Anticipating changes to future connectivity within a network of marine protected areas

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Abstract

Continental boundary currents are projected to be altered under future scenarios of climate change. As these currents often influence dispersal and connectivity among populations of many marine organisms, changes to boundary currents may have dramatic implications for population persistence. Networks of marine protected areas (MPAs) often aim to maintain connectivity, but anticipation of the scale and extent of climatic impacts on connectivity are required to achieve this critical conservation goal in a future of climate change. For two key marine species (kelp and sea urchins), we use oceanographic modelling to predict how continental boundary currents are likely to change connectivity among a network of MPAs spanning over 1000 km of coastline off the coast of eastern Australia. Overall change in predicted connectivity among pairs of MPAs within the network did not change significantly over and above temporal variation within climatic scenarios, highlighting the need for future studies to incorporate temporal variation in dispersal to robustly anticipate likely change. However, the intricacies of connectivity between different pairs of MPAs were noteworthy. For kelp, poleward connectivity among pairs of MPAs tended to increase in the future, whereas equatorward connectivity tended to decrease. In contrast, for sea urchins, connectivity among pairs of MPAs generally decreased in both directions. Self-seeding within higher-latitude MPAs tended to increase, and the role of low-latitude MPAs as a sink for urchins changed significantly in contrasting ways. These projected changes have the potential to alter important genetic parameters with implications for adaptation and ecosystem vulnerability to climate change. Considering such changes, in the context of managing and designing MPA networks, may ensure that conservation goals are achieved into the future.

Introduction

Continental boundary currents are projected to change under climate change (Wu *et al.*, 2012; Sen Gupta *et al.*, 2015). In particular, western boundary currents (WBCs) globally are forecast to strengthen due to an ongoing poleward shift of the latitude where the maximum wind stress curl occurs (Cai, 2006). Given that continental boundary currents often determine dispersal and large-scale connectivity among populations of marine organisms (Coleman *et al.*, 2011a, 2014; Cetina-Heredia *et al.*, 2015), changes to these currents may have dramatic implications for species distribution, population genetics and population persistence with resultant

alterations to entire ecosystems (Verges *et al.*, 2014; Provost *et al.*, 2016).

Networks of marine protected areas (MPAs) are an important tool for safeguarding regions crucial to metapopulation persistence (e.g., source and sink populations), and maintaining levels of connectivity (Palumbi, 2003; Roberts *et al.*, 2003; Coleman *et al.*, 2011b), which may not only ensure persistence but the long-term resilience of populations (Mumby *et al.*, 2011; Magris *et al.*, 2014; Andrello *et al.*, 2015). The size, spacing and arrangement of MPAs relative to scales of dispersal and life history of organisms (Shanks *et al.*, 2003; Durrant *et al.*, 2014), combined with local- and regional-scale oceanography (Roberts, 1997) and other environmental factors, determine the extent to which MPAs are connected and contribute to conservation goals. Moreover, given that both spatial (Castorani *et al.*,

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2015) and temporal (Blowes & Connolly, 2012) variability in dispersal distance and spread affects the likelihood of population persistence, understanding variability in dispersal and connectivity is a key component of MPA network planning (Pendoley et al., 2014). Future changes to connectivity should thus ideally be considered and anticipated in conservation initiatives to allow appropriate review of MPA designs and to ensure that MPAs achieve their conservation goals both now and into the future (Magris et al., 2014; Parsons et al., 2014).

Despite the acknowledged need to consider both extant and future connectivity, as well as its shorter-term temporal variability, in conservation planning, this task is challenging and there is much uncertainty and subjectivity in how to incorporate estimates of connectivity for multiple species and climate scenarios into management initiatives (Mundy et al., 2009; Mumby et al., 2011; Magris et al., 2014; Pendoley et al., 2014; Melia et al., 2016). The handful of studies that quantitatively examine future connectivity in a conservation context reveal significant changes to connectivity and self-seeding among MPAs that is mediated by concurrent change in species reproductive timing, larval survival and development (Andrello et al., 2015). Moreover, current spatial arrangements of MPAs are often not adequate to protect future thermal refugia that may confer long-term resilience and persistence to marine communities (Magris et al., 2014; but see Almpanidou et al., 2016) and might not even be spaced to provide effective current protection (Pendoley et al., 2014). Adaptively managing networks of MPAs that will continue to achieve conservation goals into the future will thus be dependent on understanding future changes to connectivity as well as the ability of species to genetically adapt to climatic change (Mumby et al., 2011).

A predicted 'hotspot' of climatic change is the east coast of Australia which is bathed by the East Australian Current (EAC), a poleward flowing western boundary current that has been steadily increasing in strength (Ridgway, 2007; Hill et al., 2008; Cetina-Heredia et al., 2014), and is predicted to further increase by 12% in core transport and by 35% in poleward extension by 2060 (Sun et al., 2012). Transport in eddies within the EAC has also increased in the last three decades (Cetina-Heredia et al., 2014), and longer-lived anticyclonic eddies are expected to occur more frequently (Matear et al., 2013; Oliver et al., 2015). These changes are likely to impact dispersal and connectivity within the EAC (Cetina-Heredia et al., 2015), with implications for critical population parameters (e.g., genetic diversity, inbreeding), as well as species ranges (Ling et al., 2008) and

ecological interactions (Johnson et al., 2011; Verges et al., 2014).

Along the east coast of Australia, there is a network of temperate MPAs spanning over 1000 km of shoreline (Coleman et al., 2015; Fig. 1). Extant genetic connectivity within and among these MPAs is variable and dependent on latitude, species life history and habitat (Coleman & Kelaher, 2009; Coleman et al., 2011b; Coleman, 2013). Here, we use oceanographic modelling to forecast how connectivity among this network of marine reserves is likely to be altered under forecast scenarios of climatic change. Specifically, for key benthic marine species (kelp and sea urchins; Bennett et al., 2015) we compare connectivity between contemporary and future climatic scenarios with a focus on (i) the role of each MPA as a source or sink of propagule dispersal within the network, (ii) variability in dispersal among pairs of MPAs within the network and (iii) self-seeding within each MPA. For the first time, we also examine temporal variability in connectivity within a climate change context. Anticipation of such changes will greatly enhance the ability of this network of MPAs to maintain connectivity into the future by incorporating such knowledge into legislated reviews of MPA zoning arrangements.

