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Simulating larval dispersal across the distribution of the New Zealand green-lipped mussel: insights into connectivity and source–sink dynamics

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ABSTRACT: Information about population connectivity, including the rates and routes of larval transport as well as source–sink dynamics, is important for the sustainable management of harvested species. For marine species whose primary mode of dispersal is transport during the pelagic larval stage, biophysical modelling of larval dispersal represents a valuable tool that is not subject to some of the same limitations as genetic connectivity analyses. In particular, a model that encompasses the entire distribution of a species can provide novel insights by identifying potentially important source populations or stepping-stone sites from which molecular samples may not be available. This study employed a Lagrangian particle-tracking model to simulate larval releases from all potential mussel habitats along ~15 000 km of coastline for an endemic New Zealand bivalve, the green-lipped mussel. A northern and a southern cluster with a break near Cook Strait were identified, confirming the structure reported by earlier genetic analyses and a previous biophysical modelling study. The present study revealed, for the first time, that connectivity between the 2 clusters is largely asymmetrical, with more particle transport from the south to the north. Because this study simulated spawning events across the entire distribution of the species, several previously unknown source populations and stepping-stone populations were identified. These findings highlight the utility of a multidisciplinary approach to understanding marine connectivity and provide evidence for new strategies, including the protection of source and stepping-stone populations, to sustainably manage this endemic species.

KEY WORDS: Lagrangian particle tracking · Population connectivity · Biophysical modelling · Source–sink dynamics · Genetic structure

1. INTRODUCTION

Population connectivity is the product of patterns of migration among populations within a metapopulation and is a driver of both ecological and evolutionary processes (Hanski & Gilpin 1997, Cowen & Sponaugle 2009). At ecological or demographic timescales, population connectivity describes rates of immigration and emigration among populations. Knowledge of rates and routes of connectivity is valuable to managers because of its importance in understanding species-specific connectivity for spatial planning (e.g. marine reserve networks, placement of aquaculture sites, inter-jurisdictional fisher areas, management of invasive species) as well as the identification and protection of source populations that may contribute disproportionately to larval supply (Crowder et al. 2000, Pineda et al. 2007, Muir-

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head et al. 2008, Hansen 2011, Kough et al. 2013, Coleman et al. 2017). Over longer timescales, these processes may contribute to rates of genetic divergence among populations and may produce pronounced patterns of genetic structure within a species (Slatkin 1987, Edwards & Beerli 2000, Apte & Gardner 2002). When gene flow among populations is limited, new mutations, genetic drift and localised divergent selection will result in spatially explicit genetic diversity among populations (Nosil et al. 2009). Genetic structure and the processes influencing gene flow are important for managers to consider because the overexploitation of one genetically divergent population within the metapopulation may result in a reduction of overall genetic diversity that in turn reduces the overall adaptive potential of the species to novel threats, such as climate change or emergent disease (Pita et al. 2016, Papa et al. 2021). Consequently, understanding connectivity in populations of marine organisms is critical for the management of species that support large fisheries or aquaculture industries, such as New Zealand's green-lipped mussel *Perna canaliculus*.

The green-lipped mussel is a benthic bivalve that is endemic to New Zealand and commonly found on a variety of rocky reef habitats in shallow coastal waters throughout ~15 000 km of coastline, spanning 13° of latitude (Jeffs et al. 1999). Marketed as Greenshell™ mussels, the green-lipped mussel is New Zealand's most important seafood product by export value, with NZ$337 million worth of mussels exported in 2019 (Seafood New Zealand 2020). Knowledge of population connectivity in the species is especially important because of the industry's reliance on wild-caught spat (i.e. juvenile mussels) to seed mussel farms and the high vulnerability of this species to localised overfishing (Paul 2012, Toone et al. 2023). While some mussel farms may naturally collect some spat, approximately 80% of all cultured mussels across New Zealand are grown from spat that are harvested at one site — Te Onerōa-a-Tōhe Ninety Mile Beach (NMB) in northern New Zealand (Alfaro et al. 2011, Dunphy et al. 2015). The identification of source populations that supply the mussel spat that arrives at NMB, as well as in other regions surrounding mussel farms, has been a research question of high priority (Dunphy et al. 2015, Gardner et al. 2021, Chaput et al. 2023).

Like many sessile benthic marine invertebrates, the green-lipped mussel's primary opportunity for dispersal and gene flow occurs during the pelagic larval stage (Jeffs et al. 1999, Cowen & Sponaugle 2009). Gametes are released into the water column through broadcast spawning, and fertilised embryos undergo a 3–6 wk planktonic phase during which larvae feed in the water column before settling by attaching to a substratum and metamorphosing into spat (Widdows 1991). However, this important period of their life history is not well understood owing to the difficulty of observing microscopic larvae in the open ocean, and inferences about population connectivity are most often made indirectly. One of the most commonly used indirect methods involves the comparison of haplotypic or genotypic frequencies among sampled populations using population genetic analyses (e.g. Apte & Gardner 2002, Wei et al. 2013a).

Population genetic indices such as Wright's F_{ST}, for measuring genetic distance between populations (Wright 1965), or Bayesian inference tools such as STRUCTURE or Geneland that identify clustering patterns within a metapopulation (Pritchard et al. 2000, Guillot et al. 2005) can provide valuable information about spatially explicit genetic differentiation and/or genetic connectivity. In the case of green-lipped mussels, previous analyses based on 3 different types of molecular markers have identified 2 major clusters of genetic diversity: a northern and southern group, separated by a genetic discontinuity just south of Cook Strait, which is a 22 km stretch of water between the North and South Islands of New Zealand (Apte & Gardner 2002, Star et al. 2003, Wei et al. 2013a). However, while such analyses are widely employed, these statistical approaches are unable to provide information about some of the most important questions about gene flow, including the directionality of connections within and among clusters. For example, genetic analyses have been unable, as yet, to confidently identify the source of spat that arrives at NMB (Dunphy et al. 2015, Gardner et al. 2021). While there are a few software tools that are designed to identify asymmetries in gene flow (e.g. assignment testing of individuals, 'divMigrate', 'migrateN', etc.) (Piry et al. 2004, Beerli & Palczewski 2010, Sundqvist et al. 2016), many data sets do not meet the criteria for minimum sample size and/or number of loci assayed (n = 50 in both cases for divMigrate; Sundqvist et al. 2016) for these tools to provide reliable estimates. Additionally, many genetic metrics of connectivity may reflect signals of structure that are the accumulation of multiple generations of gene flow over much longer evolutionary timescales (Hewitt 2000), making it difficult to disentangle contemporary patterns of gene flow from persistent historical signals of genetic differentiation (Apte & Gardner 2002). Finally, and most impor-

tantly, genetic inferences about population connectivity are limited to the sites sampled, a situation that has long been recognised as a major limitation of applying genetic analyses to study broad-scale connectivity (Beerli 2004, Excoffier & Heckel 2006). Thus, important stepping-stone or source populations may not be identified simply because high-resolution sampling across the entire distribution of a species is often logistically challenging and cost-prohibitive. However, another method for making predictions about gene flow in species that rely on a pelagic larval stage for dispersal that is not subject to these same limitations is biophysical modelling of larval dispersal (Hinrichsen et al. 2011, Silva et al. 2019, Swearer et al. 2019, Quigley et al. 2022).

