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Modelling the differences between El Nino and La Nina years and planktonic larval duration on dispersal across the southeast Australian biogeographic barrier

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Abstract

Phylogeographic and genetic studies have revealed complex variation in connectivity across the Southeast Australian Biogeographic Barrier (SEABB) for intertidal rocky-shore invertebrates. The objective of this study was to use Connie2 to test whether differences between El Niño and La Niña years alter the probability of larvae crossing the SEABB. The SEABB occurs on the SE corner of Australia and is the convergence site of two major ocean currents (Zeehan and East Australian Currents) as well as an historical land bridge connecting Tasmania to the mainland. It includes extensive sandy shore lacking suitable substrate for rocky-shore specialists. Study locations included coastal sites from New South Wales, Victoria, and Tasmania categorised into four regions (Barrier, Eastern, Western, and Southern). Connie2, an interactive hydrodynamic modelling tool available online, was used to evaluate connectivity via larval dispersal by comparing the effect of planktonic larval duration (PLD) from five to 120 days, season of spawning, and ENSO variability (comparing La Niña and El Niño years) on the cumulative probability of dispersal between and among populations (regions) arrayed either side of the SEABB. For all years, strong connections were detected among sites within regions, even for low to moderate (less than 20% predicted dispersal) PLDs and irrespective of season. Connectivity across SEABB (between regions) was also strongly influenced by all variables but occurred only at PLD of at least 30 days for summer spawning. Connectivity across the SEABB was strongest from west to east and south to east during La Niña events. Our findings support the importance of SEABB as a barrier to dispersal. Migration across SEABB is predicted only for summer spawners (PLD \geq 30 days). Predicted dispersal is only weakly influenced by El Niño and La Niña extremes, but connectivity may be altered by projected changes to the relative strengths of the Zeehan and East Australian Currents.

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Modelling the differences between El Niño and La Niña years and planktonic larval duration on dispersal across the southeast Australian biogeographic barrier

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Phylogeographic and genetic studies have revealed complex variation in connectivity across the Southeast Australian Biogeographic Barrier (SEABB) for intertidal rocky-shore invertebrates. The objective of this study was to use Connie2 to test whether differences between El Niño and La Niña years alter the probability of larvae crossing the SEABB. The SEABB occurs on the SE corner of Australia and is the convergence site of two major ocean currents (Zeehan and East Australian Currents) as well as an historical land bridge connecting Tasmania to the mainland. It includes extensive sandy shore lacking suitable substrate for rocky-shore specialists. Study locations included coastal sites from New South Wales, Victoria, and Tasmania categorised into four regions (Barrier, Eastern, Western, and Southern). Connie2, an interactive hydrodynamic modelling tool available online, was used to evaluate connectivity via larval dispersal by comparing the effect of planktonic larval duration (PLD) from five to 120 days, season of spawning, and ENSO variability (comparing La Niña and El Niño years) on the cumulative probability of dispersal between and among populations (regions) arrayed either side of the SEABB. For all years, strong connections were detected among sites within regions, even for low to moderate (less than 20% predicted dispersal) PLDs and irrespective of season. Connectivity across SEABB (between regions) was also strongly influenced by all variables but occurred only at PLD of at least 30 days for summer spawning. Connectivity across the SEABB was strongest from west to east and south to east during La Niña events. Our findings support the importance of SEABB as a barrier to dispersal. Migration across SEABB is predicted only for summer spawners (PLD \geq 30 days). Predicted dispersal is only weakly influenced by El Niño and La Niña extremes, but connectivity may be altered by projected changes to the relative strengths of the Zeehan and East Australian Currents.

KEYWORDS

Australia, connectivity, El Niño, La Niña, oceanographic modelling, pelagic larval duration

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1 | INTRODUCTION

Oceanographic, physical, and habitat barriers are often associated with species range limits (e.g., Gaylord & Gaines, 2000) or genetic discontinuities (e.g., Ayre et al., 2009; Henriques et al., 2016) impacting the ecosystem, evolution, and the demography of the area (Caplat et al., 2016). However, it is usually unclear whether such range limits reflect the failure of species to disperse across barriers or a failure of colonists to recruit successfully. For most marine species, exchange among populations or regions occurs primarily during a planktonic larval stage where tagging and tracking are virtually impossible. Oceanographic models are an effective tool to infer the potential of organisms to disperse across barriers under a range of conditions, for example, see Wood et al. (2014) and the review of Caplat et al. (2016). Critically, such models can incorporate interactions between the seasonal and inter-annual variability in the strength of ocean currents and timing of reproduction and planktonic larval duration (PLD) (Cowen & Sponaugle, 2009). Perhaps most importantly, online toolkits such as Connie2, which incorporate ocean models to reanalyse data (Condie et al., 2005, 2012), allow the estimation of the strength of connectivity across a range of spatial and temporal scales. They provide the opportunity to examine patterns of dispersal for a variety of species during “extreme” conditions (i.e., ENSO oscillations) or, for example, can be species specific but target dispersal on a global level (Wood et al., 2014). The importance of extreme or stochastic dispersal events in setting range limits is increasingly being recognised (Lessios & Robertson, 2006; Shanks, 2009; Williams & Hastings, 2013), and an understanding of a region's oceanography is integral in determining the likelihood of extreme dispersal events.

The southeast (SE) coast of Australia contains a prominent marine biogeographic barrier (Bennett & Pope, 1953; Hidas et al., 2007; Knox, 1963), the Southeast Australian Biogeographic Barrier (SEABB). The SEABB's effectiveness as a barrier is due to both the physical geography of the SE corner lacking suitable habitat for rocky shore invertebrates, mostly comprising a sandy shoreline at Ninety Mile beach, and the effects of major ocean currents converging in this region (Figure 1). The ability of the SEABB in setting species range limits or producing population genetic differentiation is highly variable (see the review of Colgan, 2016). There is also evidence of southward range extensions facilitated by strengthening southerly flows, potentially undermining previous genetic discontinuities (Ling et al., 2009; Poloczanska et al., 2007; Suthers et al., 2011). Understanding the conditions under which some species can cross this barrier would be a major step towards predicting species distributions under climate change and disentangling the importance of dispersal versus other biotic and abiotic factors in setting species' ranges (Waters, 2011). Dispersal among sites within regions of the SE Australian coast and across the SEABB is expected to be strongly influenced by two major sets of ocean currents: the eastward and cooler flowing Zeehan and South Australian Currents (ZC and SAC) and the warmer southward flowing East Australian Current (EAC) (Figure 1). The strength of these currents especially the EAC, are highly variable across years and seasons (Ridgway & Godfrey, 1997; Sandery & Kämpf, 2007) and are potentially sensitive to Southern Oscillation (ENSO) events (Holbrook et al., 2011; Ridgway, 2007), although Ridgway and Hill (2009) argue that ENSO events are of less importance than inter-annual variation. Nevertheless, the differences between El Niño and the reversal phase of La Niña ENSO weather patterns, including the changes to sea surface temperature (SST), sea level, wind shear, upwelling, and wave action, may influence ocean currents (Li et al., 2015), and subsequently, connectivity (larval dispersal) patterns in this region.