Materials and methods

We investigated oceanographic connectivity among a network of marine parks (gazetted MPAs) spanning 8° of latitude along the coast of New South Wales, Australia (Fig. 1). This network comprised six marine parks each containing a subnetwork of numerous spatially separated 'no-take' marine reserves interspersed with partially protected and open fished areas (Kelaher et al., 2014, 2015a). We considered connectivity between six marine parks and an additional region off Sydney at 34°S which currently lacks a marine park. The six marine parks ranged in size from ~ 22 000 to ~98 000 Ha. Five marine parks are located along the mainland coast of SE Australia, at 29°S (Cape Byron Marine Park, CBMP; Kelaher et al., 2015b), 30°S (Solitary Islands Marine Park, SIMP), 32°S (Port Stephens Great Lakes Marine Park, PSGLMP), 35°S (Jervis Bay Marine Park, JBMP) and 36°S (Batemans Marine Park, BMP). All of these sites are potentially within the influence of the East Australian Current which transports warm water (and species) from the tropics poleward. The sixth marine park is an island (Lord Howe Island) that lies at 31°S and ~600 km to the east of mainland Australia. This marine park was included in analyses because the EAC bifurcates most often between 30 and 32°S (Cetina-Heredia et al., 2014), giving rise to the Tasman Front which flows eastwards towards Lord Howe Island. South of the EAC separation, the EAC extension and meso-scale eddies dominate the circulation along the coast influencing marine parks within this region.

We chose the two dominant habitat-forming species in NSW as key species to model changes in connectivity: kelp
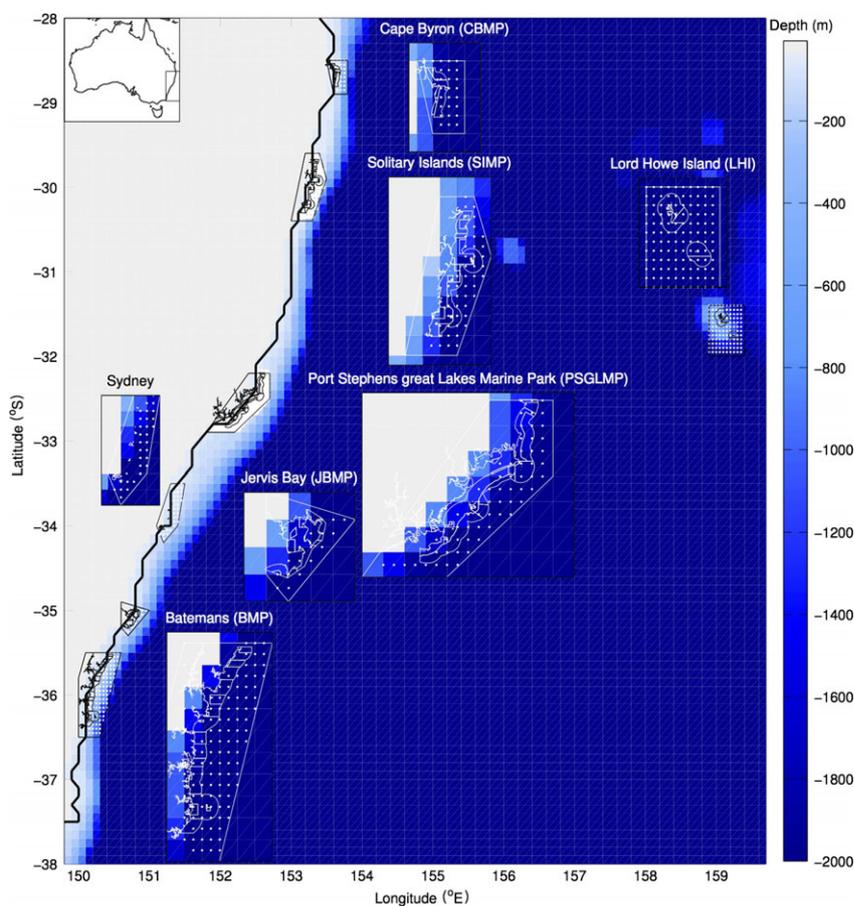
Fig. 1 Map of NSW showing a region off Sydney and networks of marine parks (along the coastline and zoomed in) used in this study. The horizontal distribution (latitude and longitude) of particle release locations (white dots) is also shown.

(*Ecklonia radiata*) and barrens forming sea urchins (*Centrostephanus rodgersii*; Andrew & O'Neill, 2000). These species were chosen because they play a disproportionately important (and interacting) role in structuring temperate marine biodiversity (e.g., Wernberg *et al.*, 2003; Coleman *et al.*, 2007). Moreover, these are key taxa in temperate marine communities that change due to protection (e.g., Shears & Babcock, 2003; Babcock *et al.*, 2010; Coleman *et al.*, 2013). Kelp does not occur on LHI so analyses of kelp connectivity were omitted at this site. *Ecklonia radiata* has a typical Laminarian alternation of generations life history strategy with large, perennial sporophytes (spore-producing individuals) alternating with microscopic gametophytes (gamete-producing individuals; Jennings, 1967). Significant dispersal likely occurs via zoospores and fertile sporophytes, which may disperse in currents when they are removed from the substratum during storms (Kirkman & Kendrick, 1997; Coleman *et al.*, 2009). *Centrostephanus rodgersii* reproduces annually by gametogenesis and spawning (Byrne *et al.*, 1998); thus, their geographical range is partly determined by larval dispersal. The onset of spawning occurs in mid to late June, and spawning is short (~1 month) at their northern limit but extends to 5 or 6 months at the southern edge of their range (Byrne *et al.*, 1998). Based on metamorphosis of cultured larvae, Hugget

et al. (2005) predict that settlement occurs from September to February. Nevertheless, settlement has been observed as late as early January (Andrew & Underwood, 1989). Hence, *Centrostephanus rodgesii* larvae take roughly 3–5 months to develop and become competent for settlement (Byrne & Andrew, 2013).