For many species, including most bivalves, maximum swimming velocities (~1 mm s^{-1}) are often several orders of magnitude lower than that of the ocean currents in which they drift (Troost et al. 2008). Thus, ocean circulation is likely to be the primary driver of dispersal for many species, so high-resolution hydrodynamic models can be used to predict how ocean currents facilitate larval transport and gene flow. Lagrangian particle-tracking models can incorporate any number of biological or behavioural parameters in the model to simulate larval dispersal events as effectively as possible. The results of these particle-tracking experiments may then be compared to population genetic analyses to identify potential oceanographic mechanisms explaining spatial genetic structure and thereby allow novel inferences about connectivity to be made (e.g. Coleman et al. 2011, 2013, Jahnke et al. 2018, Quigley et al. 2022, reviewed by Jahnke & Jonsson 2022). This multidisciplinary approach builds upon the growing field of seascape genetics, the marine counterpart of landscape genetics, which examines how environmental variables (in this case, ocean circulation) may influence patterns of genetic diversity in marine species (e.g. Riginos & Liggins 2013, Wei et al. 2013b). This combined methodology has been applied with increasing frequency over the past 10 yr, and in many cases oceanographic circulation has been shown to be an effective predictor of genetic connectivity. For example, a review of 87 studies applying the combined methodology reported an equal or stronger correlation between measures of genetic distance and dispersal probability predicted by particle-tracking experiments than that observed by isolation by distance alone (Jahnke & Jonsson 2022).

The present study builds upon previous work exploring connectivity among populations of green-lipped mussels. Quigley et al. (2022) conducted particle-tracking experiments from only the 14 sites for which genetic data were available and reported a significant relationship between F_{ST} and predicted migration rates over a single generation (Quigley et al. 2022). Here, we expand upon this work by simulating larval dispersal from not only sites where genetic samples have been taken, but from all suitable mussel habitats across the distribution of the species over 15 000 km of coastline, which are highly likely to contain mussel populations given the widespread distribution of this species across rocky habitats with a wide range of environmental conditions (Jeffs et al. 1999). This study has 3 primary objectives: (1) to examine how the inclusion of multi-generational particle transport through stepping stones in the biophysical model impacts the relationship between the population connectivity predicted by the model and that reported by population genetic data; (2) to identify important stepping stones and source populations in the country beyond those that have been sampled for genetic data; and (3) to make appropriate recommendations for management strategies based on the results of these analyses.

2. MATERIALS AND METHODS

2.1. Study area

This study covered the entire distributional range of the green-lipped mussel, which is found on rocky reefs around New Zealand's coastline. Ocean circulation at the national scale in New Zealand is defined by a generally eastward flow around both of the main islands, driven by the Tasman Front in the north and the Subtropical Front in the south (Fig. 1) (Stevens et al. 2021, Kerry et al. 2023). Prevailing currents include the East Auckland Current and the East Cape Current, which move southeast along the north and east coasts of the North Island (Roemmich & Sutton 1998), the D'Urville Current that flows southeast through Cook Strait (Heath 1971), and the Southland Current, which wraps around the southern end of the South Island, flows up the east coast, and is then deflected eastward over the Chatham Rise (Sutton 2003). Circulation on the west coast of the North Island is less well understood and is believed to be weaker and more variable than on the north and east coasts (Stevens et al. 2021, Kerry et al. 2023). Along the west coast of the South Island, the eastward current from the Tasman Sea bifurcates at around 44° S, resulting in the Fiordland Current flowing south, possibly contributing to the Southland Current

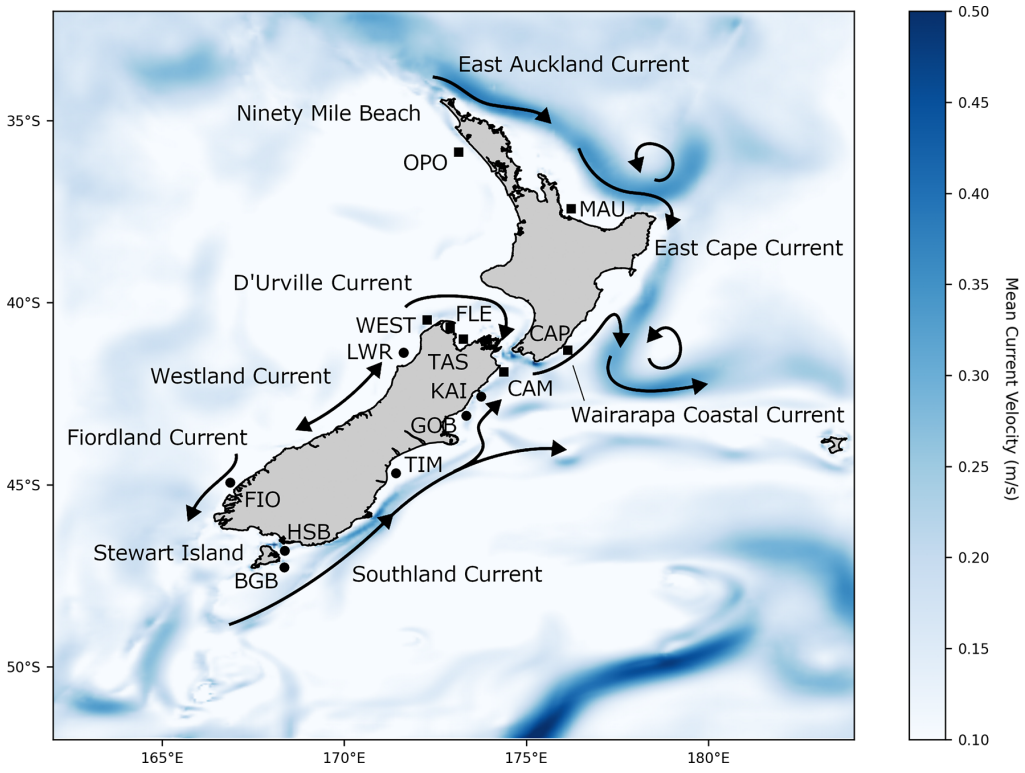

Fig. 1. Sites sampled for genetic analyses by Apte & Gardner (2002) and Wei et al. (2013a), providing data that were used for this study: Opononi (OPO, n = 27), Maunganui (MAU, n = 29), Castlepoint (CAP, n = 30), Westhaven (WEST, n = 13), Fletchers Beach (FLE, n = 14), Tasman Bay (TAS, n = 20; one individual missing data at one locus), Cape Campbell (CAM, n = 30; one individual missing data at one locus), Little Wanganui River (LWR, n = 26), Kaikoura (KAI, n = 16), Gore Bay (GOB, n = 28), Timaru (TIM, n = 22; one individual missing data at one locus), Fiordland (FIO, n = 19), Horseshoe Bay (HSB, n = 22), and Big Glory Bay (BGB, n = 20). Populations of green-lipped mussels are coded according to genetic clusters reported by Wei et al. (2013a): squares: populations in the northern cluster; circles: populations in the southern cluster. Prevailing currents around New Zealand are shown; blue shading: mean current velocity magnitudes across the 23 yr of the analysis. Reproduced with permission from Quigley et al. (2022)

(Chandler et al. 2021), while the Westland Current flows north towards the D'Urville Current and Cook Strait (Heath 1982, Chiswell et al. 2017). This flow is largely wind-driven and may be reversed at times (Stanton 1976).

2.2. Biophysical modelling

2.2.1. Hydrodynamic model

The hydrodynamic model used was the Moana Ocean Hindcast, a 25+ yr hindcast model of the oceanographic state around New Zealand configured using the Regional Ocean Modelling System version 3.9 (de Souza et al. 2023). The model domain extends from 161° E to 176° W and from 52°–31° S and is defined by a curvilinear grid with a horizontal resolution ranging from 4.1 km in the south to 5.8 km in the north. The vertical dimension is divided into 50 vertical layers that are defined by a stretching algorithm that increases resolution at the seafloor and in the surface layer (de Souza et al. 2015). This is the only multi-decadal high-resolution model freely available for the region (de Souza et al. 2023, Kerry et al. 2023), and this work relies on the assumption that oceanographic processes relevant to larval dispersal are represented by the model. The model was run from January 1993 to December 2020, and the first year was discarded as an initialisation period. The model was run at a temporal resolution of 1 h, and all particle-tracking analyses in this study were performed using hourly output fields of velocities and ocean state variables. The model also included atmospheric forcing by incorporating winds, humidity, air temperature, and sea level pressure provided by the Climate Forecast System Reanalysis, National Center for Atmospheric Research. Freshwater inputs from 42 rivers around New Zealand were included (climatological data available from https://catalogue.

data.govt.nz/dataset/river-flows), and tides were incorporated using data provided by the TOPEX/Poseidon global tidal solution (Egbert & Erofeeva 2002). Full configuration and validation of the Moana Backbone model is described by de Souza et al. (2023), with additional validation in Kerry et al. (2023).

