeast Tasmania had the highest self-recruitment (42.3%). The one *M. pyrifera* population sampled on mainland Australia was still connected to all populations sampled in Tasmania. However, the connectivity was as low as 0.00001 particles. Connectivity among the northeast Tasmanian *M. pyrifera* populations was the highest among areas. The mainland site of Skenes Creek was the least connected population in this study for *D. potatorum* (<0.03%); however, particles reached from as far south as Bicheno in northeast Tasmania (Table 2).

The majority of hindcast particles stranded within 50 km of target sites (Figures 6–8). Northeast Tasmania had the largest probable source area, with particles arriving from >100 km away (Figure 7), whereas southeast Tasmania sites had much closer sources, with particles rarely arriving from >50 km away (Figure 6). Of the mainland Victorian populations, Skenes Creek had

the most localized probable source area, being around three times smaller than other sites (Figure 8).

Combined analysis

Both *Durvillaea potatorum* and *Macrocystis pyrifera* tended to exhibit strong isolation-by-distance patterns, evidenced by strong relationships among F_{ST} and both least-cost distance and particle connectivity (Figure 5). F_{ST} tended to increase with increasing least-cost distance and decrease with increasing particle connectivity (Figure 5). These patterns were more evident in *M. pyrifera* ($R^2=0.80$) than *D. potatorum* ($R^2=0.39$; Table 3). The relationships between least-cost distance and particle connectivity were strongly correlated for both species (Figure S3).

DISCUSSION

Southeastern Australia is an ocean warming hotspot (Hobday & Pecl, 2014), and our findings provide important insights into contemporary population structure of declining autogenic ecosystem-engineers on the Great Southern Reef (GSR). Here, we have discussed our findings in the context of dispersal and connectivity.

TABLE 1 *Macrocystis pyrifera* connectivity matrix. The mean percent of particles to reach target sites. Simulations were run daily from January 1, 2008, for 10 years, resulting in the release of ~11 million particles per site. Rows are source sites; columns are target sites.

TABLE 2 *Durvillaea potatorum* connectivity matrix. The mean percent of particles to reach target sites. Simulations were run daily from January 1, 2008, for 10 years, resulting in the release of ~11 million particles per site. Rows are source sites; columns are target sites.