Current velocity outputs from the Ocean Forecast Australian Model (OFAM) forced with a contemporary and a future climate scenario were used to advect particles with the Connectivity Modelling Systems (CMS, Paris *et al.*, 2013). The OFAM contemporary scenario is forced with climatology of present atmospheric conditions, while the future scenario is forced with the 2060 forcing, constructed from the climatology of present atmospheric conditions plus air-sea flux anomalies from the CSIRO Mk3.5 climate model under an A1B emissions scenario (Chamberlain *et al.*, 2012; Sun *et al.*, 2012). The A1B scenario considers rapid economic growth, global population that peaks in the mid-century and declines thereafter, and a balanced development of alternative energy technology (Nakicenovic *et al.*, 2000). Model outputs capture the mean circulation and variability under contemporary and future atmospheric conditions but do not represent specific time periods. For this study, we use outputs from four representative 'years' of each scenario.
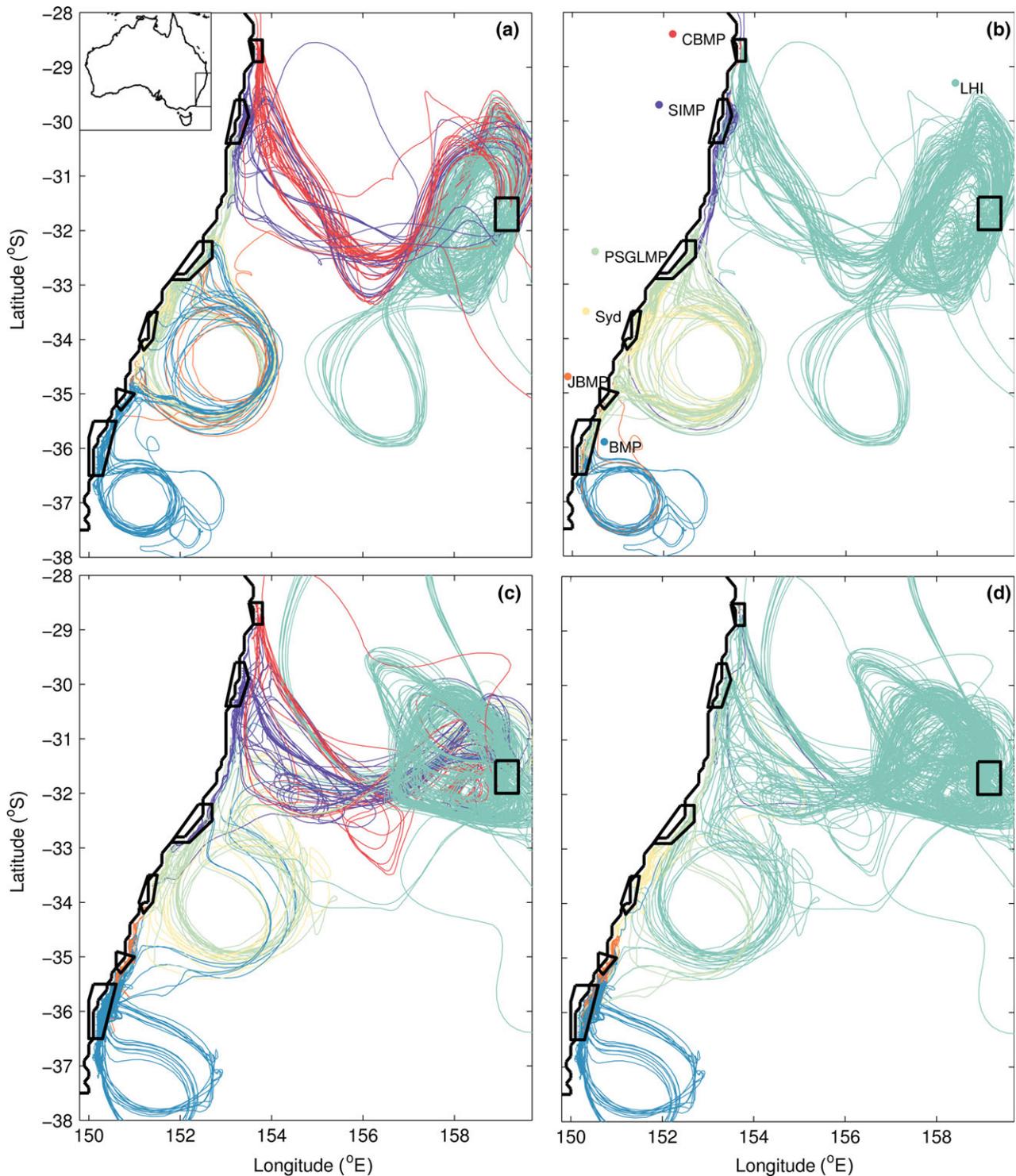
Fig. 2 Example of urchin particle trajectories that settled in Marine Parks for a contemporary year (a,b) and a future year (c,d). The trajectories are coloured by source (a,c) and sink (b,d) and show particles that achieve settlement.

Particle tracking simulations were conducted separately for each species, and particles were modified to reflect characteristics of *C. rodgersii* larvae and *E. radiata* sporophytes. We seeded particles inside the marine parks (Fig. 1) every 2 km in longitude and latitude, at 5-m depth and at 5-m increments

from there to a depth of 25 m. Because marine parks are of differing sizes (areas), the number of particles released (each day) within each marine park varied from 47 to 600 and connectivity matrices correspond to settlement proportions relative to the total number of particles released inside each

marine park. We released particles daily during the spawning season of *C. rodgersii* (June to October, Byrne *et al.*, 1998) and the reproductive season of *E. radiata* sporophytes (April to October, Coleman *et al.*, 2014), yielding a total of 1.20×10^6 and 8.55×10^5 released particles representing *E. radiata* and *C. rodgersii*, respectively, seeded over a 4-year period. Particles were considered to contribute to connectivity if they were within suitable habitat (i.e., inside an MPA) at any time 3–5 months after release (corresponding to the pelagic larval duration of *C. rodgersii*; Hugget *et al.*, 2005) or between the release time and 2 months (corresponding to the maximal potential dispersal time of *E. radiata*; Coleman *et al.*, 2014). Simulations were performed separately for four reproductive events (years) of each scenario and used to construct connectivity matrices (i.e., the number of particles exchanged among all pairs of marine parks, see Fig. 2 as an example of trajectories of particles exchanged among MPA's) for each year. The mean and standard deviation of the number of particles exchanged among marine parks were also computed for each scenario across years (Figs 4 and 5).

We compared differences between contemporary and future connectivity among all pairs of marine parks within the network. To do this, we subtracted contemporary from future connectivity matrices focusing on departures or changes from the contemporary state rather than in departures from a

hypothetical future state. Subtractions were computed element by element of the connectivity matrix, where each element represents the exchange of larvae between a pair of marine parks within the network for each year. This yielded 16 matrices of change in connectivity (i.e., 16 possible pair combinations conformed using the four contemporary and four future years). To estimate changes in connectivity as percentages relative to total contemporary connectivity, the resulting matrices of change in connectivity were normalized (element by element) by the mean across years of the number of larvae settled in the contemporary scenario. Finally, the normalized matrices of change in connectivity were averaged to obtain a single matrix of changes in connectivity (Figs 4 and 5). Both poleward (south) and equatorward (north) contemporary and future connectivity were examined to determine whether there was asymmetry in the direction of any change.