2.2.2. Particle tracking

Particle-tracking simulations were conducted using OpenDrift, an open-source Lagrangian particle-tracking tool implemented in Python (Dagestad et al. 2018). All particle tracking was performed offline, using a module designed to simulate the dispersal of bivalve larvae (a version of the model described in Norrie et al. 2020). Simulations followed the methods of Quigley et al. (2022), with a few adjustments to scale the experiment to include all suitable mussel habitat in the domain. The model domain was divided into a 0.1° × 0.1° grid, and 402 grid cells were chosen to represent all of the occurrences of shallow coastal rocky reefs around the country as mapped by New Zealand's Department of Conservation (Department of Conservation and the Ministry of Fisheries 2011) (Fig. 2). Particles were seeded in a 2500 m radius around the centroid of each grid cell, which represented rocky reef habitat. This approach was taken because high spatial resolution distribution data for *Perna canaliculus* are not available, but this species is distributed throughout the country and is abundant in a variety of rocky habitats (e.g. intertidal to subtidal, exposed to sheltered) because of its wide-ranging environmental tolerances (Jeffs et al. 1999). Because of the horizontal resolution of the model, it was not possible to release particles from the seafloor in the nearshore region. Instead, particles were released in the nearest adjacent ocean cell in the top 10 m of the water column, where mussel larvae are most often found (McQuaid & Phillips 2000, Dobretsov & Miron 2001, Helson & Gardner 2004).

Particles were released hourly for 23 yr, from January 1994 to December 2016. A total of 11 particles were released from each site for each hour, for an average of ~8000 particles released per site per month, >2 million particles released per site over the entire study, and ~900 million particles released in total. This number of particles was chosen, after sensitivity testing, to be sufficiently robust against the stochastic variation in the model (as per Quigley et al. 2022). An equal number of particles were released from each site, assumptions of which are outlined the Discussion. Particles were released every day of the year to represent the high degree of variability in the timing of mussel spawning and the presence of mussels with ripe gametes throughout the year due to trickle spawning (Jenkins 1979, Hickman & Illingworth 1980, Alfaro et al. 2001). Particles were given a settlement competency window of between 3 and 6 wk to reflect the pelagic larval duration of *P. canaliculus* (Jeffs et al. 1999), and any particles that arrived at a habitat cell during this window were considered to have settled. Experiments were run that did not force settlement when particles reached a habitat cell during the settlement competency window, and while total

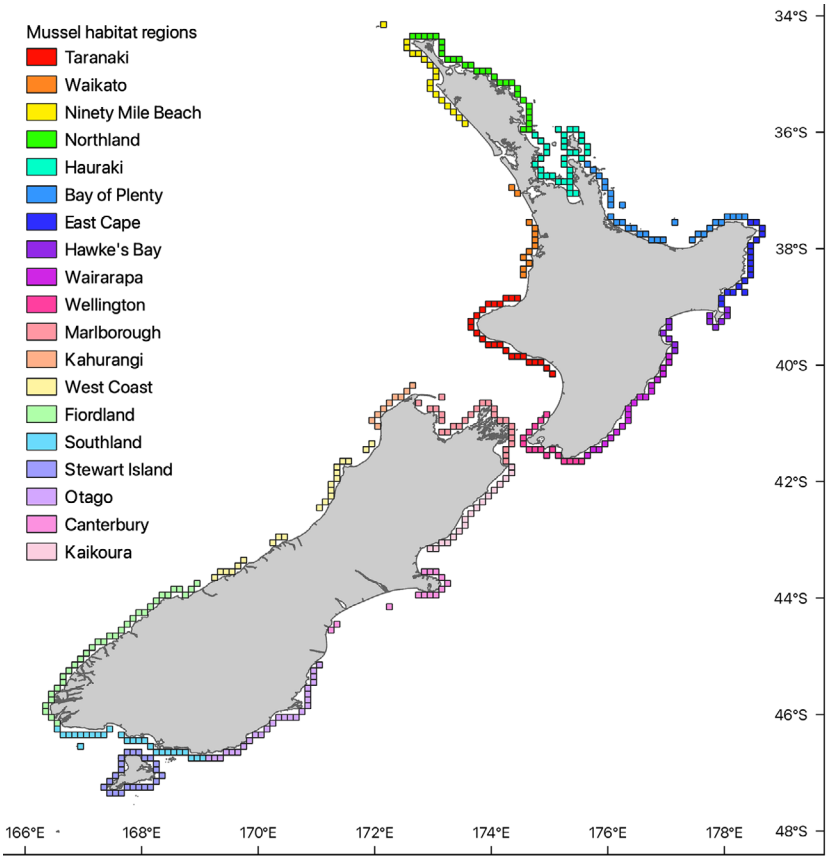

Fig. 2. Grid cells representing all occurrences of rocky reefs around New Zealand. Colour coding corresponds to regions used to organise the migration matrix in Fig. 3

Table 1. Parameters used in the particle-tracking experiment for the green-lipped mussel

Parameter	Value
Number particles released per site per hour	11
Particle release depth	0–10 m
Release period	January 1994–December 2016
Release frequency	1 h
Minimum settlement age	3 wk
Maximum settlement age	6 wk
Particle-tracking timestep	1 h
Advection scheme	Runge-Kutta 4th order
Horizontal diffusivity	0.1176 m^2 s^{-1}
Vertical diffusivity	0.01 m^2 s^{-1}

settlement success naturally decreased, overall patterns of connectivity were not markedly different. Particles that had not settled within 6 wk of release were retired. Particles that encountered the coast before the settlement competency period were returned to their position at the previous timestep using OpenDrift's 'coastline_action:previous' setting. As little is known about the larval behaviours of *P. canaliculus*, simulated larvae were treated as passive particles (Quigley et al. 2022), which seems likely given the limited swimming abilities reported for mussel larvae (Troost et al. 2008). Particles were advected using a fourth-order Runge-Kutta method and a 1 h timestep. Horizontal diffusion of 0.1164 m^2 s^{-1}, calculated using the equations in Okubo & Ebbesmeyer (1976), was included to account for variability that was not captured by the resolution of the hydrodynamic model, along with 0.01 m^2 s^{-1} of vertical diffusion (Table 1).

2.3. Data analyses

A migration matrix, *M*, was constructed from the particle-tracking results with source sites along the *j* axis (vertical) and destination sites along the *i* axis (horizontal), such that element M_{ij} shows the proportion of total settlement at site *i* that originated from site *j* (Davies et al. 2015, Cecino & Treml 2021). The diagonal of this matrix shows self-recruitment, or the proportion of recruits at site *i* that were released from site *i*, and each column sums to 1. This type of 'backward' migration matrix was chosen for comparison to the matrix of pairwise F_{ST} values instead of a 'forward' connectivity matrix (where element M_{ij} shows the proportion of total release from site *j* that arrives at site *i*) because the genetic make-up of a population is the product of all gene flow into that population from potentially multiple sources (Bodmer & Cavalli-Sforza 1968, Song et al. 2006, Bürger 2014). For example, in a forward connectivity matrix, if 100 % of larvae released from site *j* settle in site *i*, element M_{ij} would be equal to 1; however, if site *i* also receives large amounts of larvae from many other sites, the contribution of site *j* to the gene pool at site *i* may still be relatively low. Thus, a forward connectivity matrix would be misleading, as it would not account for potential inflow from other sites, and a backward migration matrix is more appropriate for comparison to metrics of genetic connectivity. Particle-transport results from all years of the simulation were added to produce a matrix representing total connectivity over the 23 yr study period. To calculate gene flow over multiple generations through stepping-stone populations, this matrix was then multiplied by itself multiple times (5, 10, 25, and 50 times).

