ORIGINAL ARTICLE

Temperate shelf water dispersal by Australian boundary currents: Implications for population connectivity

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Abstract

Boundary currents have been recognized as potential drivers of spatial heterogeneity in the ocean because of their role in physical transport and influence on large-scale coastal processes. In this study, we used particle tracking methods in a data-assimilating eddy-resolving ocean circulation model to determine the effect of multiple boundary currents on connectivity around temperate Australia during the austral winter. Results demonstrated that oceanographic connectivity was asymmetric around Australia, having greater eastward trajectories due to more favorable ocean boundary currents during this season. We validated connectivity patterns with genetic data from an ecologically important species, the kelp, Ecklonia radiata*, which has greater genetic similarity between the west and south coasts of Australia, compared with the east coast, likely due to predominantly eastward propagule dispersal. Boundary current circulation was a coarse predictor of kelp genetic connectivity on multi-generation time scales, and the nature of these relationships varied among the three boundary current systems according to mean current strength.*

Keywords: oceanography, genetic differentiation, kelp, *Ecklonia radiata*

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Introduction

[1] Australia is unique in that it is the only continent with poleward flowing boundary currents along both coastlines. Australia is flanked by the East Australian Current (EAC, the western boundary current of the South Pacific subtropical gyre) and the Leeuwin Current (LC, an atypical eastern boundary current, which flows poleward along the west coast). The LC is driven by a strong meridional pressure gradient in the eastern Indian Ocean, set up mostly by the transport of warm, low-salinity waters from the Pacific to Indian Ocean by the Indonesian Throughflow (Godfrey and Ridgway 1985; McCreary et al. 1986). Moreover, Australia is also unique in that it is the only continent with a wide southern continental shelf and a northern boundary current, the westward flowing Flinders Current (FC) at the shelf break. Seasonally, the South Australian Current flows eastward along the southern shelf (Middleton and Bye 2007) allowing for a possible connection between the eastern and western boundary currents. It is this unique confluence of ocean

circulation that has the potential to transport species and their propagules long distances (e.g., Griffin et al. 2001).

[2] Ocean boundary currents that flow along the continental margins of landmasses are critical determinants of coastal processes, such as larval retention and dispersal (e.g., Southern California, Mitarai et al. 2009; central Chile, Aiken et al. 2007; west coast of Australia, Feng et al. 2010a,), affecting global patterns of diversity, productivity, and ecological function (e.g., Dawson et al. 2005). The strength, direction, and characteristics of continental boundary currents are also key factors in determining connectivity among marine species and populations. Strong currents often promote widespread dispersal and genetic panmixia, whereas weak currents result in genetic structuring with strong relationships to distance (e.g., Coleman et al. 2011a). Mesoscale features such as eddies and upwelling can also cause nonlinear dispersal and recruitment along coastlines (e.g., Connolly et al. 2001; Broitman et al. 2005; Barth et al. 2007) and genetic patchiness (Banks et al. 2007; Barshis et al. 2011). Similarly, temporal variations in current direction can promote bidirectional and asymmetric dispersal (e.g., Feng et al. 2010a; Roughan et al. 2011) and gene flow along coastlines (Coleman et al. 2011a; Alberto et al. 2011).

[3] Although there is an emerging understanding of how oceanic circulation influences connectivity of marine organisms on regional scales, that is, within current systems (e.g., Paris et al. 2005; Mitarai et al. 2009; White et al. 2010) and at small scales (Roughan et al. 2005; Selkoe et al. 2010) there is a lack of knowledge about the role and generality of multiple, interacting current systems on large, continental scales. Understanding the individual and interactive effects of multiple boundary current systems on contemporary patterns of connectivity in marine organisms is critical because it can aid in developing robust conservation strategies that span governmental jurisdictions. It is only recently that numerical models such as the one employed here have been validated with biological data (e.g., Watson et al. 2010; White et al. 2010). Furthermore previous modeling studies (e.g., Aiken et al. 2007; Pearce et al. 2011; Roughan et al. 2011 among others) were generally not validated by biological data,

although Coleman et al. (2011a) made inferences regarding continent-wide connectivity based on genetic data, however, the circulation modeling studies available for comparison were limited to the EAC region alone. There are only a handful of numerical modeling studies that investigate large-scale connectivity, that are then validated with oceanographic data. For example, basin scale connectivity has been modeled and validated in only a few circumstances (e.g., Dawson et al. 2005 over evolutionary timescales; Banks et al. 2007; Sala et al. 2013).

[4] An eddy-resolving data-assimilating ocean model (Bluelink ReAnalysis (BRAN) system, Schiller et al. 2008) was used to investigate oceanographic connectivity both within and among the three interconnected boundary currents surrounding temperate Australia. Specifically, we examined the relationships between population genetic connectivity (population differentiation or F_{ST}) and oceanic circulation for the kelp, *Ecklonia radiata* (C. Agardh) J. Agardh. *E. radiata* is the dominant form of biogenic habitat on Australia's temperate reefs (Connell and Irving 2008) and has a fundamental influence on marine communities supporting a great diversity of fish, invertebrate and algal taxa (e.g., Irving et al. 2004; Coleman et al. 2007). We predicted that genetic and oceanographic connectivity would be correlated around temperate Australia and also at the scale of individual boundary currents. BRAN is a global model that resolves ocean circulation around Australia at a 10-km horizontal scale and has been widely used for regional connectivity studies (Feng et al. 2010a; Roughan et al. 2011; Condie et al. 2011). So far, however, investigations into continental-wide connectivity across the 50°of longitude have not been attempted. The results of this study will improve understanding of how boundary currents influence dispersal and connectivity of marine organisms on regional and continental spatial scales.

