

Variation in the strength of continental boundary currents determines continent-wide connectivity in kelp

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Summary

1. Determining the extent to which coastal oceanographic processes facilitate connectivity of marine organisms underpins our understanding of the ecology and evolution of marine communities. Continental boundary currents are a dominant physical influence on marine connectivity, but determining their effect has proved elusive because of difficulties in achieving replication of currents within the distribution of a single species.
2. Australia provides an unparalleled opportunity to address such questions because it has three replicate boundary currents within narrow latitudinal ranges that share continentally distributed species. We tested whether the strength of continental boundary currents influences coastal connectivity of a dominant foundation species (the kelp *Ecklonia radiata*).
3. Variation in the strength of different boundary currents produced entirely different patterns of connectivity in kelp with high connectivity in strong currents and low connectivity in weak currents. Spatial patterns of genetic structuring were also correlated with the nature and strength of currents.
4. *Synthesis.* This result has global implications; continental boundary currents are key drivers of marine connectivity and give predictive ability with which to understand variable ecologies of temperate coastlines world-wide.

Key-words: dispersal, *Ecklonia radiata*, ecology, gene flow, marine, oceanography, seaweed

Introduction

The effect of physical oceanographic processes on the biology of coastal organisms has become a dominant theme for a modern understanding of the ecology and evolution of marine communities. This is primarily due to the life histories of most marine organisms, in which dispersive planktonic stages precede sessile or relatively sedentary benthic adults. Physical oceanographic processes largely determine the degree of dispersal of planktonic stages and thus subsequent connectivity (exchange of genetic material) within and among populations of species. Although our understanding of coupling between physical oceanographic processes and dispersal is well devel-

oped for fish and invertebrates (e.g. Connolly & Roughgarden 1998; Botsford 2001; Broitman, Blanchette & Gaines 2005; Cowan, Paris & Srinivasan 2006; Galindo, Olsen & Palumbu 2006; Wilson *et al.* 2008; White *et al.* 2010), less is known regarding the impact of large-scale physical oceanographic processes on dispersal of marine macrophytes, the dominant habitat-forming organisms in many parts of the world.

Boundary currents are thought to be a dominant physical influence on connectivity in coastal marine systems and are among the most pervasive hydrodynamic influences along the world's coastlines. Despite their acknowledged importance to the ecology of coastal communities (e.g. via upwelling and downwelling, see references above), understanding the general effects of boundary currents on coastal connectivity has proved elusive because of the difficulties in achieving appropriate replication of currents within the distribution of a single

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species. The geography of most continents is characterized by extensive north to south coastlines with poleward or equatorward flowing boundary currents along opposite sides of landmasses. Consequently, most coastlines world-wide typically span great latitudinal gradients of temperature and other physical conditions and therefore support quite different suites of flora and fauna. Determining the general influence of continental boundary currents on connectivity and whether these currents may be used as predictive tools for estimating connectivity, is therefore necessarily confounded.

Australia is unique in having replicate boundary currents on three sides of its continent as well as having latitudinally compressed coastlines that support species with continent-wide distributions. It therefore provides an unparalleled opportunity to understand the influence of boundary currents on connectivity in marine organisms. Australia's replicate boundary currents include the Leeuwin, East Australian and Flinders currents. The Leeuwin Current (LC) flows poleward along the west coast of Australia and extends into the Great Australian Bight. The Flinders Current (FC) is an extension of the LC as it flows eastward along Australia's vast southern coastline and represents the world's only northern boundary current. On Australia's eastern coastline, the East Australian Current (EAC, essentially the western border of the South Pacific gyre) flows poleward along the coast from the tropics down to Tasmania (Fig. 1).