Information from a range of sources, including surveys of rocky shore species distributions (Hidas et al., 2007; Knox, 1963; O'Hara & Poore, 2000), and population genetic and phylogeographic studies (see Ayre et al., 2009; Dawson, 2005; Waters et al., 2005), confirm the persistent presence of SEABB as a complex barrier that historically included the Bassian Isthmus (a land bridge between the Australian mainland and Tasmania). This persistence likely reflects a range of factors including offshore current flow, persistent eddy formation, variation in water temperature, and for many rocky shore invertebrates, the presence of a sandy beach approximately 250 km in length (including Ninety Mile Beach) that lacks suitable habitat (Ayre et al., 2009). The SEABB also acts as a barrier for many subtidal species, for example, see Billingham and Ayre (1996), and Dawson (2005). Importantly, rocky shore species that have range limits (e.g., Waters et al., 2014) or display deep phylogenetic breaks at the SEABB display varying PLDs as discussed by Ayre et al. (2009). However, some rocky shore taxa with comparable PLD display no effects of the SEABB and instead form strongly interconnected (genetically homogeneous) populations arrayed along both the southwest coast and the northern section of the SE coast (Ayre et al., 2009). Taken together, these studies imply that the connectedness of populations across the barrier is not simply a function of PLD, but rather an interaction between PLD, habitat availability, and the complex oceanography of the region.

The objective of this study was to use the simulation package Connie2 to test whether differences between El Niño and La Niña (ENSO variability) alter the probability that larvae will cross the SEABB. Because the probability of crossing the barrier may also be influenced by each species' life history and geographic location, we varied PLD and time of larval release using source sites located above, below, and within the barrier. We expected that dispersal across the barrier would

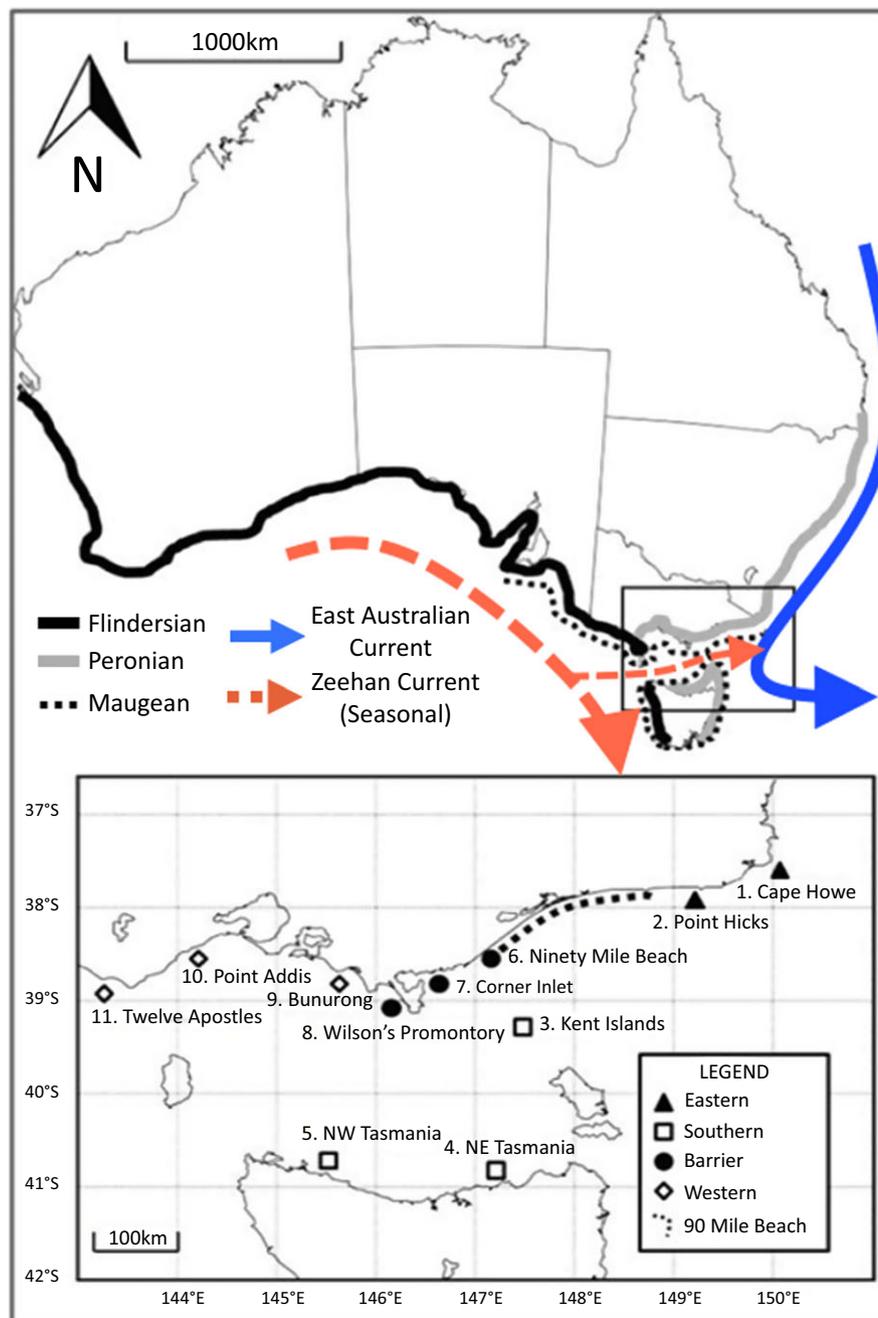


FIGURE 1 Phylogeographic provinces of southern Australia (Knox, 1963) and study sites across the Southeast Australian Biogeographic Barrier (SEABB) chosen for Connie2 simulations. Sites were categorised into four regions (Eastern, Southern, Western, and Barrier) based on their proximity and relative location to the SEABB.

be strongest in a southward direction under the influence of the EAC: for species with long PLD and summer release of larvae and under El Niño rather than La Niña conditions. Our focus was on rocky shore invertebrate taxa and on rocky headlands within four regions: within SEABB (1) and to the north (2), south (3), and west (4) of the SEABB.

