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Genetic structure of a recent climate change-driven range extension

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Abstract

The life-history strategies of some species make them strong candidates for rapid exploitation of novel habitat under new climate regimes. Some early-responding species may be considered invasive, and negatively impact on 'naïve' ecosystems. The barrens-forming sea urchin *Centrostephanus rodgersii* is one such species, having a high dispersal capability and a high-latitude range margin limited only by a developmental temperature threshold. Within this species' range in eastern Australian waters, sea temperatures have increased at greater than double the global average rate. The coinciding poleward range extension of *C. rodgersii* has caused major ecological changes, threatening reef biodiversity and fisheries productivity. We investigated microsatellite diversity and population structure associated with range expansion by this species. Generalized linear model analyses revealed no reduction in genetic diversity in the newly colonized region. A 'seascape genetics' analysis of genetic distances found no spatial genetic structure associated with the range extension. The distinctive genetic characteristic of the extension zone populations was reduced population-specific F_{ST}, consistent with very rapid population expansion. Demographic and genetic simulations support our inference of high connectivity between pre- and post-extension zones. Thus, the range shift appears to be a poleward extension of the highly-connected rangewide population of *C. rodgersii*. This is consistent with advection of larvae by the intensified warm water East Australian current, which has also increased Tasmanian Sea temperatures above the species' lower developmental threshold. Thus, ocean circulation changes have improved the climatic suitability of novel habitat for *C. rodgersii* and provided the supply of recruits necessary for colonization.

Keywords: climate change, colonization, dispersal, echinoid, ocean current, range shift, sea urchin, seascape genetics

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Introduction

The capacity of species to shift in geographical distribution is predicted to be a major influence on the likelihood of persistence or extinction in response to global warming (Thomas *et al.* 2004; Massot *et al.* 2007). In turn, climate change-facilitated range-shifts are expected to have important consequences for the functioning of newly-colonized ecosystems that must respond to the presence of novel species (Bierwagen *et al.* 2008a). Latitudinal changes in distribution have been documented in marine and terrestrial environments (Hughes 2000; Walther *et al.* 2002; Harley *et al.* 2006). Understanding the demography of range shifts and the resultant patterns of genetic population subdivision is important for predicting both the response of individual species to climate change, the subsequent effects on ecological

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communities or ecosystem-dependent primary industries, and for evaluating management responses to these novel environmental challenges (Thomas *et al.* 2004; Bierwagen *et al.* 2008b).

The primary drivers of climate change-induced range shifts are expected to be abiotic changes in environmental conditions that relate to (i) physiological thresholds and (ii) interspecific ecological interactions that alter the ability of species to persist in local habitats (Hughes 2000; Harley *et al.* 2006). These mechanisms are predicted to result in local population extinctions, but also provide opportunities for the colonization of newly suitable environments. In the marine environment, boundaries to species' distributions may also be generated by current circulation patterns (Gaylord & Gaines 2000). The effect of climate change on ocean currents could therefore drive distributional shifts by advection of planktonic larvae to new habitat (Cai *et al.* 2005).

The Tasman Sea off south-eastern Australia has warmed at a rate greater than double the global average as a consequence of the strengthening of the warm southward-flowing East Australian Current (EAC) (Bindoff & Church 1992; Ridgway 2007). Coinciding with this increase in ocean temperature has been the poleward range extension into Bass Strait and Tasmanian coastal waters by the barrens-forming diatematid sea urchin *Centrostephanus rodgersii* (Agassiz), a species unrecorded south of eastern mainland Australian waters prior to the 1960s (Fig. 1). *Centrostephanus rodgersii* is a high-dispersing species with a 3- to 4-month planktonic larval duration (Huggett *et al.* 2005) and is the dominant benthic grazing herbivore on subtidal rocky reef habitat throughout much of its range along the Australian east coast (Fletcher 1987). Its spread to Tasmania poses significant ecological and economic threats because the formation of barrens habitat results in declines of local biodiversity (Ling 2008) and fisheries productivity (Fig. 2) (Johnson *et al.* 2005). This poleward range expansion has been facilitated by warming coastal waters that now regularly exceed the lower 12 °C threshold for larval development, particularly on the open coast where rocky reefs are influenced by the EAC (Ling *et al.* 2008, 2009). Thus, the most likely demographic process of range extension is regular recruitment to a newly-accessible environment by mass larval advection from lower-latitude sources by the intensified southward flow of the EAC (Johnson *et al.* 2005; Ling *et al.* 2009). However, because the sea urchin undergoes a normal reproductive cycle and is capable of producing viable gametes in a newly suitable temperature regime in eastern Tasmania (Ling *et al.* 2008), an alternative explanation is an initial