Boundary currents tend to vary predictably in their strengths as well as volume of water transported. Typically, currents on the eastern side of landmasses (western boundary currents) are faster and stronger relative to those on the western side of landmasses (eastern boundary currents). Australia's boundary currents conform to this general pattern. The EAC is strongest reaching speeds of up to 3.6 m s^{-1} (averaging $1\text{--}1.5 \text{ m s}^{-1}$) and generates a characteristic cyclonic and anticyclonic eddy field in the austral summer and autumn (Mata *et al.* 2007). In contrast, the LC is a weaker current (averaging 0.5 m s^{-1} , Cresswell & Vaudrey 1977) and transports significantly less water than the EAC. Finally, the FC is significantly weaker than either the EAC or LC ($0.2\text{--}0.3 \text{ m s}^{-1}$; Middleton & Bye 2007). If the overall strengths of boundary currents are significant drivers of marine connectivity, then patterns of connectivity within each of Australia's boundary currents should be correlated with current strength.

We tested this hypothesis using the cosmopolitan kelp, *Ecklonia radiata* (C. Agardh) J. Agardh, the dominant form of biogenic habitat on Australia's temperate reefs (Connell & Irving 2008). Kelps are true 'foundation species' (Dayton 1975) because their presence largely determines associated community structure via alteration of local physical conditions and because they constitute key components of temperate marine food webs. *E. radiata* has a fundamental influence on shallow water marine communities in Australia by providing habitat to

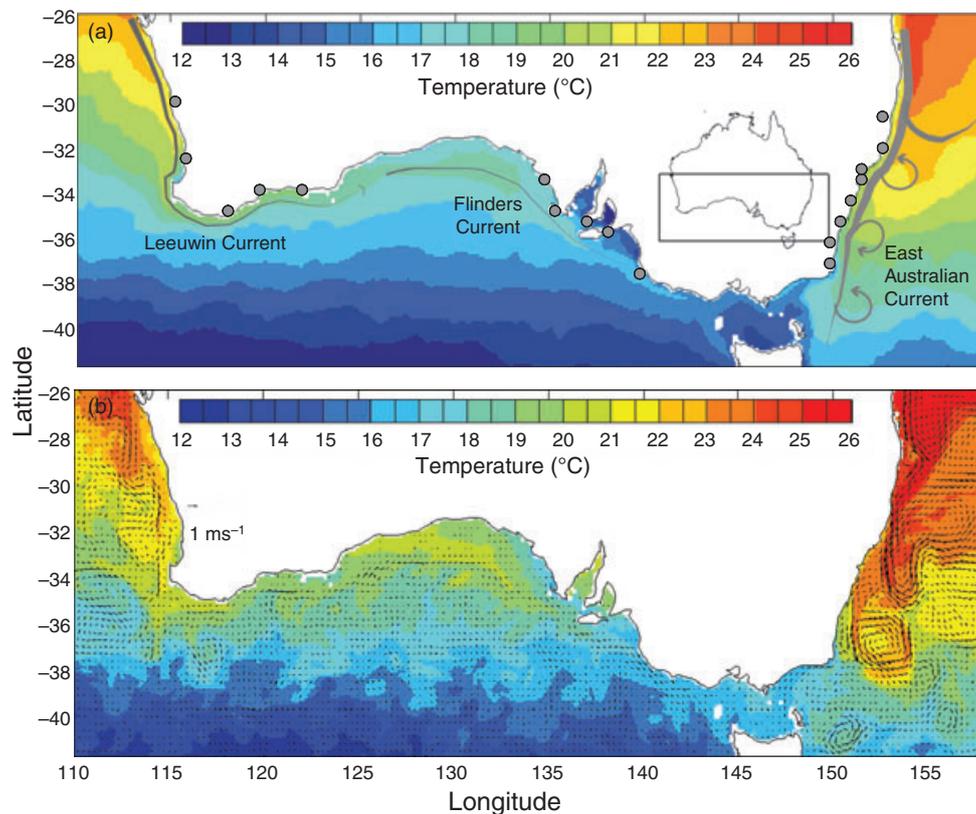


Fig. 1. Satellite images of (a) average annual sea surface temperature ($^{\circ}\text{C}$) from 2005 illustrating fundamental differences in current strength (line thickness) and extension along the coast of Australia and sampling locations (grey dots) and (b) an example of current strength and direction over a 6-day period in the austral autumn during peak kelp reproduction. Geostrophic current vectors are overlaid where the magnitude of the current is indicated by the size of the vector. Data courtesy CSIRO Marine and Atmospheric Research (BlueLink output).