2 | MATERIALS AND METHODS

2.1 | The study system and sites chosen

The EAC is typically strongest in summertime, penetrating farther south, while weakening during the winter (Tilburg et al., 2001). The current often separates from the coast at around 32°S, joining the Tasman front and shedding a continuous

series of cyclonic and anticyclonic eddies. These eddies help retain (Condie & Condie, 2016), and may move larvae of rocky-shore taxa, as documented for fish larvae, further down the SE Australian coast and into Tasmania, albeit in an irregular fashion (Booth et al., 2007). The ZC is the most easterly part of the Leeuwin Current and dominates much of the ocean circulation through the Bass Strait. Westerly winds drive an eastward flowthrough for most of the year, with some interruption by southerly winds during the summer (Sandery & Kämpf, 2007). Furthermore, the weakening of the ZC in summer is compounded by the strengthening of the EAC with greater penetration southward and into the straight (Ridgway, 2007). Due to this seasonal variation, we predicted that both the time of larval release (spawning season) and PLD would be important determinants of connectivity in the region.

Sites ($n = 11$) were selected within major regions surrounding and within SEABB to allow us to estimate connectivity within and among these regions, especially dispersal across the SEABB (Figure 1; Table S1). Movement between mainland sites on either side of the barrier would represent direct dispersal across the barrier which separates the long recognised Flindersian and Peronian biogeographic provinces (Knox, 1963) (Figure 1). However, the biogeography of the region is complex because the Island of Tasmania lying to the south, and separated from the mainland by Bass Strait, is also considered to be split between the two provinces (Figure 1). Dispersal across the barrier could also therefore be argued to occur by movement between the SE mainland and northwestern Tasmania and the southwest mainland and northeast Tasmania. Moreover, prominent landmarks, such as points and capes, were selected as they represent suitable habitat for rocky shore specialists and are likely to be exposed to larger scale circulation patterns that would aid longer distance dispersal.

2.2 | The oceanographic model

The Australian Connectivity Interface (Connie2, see <http://www.csiro.au/connie2/>) compiles 14 years of archived historical ocean current data between 1 January 1993 and 31 December 2007, and uses particle tracking techniques (particles are seeded at a rate of 25 particles [$0.1^\circ \times 0.1$ or $\sim 10 \text{ km}^2$] per grid cell per day) to estimate connectivity statistics (Condie et al., 2005, 2012). The Australasian/SE Asia region was selected as the modelling parameter in our simulations. These archived current data come from an assimilating model that has been extensively validated in this region (Schiller et al., 2008).

Connie2 estimates the probability that larvae will pass through a given cell during its dispersal from the source grid cell, providing a biologically relevant estimate of connectivity, as larvae are often able to settle over a range of days once suitable habitat presents itself (Abdul Wahab et al., 2011; McKinney & McKinney, 2002). Using Connie2, we estimated connectivity among the 11 sites within and surrounding the SEABB. For each of the 11 sites, the nearest complete offshore grid cell (i.e., the first cell directly adjacent to the coast containing no land) was selected as a source cell, and we varied the user-defined release period and dispersal duration parameters to correspond to the relevant spawning period and PLD respectively. The chosen release period of 30 days is representative of the number of approximate days in a month. For each simulation, the connectivity between the source cell and each of the 10 remaining sites was then extracted from the model outputs. Some movement of larvae among neighbouring sites on a continuous coastline would inevitably reflect the effect of nearshore, largely wind-driven currents (McQuaid & Phillips, 2000). However, here we are simulating the dispersal of larvae that have already moved off shelf as this would be essential for long-distance dispersal and especially dispersal across the Bass Strait. Since the focus is on long-distance dispersal over many tidal cycles, it was not necessary for the Connie2 model to resolve tides which the model does not explicitly do.

2.3 | Planktonic larval duration

A range of PLDs (of one, five, 10, 15, and 30 days) known as the “dispersion period” were selected and these correspond to values estimated for rocky shore specialists within this region (Ayre et al., 2009). Two longer PLDs (60 and 120 days) were included to simulate substantially long larval survival or rafting events. As accurate estimates of PLD for species of this region are typically based on a single laboratory study, this incremental increase in PLD was used to achieve a comprehensive framework that can provide estimates for a range of species rather than a few specific species. This approach was also useful because many species settle once suitable habitat is presented and not simply at the end of the estimated PLD (Abdul Wahab et al., 2011; McKinney & McKinney, 2002). Our approach also assumed that larvae disperse passively and at a depth of 5 m (as simulated by the model) in the water column. This 5 m is the mid-depth of the layer in the underlying hydrodynamic model used, so that dispersal at this depth is nominally representative of the upper 10 m layer therefore highly representative of the range to capture most of the larvae of interest. For example, see Raby et al. (1994).

2.4 | Temporal variation: ENSO and spawning season

Comparisons were made between different years to demonstrate the variability of connectivity during ENSO. Examination of one weak and one strong El Niño and La Niña event showed this variability based on average Southern Oscillation Index (SOI) values (Table 1) (Bureau of Meteorology [BOM], 2018). We chose these four events based on the strength of the SOI to include the strongest El Niño and La Niña events available in the model.

Seasonal variation was tested by comparing connectivity during the middle month for each of the four seasons: January (summer), April (autumn), July (winter), and October (spring). We selected the middle month of each season as a representative sample of the seasonal differences occurring within a year. Additionally, as simulations were conducted across the entire month (30 days), the sampling design covers in total one quarter of every year for each of the ENSO conditions chosen.