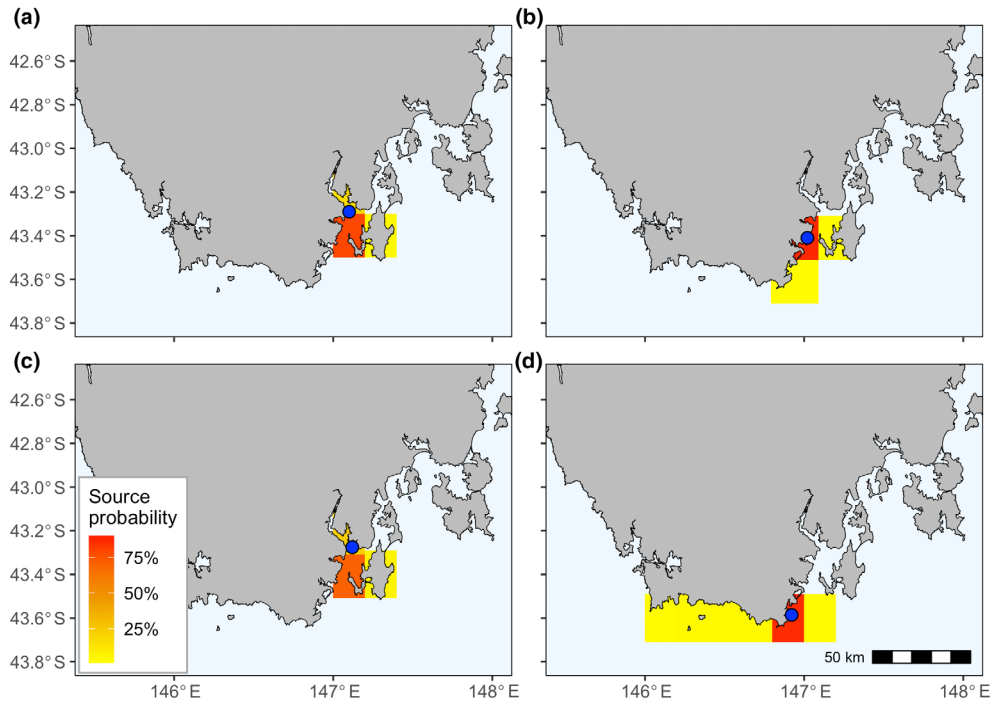


FIGURE 6 Probability of source location for hindcast particle modeling from southeast Tasmanian sites (a) Roaring Bay (*Durvillaea potatorum*), (b) Lady Bay (*D. potatorum*), (c) Charlotte Cove and Surveyors Bay (*Macrocystis pyrifera*), and (d) Fishers Point (*D. potatorum* and *M. pyrifera*).

Dispersal capability

Both *Durvillaea potatorum* and *Macrocystis pyrifera* exhibited strong regional population structure; however, as hypothesized, population structure was stronger for *D. potatorum* than *M. pyrifera*. This result is in line with previous research using lower resolution, single-gene markers (Bussolini & Waters, 2015; Fraser et al., 2009; Le et al., 2024; Macaya & Zuccarello, 2010). These results fit with the dispersal capability and life-history traits of these two species. Because of the buoyant nature of *M. pyrifera* (vs. non-buoyant *D. potatorum*), there is enhanced potential for long-distance dispersal and gene flow (Layton et al., 2022; Thiel & Gutow, 2004). Furthermore, *M. pyrifera* can reproduce year round (Buschmann et al., 2004), unlike *D. potatorum*, which is limited to reproduction during the austral winter and spring from June to October (Clayton et al., 1987). The seasonal variability in strength of the East Australian Current (EAC) means that *M. pyrifera* has the potential to disperse in a variety of oceanographic conditions (Layton et al., 2022), whereas *D. potatorum* dispersal is largely shaped by the prevailing east–west winter currents. Climate change may affect dispersal in the future as the EAC has been predicted to strengthen its southward flow (Oliver & Holbrook, 2014). More southward flow may increase the connectivity between the northeast and southeast Tasmanian populations. The connectivity modeling is limited, however, by our fine-scale understanding of kelp raft dynamics.

Furthering our understanding of specific kelp-raft parameters such as buoyancy and drag would increase the accuracy of connectivity modeling in the future.

Differences in population structure may also be due to the amount of intervening suitable habitat between populations (Durrant et al., 2018). *Macrocystis pyrifera* has a large depth range, typically down to ~30m (Graham et al., 2007), whereas *Durvillaea potatorum* is limited to rocky reefs with high wave exposure and shallower depths, <12m (Fraser et al., 2020). As such, there may be more continuously suitable habitat spread along the GSR coastline for *M. pyrifera*, further facilitating a greater connection of populations. Given southeastern Australia is a warming hotspot (Hobday & Pecl, 2014), the distinct population structuring and lack of connectivity among populations increase the vulnerability of these species to local extinctions resulting in the loss of ecosystem services provided by these habitat-forming kelp species.

Genetic relatedness

Macrocystis pyrifera sampled at the southernmost sampled site, Fishers Point, were most closely related to the mainland samples collected from southwestern Victoria. Our oceanographic connectivity analyses indicate that it is possible, albeit rare, for *M. pyrifera* from Victoria to disperse to Fishers Point. This dispersal might represent a past founder event, with rafts