Australia's Boundary Currents

[5] Australia has three unique boundary current systems. On Australia's eastern coastline, the EAC flows poleward from the tropics down to Tasmania (Fig. 1). The EAC is the strongest of Australia's currents transporting on average 22 Sv at 30° S (1 Sv = 10^6 m^3 s^{-1})
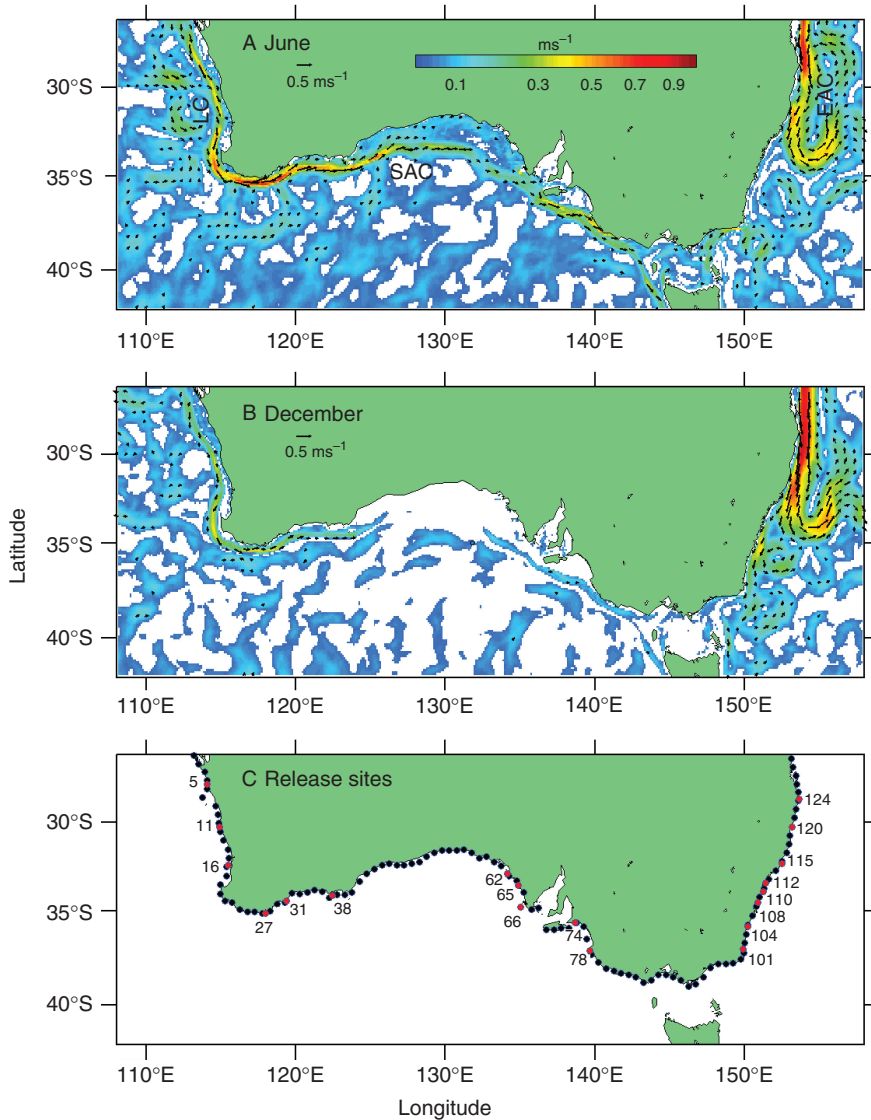
Fig. 1 Climatology of midlatitude sea surface currents (0–20 m) around Australia in June (A) and December (B) averaged over 1996–2007. The EAC, LC, and SAC denote the East Australian Current, Leeuwin Current, and South Australian Current, respectively. Note only surface currents larger than 0.05 ms⁻¹ are plotted, and the color contour scale is not linear. Locations of particle release sites in the model (C). The red dots and numbers denote the genetic sampling locations.

exchanges (Oke and Griffin 2011; Macdonald et al. 2012). The LC flows poleward along the west coast of Australia and extends eastward into the Great Australian Bight (Feng et al. 2003, Fig. 1). The LC has a typical current velocity of 0.5 ms⁻¹ (Cresswell and Vaudrey 1977; Smith et al. 1991) with a mean transport of 3.4 Sv (Feng et al. 2003), ∼20% of the EAC transport. The LC shows a distinct seasonal cycle, with its southward transport reaching a maximum during the austral winter (Smith et al. 1991; Feng et al. 2003). The FC is westward-flowing (mostly subsurface) northern boundary current along Australia's southern slope (Middleton and Cirano 2002; Fig. 1). Inshore of the FC, there is an extension of the LC, the South Australian Current (SAC), that flows eastward on the continental shelf mostly during austral winter (Fig. 1; Ridgway and Condie 2004).

Methods

Eddy-Resolving Model Simulations

[6] BRAN is based on a global ocean model, OFAM (Ocean Forecasting Australia Model), and uses an ensemble data assimilation system (Bluelink Ocean Data Assimilation System) to correct the model with satellite and in situ observations (Oke et al. 2008). Vertically the model has 47 levels, with 10-m resolution down to 200-m depth. It has been evaluated in both the EAC (Oke and Griffin 2011) and the LC (Schiller et al. 2010; Pearce et al. 2011). By adding surface wave-induced Stokes drift into BRAN, Feng et al.

(Mata et al. 2000), with average speeds of up to 1 to 1.5 ms⁻¹ (Roughan and Middleton 2004). The EAC tends to separate from the coastline around 30°–32°S forming the eastward flowing Tasman front. Downstream of the separation point, the EAC generates a vigorous cold (cyclonic) and warm core (anticyclonic) eddy field with a periodicity of ∼100 d (Mata et al. 2006). These eddies drive significant alongshore and cross-shelf

(2011b) were able to simulate the 10-month larval dispersal and settlement of western rock lobster larvae. In this study, daily BRAN estimates of ocean properties including current speed and direction in the surface to 10-m layer from 1996 to 2007 were used.