a great diversity of fish, invertebrate and algal taxa (Irving, Connell & Gillanders 2004; Anderson *et al.* 2005; Coleman *et al.* 2007). Despite their ecological importance, the influence of large-scale oceanographic processes on connectivity in kelp is almost completely unstudied. We show here that continental boundary currents are key drivers of connectivity in this important habitat-forming kelp and demonstrate the predictive ability of such currents for understanding the ecologies of temperate coastlines world-wide.

Materials and methods

Ecklonia radiata has a typical Laminarian alternation of generations life history, with conspicuous, macroscopic sporophytes (spore-producing individuals) alternating with microscopic gametophytes (gamete-producing individuals; Jennings 1967). Because microscopic gametophytes have never been found in the field, this study necessarily characterizes patterns of genetic structure of sporophytes. Patterns of genetic structure are therefore the combined effects of dispersal of zoospores and sperm (eggs are retained). Depending on the dispersal distances and settlement of zoospores, kelp can, therefore, both out-cross and potentially self-fertilize (Raimondi *et al.* 2004). Fertile sporophytes may also disperse when they are removed from the substratum during storms (Kirkman & Kendrick 1997).

Mature kelp sporophytes were sampled along 800–1200 km of coastline across each of Australia's three boundary currents (EAC, LC and FC) in 2006 (Fig. 1). This species is abundant and occurs continuously from *c.* 3–30 m depth on most rock reef along these coastlines. Given that kelp is a perennial species, the individuals sampled in this study represent a combined cohort from the previous 3–5 years. Within each current, we avoided sampling across known biogeographic breaks (Waters *et al.* 2010) or other potential barriers to dispersal. Within each boundary current a hierarchical sampling program was used with individual kelp thalli ('plants') collected within each of 2–3 sites (km to 10s km apart) at each of 5–8 locations (100s km apart, see Table S1 in Supporting Information). Individuals were genotyped using six polymorphic microsatellite loci (Dolman & Coleman 2008). Patterns of genetic diversity were characterized using a number of different descriptive measures using GENETIX ver. 4.04 (Belkhir *et al.* 2000) (results presented in Table S1). Connectivity (dispersal) was inferred from genetic differentiation estimated by testing Weir and Cockerham's F_{ST} estimates (Weir & Cockerham 1984) using permutation tests (1000 permutations, FSTAT 1.2, Goudet 1995). Pairwise F_{ST} estimates were also estimated between all pairs of locations and sites within each current. A sequential Bonferroni correction (Rice 1989) was used when examining significance levels for pairwise tests. Although estimates of population differentiation can reflect processes in addition to dispersal (e.g. population history, population size, departures from an equilibrium model etc.) meta-analyses have shown that such additional processes rarely overwhelm estimates of dispersal and that F_{ST} is still an informative statistic for characterizing connectivity (Bohonak 1999). Tests of isolation by distance were done via Mantel tests using the program IBD (Bohonak 2002).

To improve predictive ability between large-scale patterns of connectivity and physical oceanographic processes we modelled one current (EAC) at a relatively fine scale (*c.* 1–3 km resolution) to elucidate the likely direction and distance of dispersal probabilities of kelp over time scales corresponding to the multigenerational cohort of kelp sampled for genetic analyses (averaged from 2001 to 2006). Although courser-scale models exist for Australia's other coastlines (e.g.