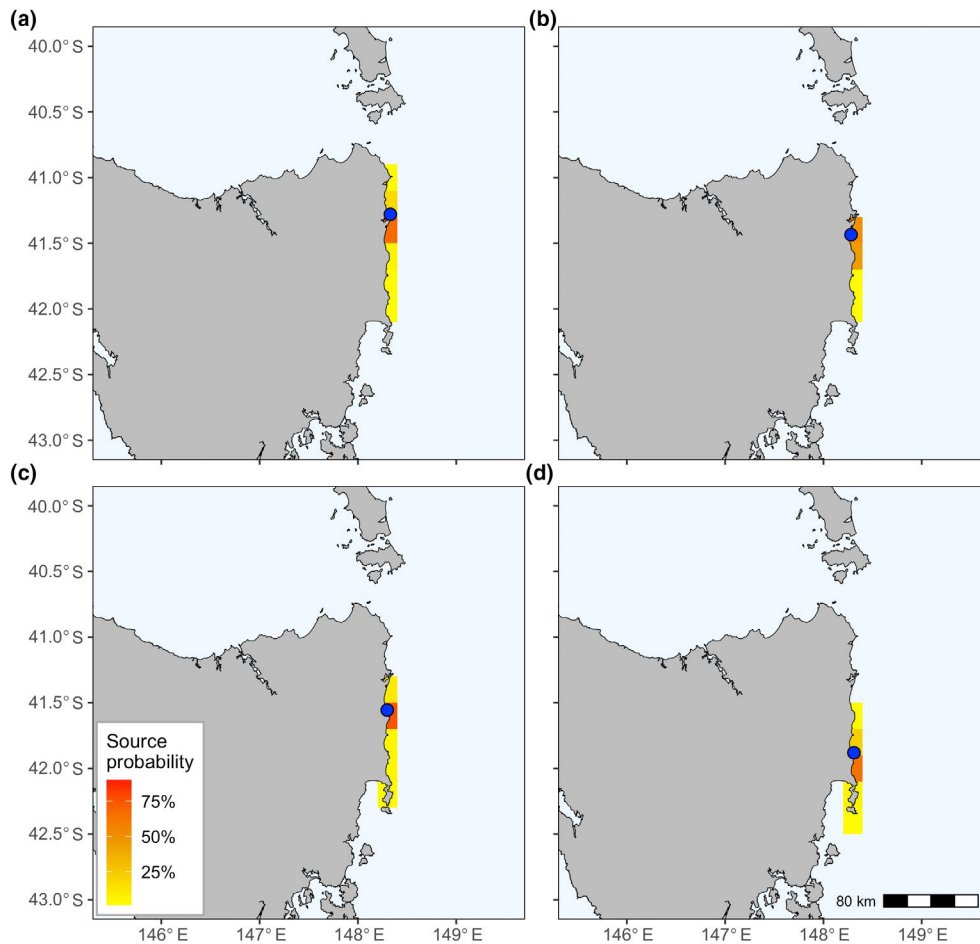


FIGURE 7 Probability of source location for hindcast particle modeling from northeast Tasmanian sites (a) St Helens (*Durvillaea potatorum* and *Macrocystis pyrifera*), (b) Shelly Point (*M. pyrifera*), (c) Four Mile Creek (*D. potatorum* and *M. pyrifera*), and (d) Bicheno (*D. potatorum*).

colonizing Fishers Point following an environmental disturbance, with subsequent offspring reaching high densities and blocking gene flow from later migrants (Fraser et al., 2018; Waters et al., 2013). However, it is surprising that there is such high genetic divergence between Fishers Point and the other southeast Tasmanian populations for *M. pyrifera*, given the relatively small geographic distances between them. The hindcast simulations indicated that rafts are most likely to come from the west. Previous work on macroalgal genetics in southeast Australia has shown strong east–west structuring but weaker north–south population structure (Durrant et al., 2015; Fraser et al., 2009; Hurd et al., 2023; Mueller et al., 2018). Populations in western Tasmania are often more similar to southwestern Victoria than either are to eastern Tasmania (Fraser et al., 2009). This east–west difference has been inferred to result from population segregation during sea level regressions in Pleistocene ice ages, during which Tasmania was connected to mainland Australia (Fraser et al., 2009). As such, we hypothesize that Fishers Point, close to the very southern tip of Tasmania, may be the

southernmost extent of this “western” genetic identity and oceanographic influence. Further sampling of *M. pyrifera* on the west coast of Tasmania and southwest Victoria could provide support for this model. Indeed, this southern point of Tasmania is where the poleward-flowing Zeehan Current of western Tasmania meets the poleward-flowing EAC of eastern Tasmania (Marchesiello & Middleton, 2000). Simulations also indicated that rafts arriving at Charlotte Cove and Surveyors Bay are unlikely to move northward from Fishers Point, raising the possibility that the transition from the western to eastern identities for *M. pyrifera* lies between these areas. The different species likely have different transition points because of their contrasting dispersal potential.