Particle Tracking

[7] We used the daily model surface velocity to investigate oceanographic connectivity from 25° S poleward to ∼40° S along both the east and west coasts, and around the entire southern portion of the Australian Continent (from ∼110° E to 155° E). Offline particle tracking was undertaken following Feng et al. (2010a). A total of 129 sites (Fig. 1C) were selected along the coast, roughly every 50 km (half degree). Additional release sites were included to incorporate the 19 *E. radiata* sampling locations as described below. The sites are at the center of the model cells adjacent to the land, or ∼5 km off the model coastline, with a minimum water depth of 20 m or deeper. Lagrangian particles ($n = 50$) were released from each site in the top layer of the model each day during April to October (austral autumn/winter when *E. radiata* reproduces) for the 12 yr from 1996 to 2007. Particles were advected passively, which is appropriate for comparison with *E. radiata*. All particles were tracked for a time period corresponding to the maximum dispersal potential time for *E. radiata* (fertile drift), which was considered to be 2 months, or 61 d. Particle tracking was undertaken in two dimensions by using a 4th order Runge–Kutta method (Feng et al. 2010a), with a 1-h time-step. A horizontal diffusivity of 20 $m^2 s^{-1}$ was used to parameterize the effect of flow structure at spatial scales smaller than the grid cell. Particle dispersal results are not different when implementing a horizontal diffusion coefficient of 20 $m^2 s^{-1}$ and are relevant to spatial scales smaller than the grid size (Okubo 1971). The particle dispersal results are not sensitive to the selection of horizontal diffusivity in the 10–50 $m^2 s^{-1}$ range.

Estimating Coastal Connectivity

[8] Coastal connectivity was defined as the probability that a water parcel leaving a source site *j* arrives at destination site *i* over a time interval *T* and is denoted as *Cji* (*T*) (Cowen and Sponaugle 2009). We regard the water

parcel as arrived if it is within a 10-km radius (i.e., one grid cell) of the destination site. The mean connection time between site *j* and site *i* can be expressed as the mean advection time,

$$
T_{ji} = \frac{\int_0^\infty C_{ji}(\tau)\tau d\tau}{\int_0^\infty C_{ji}(\tau)d\tau},
\qquad (1)
$$

where τ is time and corresponds to particle advection time before computing connectivity (C_{ji}) and can be interpreted as pelagic larval duration (PLD) or the maximum time a propagule remains viable for settlement. As we only calculate connectivity over the months that kelp reproduce (austral autumn and winter), to investigate single-generation directional connectivity time we calculate the mean advection time for each year, then ensemble average over the 12 yr of simulations to obtain the first generation connectivity matrix. If locations X to Y are connected in the first generation matrix, the connectivity is assigned as T_{ji}. If X to Y are not connected in one generation, but X to Z and Z to Y are connected in one generation, then it is assumed that X to Y will be connected in two generations and assigned a *T* value of 365 d (1 yr). Whereas for the first generation we have direct estimates of mean advection times, for subsequent generations because of the averaging process, we only obtain nominal years. This approach was continued for multiple generations adding 365 d to *Tji* each generation until all sites are connected. Note that site Y is not necessarily the sampling site it is just a "stepping stone" for connectivity. At the end of the 8 yr the multigenerational matrix was reduced to include only those sites where genetic samples were taken. To compare with genetic data, mean connectivity time was defined irrespective of direction; that is, we took the average connectivity time from X to Y and Y to X, Similarly, we defined the minimum connectivity time as the minimum time between X to Y and Y to X, again, irrespective of direction. Asymmetry in connectivity time for each boundary current was investigated by taking the difference in connectivity times for each pair of sites from the bidirectional matrix.

Ecklonia radiata

[9] Mature kelp sporophytes (attached adult plants) were sampled along 800–1200 km of coastline within each of Australia's three boundary currents in 2006 as described in Coleman et al. (2011a) (Fig. 1C). An additional two locations were sampled at the low-latitude margins of this species distribution; Byron Bay within the EAC (28.6363° S, 153.62359° E) and Kalbari within the LC (27.74197° S, 114.14358° E). Given that kelp is a perennial species, the individuals sampled in this study represent a combined cohort from the previous 3–5 yr. Within each boundary current a hierarchical sampling program was used with individual kelp thalli ("plants") collected within each of two to three sites (km to 10s of km apart) at each of five to eight locations (100s of km apart). A total of 1501 individuals from 19 locations (8 in the EAC, 5 in the LC-extension/FC and 6 in the LC) were genotyped by using six polymorphic microsatellite loci (Dolman and Coleman 2009) as described in Coleman et al. (2009).

Estimating Genetic Connectivity

[10] Connectivity (dispersal) was inferred from genetic differentiation estimated by using genetic fixation (F_{ST}) estimates. A pairwise F_{ST} (connectivity) matrix among all pairs of locations was generated in FSTAT (Goudet 1995). We identified potential first-generation migrants by using GeneClass 2 (Piry et al. 2004) as an indirect measure of past dispersal. Assignment tests are limited by the number of potential "source" populations sampled. That is, an individual will be assigned to one (the most likely) source population, even if there is a low probability that it came from that population. To assess this problem, Gene Class 2 uses Monte Carlo resampling techniques to compute the probability of an individual belonging to each given source population. Tests were done using the Rannala and Mountain (1997) Bayesian method of computing genotypes because this method often performs better than distance-based methods (Cornuet et al. 1999; Berry et al. 2004), particularly when the number of loci and number of replicates are small (Cornuet et al. 1999). Since migration is bidirectional and each population can act as both a source and destination, we first created a triangular matrix of the total number of migrants between all pairs of populations by adding the number of migrants between each pair of populations regardless of direction of migration. This matrix was then transformed into the percentage of individuals that were migrants between all pairs of populations by dividing by the total sample size for each pair of populations. We also estimated asymmetry in dispersal by calculating the differences in the matrices of bidirectional migration and converting these values into the percentage of migration events that indicated trends for net poleward or equatorward migration. For each site we also generated estimates of observed and expected heterozygosity, allelic diversity, and F_{IS} (inbreeding coefficient).