AusConnie, Condie *et al.* 2005), at the time of publication this remains the only model available that can track particle dispersal at the fine spatial scales (1–3 km) that are relevant to nearshore marine organisms. A configuration of the Princeton Ocean model (POM; Blumberg & Mellor 1987) was used to model currents at latitudes corresponding to where kelp was sampled. We used the configuration of Roughan *et al.* (2010), a reanalysis of the coastal ocean state off south-east Australia that is forced by Bluelink products (Oke *et al.* 2008; Schiller *et al.* 2008). A series of particle-tracking simulations were conducted whereby particles were released in the surface waters above the 25 m isobath at sites corresponding to where kelp was sampled (grouped into $17 \times 0.5^\circ$ latitudinal intervals from 29 to 37°S for graphical representation). Particles were released at a depth of 0–3 m below the surface. Ten particles were released from each release site on model days 0, 5, 10, 15 and 20. When a particle reaches a boundary it stops propagating. Settlement is considered to have occurred when a particle comes within a third of a grid box off the coast within each latitudinal band (i.e. in surface waters). Particles that were swept offshore were disregarded and particles were not allowed to settle in their release latitude band. We modelled dispersal using an average 30-day dispersal period. We used Mantel tests to determine whether there was a correlation between predicted dispersal probabilities and geographic distance as well as genetic differentiation for both poleward and equatorial dispersal probabilities.

Results

Consistent with our predictions, the magnitude of genetic differentiation within kelp populations varied greatly among Australia's replicate boundary currents and was correlated to the peak strength of these currents. There was weak connectivity within the FC ($F_{ST} = 0.211$), relatively stronger connectivity within the LC ($F_{ST} = 0.11$) and the highest connectivity within the EAC ($F_{ST} = 0.046$). F_{ST} is an estimate of relative genetic diversity within a subpopulation compared to the total population and varies from 0 to 1 with small estimates indicating high connectivity and large estimates indicating low connectivity. $F_{ST} > 0.2$ (effectively corresponding to 1 migrant per generation) is considered to indicate low connectivity.

There was also a striking relationship between spatial patterns of genetic structure and relative current strength. There was a strong positive correlation between genetic differentiation and geographic distance within the weakest current (FC Mantel test: $Z = 2281.67$, $r = 0.84$, $P \leq 0.05$, Fig. 2), a weaker but significant correlation within the relatively stronger LC (Mantel test: $Z = 1077.6125$, $r = 0.7025$, $P < 0.05$; Fig. 2) and no correlation within the fastest current (EAC Mantel test: $Z = 272.553$, $r = 0.1225$, $P > 0.05$, Fig. 2).

There was also much small-scale genetic differentiation within each current. Pairwise tests between kelp populations within all currents were almost always significant with 83%, 92% and 93% of pairwise F_{ST} estimates between sites being significant within the EAC, LC and FC respectively (see Table S2). Moreover, estimates of F_{IS} were significantly positive or negative in *c.* 50% of sites (Table S1), indicating deviations from random mating. F_{IS} is an estimate of inbreeding of individuals relative to the subpopulation. F_{IS} estimates range from -1 to 1 with negative estimates indicating an excess of heterozygotes and positive estimates an excess of homozygotes.