Durvillaea potatorum from St Helens appeared to be genetically distinct, with minimal admixture with nearby populations. St Helens also had the highest self-recruitment (~50%) based on the particle modeling and a higher probability of rafts originating from the north in the hindcast analysis (~20% from northeast populations). There could be more closely related populations to the north which were not sampled, limiting the conclusions

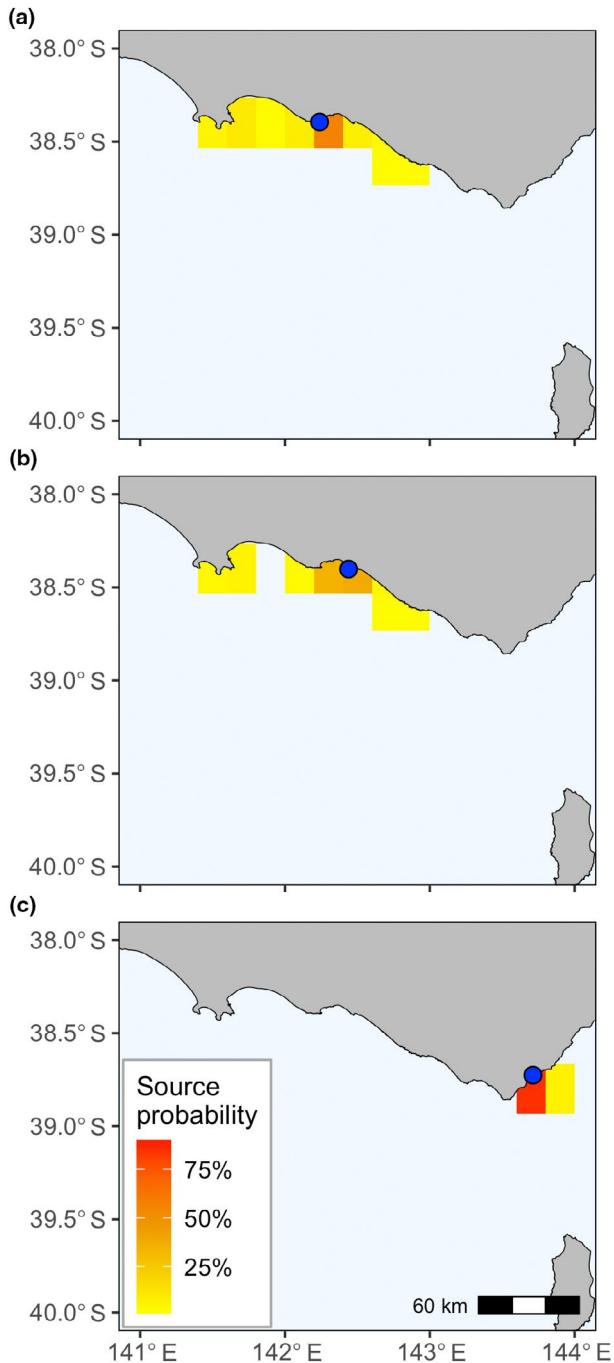


FIGURE 8 Probability of source location for hindcast particle modeling from mainland Victorian sites (a) The Passage (*Durvillaea potatorum*), (b) Keyhole and Breakwater Reef (*Macrocystis pyrifera* and *D. potatorum*), and (c) Skenes Creek (*D. potatorum*).

that can be made from this study. The modeled potential connectivity of *D. potatorum* between southwestern Victoria and Tasmania was very low, and the simulations revealed the capacity for north–south dispersal but not vice versa. The isolation of *D. potatorum* at St Helens from the other sampling locations is logical given relatively limited east–west flow through Bass Strait and the behavior of the dominant poleward flowing Zeehan and East Australian Currents (Weber et al., 2017).

TABLE 3 Results of multiple regression of distance matrices for *Durvillaea potatorum* and *Macrocystis pyrifera*.