[11] Relationships between pairwise F_{ST} and percentage of migrant matrices, and both mean and minimum oceanographic connectivity matrices were assessed via Mantel tests. We also tested for relationships between oceanographic connectivity and geographic distance. Relationships between estimates of observed and expected heterozygosity, allelic diversity, and F_{IS} for each location were tested against estimates of self-seeding time for that location (the diagonal of a matrix) by using the Pearson Moment correlation. All analyses were done on the continental-wide data set to examine large-scale patterns and also for each boundary current separately.

Results

[12] The LC and the SAC are distinctly stronger in austral winter compared with austral summer, mostly due to seasonal variations of regional wind regimes (e.g., Feng et al. 2003), while the EAC is stronger in austral summer than winter (Fig. 1). There appears to be a restriction of surface current at Bass Strait (between the mainland and Tasmania). During autumn to early winter at the beginning of the reproductive season, there were dominantly southward and eastward trajectories off the west and south coast and dominantly southward flow off the east coast (see Fig. 2A for a representative year corresponding to the cohort of kelp sampled). In Bass Strait, the eastward trajectories and westward trajectories meet on the east side of the strait. Near the end of the reproductive season (illustrated by October 2003 corresponding to the cohort of kelp sampled; Fig. 2B), there were enhanced eddy activities in both the LC and
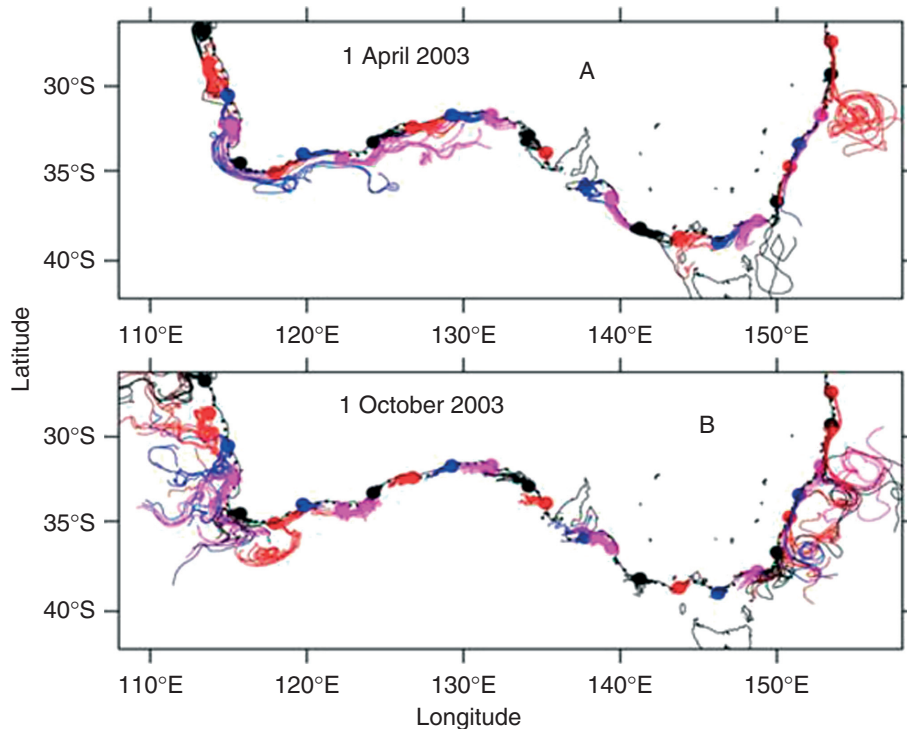
Fig. 2 Representative 60-d trajectories of particles, released on 1 April 2003 (A) and 1 October 2003 (B) (the beginning and end of the *E. radiata* reproductive season). The solid circles are the release sites of the passive particles. Different colors of trajectories are used for ease of visualization.

the EAC, and strong cross-shelf exchanges replaced the alongshore dispersal in both current systems (Fig. 2B). Off the south coast, the SAC became weaker or weakly reversed, thus, the alongshore connectivity also became interrupted.

[13] The continental scale model of single generation oceanographic connectivity time during the reproductive season of *E. radiata* (austral autumn and winter) showed distinct patterns for each current system (Fig. 3A). Oceanographic connectivity was asymmetric within the LC with shorter connectivity times corresponding to the poleward flow of this current (Fig. 3A). Within the EAC oceanographic connectivity was also relatively asymmetrical with more poleward dispersal and shorter connectivity times at lower latitudes relative to more equatorward connectivity from higher latitudes (Fig. 3A). Within all of the currents ~71%–83% of migration events occurred in a net poleward direction (or easterly for the SAC) with 17%–29% in a net equatorward direction (or westerly for the SAC).

Oceanographic connectivity also exhibited distinct patterns among the three currents with the SAC generally having longer connectivity times but shorter dispersal distances between all pairs of sites (Fig. 3). Over multigenerations, there appeared to be greater oceanographic connectivity (faster dispersal times) among distant sites from West (LC) to East (EAC) than vice versa, due to the fact that the LC extension is more effective in overcoming the FC and thus transporting particles eastward during the austral winter (Fig. 3B). It takes 8 yr for all the sampling sites to be connected in both directions.