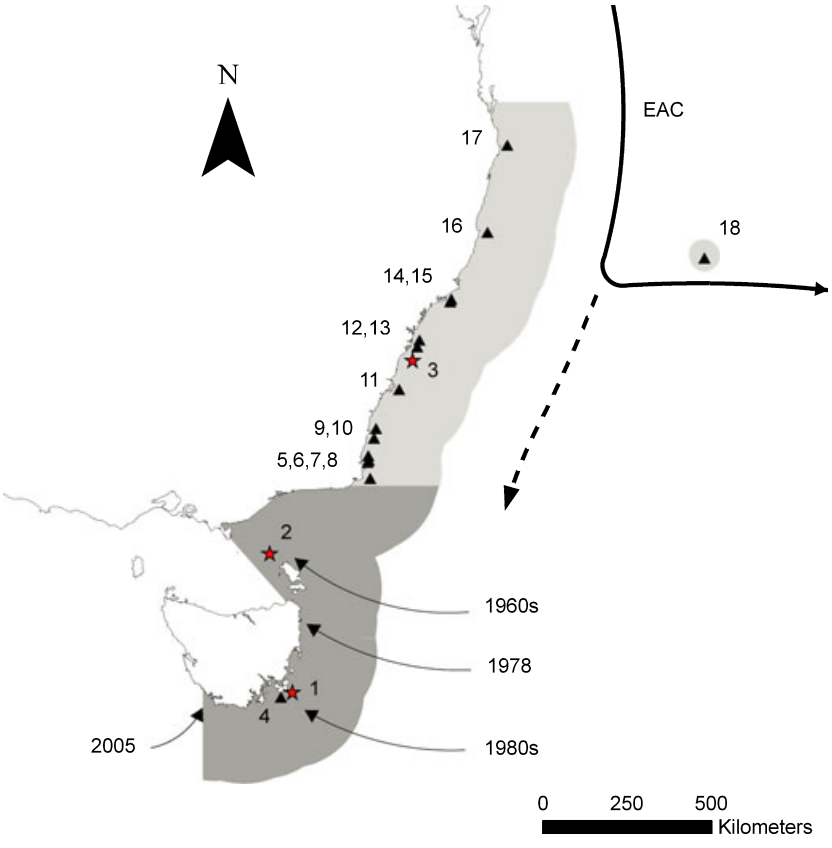

Fig. 1 Locations in which *C. rodgersii* was sampled in 2000 (1–3) and 2005 (4–18). The arrows indicate the year of first detection of *C. rodgersii* in the newly colonized portion of its range. The pale grey region covers the historical latitudinal distribution of *C. rodgersii* along the mainland Australian coast. The darker grey region covers the recently colonised portion of the species' range. *C. rodgersii* is found on shallow rocky reefs within these areas. The predominant ocean current of the region, the EAC, is presented as a solid line turning east as the Tasman Front. The EAC annually extends southward, being strongest in the summer months (broken line).