Species	Predictor	Coefficient	p-value
<i>Durvillaea potatorum</i>	Intercept	0.3712	0.879
	Least cost distance	0.0005	0.019
	Particle connectivity	−0.0013	0.031
	$R^2=0.394$, $F=10.73$, $p=0.019$		
<i>Macrocystis pyrifera</i>	Intercept	0.2623	0.028
	Least cost distance	0.0002	0.031
	Particle connectivity	−0.0013	0.028
	$R^2=0.803$, $F=24.39$, $p=0.007$		

Population genetics and connectivity

Both *Durvillaea potatorum* and *Macrocystis pyrifera* exhibited evidence for isolation-by-distance; however, these patterns were much stronger in *M. pyrifera* than in *D. potatorum*. We suggest that this pattern is the result of greater predictability in admixture of *M. pyrifera* populations. As *D. potatorum* is less dispersal-capable, localized geographic factors and historic contingencies are more likely to shape this the population structure of this species (Fraser et al., 2020), leading to greater departures from isolation-by-distance patterns. In contrast, *M. pyrifera* is a highly dispersive species and, thus, is expected to align better with isolation-by-distance patterns (Alberto et al., 2011). Notably, *M. pyrifera* F_{ST} was strongly associated with particle connectivity, whereas this relationship was weaker in *D. potatorum*. Although this could be the result of localized influences on *D. potatorum* coupled with reduced dispersal ability, it could also be explained by the particle characteristics used in our modeling better aligning with those of a buoyant kelp species. Nevertheless, given that *D. potatorum* is expected to disperse via entanglement with buoyant rafts (Kelly et al., 2021), it is difficult to be sure which explanation is more likely. Interestingly, *D. potatorum* tended to have much lower observed heterozygosity than *M. pyrifera*. This phenomenon is likely explained by reduced population connectivity leading to reduced genetic diversity in *D. potatorum* relative to *M. pyrifera*. Similar findings of low heterozygosity were observed for *D. amathiae* in southeast Australia (New South Wales and Victoria; Nimbs et al., 2025).

CONCLUSIONS

Our results revealed intriguing population structure and connectivity patterns in large habitat-forming kelp taxa in southern Australia, and future analyses should aim to include more sampling sites to determine the locations

of barriers and pathways for gene flow across this area. The unique genetic structuring of *Durvillaea potatorum* and the low connectivity among populations has emphasized the potentially concerning vulnerability of this species to climate change and local stressors such as marine heat waves. The potential vulnerability of *D. potatorum* is even more alarming given its endemism, more limited-dispersal capacity, and probable range reductions and the absence of poleward habitat for this species to move toward. Therefore, it is important to identify species that rely on *D. potatorum* for habitat and to develop strategies to reduce the potential impacts for these species if range retractions continue. The loss of these habitat-forming autogenic ecosystem engineers will affect ecosystem functioning of the GSR and, consequently, affect the human livelihood derived from that functioning.

AUTHOR CONTRIBUTIONS

Finn J. Ryder: Conceptualization (equal); formal analysis (lead); investigation (equal); methodology (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **William S. Pearman:** Conceptualization (equal); formal analysis (lead); investigation (equal); methodology (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **Cayne Layton:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); writing – review and editing (equal). **Elahe Parvizi:** Conceptualization (equal); investigation (equal); methodology (equal); writing – original draft (supporting); writing – review and editing (equal). **Craig Johnson:** Conceptualization (equal); supervision (supporting); writing – review and editing (equal). **Alecia Bellgrove:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); writing – review and editing (equal). **Ceridwen I. Fraser:** Conceptualization (equal); funding acquisition (lead); project administration (lead); resources (equal); supervision (lead); writing – review and editing (equal).

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SUPPORTING INFORMATION

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

Figure S1. Principal component analysis of *Durvillaea* sequencing data. The left most cluster was discarded from primary analyses as these samples belonged to *D. amatheiae*.

Figure S2. Admixture cross validation error for *Macrocystis pyrifera* and *Durvillaea potatorum*.

Figure S3. Least-cost distance and number of particles reaching each site (log scale) for *Durvillaea potatorum* (blue) and *Macrocystis pyrifera* (red).

Table S1. Details of sampling sites and replication.

Table S2. Proportion of samples clustering with each ADMIXTURE group for *Macrocystis pyrifera*. $K=3$.

Table S3. Proportion of samples clustering with each ADMIXTURE group for *Durvillaea potatorum*. $K=5$.

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