2.3.1. Source–sink dynamics

To identify source–sink dynamics in the system, 4 metrics of larval connectivity were calculated for each of the 402 coastal grid cells representing mussel habitat sites (Ospina-Alvarez et al. 2020). Each of these measures included particles released from and settled at the same site:

(1) Source total: the percentage of particles released from a site that successfully settled at any site; i.e. out-strength of the vertex in the migration matrix (Barrat et al. 2004).
(2) Source diversity: the percentage of all sites to which a site contributed particles; i.e. out-degree of the vertex in the migration matrix (Vasudev 2006).
(3) Sink total: the number of particles that settled in a site divided by the total number of particles released in the model; i.e. in-strength of the vertex in the migration matrix (Barrat et al. 2004).
(4) Sink diversity: the percentage of all sites from which a site received particles; i.e. in-degree of the vertex in the migration matrix (Vasudev 2006).

Additionally, important stepping-stone populations were identified by calculating the betweenness centrality (the percentage of shortest paths between all pairs of sites that pass through a given site) of all habitat sites in the model using the 'NetworkX' package in Python (v.2.8) (Newman 2001, Hagberg et al. 2008, Treml et al. 2008).

2.3.2. Comparison of connectivity estimates for particle tracking and genetic data

The relationship between the simulated migration matrix and observed genetic connectivity was examined by performing a variation of the Mantel test between a pairwise matrix of F_{ST} and a subset of the migration matrix that only included sites for which there were genetic data (see Quigley et al. 2022; code available at https://doi.org/10.5281/zenodo.7908628). Genetic analyses for this study relied on mussel samples that were collected and analysed by Apte & Gardner (2002) and Wei et al. (2013a). Because F_{ST} cannot provide an estimate of self-recruitment, the diagonal was excluded from both matrices. In addition, because F_{ST} is a symmetric measure of genetic distance, the migration matrix was transformed to be symmetric by taking the mean of transport A→B and B→A, and only one triangle (i.e. one half) of each matrix was used (following De Wit et al. 2020). This was done for each of the multigenerational migration matrices (5, 10, 25, and 50 generations).

3. RESULTS

3.1. Particle-tracking model

Of the ~900 million particles released over the 23 yr period, 48.7% successfully reached a settlement habitat site during the 3–6 wk competency period and were considered to have settled. It is important to note that realised settlement success rates of mussel larvae are likely to be several orders of magnitude lower than those reported here, as this particle-tracking experiment did not include mortality during the pelagic or post-settlement stages but instead represents a relative measure of possible larval transport. The migration matrix showed that the majority of settlement happened locally, with transport centred around the matrix diagonal (Fig. 3). Some areas of the country are well connected beyond local dispersal, such as the populations located around Cook Strait (Wellington, Marlborough, Kahurangi, and Kaikoura), the northeastern populations (Northland, Hauraki, and Bay of Plenty), and the populations around the southern end of the South Island (Southland and Stewart island). By multiplying the matrix by itself to simulate transport over multiple generations, the connections that occur through stepping stones between more distant populations began to emerge. The multi-generational connectivity matrices show that after 50 generations, the matrix had reached a stable state (Fig. 4). This analysis revealed that while particles released from Taranaki, Wellington, and all of the South Island populations were dispersed throughout the system after 25 generations, particles from the majority of the North Island sites were not well connected to the south and were either retained locally or advected eastward out of the system.

3.2. Source–sink dynamics

Source–sink dynamics were largely subject to local processes, but some large asymmetries in the connectivity matrix seem to be driven by mesoscale currents, such as the triangles above the diagonal in the bottom-left and top-right of the matrix, representing

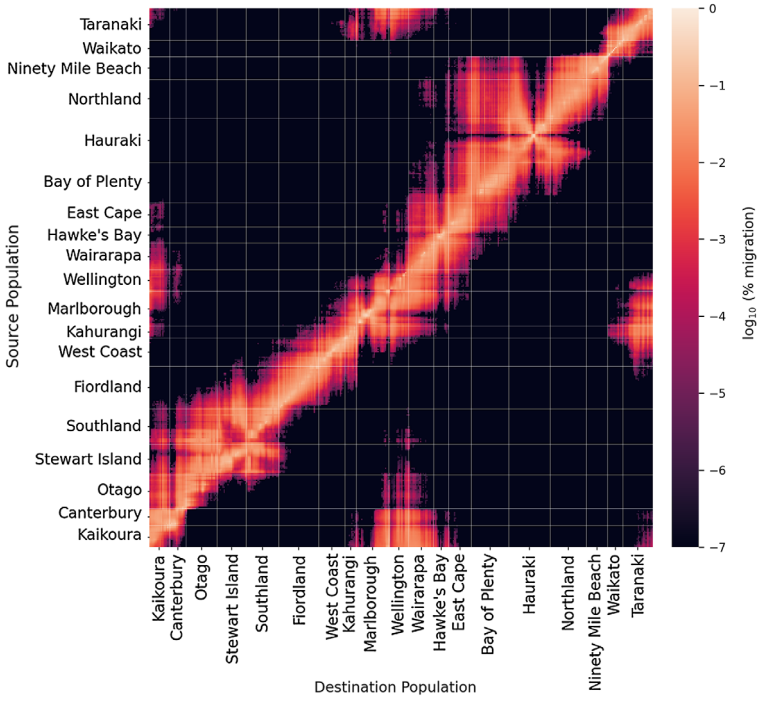

Fig. 3. Migration matrix of modelled successful larval exchange among all sites of suitable habitat for green-lipped mussels around New Zealand. Each element in the matrix shows the proportion of total settlement in each destination site (columns) that originates from each source site (rows). Populations are ordered to maximise structure and follow clockwise from Taranaki around the North Island, through Cook Strait, and then counter-clockwise around the South Island (as per sites and regions defined in Fig. 2). Self-recruitment can be seen along the diagonal