To assess future changes in each marine park acting as a source (total dispersal into any other park in the network, minus self-seeding), acting as a sink (total dispersal from any other park in the network, minus self-seeding) and level of self-seeding within each marine park (the number of particles self-seeding), we did multivariate analyses in PERMANOVA using Euclidean distances. This was performed for each marine park separately with the factors being time (contemporary and
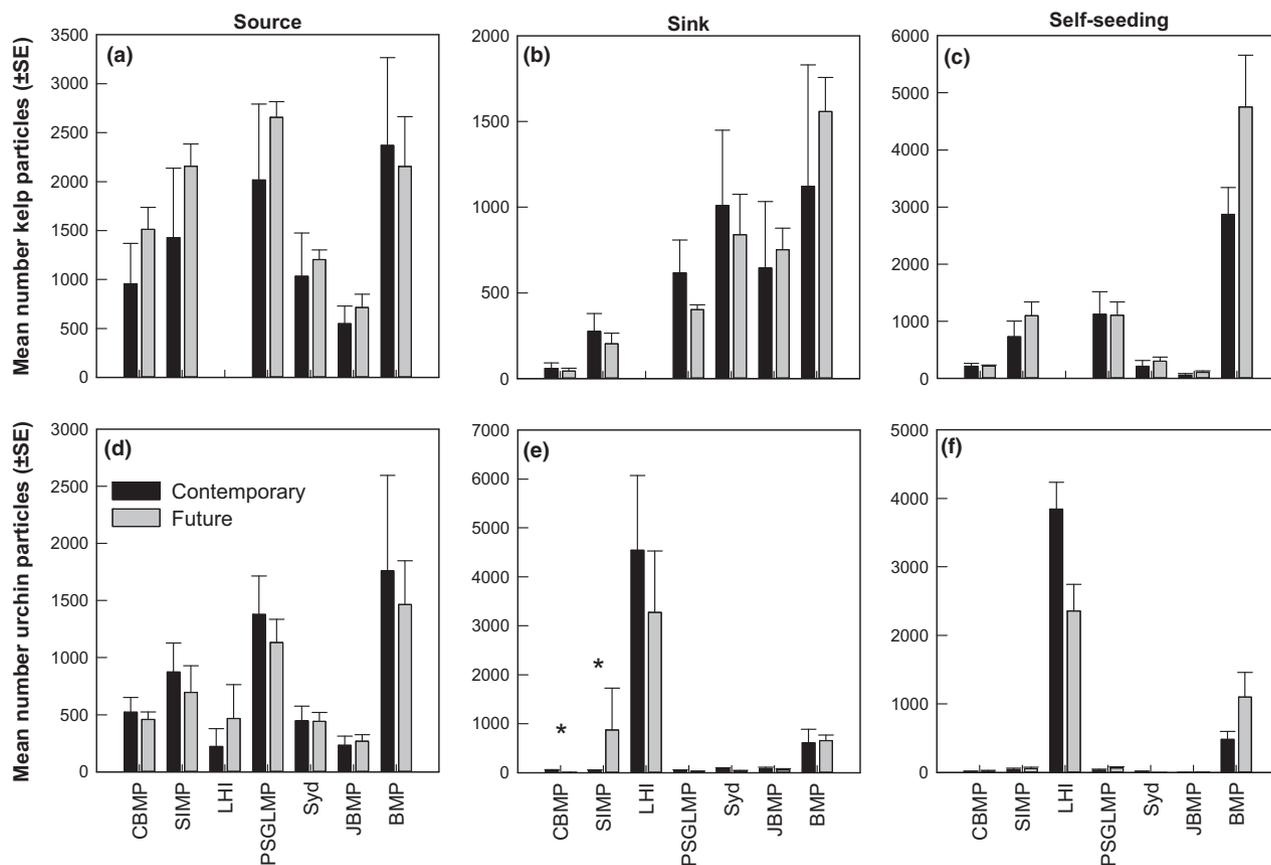
Fig. 3 Mean number of particles dispersing into the network from each marine park (source; a, d) and into each marine park from elsewhere in the network (sink; b, e) and self-seeding within each marine park (c, f) in the contemporary (black) and future (grey) climate scenarios for urchins and kelp.

future, fixed) and marine park source or sink (fixed, $n = 5$ and 6 for kelp and urchins, respectively) with $n = 4$ years of each scenario being the replicates. We were primarily concerned with the factor 'time' (see Fig. 3).

Results

Change in connectivity among populations of kelp

For kelp, connectivity among marine parks within the network varied greatly among years in both the contemporary and future scenarios, and this variation resulted in no statistical difference in each park acting as a source or sink between contemporary and future scenarios (PERMANOVA, Time: $P > 0.05$ for all parks, Fig. 3a, b). Either self-seeding of kelp particles within all marine parks did not change (CMBP and PSGLMP), or there was a trend for it to increase (all other parks, Fig. 3c and diagonal in Fig. 4). Self-seeding increased twofold in BMP and JB (Fig. 3c), but pairwise tests did not reveal any statistical difference despite a significant time × park interaction (PERMANOVA, $P > 0.05$ for all pairwise tests). Again, variation in self-seeding within each marine park was high in both future and contemporary scenarios (Fig. 3c and diagonal in Fig. 4).

The percentage and direction of change in connectivity among pairs of marine parks varied greatly, and variation among years was high in both the contemporary and future scenarios (Fig. 4). In general, there appeared to be a trend for poleward connectivity among pairs of marine parks to increase (reds, top right of matrix) and equatorward connectivity to decrease (blues, bottom left of matrix) (Fig. 4).