2.5 | Statistical analysis

The outcomes of using each of the 11 selected sites as a source and sink of larvae and contrasting them to yearly seasonal variation across a range of PLDs are summarised graphically, comparing intra- or within-region (Figure 2) and inter-regional (between regions) dispersal (Figure 3). Connectivity matrices for each year are presented as Appendix S1 (Figure S1, EN 1997–1998; Figure S2, EN 2002–2003 Figure S3, LN 1999–2000; Figure S4, 2000–2001, Table S2 and file “Connectivitymatrices Rdata” for raw data values). Connectivity data exhibited overdispersion and excessive zeros and thus zero-inflated negative binomial (ZINB) regression was used to model the effects of season, ENSO, or direction on connectivity. This approach works by firstly modelling the existence of a connection as a binary presence or absence response. If a binary response is present, then the strength of this connection can be subsequently modelled using the negative binomial distribution (used for overdispersed data) (Zuur et al., 2009). Additionally, likelihood ratio tests (LRTs) were run on the ZINB model to test the overall effect of year and ENSO. The LRT determines the contribution of a single (random or fixed) factor by comparing the fit for models with and without the factor (Bolker et al., 2009). All models were implemented using the “pscl” package (Jackman, 2017), and open-source R software v 3.2.1 (R Core Team, 2012).

3 | RESULTS

3.1 | Intra-regional dispersal

Intra-regional dispersal (connectivity between locations within regions: Eastern, Barrier, Southern, and Western) were generally the strongest links made. However, the strength and timing of connection varied markedly among regions. The most reliable and strongest connections occurred among sites within the Barrier and Eastern regions (Figure 2, see Appendix S1). These intra-regional connections were predicted at PLD as low as five days across all seasons.

Intra-regional connections were predicted to be strongest (high probability [%] of dispersal) and statistically significant during the July period (ZINB, $z_{13} = 2.6$, $p = 0.0002$). This trend was most prominent within the Barrier region, where the strongest intra-regional connections were detected (ZINB, $z_{13} = 5.9$, $p < 0.0001$). During April, July, and October larval

TABLE 1 Southern Oscillation Index (SOI) values for the four ENSO events (Bureau of Meteorology (BOM), 2018) used (El Niño: italic, La Niña: bold) with the months used to represent spawning season denoted by an asterisk. El Niño and La Niña events are defined as one year in length and commence in April and July respectively. Plain numbers were not included in the sampling design.

Year	Jan*	Feb	Mar	Apr*	May	Jun	Jul*	Aug	Sep	Oct*	Nov	Dec
1997	4.1	13.3	-8.5	-16.2	-22.4	-24.1	-9.5	-20	-15	-17.8	-15	-9.1
1998	-23.5	-19.2	-28.5	-24.4	0.5	9.9	14.6	9.8	11.1	10.9	12.5	13.3
1999	15.6	8.6	8.9	18.5	1.3	1	4.8	2.1	-0.4	9.1	13.1	12.8
2000	5.1	12.9	9.4	16.8	3.6	-5.5	-3.7	5.3	9.9	9.7	22.4	7.7
2001	8.9	11.9	6.7	0.3	-9	1.8	-3	-8.9	1.4	-1.9	7.2	-9.1
2002	2.7	7.7	-5.2	-3.8	-14.5	-6.3	-7.6	-15	-7.6	-7.4	-6	-10.6
2003	-2	-7.4	-6.8	-5.5	-7.4	-12	2.9	-1.8	-2.2	-1.9	-3.4	9.8