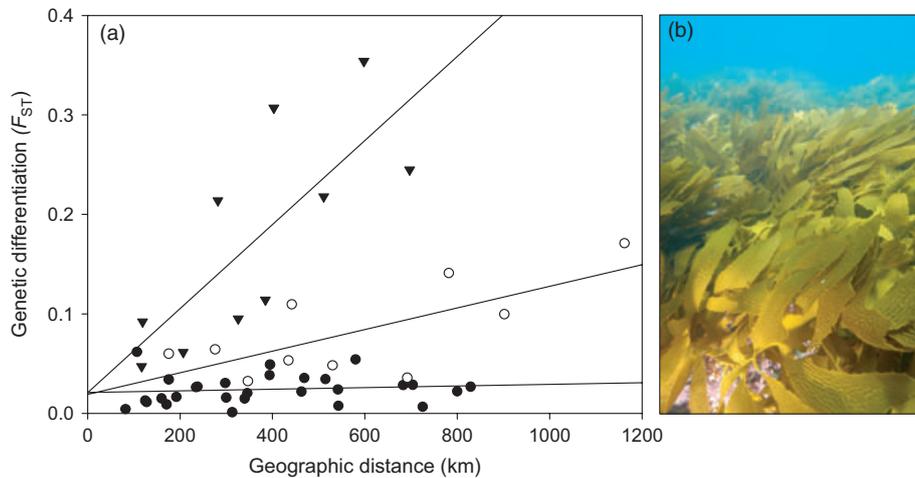


Fig. 2. (a) Patterns of isolation by distance [pairwise genetic differentiation (F_{ST}) estimates and geographic distances between locations] among kelp populations within the Flinders Current (▼), Leeuwin Current (○) and East Australian Current (●). Regression lines are shown for each boundary current. (b) A typical kelp forest off southern Australia.

Modelling revealed that the poleward flow of the EAC facilitated predominately poleward transport of particles; however, there was equatorward transport of particles particularly from higher latitudes (Fig. 3). Equatorward transport occurred mostly when particles were released in the austral winter when the EAC is at its weakest (data not presented). Correlations revealed that both poleward (Mantel test $Z = 51221.5$, $r = -0.455$, $P < 0.001$) and equatorward (Mantel test $Z = 13612.5$, $r = -0.363$, $P < 0.001$) dispersal probabilities

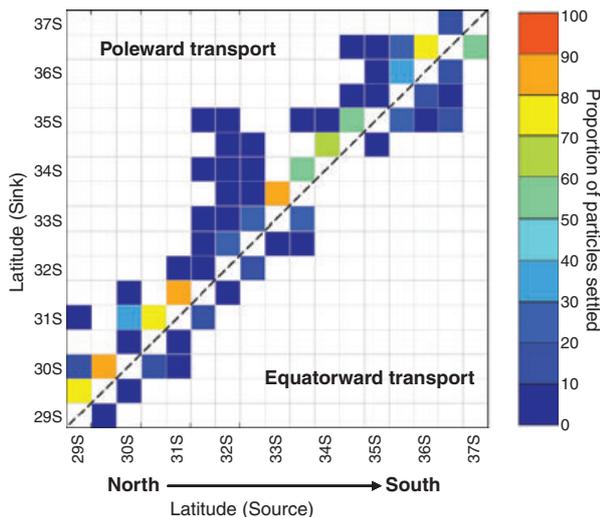


Fig. 3. Connectivity matrix for the East Australian Current (EAC) showing the probability that a particle originating near the coast at one latitude will reach or settle at another latitude near the coast. Equatorward and poleward dispersal of particles are shown on the bottom right and top left of the matrix respectively. Grid boxes are $\frac{1}{2}$ degree of latitude. Data are 2001–2006 averages and dispersal occurred over a 30-day period at latitudes corresponding to where kelp was sampled. Particles were not allowed to sink in their original latitude. Further, not all particles reached a $\frac{1}{2}$ -degree latitude band along the coast (i.e. were swept offshore), so probabilities do not add to 100.

were negatively correlated with distances between sites. There was, however, a lack of correlation between genetic differentiation and both poleward (Mantel tests, $Z = 31.844$, $r = 0.0335$, $P > 0.05$) and equatorward (Mantel tests, $Z = 6.175$, $r = -0.139$, $P > 0.05$) predicted dispersal probabilities.

Discussion

This study utilized the unique geography of the Australian continent to compare patterns of connectivity and genetic structure among replicate boundary currents using a cosmopolitan species. Consistent with our predictions, the magnitude of genetic differentiation within kelp populations varied greatly among Australia's replicate boundary currents and was correlated to the peak strength of these currents. Moreover, spatial patterns of genetic structure were also correlated to current strength. These results demonstrate the predictive ability of such currents in developing models of connectivity for coastlines world-wide.