Change in connectivity among populations of sea urchins

For urchins, connectivity among marine parks within the network varied greatly among years in both the contemporary and future scenarios, and there was thus little overall statistical difference between scenarios in terms of marine parks acting as a source or a sink (PERMANOVA, Time: $P > 0.05$, Fig. 3d, e). The exception was the two lowest latitude marine parks (CBMP and SIMP) which received significantly less (CBMP) or more (SIMP) dispersal from elsewhere in the network under a future climate scenario (PERMANOVA, $P < 0.05$ for time × park interaction and for pairwise tests involving CBMP and SIMP). Self-seeding tended to increase marginally in most marine parks except LHI (Figs 3a and 5), but not
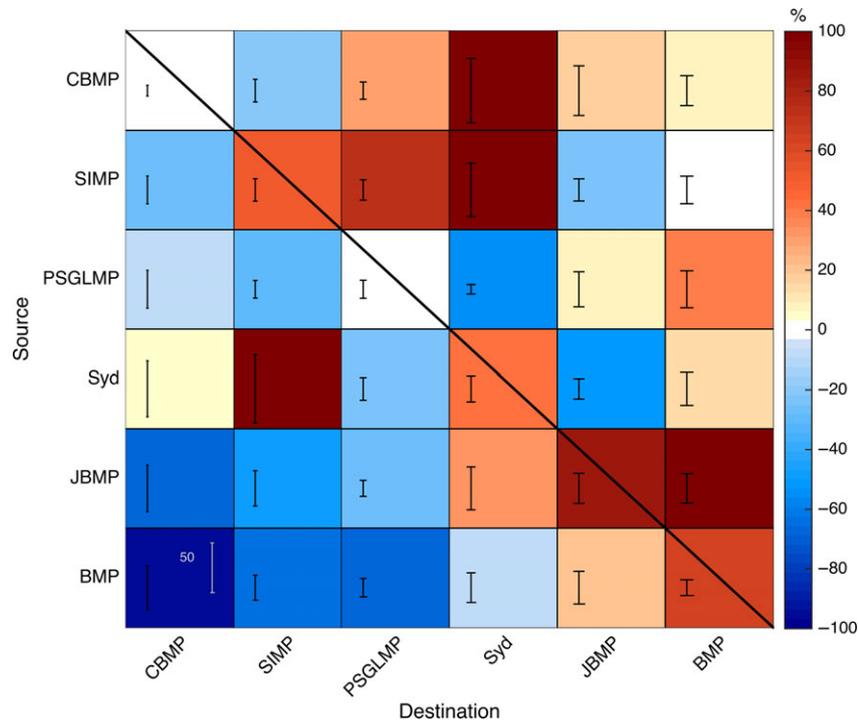
Fig. 4 Mean normalized difference (future minus contemporary) of connectivity among pairs of marine protected areas (MPAs) for *Ecklonia radiata*. Normalized connectivity difference is settlement proportion relative to the number of particles that settle in the contemporary scenario at each marine park. The error bars inside each square indicate the standard error across the normalized difference matrices for each pair of parks; a scale for the error bar magnitude is show in the bottom left of the figure. Both equatorward connectivity (bottom left of matrix) and poleward (top right of matrix) connectivity are shown.
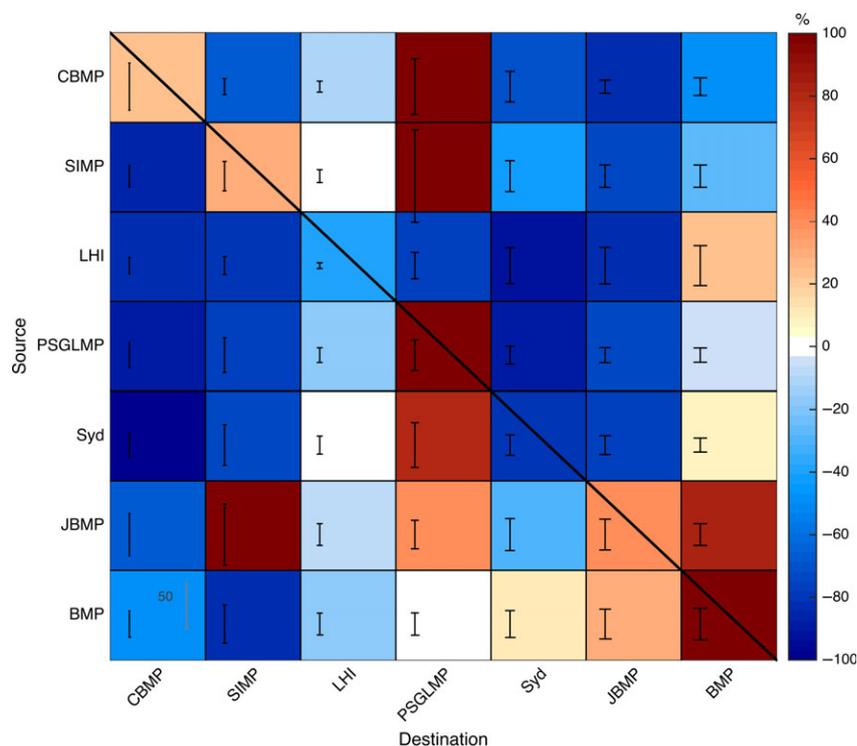
Fig. 5 Mean normalized difference (future minus contemporary) of connectivity among pairs of marine protected areas (MPAs) for *Centrostephanus rodgersii*. Mean normalized difference in connectivity is settlement proportion relative to the number of larvae that settle in the contemporary scenario at each marine park. The error bars inside each square indicate the standard error across normalized difference matrices for each pair of marine parks; a scale for the error bar magnitude is show in the bottom left of the figure. Both equatorward connectivity (bottom left of matrix) and poleward (top right of matrix) connectivity are shown.

significantly so (PERMANOVA, all pairwise tests for time × park interaction $P > 0.05$).

For sea urchins, connectivity among most pairs of marine parks tended to decrease in a future relative to contemporary climate scenario (Fig. 5), and this was the case for both poleward connectivity and equatorward connectivity (blues in Fig. 5). Interestingly, both future connectivity and contemporary connectivity into LHI were almost always extremely variable (Fig. 5) relative to all other parks.

Discussion

Planning the spatial distribution of MPAs to ensure they maintain connectivity both now and under future climatic scenarios is an important design criterion, but incorporating this objective is hindered by a lack of quantitative data (Magris *et al.*, 2014; Pendoley *et al.*, 2014), intricacies associated with species' ability to adapt (Mumby *et al.*, 2011), and biological responses (Andrello *et al.*, 2015) to climatic changes. Here, we use oceanographic modelling to quantitatively determine likely future changes to connectivity among a network of marine parks spanning over 1000 km of coastline. Climate-induced change in overall connectivity within

the network generally did not exceed temporal variation within scenarios. However, despite temporal variation we found notable large and often asymmetrical changes to connectivity among specific pairs of marine parks and a tendency towards an increase in self-seeding. In the light of the nonsignificance of these patterns due to large variation in dispersal within each climatic scenario, they should be cautiously discussed in the review and design of spatial arrangements of marine parks.

Contrary to expectations, overall connectivity within the network of marine parks generally did not change significantly because variation among years within both contemporary and future climatic scenarios was great, making statistical analyses difficult. This great variation may have arisen due to our use of only 4 years of data for each climatic scenario, a limitation of computation time and data storage. Modelling capabilities that allow comparisons of more years under each scenario will be important for future studies to better understand temporal variability as well as enhance predictions about change. Predictions may be further refined and matched to spatial management initiatives by downscaling models under future scenarios to allow finer spatial resolution of likely changes to connectivity

closer to the coast. In addition, incorporating information on variation in habitat availability, organismal behaviour and biological responses to climate change (e.g., larval survival and pelagic larval duration (PLD), Cetina-Heredia *et al.*, 2015) will also further refine predictions about future change to connectivity and provide the best possible scientific information to conservation managers.