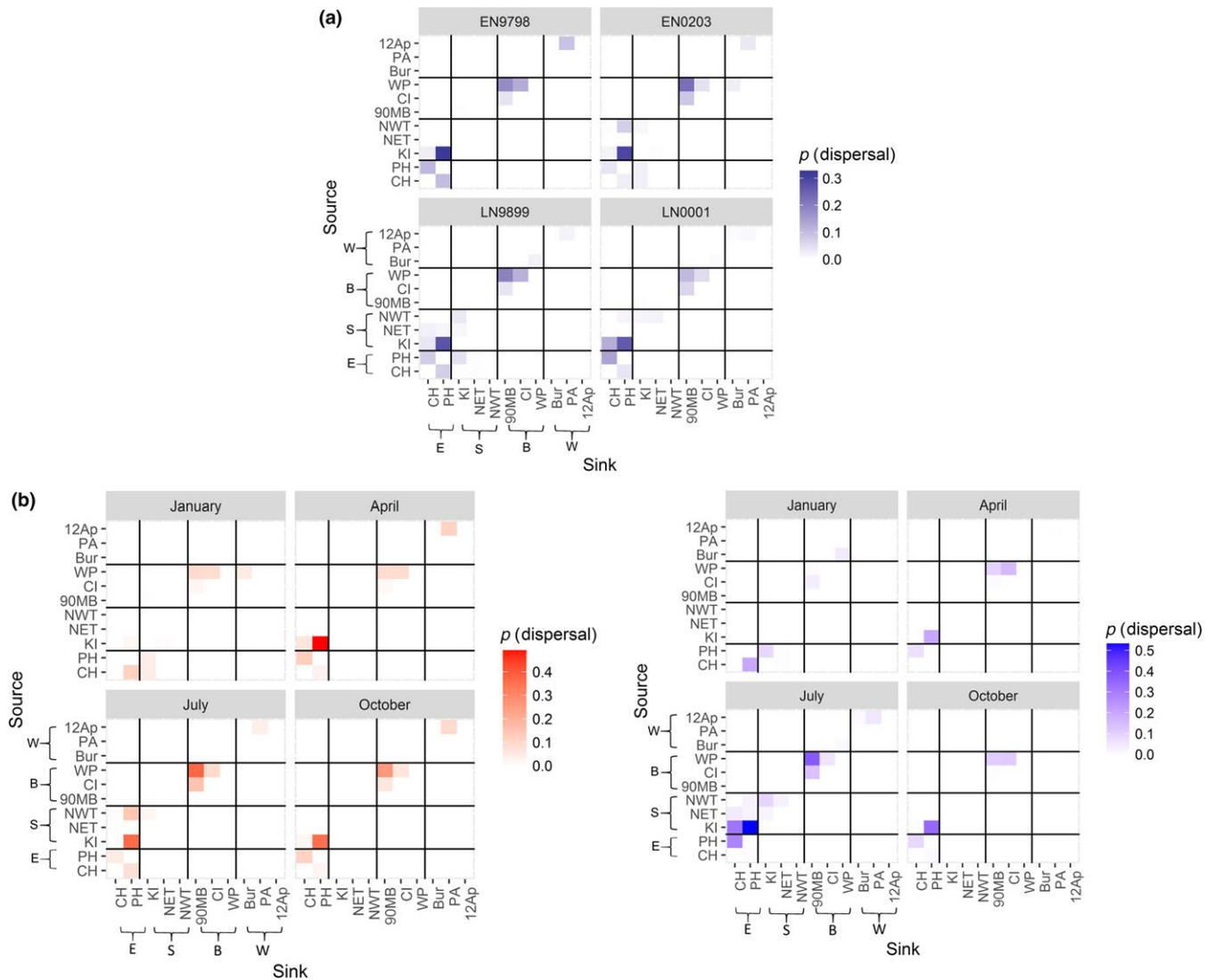


FIGURE 2 Matrices show the cumulative probability of dispersal between source (y axis) and sink (x axis) locations on the southern Australian coast (see Figure 1 for locations). Data are the average of two El Niño and two La Niña (a) years (labelled EN and LN respectively). The matrices allow comparison across planktonic larval durations (PLDs) ranging from five to 120 days and for release periods across all seasons (a), and each of the four seasons (b) for the mean of the two El Niño (left image) and La Niña (right image) years. Each of the matrices are colour coded based on simulated larval dispersal shown as probabilities (%), for the regions named Western (W), Southern (S), Eastern (E) of the Southeast Australian Biogeographic Barrier (SEABB), and at the SEABB or Barrier (B), and sites within regions. Site abbreviations: 12Ap: Twelve Apostles; 90 MB: Ninety Mile Beach; Bur: Bunurong; CH: Cape Howe; CI: Corner Inlet; KI: Kent Islands; NET: Northeast Tasmania; NWT: Northwest Tasmania; PA: Point Addis; PH: Point Hicks; WP: Wilson's Promontory.

dispersal was almost exclusively in a west to east direction for the Barrier, Southern, and Western regions, even at extended PLDs of 60 days (Figure 2). Intra-regional connectivity was almost exclusively from west to east except in the Eastern region where east to west transport was significantly stronger than in the other regions (ZINB, $z_{14} = 5.0$, $p < 0.0001$). This east to west transport was significantly greater during peak flows of the EAC in January, and indeed there was a significant interaction between direction of transport and season (ZINB, $z_{14} = 5.5$, $p < 0.0001$). The ENSO La Niña and El Niño conditions did not have a significant effect upon intra-regional dispersal in the Eastern, Barrier, or Southern regions, however connectivity was higher under El Niño conditions in the Western region (ZINB, $z_{14} = 3.7$, $p = 0.0002$).

Connections among sites within the Southern and Western regions were weak, rarely formed at PLD of less than 30 days, and were strongest during July. As was seen within the Barrier, connections in the Southern region were predominantly in a west to east direction (northern Tasmania acts as source for Kent Islands). This pattern was reversed during January when the dominant west to east flow of the ZC is reversed by the extension of the EAC further into Bass Strait

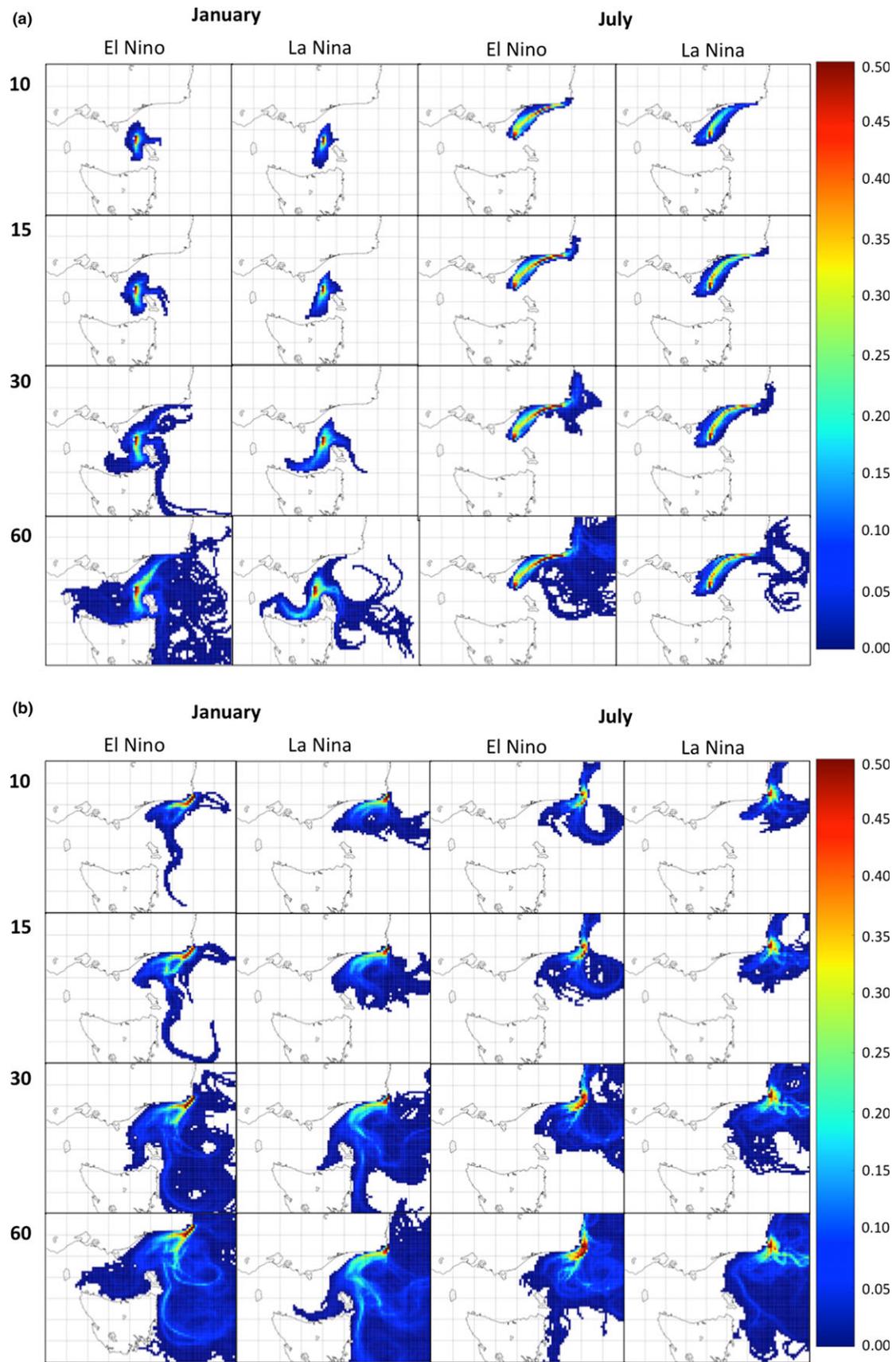


FIGURE 3 Plots of the cumulative probability of predicted dispersal using Kent Islands (a) and Cape Howe (b) as source locations for the average of two El Niño and two La Niña years. Figure represents dispersal in January (summer) compared with July (winter) for a range of planktonic larval durations.