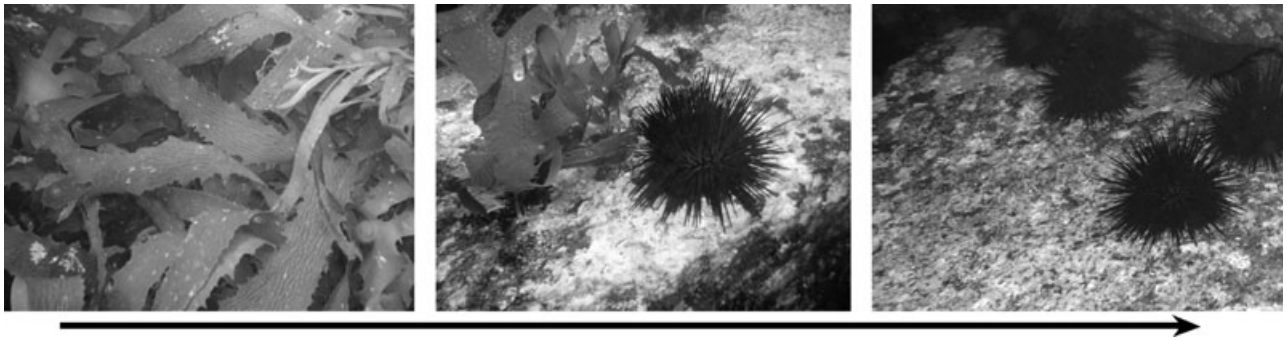

Fig. 2 Recently observed phase shift in eastern Tasmania from macroalgal dominated habitat to sea urchin barrens as a result of overgrazing by *C. rodgersii*. The image is a time series of the same reef patch. The barrens habitat is patchily distributed throughout eastern Tasmania with widespread barrens (hundreds of metres) currently observed on reefs in the north east and mid-east coasts, while smaller incipient barrens patches (one to tens of metres) are observable over much of the east coast (Johnson *et al.* 2005) (Photo: SD Ling).

founder effect followed by rapid intrinsic population growth.

The demographic processes that differ between these alternative range expansion scenarios, including dispersal, population growth rates and founder effects, leave potentially detectable signatures in the genetic structure of the newly established demes. However, marine broadcast-spawning species commonly have been found to demonstrate unusual patterns of spatial genetic structure driven by processes resulting from the life histories of these species (Hellberg 2009). As expected, genetic structure in some species has been associated with dispersal ability predicted from pelagic larval duration or developmental mode (Sherman *et al.* 2008). However, factors such as habitat specificity and larval behaviour potentially contribute to local larval retention, even in species with long larval durations (Queiroga & Blanton 2004; Kelly & Palumbi 2010). The relationship between genetic structure and distance may be driven by different processes at different scales (Hellberg 2009) and factors other than dispersal may often be the primary drivers of spatial genetic patterns. On the fine scale, 'chaotic genetic patchiness' (Johnson & Black 1984) has been observed in several species, most likely generated by very low effective (N_e) to census (N_c) population sizes, leading to genetic differentiation between generations (Hedgecock 1994; Moberg & Burton 2000; Levitan 2005; Hauser & Carvalho 2008). Together with cohesion of genetically-similar larval groups and spatio-temporal variation in settlement and recruitment rates, these processes lead to patchy patterns of genetic structure (Selkoe *et al.* 2006). In *C. rodgersii*, fine-scale patchy genetic structure was associated with larval retention along complex coastlines and spatiotemporal variation in recruitment due to ocean circulation variability (Banks *et al.* 2007).

In contrast, to the fine-scale pattern, Banks *et al.* (2007) found *C. rodgersii* genetic structure over thousands of kilometres to be weak, consistent with high levels of long-distance dispersal and no effective biogeographic boundaries. Studies of other marine species with planktonic larvae in this region have found an absence of major structure over large scales (Murray-Jones & Ayre 1997; Piggott *et al.* 2008; Sherman *et al.* 2008; Curley & Gillings 2009). These results and the presence of the strengthening poleward EAC make high-dispersing species in this region prime candidates for rapid colonization of higher-latitude habitats that become climatically suitable under global warming.

In this study, we characterized the patterns of genetic diversity and population structure associated with the poleward range extension of *C. rodgersii*. We analysed microsatellite data from the newly colonized region (Bass Strait and coastal Tasmanian waters) and the species' historical eastern mainland Australian range. We used a series of statistical analyses to test for evidence of founder effects during range expansion and to evaluate the relative connectivity of recently founded demes, which enabled us to infer how this species has extended its range in association with recent ocean circulation changes.