[14] On continental scales, there were positive correlations between genetic connectivity (F_{ST}) and both mean (Mantel tests $Z = 21847$, $r = 0.53$, $p < 0.001$) and minimum ($Z = 15033$, $r = 0.54$, $p < 0.001$) multigenerational oceanographic connectivity (Fig. 4). Similarly, there were negative correlations between the percentage of each pair of populations that were considered first-generation migrants between locations and mean ($Z = 39265$, $r = -0.41$, $p < 0.001$) and minimum ($Z = 19897$, $r = -0.46$, $p < 0.001$) multigenerational oceanographic connectivity (Fig. 4). For single generational time scales (<60 d) there was no correlation between F_{ST} and oceanographic connectivity ($p > 0.05$).

[15] On the scale of individual boundary current systems there were positive correlations between F_{ST} and multigenerational mean oceanographic connectivity time within the EAC ($Z = 102.55$, $r = 0.504$, $p = 0.038$, Fig. 5) and the LC ($Z = 582.67$, $r = 0.63$, $p = 0.007$, Fig. 5). Despite a strong trend for a positive correlation between oceanographic connectivity time and F_{ST} for the SAC, large variation in F_{ST} values and

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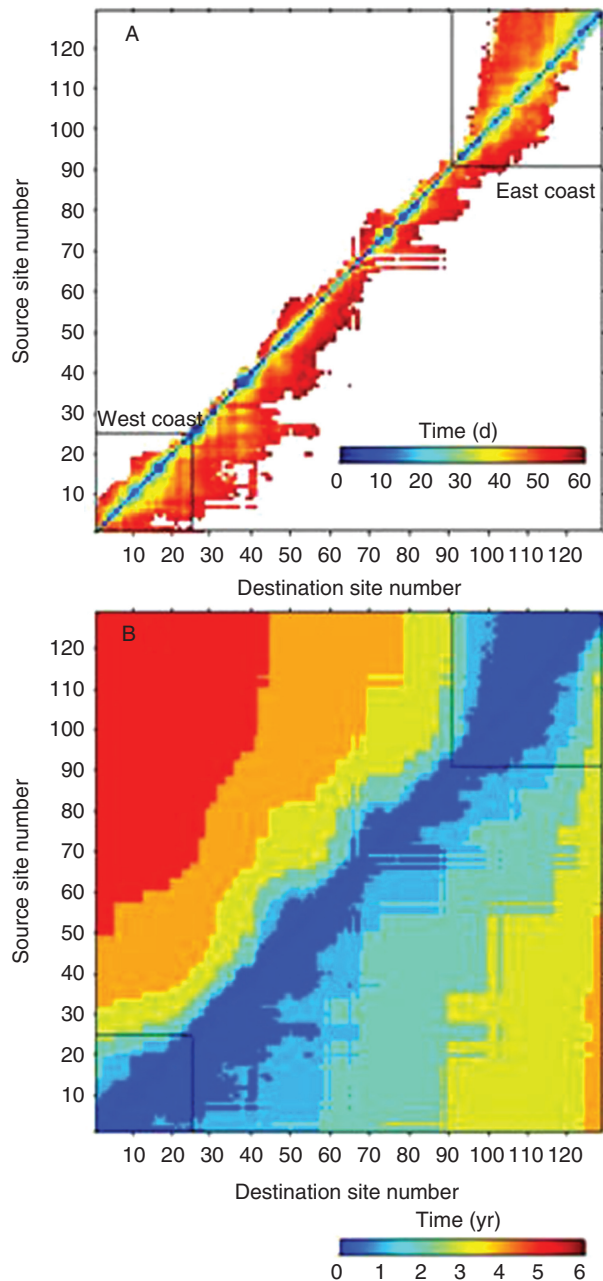
Fig. 3 Single generation (A) and multigeneration matrix (B) of ensemble average oceanographic connectivity time (d) among different sites over the April–October months (peak *E. radiata* reproduction) in 1996–2007. The white spaces in A denote no connectivity within the particle tracking period. Site number locations are presented in Fig. 1C.
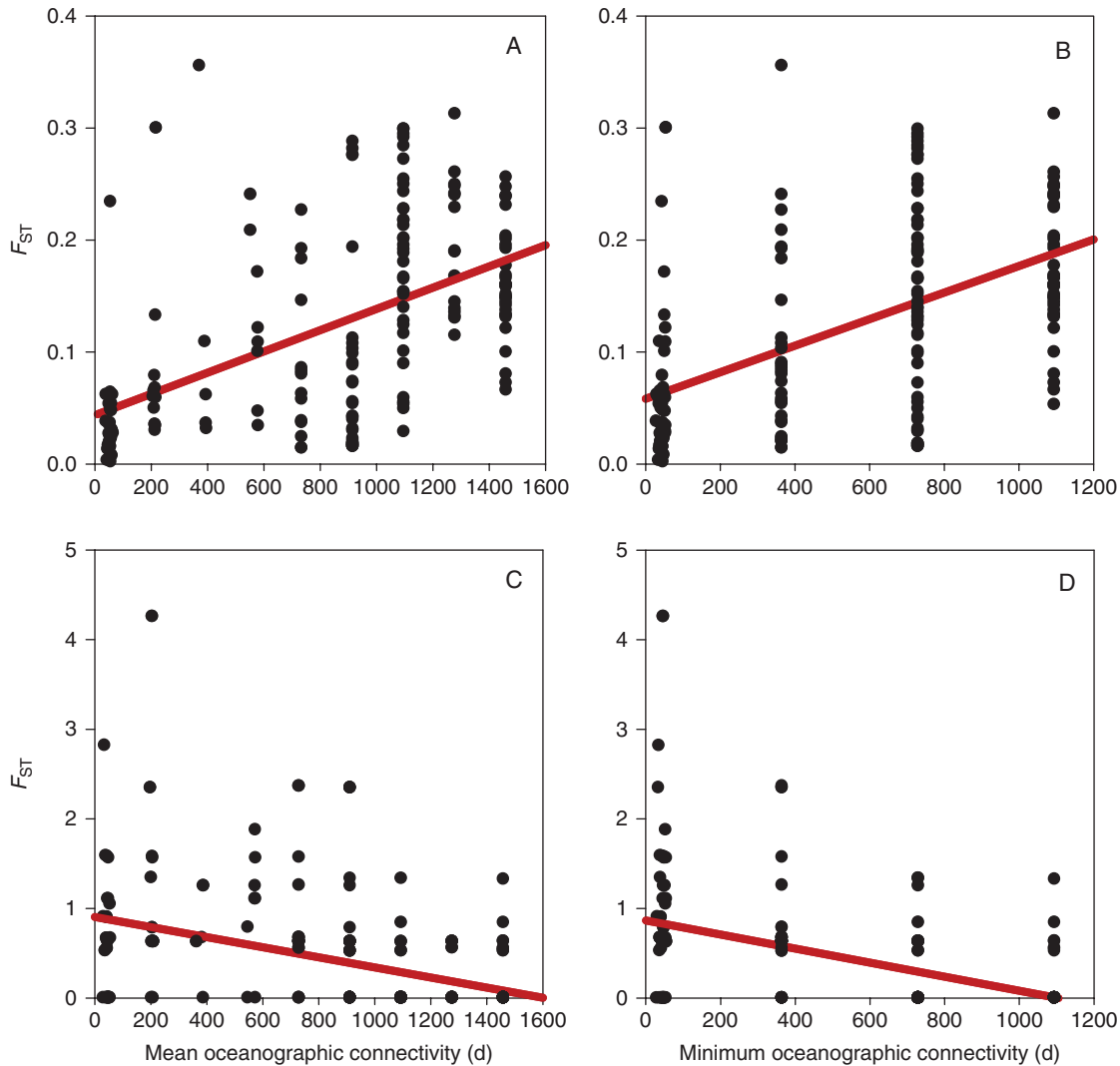
pairwise estimates exceeding this value so these outliers were excluded from analyses and only single-generational patterns examined. Single-generational minimum and maximum oceanographic connectivity time (<60 d) was not correlated with F_{ST} for any current (Mantel tests $p > 0.05$). When each current was examined separately, there was no correlation between the percentage of individuals from each pair of populations that were considered first-generation migrants between locations and mean or minimum connectivity time (Mantel tests $p > 0.05$). There were no correlations between estimates of observed and expected heterozygosity, allelic diversity, and F_{IS} for each location with self-seeding time for that location (all self-seeding times <20 d).