(Kent Islands act as source for northern Tasmania). In the western region, connections were less likely with the only reliable connection occurring between the Twelve Apostles and Point Addis. Again, this connection was weakest in January (less than 1%) and was significantly stronger during El Niño (10%) compared with La Niña (2%) at PLD 60 days (ZINB, $z_{14} = -3.7$, $p = 0.0002$ (Figure 2), thus supporting the prediction that there is a difference between the two ENSO cycles.

Importantly, the model predicted at least some intra-regional connectivity within all the mainland regions at PLD of 15 days (Figure 2). This would allow successful intra-regional dispersal of many rocky shore taxa. Indeed, dispersal within Eastern and Barrier regions was predicted at a PLD of 10 days across all seasons under El Niño and in July and October under La Niña. Overall, intra-regional connections were predominantly west to east and therefore at their strongest later in the year, when the western flowing ZC is at its peak (and the EAC at its weakest). Connections within the East and the Barrier regions were the strongest and most consistent while the ENSO signal was generally weak and non-significant (Figure 2).

3.2 | Inter-regional dispersal

Connectivity between regions was estimated to be rare and required long PLDs, but outcomes were consistent with dominant patterns of the major ocean currents. For example, the strongest and most predictable inter-regional connections were made between the Southern and Eastern regions due to the predominant west to east flow of the ZC, but these were severely disrupted by the weakening of this flow during summer. Connectivity between the Southern and Barrier regions was also commonly predicted at the PLD of 30 days. However, connectivity between other regions was generally weak and inconsistent, requiring vastly extended PLD or very specific release periods (Figure 2).

At a PLD of 15 days, inter-regional movements were restricted solely from west to east between Kent Islands (Southern region) to the Eastern region during April, July, and October, with a pronounced reversal of direction of movement during January. For example, in July under La Niña conditions and for a PLD of 15 days, the probabilities of dispersal from Kent Islands (KI) to Cape Howe (CH) and Point Hicks (PH) were 24% and 40% respectively (Figure 2b). This contrasts with January simulations when connections to these Eastern sites were not observed until PLD reached 120 days, and even then, dispersal was unlikely with probabilities of 1% and 6% respectively (Figure 2). This was the strongest and most reliable inter-regional connection (see below for full description of stepping stone dispersal across the SEABB). In July, under La Niña conditions, a very weak connection (1.2%) between Bunurong (Bur) from the Western region and Wilson's Promontory (WP) of the Barrier region was formed at a PLD of 15 days. However, these sites are close to each other (Figure 1) and therefore, are not representative of strong inter-regional movement.

At 30 days PLD, inter-regional connections were established. Very weak dispersal (less than 0.5%) between the Barrier (90 Mile Beach [MB]) and Southern regions (KI) was predicted during January for La Niña and during January and July for El Niño (Figure 2). During July, for both ENSO conditions, weak to moderate connections (5%–15%) were also predicted between the two northern Tasmanian sites (northwest and northeast Tasmania). Connectivity between the Western and Barrier regions was weak, with dispersal predominantly limited to movement from Bur (weak at less than 5% probability) to the other Western sites during January under El Niño conditions at PLDs of 60 and 120 days (Figure 2). Connectivity between the Barrier and Southern sites was only predicted for PLD of 60 days and 1% probability. However, during January and October at a PLD of 120 days, weak connections (1%–10%) were established between northwest Tasmania and the Barrier sites (Figure 2). Regardless of the ENSO La Niña or El Niño condition, no direct connections were predicted from the Eastern to Western regions during any season, and movement from the west to the east was only found from Bur (the most easterly of the Western sites) during January under La Niña conditions (specifically for the 2000–2001 event, see Appendix S1, Figure S4) at a PLD of 120 days (1%–37%) from all Barrier sites (WP, CI, and 90 MB) to both Eastern sites (CH and PH). The strongest dispersal predicted was at a PLD of 120 days for El Niño from WP to both CH (14%) and PH (37%), from CI to PH (15%), and from 90 MB to PH (31%) (Figure 2b). Based on our simulations, the analyses indicated that direct trans-barrier dispersal is virtually impossible for most intertidal taxa across our 11 sites as direct connections (non-stepping stone) between the Barrier and Eastern regions were not observed until the PLDs exceeded 60 days. Under La Niña conditions, weak dispersal was predicted only in January and in an exclusively west to east direction from all three Barrier sites to PH (WP: 9%, CI: less than 0.5%, 90 MB: 6%; Figure 2b). Under El Niño, west to east connectivity was even less (less than 1%) and only occurred from 90 MB to PH during January and July, while extremely weaker at less than 0.5% dispersal probability for east to west connections (PH to 90 MB and WP) were observed during January, which were only strengthened slightly at PLD of 120 days (1%–3%; Figure 2a). These results show that direct trans-barrier dispersal requires extended PLDs, summer spawning, and is almost exclusively restricted to west to east movement.

3.3 | Stepping stone larval dispersal

Because of the low probability of direct trans-barrier dispersal, the likelihood of stepping stone dispersal across the barrier was also investigated by generating cumulative probability plots of larval dispersal generated using KI and CH as source locations. The predominant west to east flow of the ZC appears to have influenced the strongest and most consistent inter-regional connections observed in this study, linking southern regions, and CH and PH to the SE Australian coast (Barrier region) during April, July, and October, while this connection was reversed during January (see cumulative probability plots of larval dispersal generated using the KI and CH as source locations; Figure 3). When KI was modelled as the source (Figure 3a) it provided a strong connection to the SE mainland coast (CH and PH) during July even for taxa with PLD of five days for both El Niño and La Niña events. In contrast, during January, these connections were only present at a PLD of 30 and 60 days during El Niño and La Niña periods respectively. Furthermore, the magnitude of the connectivity between KI and the SE mainland coast varied enormously, both between seasons and ENSO El Niño and La Niña events. At PLD of 60 days the cumulative probability in July was approximately seven times larger than in January (41% and 6% respectively) during El Niño, but was over 1,400 times (94% and 0.07%) during La Niña events. Despite the seasonal reversal of flow and variability due to ENSO, the strength of this inter-regional connection may facilitate an alternative pathway for larvae to disperse across the SEABB.