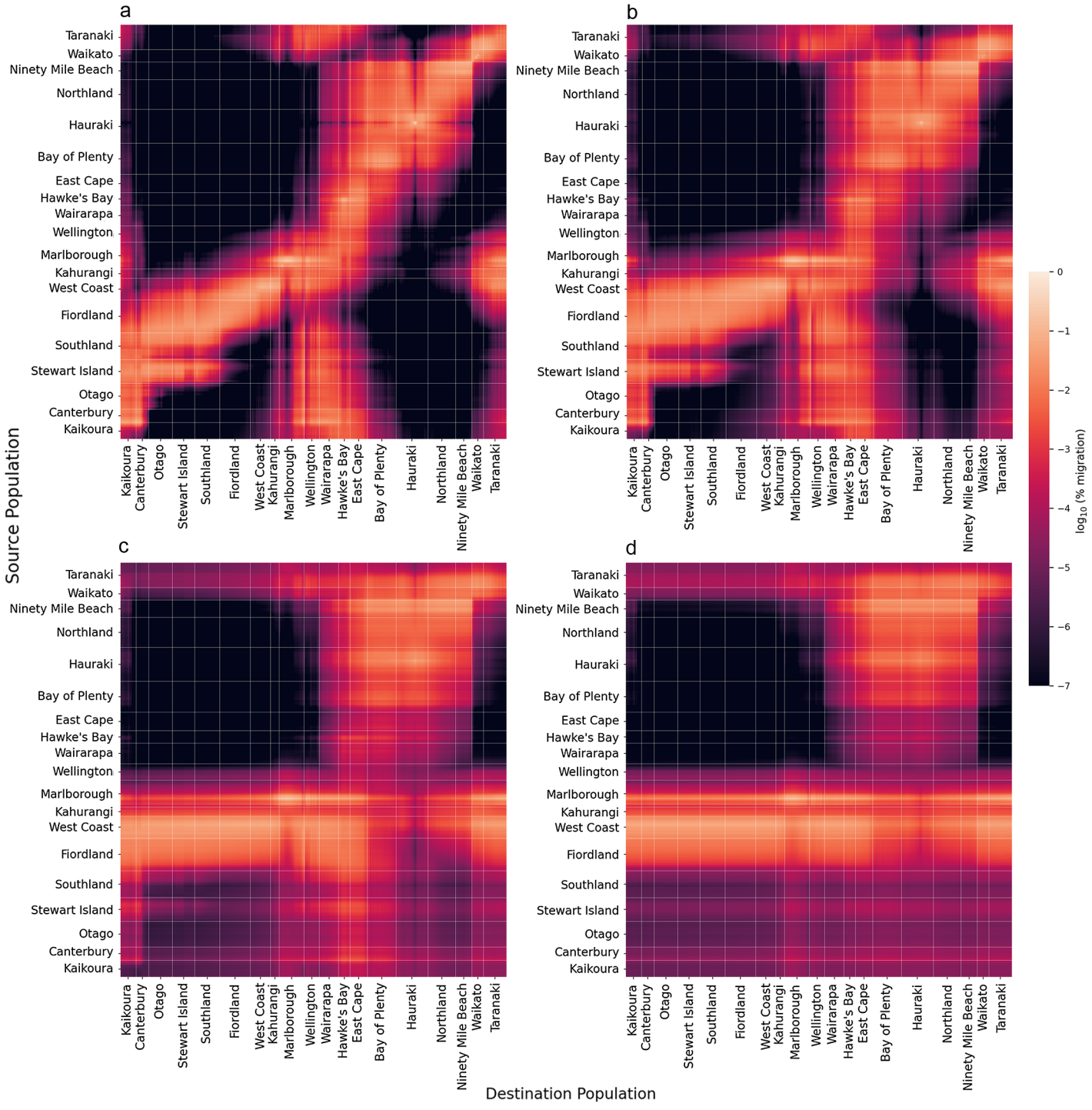

Fig. 4. Multigenerational connectivity matrices for (a) 5, (b) 10, (c) 25, and (d) 50 generations of modelled successful larval exchange among all coastal sites of suitable habitat for green-lipped mussels around New Zealand (refer to Fig. 3 for further details)

directional particle transport by the Southland Current and East Auckland Current, respectively (Fig. 3). Total settlement success rates (source total) varied among regions from 89% (multiple sites in the Waikato region) to only 10% (multiple sites in the eastern Bay of Plenty and East Cape regions) (Fig. 5). Other regions that showed high source totals include Southland, Stewart Island, the West Coast of the South Island, the Hauraki Gulf, and populations in the western Marlborough region that correspond to

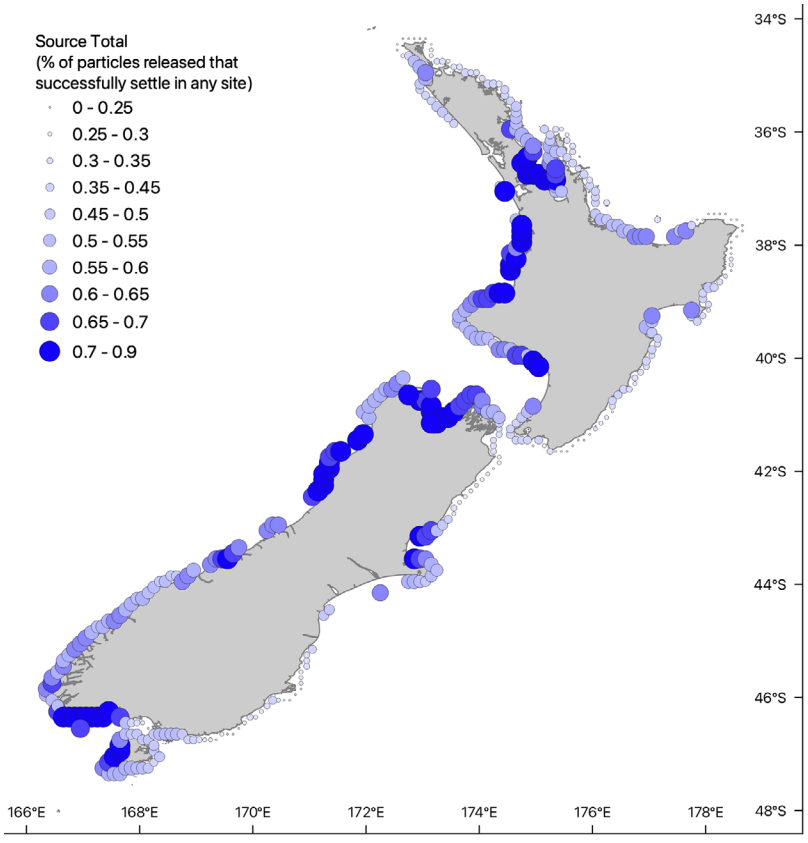

Fig. 5. Source total. The colour and size of the circles represent the total number of particles released from each site that successfully settle in any coastal site containing suitable habitat for green-lipped mussels around New Zealand (as a percentage of the total number of particles released)

Tasman Bay. However, some sites that exhibited high source total contributed particles to a small number of unique populations (low source diversity). For example, Waikato, which showed the highest rates of source total, showed the lowest rates of source diversity, contributing particles to ~10% of total sites in the model (Fig. 6). The sites with the highest source diversity were in the Kahurangi region, which contributed at least one particle to recruitment at ~40% of sites in the system (Fig. 6). High source diversity was also observed throughout the Marlborough and western Wellington regions, in Northland, and in Southland. Total recruitment at each site (sink total) varied from 0.7% of total particles released (multiple sites in Wellington and Southland) to 0.01% (certain sites in Southland, Stewart Island, and Marlborough) (Fig. 7). The sites that received particles from the highest number of unique sites (sink diversity) were along the east coast of the North Island (East Cape, Hawke's Bay, Wairarapa, and Wellington) and the northern South Island (Kaikoura), which received particles from ~50% of sites in the system (Fig. 8). The regions where sites received particles from the fewest number of unique sites were NMB, Waikato, West Coast of the South Island, and Fiordland (<20% of sites). In some cases, high sink total corresponded with high sink diversity (e.g. Wellington, southern Kaikoura, and the eastern Bay of Plenty), while other populations with

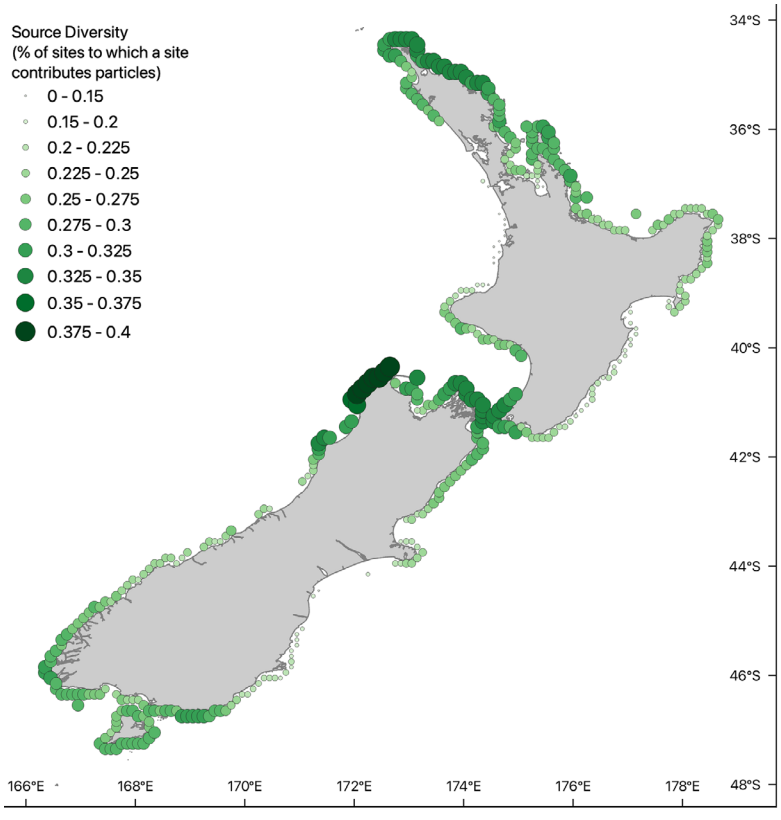

Fig. 6. Source diversity. The colour and size of the circles represent the percentage of all coastal sites containing suitable habitat for green-lipped mussels around New Zealand to which a source site contributes particles