Nevertheless, our study represents the first to examine temporal variability in connectivity among MPAs within both a contemporary and a future scenario and, therefore, to statistically examine future change. Given our finding of high temporal variability within climate scenarios, future studies should consider temporal variability to allow robust assessment when assessing absolute change, particularly given that temporal variation in dispersal is a key factor influencing population persistence (Blowes & Connolly, 2012). Even modest absolute change (3–10%) in overall connectivity metrics between contemporary and future climatic scenarios has previously been interpreted as meaningful in conservation settings (Andrello *et al.*, 2015), and may have genetic implications for populations. Absolute change in connectivity between many of the different pairs of marine parks studied here often far exceeded these estimates (up to 100% change), which should at least be considered (albeit cautiously) in the review and design of marine parks despite temporal variability within scenarios.

There were notable patterns in the intricacies of connectivity among pairs of marine parks, and these changes may have important implications for the geographical scale on which parks are reviewed. For kelp, poleward connectivity among most pairs of marine parks tended to increase. This is consistent with predicted strengthening of the EAC (Sun *et al.*, 2012), which likely facilitates longer distance transport of propagules among marine parks. Interestingly, the formation of more stable and longer-lived eddies is also predicted along south-east Australia (Oliver *et al.*, 2015), suggesting that increases to connectivity will not necessarily be linear in nature (stepping-stone; Kimura & Weiss, 1964) but that eddies may facilitate 'jumps' in dispersal. Increased poleward connectivity may have a number of genetic and demographic implications for kelp populations. If lower-latitude populations are better adapted to cope with warming temperatures, then increased connectivity may facilitate enhanced adaptation of populations at higher latitudes, which will experience increasingly warmer temperatures. For kelp (*E. radiata*), however, this may not be the case. Rather, low-diversity populations at low-latitude margins (Coleman *et al.*, 2011a) may lack the genetic diversity and physiological versatility to cope with future conditions (Wernberg *et al.*, 2016), and thus, increased poleward connectivity would not boost resilience of higher-latitude populations.

The trend towards an increase in poleward connectivity in kelp may be exacerbated by a general decrease in equatorward connectivity. This is particularly concerning given that lower-latitude kelp populations have already undergone climate-mediated range retractions (Smale & Wernberg, 2013; Verges *et al.*, 2014) which may be driven by lower genetic diversity (Coleman *et al.*, 2011a) conferring an inability to respond to thermal stress (Wernberg *et al.*, 2016), as well as increased herbivory (Verges *et al.*, 2014). The likelihood of lower-latitude populations recovering via recolonization from genetically diverse propagules at higher latitudes may thus be hindered under future climate scenarios resulting in continued poleward shifts in kelp distribution. Protecting important sources of equatorward connectivity in future marine park designs may thus be important for maintaining the resilience of kelp populations. Given that equatorward connectivity marginally increased (albeit nonsignificantly) only in adjacent networks of marine parks (e.g., BMP to JBMP, JMBP to SYD; Fig. 4), this could be achieved by ensuring the spacing among parks does not decrease and existing networks are maintained.

Similarly, for urchins, despite little change in overall connectivity within the entire network of marine parks, lower-latitude parks significantly changed their role as a sink in contrasting ways under a future scenario. Poleward and equatorward connectivity among pairs of marine parks showed a tendency to decrease in the future for urchins, and this is likely driven by the strengthening of the EAC (Oliver & Holbrook, 2014) and the long pelagic larval duration (PLD) of this species (3–5 months), resulting in more larvae transported to higher latitudes and outside the network of parks examined here. Although temperature-mediated decreases to larval PLD, dispersal distance and connectivity (e.g., see review by Lett *et al.*, 2010) may offset increased transport, this is unlikely to be the case for the urchin species studied here. Larvae of *C. rodgersii* have a wide thermal tolerance (Hardy *et al.*, 2014), and periodic incursions of warm, EAC water into higher latitudes have been shown to facilitate increased larval arrival, survival and establishment in cooler, higher-latitude areas (Ling *et al.*, 2008), contributing to the large reduction in abundance of giant kelp (*Macrocystis pyrifera*) forests (Johnson *et al.*, 2011). Thus, conservation managers in regions at higher latitudes will greatly benefit from understanding how the magnitude and spatial variability of urchin dispersal is likely to change under future climate scenarios, so that marine parks can be designed or reviewed to allow an increase in the

resilience of important *M. pyrifera* forests that underpin biodiversity and local productivity. Although our study did not disentangle the effects of increased temperature on larval survival from concurrent increased poleward connectivity (but see Cetina-Heredia *et al.*, 2015), it is likely that urchin larvae in northern NSW will begin to experience temperatures that exceed their thermal maxima (~22 °C; Hardy *et al.*, 2014). Thus, although poleward transport in ocean currents may theoretically increase, this may be offset by a decrease in larval survival, particularly at lower latitudes and possibly a poleward range retraction once extant adult populations expire.

An important aspect of MPA design is the extent to which protected areas can be self-sustaining (Almany *et al.*, 2007), particularly in the light of increasing habitat loss and fragmentation in surrounding unprotected areas. In the network of marine parks studied here, self-seeding (particle retention) of both species generally increased (albeit not significantly) in most parks and increased twofold for both species in higher-latitude marine parks. Such increase is likely a consequence of higher eddy activity, particularly polewards of latitudes where the EAC separates (Cetina-Heredia *et al.*, 2015) where SYD, JBMP and BMP are located. The conservation implications of greater local retention are likely to be positive and confer population persistence (Figueiredo *et al.*, 2014; Castorani *et al.*, 2015). At lower latitudes where thermal stress is greatest, marginal increases in retention may mean that locally adapted genotypes are retained within protected areas. In addition, given that higher-latitude populations may have higher genetic diversity (kelp; Coleman *et al.*, 2011b), greater self-seeding under future climatic scenarios likely confers long-term resilience and persistence of populations in these marine parks.

Ongoing management of MPAs following a review of the spatial arrangement and effectiveness of different management zones is a common requirement around the world to ensure MPAs achieve their goals into the future, but the extent to which this occurs is not clear. Anticipation of future changes to connectivity (and the variability surrounding predicted changes) will assist with such management processes by (i) identifying key additional areas to be considered for protection into the future and (ii) providing insight into the future effectiveness of current spatial arrangement of MPAs and how this may be best modified to maintain connectivity. Anticipating changes to connectivity, particularly for organisms that underpin biodiversity (e.g., habitat formers) and those that are key components of marine food webs, is important if MPAs are to achieve their conservation goals in a future of rapid environmental change.

References

Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science*, **316**, 742–744.

Almpanidou V, Costescu J, Schofield G, Türkozan O, Hays GC, Mazaris AD (2016) Using climatic suitability thresholds to identify past, present and future population viability. *Ecological Indicators*, **71**, 551–556.

Andrello M, Mouillot D, Somot S, Thuiller W, Manel S (2015) Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. *Biodiversity Research*, **21**, 139–150.

Andrew NL, O'Neill AL (2000) Large-scale patterns in habitat structure on subtidal rocky reefs in New South Wales. *Marine and Freshwater Research*, **51**, 255–263.