3.4 | Variation among individual El Niño and La Niña ENSO Events

Major connectivity patterns such as the strong west to east movement (both intra- and inter-regionally) during April–October were mostly consistent across years. Surprisingly at a broad level, no significant effect was found of either year (LRT $\chi^2_3 = 1.6$, $p = 0.66$) or ENSO (LRT $\chi^2_1 = 1.1$, $p = 0.28$) on dispersal patterns, despite observable differences evident in our simulation data. For example, in the 2002–2003 El Niño event, the strongest west to east connection occurred during April and July, while during the 1997–1998 event, the July connections weakened. April and October then became the strongest months for predicted dispersal. Furthermore, throughout the 2002–2003 El Niño, a strong southward penetration of the EAC (reversal of dominant west to east connectivity patterns) influenced movement within Eastern, Southern (≤ 15 days), and Barrier regions during January. In contrast, during the 1997–1998 El Niño, no inter-regional connections were made from the East to either the Barrier or the South. Similarly, though for La Niña, the southward penetration from the east to KI in January did not occur even at the incredibly high PLD of 120 days in the 2000–2001 La Niña but occurred at PLDs up to 15 days during the 1998–1999 La Niña (see Appendix S1, Figure S3).

4 | DISCUSSION

Our modelling of patterns of connectivity on the SE Australian coast supports that the SEABB does act as a barrier to dispersal for many planktonically dispersing rocky shore species (Ayre et al., 2009; Hidas et al., 2007; Knox, 1963; Waters et al., 2005). Predicted dispersal across the barrier between mainland sites was largely limited to summer spawning taxa with an unusually long PLD of 120 days and was only expected to allow movement from a west to east direction. Furthermore, although the effects of weather and climate events such as the ENSO on the EAC have previously been reported to be weak (Ridgway, 2007; Ridgway & Godfrey, 1997), this was also supported in our study; trans-barrier dispersal was only consistently detected during La Niña periods. Overall, our results closely match the outcomes of a growing number of population genetic and phylogeographic studies that have emphasised the strength of connectivity among mainland sites to the east and west of the SEABB (Banks et al., 2007; Sherman et al., 2008; York et al., 2008), and both the persistent separation of some rocky shore species (Hidas et al., 2007; McWilliam et al., 2013), and genetic lineages with range limits to the northeast and southwest of this barrier (Ayre et al., 2009; Ruis & Teske, 2013).

Historic phylogeographic treatments have been unclear regarding the role of the SEABB in separating the biota of the northeast coast of Tasmania from the eastern mainland coast (Ayre et al., 2009). Indeed, both the northeast Tasmanian coast and the SEABB region have long been considered regions of overlap between the Peronian Province to the northeast and the Maugean province representing southwest Victoria and western Tasmania (Knox, 1963). More recently, there is evidence of an overlap between the eastern warm temperate and cool temperate zones of these regions (Cresswell, 2000). Importantly, our data help to clarify the nature and location of the SEABB. Indeed, our data together with recent genetic studies (Aguilar et al., 2015; Fraser et al., 2009; Waters et al., 2005), of both intertidal and subtidal taxa, show strong connectivity between the NE and NW Tasmanian populations and indeed between the Tasmanian populations and KI in

southwestern Victoria, confirming that the SEABB does separate the biota of Tasmania and southwest Victoria from that of the SE mainland coast.

Our estimates of strong connectivity among sites arrayed along the southern coast of mainland Australia on either side of the SEABB support the large number of genetic studies that have reported either homogeneous population structures or limited evidence of isolation by distance for taxa with a wide range of spawning times and PLDs within these regions (Banks et al., 2007; Sherman et al., 2008). A strong relationship between PLD and the strength of connection within regions was found, with movement within both the Eastern and Barrier regions predicted for PLDs less than 10 days and within the Western region for PLDs less than 15 days, promoting genetic homogeneity within regions. Typically, however, predicted connectivity was consistent year round for the Eastern region, but greater during July and October for the Barrier and Western sites. This seasonal discrepancy is explained by the relative strengths of the SE flowing EAC, which strengthens during the summer, subsequently weakening the west to east flow of the LC and ZC which are at their peak during winter (Ridgway, 2007; Sandery & Kämpf, 2007). Surface transport of particles has also been shown to weaken during summer in the LC and ZC (Ridgway & Condie, 2004). In some species, such as the barnacle *Catomerus polymerus*, the predominant period of larval release coincides with the winter strengthening of the ZC, helping to create genetic homogeneity within Western sites and connect southwestern Victoria with Tasmania (Aguilar et al., 2015; York et al., 2008). Further, Bruce et al. (2001) reported that the July to August spawning of the blue grenadier fish is also consistent with these winter flow patterns and suggested that larval movement from the Bass Strait into New South Wales (Bermagui) is possible (Southern to Eastern sites).

In contrast to the strong connectivity predicted to occur within regions, our data indicate that direct connectivity across the SEABB is extremely unlikely for most taxa, requiring PLD of at least 30 days. Furthermore, transbarrier connectivity was predicted to occur almost exclusively in a west to east direction during summer months. This result appears counterintuitive as the west to east flow of the ZC is typically weakened in summer (Figure 2) by changing wind regimes (Sandery & Kämpf, 2007), and a strengthening of the EAC into the Bass Straight (Ridgway, 2007). However, the great majority of these trans-barrier connections were predicted for La Niña years when west to east connections may be enhanced further by the strengthening of the Leeuwin Current to the west (Ridgway, 2007), in turn, strengthening the ZC's eastward flow. Regardless of the underlying oceanographic causes, direct trans-barrier dispersal appears to be very unlikely for most species, adding further evidence for the effectiveness of the SEABB.