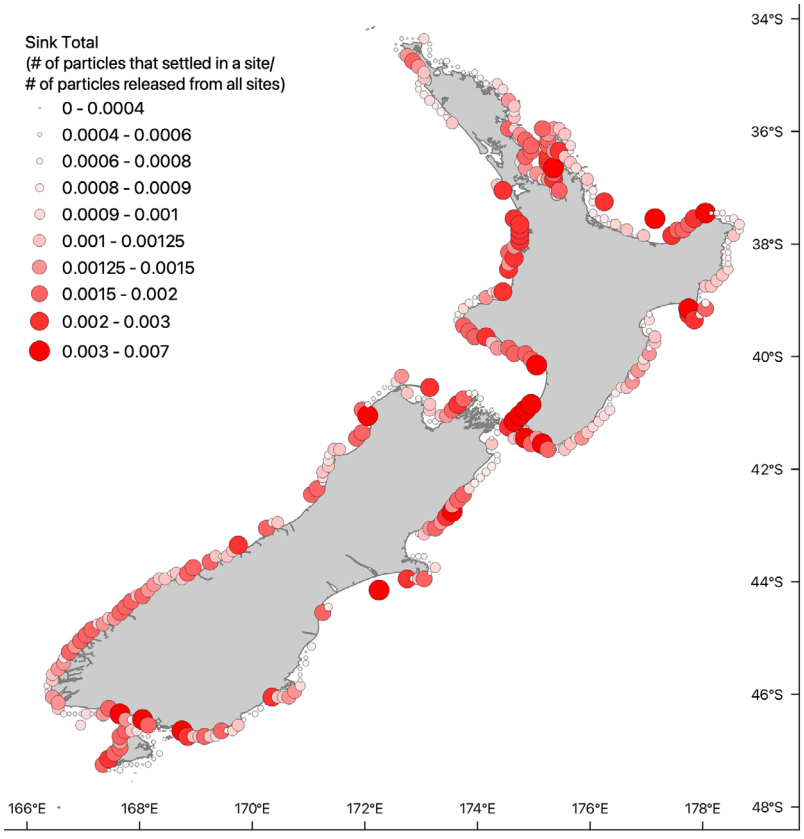

Fig. 7. Sink total. The colour and size of the circles represent the total number of particles that settle in each coastal site containing suitable habitat for green-lipped mussels around New Zealand divided by the total number of particles released from all sites

high sink total showed low sink diversity (e.g. Waikato and populations deep within the Hauraki Gulf). The highest levels of betweenness centrality were observed around the Cook Strait region (Kahurangi, Marlborough, and Wellington, with additional hotspots in Fiordland and the Hauraki Gulf (Fig. 9).

3.3. Comparison of particle-tracking model and genetic data

The variation of the permutational Mantel test performed between the pairwise F_{ST} matrix and the migration matrix revealed a significant relationship (Pearson's correlation coefficient [r] = −0.293, p = 0.005), consistent with the findings of Quigley et al. (2022). However, the strength of the relationship did not increase when compared to the multigeneration matrices as opposed to the single generation matrix (Fig. 10).

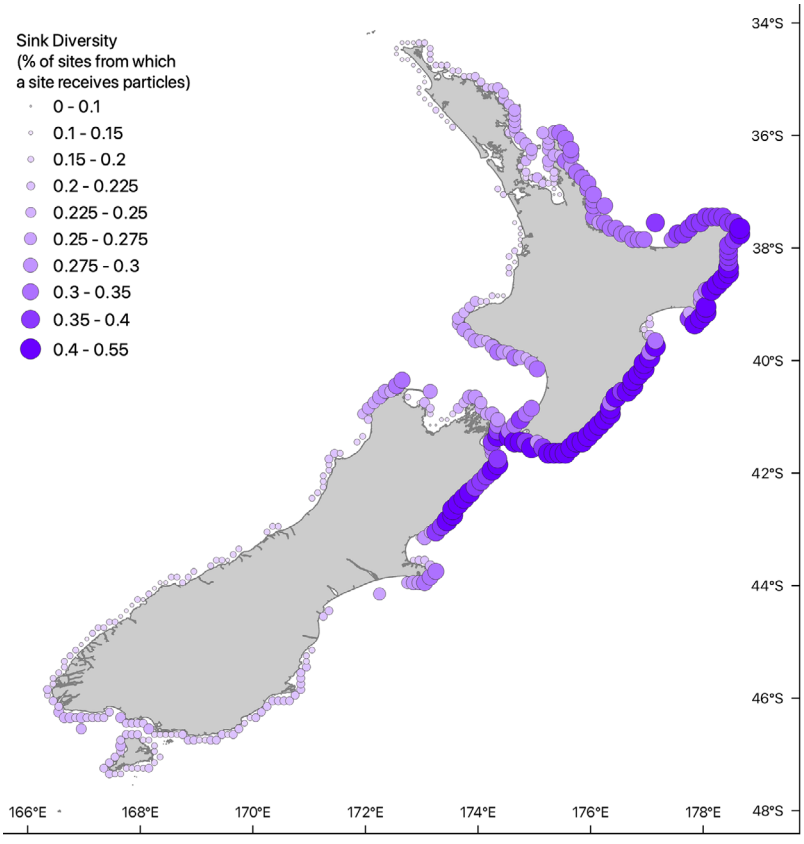

Fig. 8. Sink diversity. The colour and size of the circles represent the percentage of all coastal sites containing suitable habitat for green-lipped mussels around New Zealand from which a site receives particles

4. DISCUSSION

This study explored how a Lagrangian particle-tracking experiment that simulated larval dispersal from all suitable habitat locations over multiple generations within the full distribution of a species can provide new insights into connectivity that other methods may fail to capture. By including all possible mussel habitat in the model, it was possible to identify potentially important source, sink, and stepping-

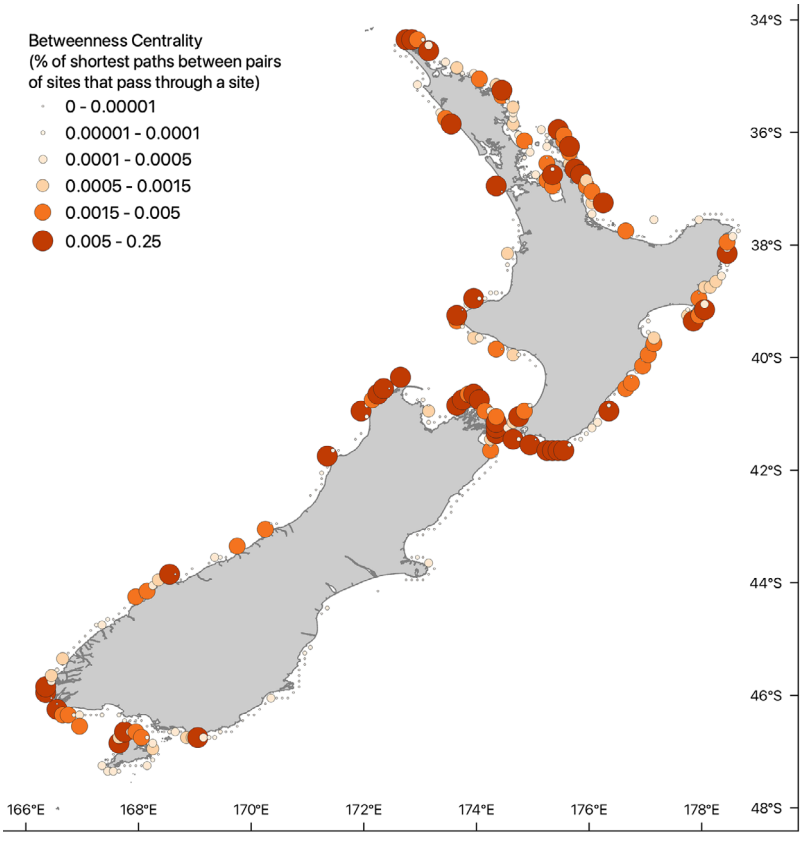

Fig. 9. Map of betweenness centrality for green-lipped mussels at each site. The colour and size of the circles represent the percentage of shortest paths between all sites in the system that pass through a given site

stone populations in the system that could not be identified by genetic analyses alone or by previous biophysical modelling confined to only sites for which mussel genetic data were available (Quigley et al. 2022). In addition, it was possible to estimate multigenerational connectivity through stepping stones, although this did not result in an overall improved fit of the biophysical model predictions to genetic distance.