Methods

Genetic data collection

We sampled 474 *C. rodgersii*, including 93 in 2000 and 384 in 2005, from sites within the historical range of the species and the newly colonized southern region (Fig. 1, Table 1). We collected gonad tissue from mature adults, extracted DNA and genotyped all samples at the eight microsatellite loci CRO1-6, CRO2-7,

Table 1 Sampling sites for *Centrostephanus rodgersii* in 2000 and 2005. Number of samples (N_S), expected heterozygosity (H_S), number of alleles (N_A), allelic richness (AR) and F_{IS} are presented, as well as the proportion of locus pairs at which linkage disequilibrium was detected at a 5% significance level (LD_{SIG05}) and mean *M*-ratio. Population-specific F_{ST} (mean estimate), as estimated in GESTE 2, is presented with the 95% highest probability density interval

Location name	Site	Year	N_S	H_S	N_A	AR	F_{IS}	LD_{SIG05}	*M*-ratio	F_{ST} (GESTE)	F_{ST} (95% HPDI)
Tasman Peninsula—Fortescue Bay	1	2000	27	0.592	9.333	6.542	0.083	0.036	0.421	0.016	0.007–0.027
Deal Island	2	2000	42	0.615	9.667	6.096	0.111	0.107	0.424	0.018	0.007–0.029
Shell Harbour—Bass Point	3	2000	21	0.607	6.500	5.388	0.159	0.000	0.428	0.043	0.020–0.068
Tasman Peninsula—Safety Cove	4	2005	26	0.608	8.333	6.521	0.022	0.000	0.484	0.029	0.015–0.047
Cape Howe	5	2005	30	0.599	9.000	6.264	−0.019	0.000	0.469	0.021	0.009–0.033
Eden—Ross Bay	6	2005	26	0.668	7.667	6.245	0.023	0.067	0.447	0.045	0.027–0.063
Eden—Leonard's Island	7	2005	30	0.596	8.833	6.470	0.092	0.133	0.517	0.062	0.038–0.088
Merimbula wharf	8	2005	25	0.626	8.000	6.284	0.030	0.133	0.455	0.046	0.026–0.069
Bermagui	9	2005	25	0.600	7.333	5.900	0.066	0.000	0.395	0.042	0.022–0.063
Dalmeny	10	2005	25	0.604	7.167	6.027	0.024	0.000	0.493	0.026	0.013–0.043
Jervis Bay	11	2005	29	0.638	8.167	6.006	−0.049	0.000	0.514	0.034	0.015–0.054
Botany Bay—Bare Island	12	2005	19	0.653	7.500	6.595	−0.030	0.000	0.514	0.032	0.016–0.051
Port Jackson—Little Manly	13	2005	25	0.617	7.333	5.742	−0.029	0.000	0.475	0.033	0.019–0.049
Port Stephens—Boat Harbour	14	2005	19	0.603	7.167	6.680	0.128	0.000	0.504	0.044	0.026–0.064
Nelson's Bay	15	2005	25	0.615	7.333	6.540	0.022	0.000	0.420	0.032	0.015–0.051
South West Rocks	16	2005	30	0.645	8.167	6.444	0.087	0.000	0.472	0.044	0.023–0.067
Byron Bay—Julian Rocks	17	2005	25	0.586	7.000	5.563	0.064	0.067	0.560	0.063	0.040–0.091
Lord Howe Island	18	2005	25	0.651	8.000	6.755	−0.057	0.000	0.470	0.020	0.008–0.033

CRO2-9, CRO3-4, CRO3-10, CRO3-12A, CRO3-22 and CRO3-58 as described in Banks *et al.* (2006).

Genetic diversity

We tested for linkage disequilibrium (LD) among loci within populations and for departures from Hardy–Weinberg (H–W) expected genotype proportions using GENEPOP 3.4 (Raymond & Rousset 1995). We used FSTAT 2.9.3 (Goudet 1995) to calculate expected (H_E) heterozygote proportions within samples, allelic richness (AR) standardized by sample size and F_{IS} within samples.