In order to evaluate the effectiveness of the SEABB in restricting dispersal based on our simulations for the 11 selected sites, the promotion of multigenerational migration across the complex barrier via stepping stone dispersal must also be considered. One possible pathway would be to utilise the Southern sites (KI, northeast and northwest Tasmania) to cross the barrier. Our data, however, suggest that this would only be possible for species with both long PLD (mostly greater than 60 days) and either extended spawning periods or the capacity to vary their spawning period to match opportunities for dispersal. Importantly, while dispersal was often predicted to occur between both the Eastern and Barrier sites and KI for PLDs less than 15 days, dispersal between KI and northern Tasmania was only predicted for PLDs greater than 30 days and most commonly in July (Figure 2). Similarly, connectivity between the Western and Barrier sites was only predicted to occur for species with PLDs greater than 60 days, while dispersal from the Barrier to sites to the East were predicted to be most effective during January and April. Therefore, while our data do indicate that the KI group and sites within the barrier region could function as biological stepping stones, only species with long PLD and vastly extended or flexible spawning periods would be able to use these to establish a viable genetic connection across the barrier. Large-scale spatial variation in the timing of spawning or larval release is virtually unstudied on temperate Australian shores and may be a critical barrier to either direct or stepping stone migration for many taxa. Our data may also overestimate the potential for dispersal using sites within the mainland barrier region because this region represents an extensive area of sandy beach and mangrove swamp that provides little potential substrate for rocky shore specialists (see Ayre et al., 2009). The species reported by Ayre et al. (2009) display no genetic effect of the SEABB and were typically able to utilise unusual habitat within this region (*Tetraclitella purpurascens*), had long PLD (*Bembicium nanum*, *Meridiastra calcar*), or rafted dispersal (*Parvalustra exigua* and *Haustrum vinsosa*).

The biological implications of any modelling study such as this must be interpreted with some caution and consideration of both deliberate and unavoidable limitations of the study. For example, in attempting to summarise patterns of dispersal within this region we have used only a single month replicated across four years to capture predicted patterns of dispersal within each season. However, simulations were conducted over the entire month, capturing data for one quarter of each year, thus representing a significant portion of the potential seasonal variation occurring annually. Similarly, in applying the model we selected specific values for PLD and have opted to allow dispersal to occur only within the surface layer. The capacity to control PLD is an important strength of the modelling approach as it allowed us to select PLDs that are representative of published values for intertidal taxa. However, we do acknowledge that published PLDs are typically crude

estimates of actual larval competency and may typically overestimate dispersal due to, for example, high mortality rates (Cowen & Sponaugle, 2009; Faurby & Barber, 2012; Siegel et al., 2003). Moreover, larvae rarely disperse in a passive fashion and at a single depth; rather, larvae often descend to slower undercurrents (Shanks, 2009; Shanks et al., 2003) or form gregarious monospecific aggregations in response to chemical cues (Pawlik, 1992; Toonen & Pawlik, 1994), promoting larval retention, making realised dispersal much lower than predicted by passive dispersal models. Environmental triggers such as favourable temperature may also promote settlement and establishment of larvae, again increasing the gap between realised and potential dispersal (Lathlean et al., 2015; O'Connor et al., 2007).

Perhaps the greatest assumption of any study that attempts to predict connectivity is that dispersal is a good proxy for connectivity. We recognise that trans-SEABB dispersal either via stepping stone or long distance dispersal may be limited by regional environmental variation or by biotic interactions such as competition and predation (Coulson et al., 2011; Waters, 2011). Indeed there are striking variations in substrates, SST, and climates across regions of interest and considerable variation in community structure (Hidas et al., 2007; Lathlean et al., 2012). Further refinement of this modelling approach will therefore require not only better oceanographic models or more detailed application and comparisons, for example, with non-ENSO or “neutral” years. However, we emphasise that extreme instead of neutral years were used to identify major differences between ENSO events. Moreover, as we hypothesised, based on the knowledge of circulation patterns of the ZC and EAC, there was greater seasonal variability and there was not a significant effect of ENSO on dispersal. Further research could focus on reporting across the entire spectrum of ENSO variability, but it seems unlikely to shed more light on the matter as there were no differences found at the extremes used in this study. Also, more precise knowledge of life histories and biotic interactions are necessary. We argue, nonetheless, that this study provides a framework which enables us to predict dispersal and explain genetic divergences and homogeneities, and is the most comprehensive attempt to predict dispersal within this region.

In conclusion, our data provide a contemporary explanation for the continued separation by the SEABB of both species (Hidas et al., 2007; Knox, 1963; McWilliam et al., 2013) and genetic lineages (Ayre et al., 2009; Beck & Styan, 2010; Waters, 2008; York et al., 2008), which like several other biogeographic barriers worldwide display genetic divergences consistent with successive glacial events since the Pleistocene (Barber et al., 2000; Patarnello et al., 2007; Wiley, 1988). The SEABB has historically been associated with the vicariant Bassian Isthmus; however, our results emphasise that for some rocky shore species contemporary patterns of current movement together with a lack of suitable substrate for most rocky shore specialists (Ayre et al., 2009) form an almost impenetrable barrier to direct migration between mainland communities either side of the barrier for virtually all species. Moreover, stepping stone dispersal via the KI and northern Tasmania is likely to be limited by regional differences in the timing of potential dispersal events. These data are largely congruent with the outcomes of the small number of studies that have tested for evidence of phylogeographic separation of southeast and southwest lineages, and for which we have knowledge of spawning time and PLD (Waters et al., 2005; York et al., 2008). Nevertheless, our current paper and targeted application of *Connie2* or alternative models can provide a framework for a more detailed understanding of both differences in community structure between areas to the southeast and southwest of the SEABB and globally for other barriers.

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DATA ACCESSIBILITY

All data supporting this study is provided as supplementary information accompanying this paper.

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SUPPORTING INFORMATION

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

Appendix S1. Cumulative probability matrices for each of the four ENSO events simulated.

Figure S1. El Niño 1997–98 and key legend.

Figure S2. El Niño 2002–03 and key legend.

Figure S3. La Niña 1998–99 and key legend.

Figure S4. La Niña 2000–01 and key legend.

Table S1. Site co-ordinates (latitude and longitude) for locations used in the study.

Table S2. Data supplied in the 'Connectivitymatrices Rdata' file. Each matrix in the file is an [11:11] named matrix containing the connectivity data for summaries of ENSO events and Seasons for each PLD (5, 10, 15, 30, 60 and 120) used in the study.

Data S1. Connectivitymatrices Rdata file.

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