4.1. Population structure and connectivity among clusters

The present study identified 2 main blocks of connectivity in the migration matrix, with a northern and a southern cluster. This is consistent with previous population genetic analyses and a previous biophysical modelling study (Apte & Gardner 2002, Star et al. 2003, Wei et al. 2013a, Quigley et al. 2022). These clusters are especially visible in the migration matrix representing 50 generations of modelled larval dispersal. Over multiple generations, particles released from the southern cluster are eventually transported throughout coastal New Zealand (i.e. throughout the full distributional range of the mussel), while transport from the northern cluster southwards is much more limited. This pattern of modelled particle connectivity is at odds with the hypothesis from genetic data for green-lipped mussels, particularly from a mitochondrial DNA data set, that the north–south differentiation is driven by some sort of restriction of gene flow from south to north. This assumption is based on the presence of a unique haplotype that occurs only in southern populations in the mtDNA data (Apte & Gardner 2002). However, phylogeographic studies of other marine invertebrates exhibiting a similar barrier to gene flow just south of the Cook Strait region do not report the presence of private alleles in southern populations (e.g. Goldstien et al. 2006, Veale & Lavery 2011), and the biophysical model here found no evidence of a barrier to gene flow from south to north.

4.2. Multigenerational connectivity

The inclusion of all possible stepping-stone populations in the biophysical model allowed for calculations of multigenerational transport by multiplying the connectivity matrix by itself a number of times (5, 10, 25, and 50 generations). Because of the large spatial scale of the study, many of the sites, including locations where genetic samples have been taken, were not connected by particle transport in only one generation. Therefore, when comparing genetic connectivity to the single generation migration matrix produced by the particle-tracking data, most connections in the biophysical matrix were zero. This is expected, given the distance (mean of ~1000 km) between pairs of the 14 sampling sites. However, genetic data identified that green-lipped mussels form at least 2 well-mixed clusters, with a limited amount of transport between them (Apte & Gardner 2002, Star et al. 2003, Wei et al. 2013a). This suggests that gene flow is occurring even between populations where no transport is predicted by particle-tracking data for a single generation, presumably through non-sampled stepping-stone sites. Applying a robust biophysical modelling approach that includes all possible stepping-stone populations has

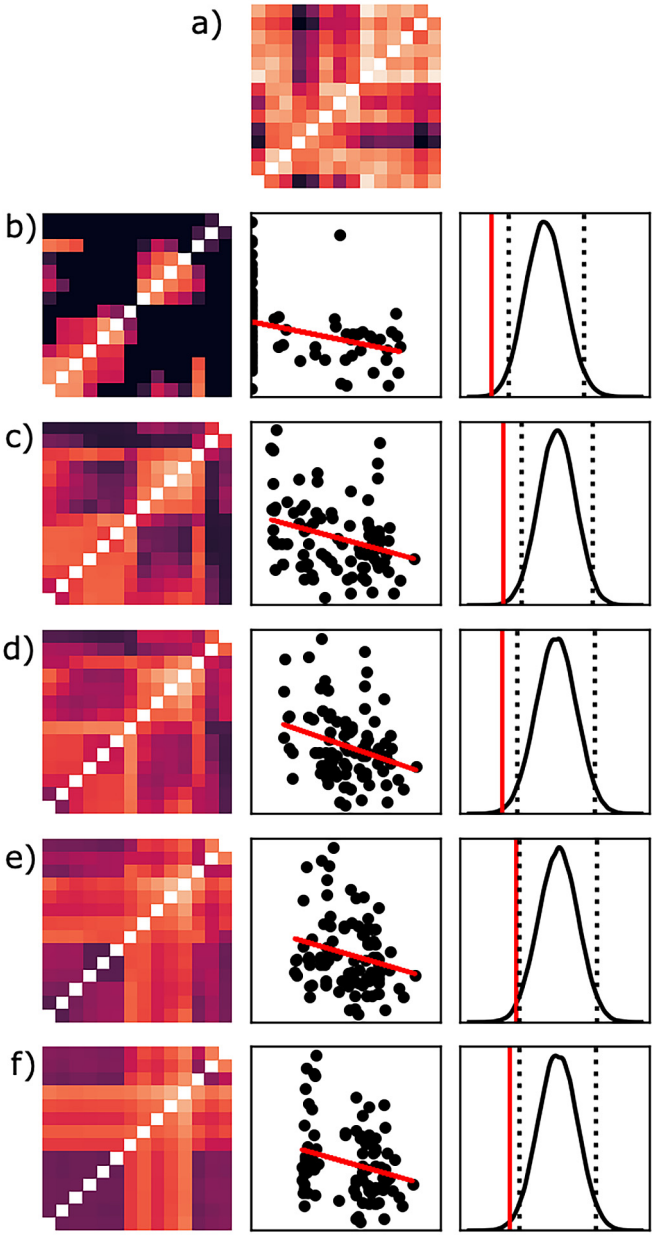

Fig. 10. Comparisons of multigenerational green-lipped mussel migration matrices to the pairwise F_{ST} matrix. (a) Pairwise F_{ST} matrix (Wei et al. 2013a). Ordering of the populations follows the same pattern as the migration matrix in Fig. 3 (From top to bottom and left to right: OPO, MAU, CAP, TAS, FLE, WEST, LWR, FIO, HSB, BGB, TIM, GOB, KAI, CAM). (b–f) Left panel: the migration matrix, subsampled to show only sites representing the 14 populations sampled for genetic analysis; middle panel: pairwise relationships between elements in one triangle of the migration matrix and one triangle of the F_{ST} matrix plotted as points, with a line showing the best fit of the data; right panel: distribution of correlation coefficients between the migration matrix and 1 000 000 permutations of the pairwise F_{ST} matrix. Dotted lines enclose 95% of the distribution; solid line: correlation coefficient of the unpermuted data. (b) One generation: Pearson's correlation coefficient (r) = −0.293, p = 0.005; (c) 5 generations: r = −0.307, p = 0.003; (d) 10 generations: r = −0.284, p = 0.006; (e) 25 generations: r = −0.228, p = 0.03; (f) 50 generations, r = −0.26, p = 0.013

allowed for the estimation of these multigenerational connections. However, comparing the pairwise F_{ST} matrix to the multigenerational migration matrices (5, 10, 25, and 50 generations) did not improve the strength of this relationship. This is consistent with the findings of a review of studies that brought together genetic connectivity data with particle-tracking models (Jahnke & Jonsson 2022), which found that including stepping stones did not improve the correlation of the 2 data sets. However, some studies have shown that this may still be a valuable approach, especially for studies on spatial scales of 100s of km (Jahnke et al. 2018, De Wit et al. 2020).