[16] Mean mutigenerational oceanographic connectivity was positively correlated with geographic distances between sites within the LC ($Z = 2506225$, $r = 0.67$, $p = 0.02$) and SAC ($Z = 337137$, $r = 0.82$, $p = 0.029$) but not the EAC ($Z = 3715323$, $r = 0.19$, $p > 0.05$). Minimum multigenerational oceanographic connectivity was strongly correlated with distances between sites within the EAC ($Z = 1710114$, $r = 0.79$, $p < 0.001$), LC ($Z = 487678$, $r = 0.54$, $p < 0.004$), and SAC ($Z = 2217093$, $r = 0.77$, $p < 0.008$).

Discussion

[17] The flow of boundary currents has been recognized as a potential explanation for regional differences in biomass, recruitment (Connolly et al. 2001; Menge et al. 2003; Broitman et al. 2005), and genetic structure of marine biota (Banks et al. 2007; Fraser et al. 2009; Coleman et al. 2011a). Our results extend this model to a continental scale to incorporate multiple boundary currents by demonstrating that current flow is a coarse predictor of connectivity across vast distances and contrasting seascapes.

[18] On continental scales, multigenerational oceanographic connectivity was positively correlated with genetic connectivity in the habitat-forming kelp, *E. radiata*. This pattern was largely driven by populations for which oceanographic and genetic connectivity were both extremely high (short times and low F_{ST} estimates). Given that oceanographic connectivity was also strongly correlated with geographic distance, this likely represents populations that were close

smaller sample sizes meant that this was not significant ($Z = 499.86$, $r = 0.55$, $p = 0.08$, Fig. 5). Minimum oceanographic connectivity times within each boundary current were typically less than 60 d with only four

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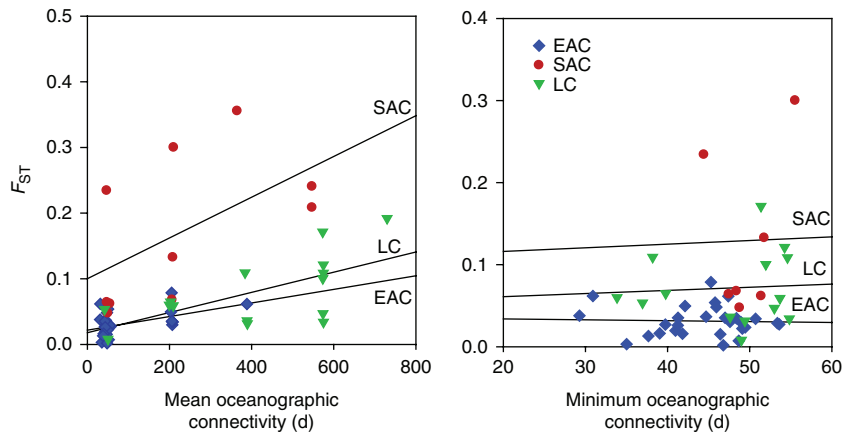
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Fig. 4 Correlations between mean and minimum multigenerational oceanographic connectivity time and F_{ST} (A and B) and number of migrants (C and D) around Australia. Points represent pairwise F_{ST} estimates and corresponding oceanographic connectivity times between sites within each boundary current. Lines represent regression lines.