We used regression analysis of expected and observed heterozygosity and allelic diversity data at the site and individual level to investigate the sources of variation in the genetic diversity data. Per-locus, per-site H_E and allelic diversity (AD) were analysed with generalized linear models (GLMs; McCullagh & Nelder 1983) fitted in GENSTAT 11 (Payne 2008). Locus, sample size (*n*: number of alleles sampled), year (2000 or 2005), site and extension zone (*Ext_Zone*: Bass Strait and Tasmanian sites) were the candidate explanatory variables. Observed heterozygosity (H_O) of individual diploid genotypes was analysed as a binary variable in a logistic generalized linear mixed model (GLMM; Schall 1991). Individual ID was included as a random effect. We hypothesized that if the *C. rodgersii* range extension progressed via one or a series of bottlenecks with little or no ongoing connectivity, we would detect a reduction in genetic diversity in the extension zone (Excoffier *et al.* 2009).

Bottleneck tests

We tested for genetic evidence for population bottlenecks in the extension zone samples, using a set of mainland Australian samples as 'controls'. First, we used the heterozygosity excess test with a two phase microsatellite mutation model (with 5% of mutations greater than one repeat unit) implemented in the software Bottleneck (Cornuet & Luikart 1996). A second test employed Garza and Williamson's M-ratio statistic (Garza & Williamson 2001), the mean ratio of the number of alleles to the range in allele size. Instead of estimating the critical M-ratio to identify putative population bottlenecks, we used a GLM with identity link function to test for consistent variation between sites, loci, years and between the extension and pre-extension zones of the species' range in the M-ratio statistic over the eight loci genotyped.

F_{ST} and hierarchical analysis of molecular variance

We used GENETIX 4.05 (Belkhir *et al.* 2004) to estimate F_{ST} using Raufaste & Bonhomme's (2000) bias-corrected version of Robertson & Hill's (1984) estimator ($\theta_{RH'}$). Raufaste & Bonhomme (2000) found this estimator to have lower variance than Weir & Cockerham's (1984) θ

in situations of low differentiation, as is the case for *C. rodgersii* (Banks *et al.* 2007). $\theta_{RH'}$ was tested for significance with 10 000 permutations. We used Arlequin 3.11 (Excoffier *et al.* 2005) to conduct a hierarchical analysis of molecular variance (AMOVA) with groups structured into new (Tasmanian) and pre-range extension zones. Meirmans' standardization of F statistics (by their maximum possible values) was conducted following data transformation in Recode_Data (Meirmans 2006). These analyses were conducted separately for the 2000 and 2005 data.

Genetic distances and partial Mantel tests

We used four genetic distance statistics to investigate differentiation among populations, with specific reference to pairwise population comparisons involving samples from the range extension zone. These methods use the genotypic data in different ways, ranging from allele frequency-based statistics to those based on multilocus genotypic arrays. We estimated:

1 Pairwise population F_{ST} values, estimated by $\theta_{RH'}$ in GENETIX 4.05 (Belkhir *et al.* 2004) and tested for significance with 1000 permutations.
2 Jost's *D*, estimated using the web program SMOGD (Crawford 2009).
3 Paetkau *et al.*'s (1997) D_{LR}, based on multilocus genotype likelihoods estimated in GENECLASS 2 (Piry *et al.* 2004).
4 Multilocus genotypic autocorrelation among populations (r_{pop}).

We used pairwise population comparisons as 'distance bins' for a multilocus spatial autocorrelation analysis implemented in Genalex 6 (Smouse & Peakall 1999; Peakall & Smouse 2006) with 10 000 permutations. This analysis yields a pairwise population-level genetic similarity estimate based on multilocus genetic distances among individuals, but does not take any allele frequency data into account.

We used partial Mantel tests implemented in FSTAT 2.9.3 (Goudet 1995) to determine whether the range extension zone explained a significant component of the variation in each genetic distance measure, after known environmental correlates of spatial genetic structure in *C. rodgersii* (Banks *et al.* 2007) were taken into account. These include coastal topography (i.e. lower connectivity of sites 'protected' by complex coastlines), measured as the length of coastline within a 20 km radius of each site (CL_{20}: summed over pairs of sites for pairwise comparisons in this study), and interannual sea surface temperature variability (SST_{SD}) during the planktonic larval period. SST variability is indicative of ocean circulation variability and hence unpredictable larval transport and recruitment to sites with high interannual variation in SST, measured here as the interannual SD. This statistic was multiplied across pairs of sites for pairwise comparisons, as an exploratory analysis indicated that high differentiation was primarily between sites which both had high SST_{SD} values (as opposed to high vs. low SST_{SD}). No pattern of isolation by distance was previously detected over thousands of kilometres in this high-dispersing species, using either Euclidean or 'marine' distances (Banks *et al.* 2007). Partial Mantel tests were conducted with the SST_{SD}, CL_{20}, *Ext_Zone* [pairwise comparisons between sites in the pre-extension (historical) and extension zones for the species' range] and YEAR (2000 or 2005) variables.