Andrew NL, Underwood AJ (1989) Patterns of abundance of the sea urchin *Centrostephanus rodgersi* (Agassiz) on the central coast of New South Wales, Australia. *Journal of Experimental Marine Biology and Ecology*, **131**, 61–80.

Babcock RC, Shears NT, Alcala AC *et al.* (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences USA*, **107**, 18256–18261.

Bennett S, Wernberg T, Connell SD, Hobda AJ, Johnson CR, Poloczanska ES (2015) The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. *Marine and Freshwater Research*, **67**, 47–56.

Blowes SA, Connolly SR (2012) Risk spreading, connectivity, and optimal reserve spacing. *Ecological Applications*, **22**, 311–321.

Byrne M, Andrew N (2013) *Centrostephanus rodgersii*. In: *Sea Urchins: Biology and Ecology* (ed. Lawrence JM), pp. 243–256. Elsevier, Amsterdam, the Netherlands.

Byrne M, Andrew NL, Worthington DG, Brett PA (1998) Reproduction in the diadematoid sea urchin *Centrostephanus rodgersii* in contrasting habitats along the coast of New South Wales, Australia. *Marine Biology*, **132**, 305–318.

Cai W (2006) Antarctic ozone depletion causes an intensification of the Southern Ocean super-gyre circulation. *Geophysical Research Letters*, **33**, L03712.

Castorani MCN, Reed DC, Alberto F *et al.* (2015) Connectivity structures local population dynamics: a long term empirical test in a large metapopulation system. *Ecology*, **96**, 3141–3152.

Cetina-Heredia P, Roughan M, van Sebille E, Coleman MA (2014) Long-term trends in the East Australian Current separation latitude and eddy driven transport. *Journal of Geophysical Research Oceans*, **119**, 4351–4366.

Cetina-Heredia P, Roughan M, Van Sebille E, Feng M, Coleman MA (2015) Strengthened currents override the effect of warming on lobster larval dispersal and-survival. *Global Change Biology*, **21**, 4377–4386.

Chamberlain MA, Sun C, Matear RJ, Feng M, Phipps SJ (2012) Downscaling the climate change for oceans around Australia. *Geoscientific Model Development*, **5**, 1177–1194.

Coleman MA (2013) Dispersal of the habitat-forming kelp, *Ecklonia radiata* within and among estuaries and open coast. *PLoS One*, **8**, e64667

Coleman MA, Kelaher BP (2009) Connectivity among fragmented populations of a habitat-forming alga, *Phyllospora comosa* (Phaeophyceae, Fucales) on an urbanised coast. *Marine Ecology Progress Series*, **381**, 63–70.

Coleman MA, Vytopil E, Goodsell PJ, Gillanders BM, Connell SD (2007) Depth and mobile invertebrates: evidence of a widespread pattern in biodiversity. *Marine and Freshwater Research*, **58**, 589–595.

Coleman MA, Connell SD, Gillanders BM (2009) Dispersal and gene flow in the habitat-forming kelp, *Ecklonia radiata*: relative degrees of isolation across an east-west coastline. *Marine and Freshwater Research*, **60**, 802–809.

Coleman MA, Roughan M, McDonald H, Connell SD, Gillanders BM, Kelaher BP, Steinberg PD (2011a) Variation in the strength of continental boundary currents determines patterns of large-scale connectivity in kelp. *Journal of Ecology*, **99**, 1026–1032.

Coleman MA, Chambers J, Knott N, Malcolm H, Harasti D, Jordan A, Kelaher BP (2011b) Connectivity within and among a network of temperate marine reserves. *PLoS One*, **6**, e20168

Coleman MA, Palmer-Brodie A, Kelaher BP (2013) Conservation benefits of a network of marine reserves and partially protected areas. *Biological Conservation*, **167**, 257–264.

Coleman MA, Feng M, Cetina-Heredia P, Roughan M, Connell SD (2014) Temperate shelf water dispersal of Australian boundary currents and implications for population connectivity. *Limnology and Oceanography: Fluids and Environments*, **3**, 295–309.

Coleman MA, Bates AE, Stuart-Smith RD *et al.* (2015) Functional traits reveal early responses in marine reserves following protection from fishing. *Diversity and Distributions*, **21**, 876–887.

Durrant HMS, Kelaher BP, Burridge CP, Barrett NS, Edgar GJ, Coleman MA (2014) Implications of macroalgal isolation by distance for networks of marine protected areas. *Conservation Biology*, **28**, 438–445.

Figueiredo J, Baird AH, Harii S, Connolly SR (2014) Increased local retention of reef coral larvae as a result ocean warming. *Nature Climate Change*, **4**, 498–502.

Hardy N, Lamare M, Uthicke S, Wolfe K, Doo S, Dworjanyn S, Byrne M (2014) Thermal tolerance of early development in tropical and temperate sea urchins: inferences for the tropicalization of eastern Australia. *Marine Biology*, **161**, 395–409.

Hill KL, Rintoul SR, Coleman R, Ridgway KR (2008) Wind forced low frequency variability of the East Australian current. *Geophysical Research Letters*, **35**, L08602.

Hugget MJ, King CK, Williamson JE, Steinberg P (2005) Larval development and metamorphosis of the Australian diadematoid sea urchin *Centrostephanus rodgesii*. *Invertebrate Reproduction and Development*, **47**, 197–204.

Jennings J (1967) The development of the gametophyte and young sporophyte of *Ecklonia radiata* (C. Ag.) J. Ag. (Laminariales). *Journal of the Royal Society of Western Australia*, **50**, 93–96.

Johnson CR, Banks SC, Barrett NS *et al.* (2011) Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology*, **400**, 17–32.

Kelaher BP, Coleman MA, Broad A, Jordan A, Davis AR (2014) Changes in fish assemblages following the establishment of a network of no-take and partially protected marine protected areas. *PLoS One*, **9**, e85825.

Kelaher BP, Page A, Dasey M, Maquire D, Reed A, Jordan A, Coleman MA (2015a) Strengthened enforcement enhances marine sanctuary performance. *Global Ecology and Conservation*, **3**, 503–510.

Kelaher BP, Tan M, Figueira WF *et al.* (2015b) Fur seal activity moderates the effects of an Australian marine sanctuary on temperate reef fish. *Biological Conservation*, **182**, 205–214.

Kimura M, Weiss GH (1964) The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics*, **49**, 561–576.

Kirkman H, Kendrick GA (1997) Ecological significance and commercial harvesting of drifting and beach-cast macro-algae and seagrasses in Australia: a review. *Journal of Applied Phycology*, **9**, 311–326.

Lett C, Ayata S-D, Huret M, Irisson J-O (2010) Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress in Oceanography*, **87**, 106–113.