together within individual boundary current systems. On contemporary time scales, two of the three modes of dispersal of kelp (sperm and zoospores) are likely to disperse only on scales <10s km within any given reproductive event (Reed 1990; Gaylord et al. 2002; Gaylord et al. 2006), hence resulting in high connectivity between neighboring locations for which oceanographic connectivity times were low. This is particularly true within fast-flowing boundary currents that facilitate fast connectivity times and bidirectional dispersal such as the EAC (Roughan et al. 2011) where there is little genetic differentiation (Coleman et al. 2011a, 2011b;

Coleman 2013). Despite positive correlations between oceanographic and genetic connectivity on multigenerational time scales, similar patterns did not exist on the scale of single generations (<60 d). That is, locations that were connected oceanographically within 60 d displayed no relationship between oceanographic connectivity time and genetic differentiation. This suggests that the spatial scales over which currents are able to transport propagules over a given 60-d period is not a barrier to dispersal for this kelp. This may be related to the fact that dispersal over this time period may occur in either a poleward or equatorward direction, thus eliminating

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Fig. 5 Correlations between mean and minimum multigenerational oceanographic connectivity time and F_{ST} for each of Australia's three boundary currents (A and B). EAC, East Australian Current; SAC, South Australian Current; and LC, Leeuwin Current. Lines represent regression lines.

patterns between genetic differentiation and oceanographic connectivity. Within the EAC for example, dispersal was asymmetric, with more poleward dispersal and shorter connectivity times at lower latitudes relative to more equatorward connectivity from higher latitudes. Over longer time periods (e.g., across a single ~7-month reproductive season) genetic differentiation is likely to be variable because kelp propagules or fertile drift may move on or offshore. For example, at the end of the *E. radiata* reproductive season trajectories were mostly offshore on the east and west coasts but were mostly alongshore early in the reproductive season (Fig. 2). Similarly, within a reproductive season on Australia's southern coastline, dispersal direction from a single location may reverse (Fig. 2).

[19] Despite significant correlations between genetic and oceanographic connectivity, there was large variation in genetic connectivity for any given estimate of oceanographic connectivity. For example, there were some pairs of populations where genetic connectivity was low despite high oceanographic connectivity and short distances between populations, indicating that factors other than boundary currents and distance are likely to determine patterns of dispersal and gene flow. For example, gene flow in marine algae has been shown to be restricted by local geography including the presence of unsuitable habitats such as sandy beaches or estuaries (Faugeron et al. 2001; Billot et al. 2003;

Coleman and Kelaher 2009) and differences in the availability of rocky reef or habitat between sites (Coleman and Brawley 2005; Alberto et al. 2010). Indeed, most locations in this study were separated by multiple estuary openings, sandy beaches, and protruding headlands that punctuate the coastline and across which propagules or fertile wrack must disperse to facilitate gene flow. Furthermore, the amount of available rocky reef varies with latitude along Australian coastlines and may play a role in increasing variation in estimates of genetic structure among pairs of populations. Indeed, patchier, low-latitude populations of *E. radiata* generally exhibit greater genetic structuring than similarly spaced reefs at higher latitudes (Coleman et al. 2011b). To evaluate these hypotheses, oceanographic models would have to incorporate subtidal habitat mapping data on continental scales, a task which is currently beyond our financial and technical capabilities.

[20] General descriptive results from the oceanographic model appear to correlate well with observed patterns of continental connectivity and ecological variation in this kelp species. The apparent restriction point at Bass Strait may contribute to great genetic (Coleman et al. 2011a), biological (e.g., Wernberg et al. 2003; Fowler-Walker et al. 2005; Connell 2007), and ecological (e.g., Fowler-Walker and Connell 2002; Russell et al. 2005; Connell and Irving 2008) differences between the east compared with west and southern coastlines of Australia for *E. radiata*. However, such differences may also be due to the closure of Bass Strait during the Pleistocene and historical isolation of eastern and southern populations, despite some amount of present day gene flow (e.g., Kassahn et al. 2003). Although surface flow across Bass Strait is restricted during summer (Fig. 1B), particle trajectories show that water transport across the Strait also occurs (Fig. 2A). In addition, van Sebille et al. 2012 have quantified the westward transport of water from the Australian east coast (north of

35°S), along the south, and into the west (north of 35°S) by using a Lagrangian approach and identifying pathways by which kelp populations from eastern and western Australia could connect. Moreover, these authors found that 90% of particles took 3–10 yr to complete such trajectories. Concurrently, this study found that such populations would only be connected after 6 yr or multiple generations (Fig. 3) through intermediate populations or stepping stones. We have previously found greater genetic differences between *E. radiata* on the eastern (NSW; New South Wales) coast compared with both the southern (SA; Southern Australia) and western (WA; Western Australia) coasts but lower differentiation between the south and west coasts (Coleman et al. 2011a). Such patterns are obviously also facilitated by greater oceanographic connectivity (faster dispersal times, i.e., 3 yr or multiple generations, see Fig. 3B) from west (LC) to east (EAC) than vice versa, due to the fact that the LC extension is more effective in overcoming the FC and thus transporting particles eastward. Connectivity from western to eastern populations implies that dispersal occurs from south to north along the east coast of Australia. Although the EAC flows mainly south, both cyclonic and anticyclonic eddies are often formed between 30 and 34°S (e.g., Bowen et al. 2005), allowing the northward transport of particles. Such features are well depicted in BRAN (Oke and Griffin 2011) and provide a mechanism by which the dispersal of kelp spores from south to northern populations might occur either close to shore when trapped in cyclonic eddies, or offshore and back into the coast when recirculating within an anticyclonic eddy.