Coincident with the strong correlation between boundary current strength and connectivity of kelp was the striking relationship between spatial patterns of genetic structure and geographic distance. There was strong isolation by distance within the relatively weaker currents (FC, LC) and no pattern within the strongest current (EAC). This suggests that, on the scale of continental boundary currents (*c.* 1000 km), weaker currents may facilitate linear, 'stepping stone' patterns of dispersal that are correlated with distance. In contrast, stronger and pervasive currents may promote high connectivity and lack of isolation by distance resulting in 'mosaic' patterns of genetic structure.

Nearshore circulation patterns can be notoriously complex and fine-scale oceanographic models are a key component for understanding patterns of connectivity in coastal marine organisms (White *et al.* 2010). Modelling of nearshore dispersal probabilities within Australia's strongest boundary cur-

rent (EAC) revealed that while dispersal was primarily poleward, equatorward dispersal was common, particularly at higher latitudes. Equatorward dispersal arises due to both the weakening of this current in winter (Ridgeway & Godfrey 1997) and the resulting equatorward flowing counter current, as well as eddies commonly shed in the austral summer and autumn (Mata *et al.* 2007), potentially transporting propagules equatorward or in a nonlinear fashion. Combined with the fact that estimates of genetic differentiation (F_{ST}) between any two locations reflect multigenerational exchange of genetic material from both poleward and equatorward sources, it is not surprising that there was no correlation between genetic differentiation and both predicted dispersal probabilities and geographic distance. These results are consistent with a lack of clear spatial genetic structuring in a range of planktonically dispersing organisms within the EAC (Hunt & Ayre 1989; Banks *et al.* 2007; Piggott *et al.* 2008; Sherman, Hunt & Ayre 2008; Coleman & Kelaher 2009; Curley & Gillings 2009) and suggest that the complex nature of this current may produce ubiquitous patterns of connectivity across taxa.

Australia's coastlines vary in factors other than simply the strength and nature of continental boundary currents and these variations present alternative hypotheses to explain the observed patterns of connectivity in kelp. For example, differences in the availability of rocky reef or kelp forest habitat between sites (Alberto *et al.* 2010) or the continuity of coastlines (e.g. number of estuaries, inlets, unsuitable habitat between sites; Faugeton *et al.* 2001) may influence dispersal and connectivity. However, neither of these variables showed any correlation with patterns of genetic structuring of kelp within each of Australia's boundary currents (Mantel tests $P > 0.05$, data not presented). There is also an emerging body of literature showing distinct differences in the ecologies of kelp forests among Australia's coastlines and these ecological variations may also explain patterns of connectivity. In particular, kelp forests on Australia's east coast are consistently different with respect to morphology (Wernberg *et al.* 2003; Fowler Walker, Connell & Gillanders 2005), percentage cover (Connell 2007; Connell & Irving 2008) and relationships to associated biota (Fowler Walker & Connell 2002; Irving, Connell & Gillanders 2004). Moreover, the ecological processes that structure kelp forests differ among coastlines with grazing by sea urchins and subsequent barrens habitat prevalent on the east coast (Connell & Irving 2008) vs. eutrophication on Australia's oligotrophic southern coastline (Russell *et al.* 2005; Gorman, Russell & Connell 2009). Such factors have the potential to influence a suite of demographic and reproductive traits including productivity and subsequent reproductive output, fertilization success, dispersal and post-settlement survival (e.g. Graham 2003). Whether variations in the ecology of kelp forests structures connectivity (or connectivity structures ecology) requires ongoing research on these broad, continental spatial scales.