4.3. Identifying source–sink dynamics and populations of interest

A significant benefit of including all possible habitat locations when simulating larval dispersal for a species is the ability to identify source populations and stepping-stone sites that would otherwise go unrecognised. This subject, which is important for managers to understand (Pulliam 1988, Crowder et al. 2000, Hansen 2011), can be complex and may be resource-intensive to answer using molecular tools alone (Muirhead et al. 2008, Heinrichs et al. 2019). While previous population genetic analyses have been able to identify 2 primary genetic clusters in New Zealand green-lipped mussels (Apte & Gardner 2002, Star et al. 2003, Wei et al. 2013a), they were unable to describe the directionality of connections within and between these groups. Analytical tools such as divMigrate and GENECLASS2, which are designed to identify asymmetries and directionality of gene flow, often require large sample sizes (~50 individuals per site) and high numbers of assayed loci (~50 loci per individual) to produce reliable estimates (Piry et al. 2004, Sundqvist et al. 2016), and therefore many publicly available data sets cannot be used in such analyses. Even when these analyses can be applied successfully to a species, inferences about source–sink dynamics and stepping-stone populations are limited to the populations sampled. While sample sites may be selected with prior knowledge about potentially important populations in the species, the possibility remains that other non-sampled populations unknown to researchers may play important roles in population dynamics. As identification and protection of a source population in a species may

result in increased harvest pressure on adjacent populations, it is important to be confident that potentially significant populations are not overlooked when planning management strategies (Crowder et al. 2000). Because molecular sampling of all known populations of a species is cost-prohibitive and logistically infeasible, Lagrangian particle-tracking experiments can be used efficiently to inform management decisions and identify areas of interest for future study, including informing site selection for additional genetic sampling.

Source–sink dynamics of New Zealand green-lipped mussels are driven by both local and mesoscale processes. On the local scale, geographic features such as the partially enclosed Hauraki Gulf and the Marlborough Sounds lead to increased retention of particles. At the mesoscale, strong prevailing currents may facilitate larval transport, as is seen at Kahurangi Point and along the Northland coast, where the D'Urville Current and East Auckland Current, respectively, result in widespread dispersal of particles to other habitats in other regions. In other cases, boundary currents may be responsible for advecting particles too far offshore for them to return to the coast and settle successfully, as the Southland Current does for many of the particles released from the Otago coastline. At the national scale, the main west-to-east fronts that drive New Zealand's current regime (the Tasman Front in the north and the Subtropical Front in the south) seem to play an important role in source–sink dynamics: populations along the east coasts of New Zealand (East Cape, Wairarapa, Wellington, and Kaikoura) receive particles from a far greater number of sites, while many west coast populations (NMB, Waikato, West Coast, and Fiordland) receive particles from far fewer populations and likely rely much more on local recruitment, including self-recruitment.

Analyses such as those described in this paper are useful for identifying notable regions for future study of green-lipped mussel connectivity. Mussel populations at Kahurangi, Marlborough, and Wellington that displayed high betweenness centrality in the migration matrix play an important role as stepping-stone populations that link the 2 primary genetic clusters (north and south) because of their central locations and because currents in the region lead to widespread dispersal of simulated larvae. Notable potential source populations were identified, including the Canterbury populations north of Banks Peninsula, for their role in supplying larvae to populations along the Kaikoura coast and the Southland and Stewart Island populations that show high levels of self-recruitment and also contribute to settlement at Otago, where self-recruitment is low. Additionally, it is important to identify populations with low sink diversity that receive particles from the fewest number of other sites in the system, such as NMB, Waikato, and the West Coast of the South Island. While total settlement at these sites may be high, these populations are largely reliant on self-recruitment and are therefore more susceptible to local disturbances (Thorrold et al. 2001, Madduppa et al. 2014). This is especially noteworthy in the case of the NMB populations because of their role in maintaining New Zealand's Greenshell™ mussel aquaculture industry; as noted previously, 80% of all cultured mussels originate from mussel spat harvested at NMB (Alfaro et al. 2011). Recent regionally focused Lagrangian particle-tracking work has provided evidence that the majority of spat that arrive at NMB originate from local sources (Chaput et al. 2023), and this national-scale study supports those findings.

4.4. Limitations and areas for future research

A limitation of this approach is the need to assess *in situ* mussel abundance, fecundity, and recruitment at locations of interest identified by the biophysical model. Because these data were not available in the present study, the same number of particles was released from each site where any coastal rocky reef was present in that 0.1° × 0.1° grid cell. While this is reasonable for a modelling approach, it does not represent the ecological reality of site-specific mussel abundances, densities, or sizes. For example, while the biophysical model identified the Wellington region as an important stepping stone for national-scale connectivity, large *Perna canaliculus* populations in this region were — and still are — notably absent (Gardner 2000). For this reason, additional field data about mussel abundance and size at potentially important source or stepping-stone populations will be useful to help inform management decisions. While collecting information on every mussel reef at a large scale may not be feasible or cost-effective, the results highlighted in this study can be used to target specific populations of significance to fill this knowledge gap.

4.5. Management recommendations

This work has identified several mussel populations as priorities for further study and conservation

(Fig. 11). These include potentially important source populations in Canterbury, Southland, and at Stewart Island; stepping-stone populations connecting the northern and southern genetic clusters at Kahurangi, Marlborough, and Wellington; and populations that are heavily reliant on self-recruitment in the Waikato and NMB regions. Assessment of mussel abundance, fecundity, and recruitment at these sites is recommended so that appropriate management decisions may be taken.

As the entire range of *P. canaliculus* falls within New Zealand's jurisdiction, conclusions presented by the present study regarding source–sink dynamics, important stepping-stone populations, and populations susceptible to local disturbances are readily applicable to management decisions. However, this is very often not the case because the distribution of many managed species traverse jurisdictions within and among countries and across maritime boundaries (Kough et al. 2013). As the harvest of individuals in one region may have immediate impacts on populations in other regions, an approach that considers source–sink dynamics across borders, whether they be international or regional within a nation, is critical to the successful management of widely dispersing marine species.

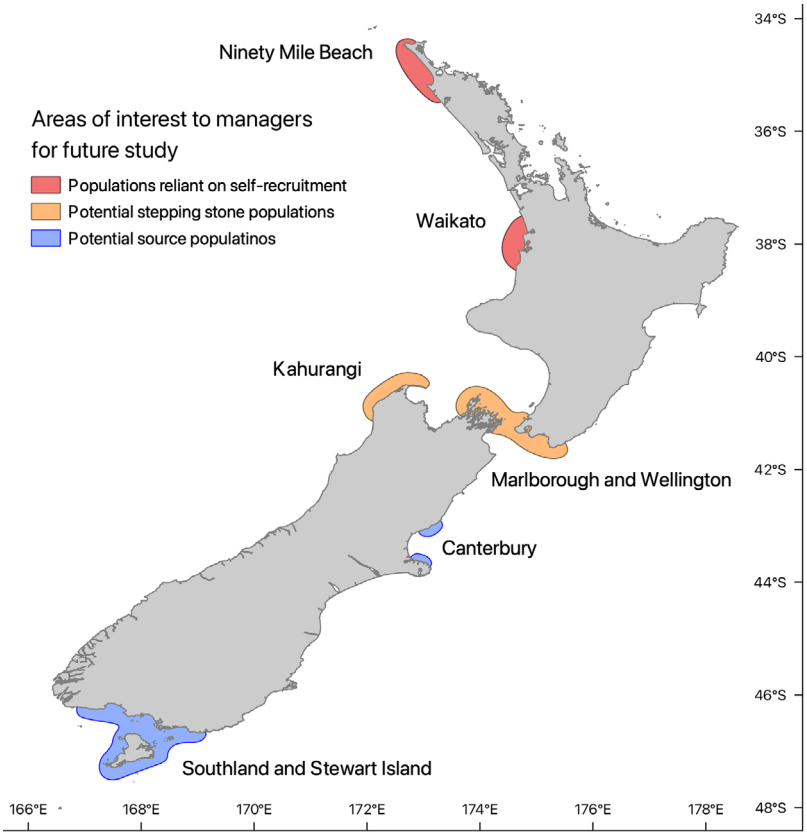

Fig. 11. Areas of potential interest to managers for future study of green-lipped mussels. Colour legend represents the reason for the significance of a population to the health of the metapopulation

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