[21] When Australia's three boundary currents were analyzed separately, there were strong correlations between multigenerational mean oceanographic and genetic connectivity and the strengths of these relationships were inversely proportional to the strength of each current. The strongest relationships between genetic and oceanographic connectivity existed within the weak LC extension/FC and with a weaker relationship in the strong EAC. This is in contrast to a previous study that found no correlation between gene flow and oceanography in the EAC (Coleman et al. 2011a). This discrepancy may be due to the different modeling methods, with ocean connectivity time (cf. this study and Alberto et al. 2011) potentially being a better descriptor of kelp genetic connectivity than particle tracking techniques (Coleman et al. 2011a). Moreover, within the EAC there was no relationship between ocean connectivity time and distance indicating that this method may also be more representative of the way the constant formation of eddies and consequent particle transport along non-straight but convoluted trajectories influences dispersal of propagules.

[22] Understanding how variations in the strength of Australia's boundary currents influenced connectivity is important because such variations (e.g., within the EAC) have been shown to have effects on marine life including range expansions of warm-water species (Figueira and Booth 2010; Ling 2008) and loss of giant kelp (*Macrocystis pyrifera*, Edyvane 2003). Similarly, variations in the strength of the LC are correlated with variable recruitment of species including fish and lobster (e.g., Fletcher et al. 1994; Caputi et al. 2010; Feng et al. 2011a). Given that Australia's boundary current systems are predicted to change in contrasting ways under future scenarios of climate change, these variations in oceanographic–biological coupling will have critical implications for connectivity. The LC–LC extension system has weakened by 10%–30% in the past 50 yr (Feng et al. 2004) and is predicted to weaken a further 15% by 2060 (Sun et al. 2012), although strong decadal variation has been observed (Feng et al. 2010b). In contrast, the EAC has been steadily increasing in strength (Ridgway 2007; Hill et al. 2008) and is predicted to further increase by 12% in the core transport, and 35% in the EAC poleward extension by 2060 (Sun et al. 2012). This is likely to result in greater genetic connectivity in the EAC but reduced connectivity in the LC and FC with implications for critical population parameters such as genetic diversity, inbreeding, and adaptive ability. Combined with concomitant climate-induced stressors such as increases in sea surface temperature, this may compromise the dynamics and functioning of organisms along Australia's temperate coastlines.

[23] There are limitations in both the model used in this study and the estimates of genetic differentiation. One limitation that must be noted is that the oceanographic model does not yet include tides, which may

be important in shallow regions adjacent to the continental shelf where kelp lives. Another potential limitation of using this model is that it may not accurately reflect other continental shelf processes. However, forecasted or precise predictions of dispersal was not the aim of this study, instead we explored to what extent broad circulation patterns of boundary currents explained single and multiple generation dispersal. Population genetics provide a means of assessing connectivity integrated over many generations (Kool et al. 2013). Similarly, simulation of particle dispersal over several years allows building an ensemble matrix of mean connectivity time, and its projection is an effective method to obtain oceanographic connectivity over multiple generations (Kool et al. 2011). Comparison of genetic and oceanographic connectivity can then be used to support physical mechanisms driving the development of genetic structure over time due to migration. BRAN, a product comprising an eddy-solving global ocean circulation model, and an ensemble data assimilation system, provides the ideal tool to model oceanographic connectivity from particle tracking simulations over decades and spatial scales that encompass the east, south, and west coasts of Australia. More important, the level of agreement between the genetic and modeled oceanographic connectivity gives an insight of how relevant mechanisms neglected in the hydrodynamic model (e.g., flow structure at smaller spatial scales than BRAN's grid cell size), or biological mechanisms (e.g., postsettlement processes) are important to the dispersal of kelp around the Australian coastline.

[24] The significant correlation between the continental-wide F_{ST} data and the multigeneration minimum and mean connectivity time suggests that structural patterns of populations are able to form on the basis of large-scale dispersal caused by Australian boundary currents. Nevertheless, nonsignificant correlations between genetics and single generation mean or minimum connectivity time suggests that mechanisms that are not captured in the hydrodynamic model might also cause dispersal of propagules between populations. Future downscaling of models and incorporation of processes such as tides will be valuable in understanding the connectivity of marine organisms on the continental shelf. Improvements in the genetic data could also be

valuable for refining relationships between genetic and oceanographic connectivity. For example, only six microsatellite loci were available for use in this study due to widely acknowledged difficulties with molecular techniques when working with algae and finding microsatellite regions (e.g., polymerase chain reaction–inhibiting compounds in the algal thallus). New molecular techniques that cover greater portions of the genome (e.g., genotyping by sequencing) will give more precise estimates of genetic differentiation and increase the robustness of population genetic analyses.

Significance to Aquatic Environments

[25] Developing models of ocean circulation that accurately reflect patterns of dispersal of marine organisms is important for understanding and identifying drivers of connectivity in the oceans. The continental-scale model presented here was correlated with genetic connectivity of an important kelp species on multigenerational time and large-spatial scales suggesting that structural patterns of populations are able to form on the basis of large-scale dispersal caused by Australian boundary currents. Nevertheless, nonsignificant correlations between genetic differentiation and single-generation connectivity times suggests that the hydrodynamic model used here was not an accurate predictor of connectivity over short-spatial and temporal scales and that mechanisms that are not captured in this model are important in determining dispersal. This model did, however go further in explaining genetic patterns of kelp within the East Australian Current where ocean circulation is complex and dispersal is more bidirectional and not correlated with distance. Future downscaling of models and incorporation of processes such as tides will be valuable in understanding the connectivity of marine organisms on the continental shelf. The results of this study will improve understanding of how boundary currents influence dispersal and connectivity of marine organisms on regional and continental spatial scales. Understanding patterns of continental oceanographic connectivity may also help explain large-scale heterogeneity in species distribution, ecology, and biology and thereby aid in developing robust conservation strategies that span governmental jurisdictions.

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