Although boundary currents drive connectivity across large-scales, small-scale processes are important considerations and have the potential to structure dispersal of kelp propagules (e.g. Gaylord *et al.* 2006) and subsequent population connec-

tivity. Indeed, we observed significant population differentiation at smaller spatial scales, even among neighbouring kelp populations on rocky reefs km to 10s of km apart. The existence of both large- and small-scale genetic differentiation may be explained by the contrasting dispersal abilities of the multiple life history stages of kelp. Dispersal of sperm is likely to occur only on the scale of centimetres over which pheromones from eggs are effective (e.g. giant kelp, *Macrocystis pyrifera*, Reed 1990). In contrast, zoospores may disperse kilometres from their point of origin (Gaylord *et al.* 2002, 2006; Reed, Schroeter & Raimondi 2004) and fertile drift material even further (Hernández-Carmona, Hughes & Graham 2006). Moreover, kelp populations inhabiting each site were unique with respect to patterns of mating (i.e. random mating vs. outcrossing vs. selfing) indicating that location-specific factors (e.g. kelp forest density or size; Gaylord *et al.* 2006) can determine local population dynamics. Thus, small-scale biological and oceanographic processes (Largier 2003) are also important considerations in understanding the dynamics of kelp populations, particularly for recognizing the locations and scales of protection for species that found entire communities.

An understanding of connectivity is considered an important component of conservation and management strategies (Wayne & Morin 2004). The results of this study have important implications for the conservation and management of kelp forests, particularly given that anthropogenic stressors are beginning to precipitate significant changes in macroalgal habitats world-wide (e.g. Dayton *et al.* 1998; Steneck *et al.* 2002; Airoidi & Beck 2007; Coleman *et al.* 2008; Connell *et al.* 2008). Because generalizations cannot be made about connectivity, conservation and management strategies must be based on sound knowledge of specific coastlines. For example, conservation strategies for kelp forests on coastlines with high connectivity (e.g. Australia's east coast) must account for the patchy nature of genetic structuring and complex patterns of dispersal. Identification of 'sources' of propagules that might be protected or given high conservation priority may be difficult along such coastlines, and this emphasizes the need for representative networks of connected marine reserves. In contrast, on coastlines with relatively poor connectivity (e.g. Australia's southern coastline) determining the size and spacing of marine reserves requires careful consideration. Along such coastlines, recovery following loss or fragmentation of ecologically important habitats such as kelp forests may be slow or may never occur at all, depending on the spatial extent of loss. With conservation strategies increasingly moving towards the conservation of habitat as opposed to species, the ability to predict spatial and temporal dynamics of habitat-forming macroalgae is of immense benefit to the conservation and management of kelp forests and the biodiverse assemblages they support.

Dispersal in marine environments is structured by a multitude of factors operating at different spatial scales. The influence of physical factors on scales of dispersal are superimposed on intrinsic differences in species biology and life history including timing of reproduction, propagule motility, behaviour, competency periods and developmental times (e.g. Brad-

bury *et al.* 2008). Further, actual patterns of dispersal can be altered by spatial and temporal variability in settlement or recruitment and subsequent survival and population dynamics (e.g. Johnson & Black 1982). Despite these complexities, we have shown that a dominant physical force (the strength of continental boundary currents) can structure patterns of dispersal and determine connectivity on large, continental spatial scales.

The strong physio-biological coupling between connectivity and boundary current strength has broad implications for developing models of large-scale connectivity for the world's coastlines. Continental boundary currents vary in predictable ways around the globe, and such consistent variations in physical environments may prove to be universal determinants of large-scale connectivity in the oceans. Knowledge of how physical factors structure connectivity is a key step forward in understanding how contemporary processes drive variation in coastal ecologies under both present and forecast scenarios of anthropogenic change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Number of individuals sampled (n), total number alleles, expected and observed heterozygosity (H_e and H_o respectively) and F_{IS} (a measure of inbreeding within populations) for each site in Australia.

Table S2. Pairwise F_{ST} estimates between all locations.

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