Ling SD, Johnson CR, Frusher S, King CK (2008) Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range. *Global Change Biology*, **14**, 1–9.

Magris RA, Pressey RL, Weeks R, Ban NC (2014) Integrating connectivity and climate change into marine conservation planning. *Biological Conservation*, **170**, 207–221.

Matear RJ, Chamberlain MA, Sun C, Feng M (2013) Climate change projection of the Tasman Sea from an eddy-resolving ocean model. *Journal of Geophysical Research Oceans*, **118**, 2961–2976.

Melia P, Schianina M, Rossetto M, Gatto M, Fraschetti S, Casagransi R (2016) Looking for hotspots of marine metacommunity connectivity: a methodological framework. *Scientific Reports*, **6**, 23705.

Mumby P, Elliott IA, Eakin CM *et al.* (2011) Reserve design for uncertain responses of coral reefs to climate change. *Ecology Letters*, **14**, 132–140.

Mundy PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate change and coral reef connectivity. *Coral Reefs*, **28**, 379–395.

Nakicenovic N, Alcamo J, Davis G (eds) (2000) *Emissions Scenarios*: *A Special Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, Cambridge.

Oliver ECJ, Holbrook NJ (2014) Extending our understanding of South Pacific gyre ''spin-up'': modelling the East Australian Current in a future climate. *Journal of Geophysical Research Oceans*, **119**, 2788–2805.

Oliver ECJ, O'Kane TJ, Holbrook NJ (2015) Projected changes to Tasman Sea eddies in a future climate. *Journal of Geophysical Research Oceans*, **120**, 7150–7165.

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications*, **13**, S146–S158.

Paris CB, Helgers J, van Sebille E, Srinivasan A (2013) Connectivity modelling system: a probabilistic tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environmental Modelling and Software*, **42**, 47–54.

Parsons EMC, Favaro B, Aguirre AA *et al.* (2014) 71 important questions for the conservation of marine biodiversity. *Conservation Biology*, **28**, 1206–1214.

Pendoley KL, Schofield G, Whittock PA, Ierodiaconou D, Hays GC (2014) Protected species use of a coastal marine turtle migratory corridor connecting Australian MPAs. *Marine Biology*, **161**, 1455–1466.

Provost EJ, Coleman MA, Dworjanyn SA *et al.* (2016) Direct and indirect effects of future oceans at the low latitude margins of kelp forest distribution. *Global Change Biology*, **23**, 353–361.

Ridgway KR (2007) Long-term trend and decadal variability of the southward penetration of the East Australian current. *Geophysical Research Letters*, **34**, L13612.

Roberts CM (1997) Connectivity and management of Caribbean Reef Corals. *Science*, **278**, 1454–1457.

Roberts CM, Bustmante RH, Dugan J *et al.* (2003) Application of ecological criterion in selecting marine reserves and developing reserve networks. *Ecological Applications*, **13**, S215–S228.

Sen Gupta A, Brown JN, Jourdain NC, van Sebille E, Ganachaud A, Verges A (2015) Episodic and non-uniform shifts of thermal habitats in warming Ocean. *Deep-Sea Research II*, **13**, 59–72.

Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications*, **13**, S159–S169.

Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series*, **246**, 1–16.

Smale DA, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B*, **280**, 20122829.

Sun C, Feng M, Matear RJ, Chamberlain MA, Craig P, Ridgway KR, Schiller A (2012) Marine downscaling of a future climate scenario for Australian boundary currents. *Journal of Climate*, **25**, 2947–2962.

Verges A, Steinberg PD, Hay ME *et al.* (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society of London, Series B Biology*, **281**. doi: 10.1098/rspb.2014.0846.

Wernberg T, Coleman MA, Fairhead A, Miller S, Thomsen MS (2003) Morphology of *Ecklonia radiata* (C. Ag.) J. Agardh. along its geographic distribution in Southwestern Australia and Australasia. *Marine Biology*, **143**, 47–55.

Wernberg T, Bennett S, Babcock RC *et al.* (2016) Climate driven regime shift of a temperate marine ecosystem. *Science*, **353**, 169–172.

Wu L, Ca W, Zhang L *et al.* (2012) Enhanced warming over the global subtropical western boundary currents. *Nature Climate Change*, **2**, 161–166.

Graphical Abstract

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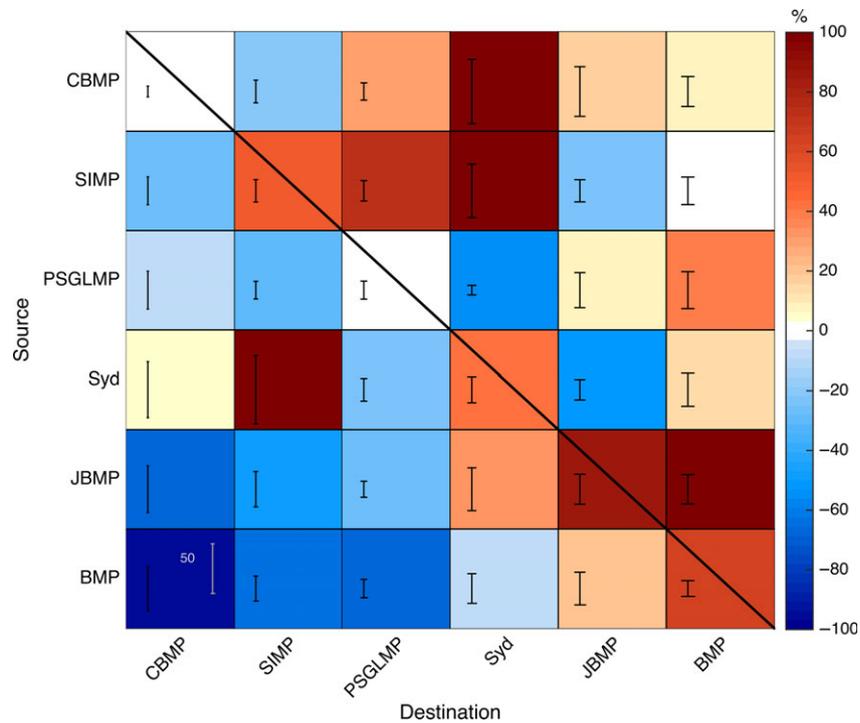
Planning marine protected areas (MPAs) to ensure they maintain connectivity under future climatic scenarios is an important design criterion that is rarely quantitatively incorporated. We use oceanographic modelling to show that climate-induced change in connectivity within a large network of MPAs did not exceed temporal variation within future and contemporary scenarios. However, notable changes to absolute connectivity among specific pairs of MPAs and a tendency towards an increase in self-seeding should be cautiously considered in the review and design of MPAs.