Bayesian inference of population-specific F_{ST} and its environmental influences

We used GESTE 2 (Foll & Gaggiotti 2006) to estimate, via generalized linear models, the relationship between population-specific F_{ST} values and a set of environmental variables. These variables included single-population versions of the *Ext_Zone*, SST_{SD} and CL_{20} variables tested against the pairwise genetic distance data. We included year as a variable to account for temporal patterns of differentiation.

Structure analysis

We used the program Structure 2.2 (Pritchard *et al.* 2000; Falush *et al.* 2003) to address the question of whether there is genetic support for any population subdivision and whether this is consistent with the newly-founded Tasmanian populations being demographically discrete. Our simulations used admixture and no admixture models. We considered the former more biologically plausible, but the latter may be more sensitive to subtle structure. Our models used correlated allele frequencies (the prior mean and SD of F_{ST} were 0.005 and 0.025, respectively) and we used no prior information on the population of origin of each individual. We compared models in which the parameter alpha was inferred separately for each population and together for all populations and reached the same biological conclusions. Therefore, the results we present are based on models with a uniform prior for alpha of 1 (maximum 10). Five replicate simulations were conducted for each value of *K* (the number of groups) and featured a burn-in and final run, each of length 10^6. We compared models featuring *K* values from one to one plus the maximum number of sites sampled in each year (four in the year 2000 and 16 in 2005).

Modelling of alternative range expansion scenarios

To complement the above analyses, we simulated genetic diversity under a set of demographic range expansion scenarios. Our primary aim was to determine whether we had the power to reject certain demographic scenarios. These scenarios featured the presence or absence of a founder effect, varying immigration rates to the range extension zone and a range of population growth rates.

The demographic models were simulated in SPLATCHE (Currat *et al.* 2004), followed by coalescent genetic simulations. Population structure was represented by a series of 2-degree square geographic cells with carrying capacities of 10 000 individuals. These represented demes within the historical distribution of the species (Australian mainland coast) and two stages of the southward range extension (Bass Strait and north-east Tasmania and southern Tasmania). The true population sizes in these regions are likely to be much larger, but broadcast-spawning marine invertebrates are thought to have a high ratio of census population size to effective population size (Hedgecock 1994). The dispersal probability among established demes was 0.2, such that 2000 effective migrants are expected to be exchanged per deme per generation. For each demographic scenario, we conducted 500 replicate simulations, in which 5000 generations were simulated in the pre-extension zone of the species' range prior to colonization of the Bass Strait and Tasmanian waters. Progression of colonization corresponded to the first records of *C. rodgersii* in each region (Fig. 1; Ling *et al.* 2008).

Immigration rates varied between the alternative model scenarios. We contrasted LOW (5% of the rate among established 'historical' demes), MEDIUM (20%) and HIGH (100%: no reduction in migration to new demes relative to within the species previous range) migration levels. The population growth rates used were 10%, 20% and 40%, with these upper values enabling population growth, in the absence of high immigration, that compared to the observed rates of density increase in Tasmanian sites (Ling *et al.* 2009). The founder effect (FE) models featured immigration for only a single generation corresponding to the generation of first colonization in the ongoing immigration (OI) models. The FE models under LOW, MEDIUM and HIGH migration rates involved founder numbers of 50, 200 and 1000, respectively.

Following the simulations, we sampled genetic data to estimate allelic richness (AR) and pairwise F_{ST} over eight microsatellite loci at generations corresponding to the years 2000 and 2005 (for the same number of individuals that we sampled in the field). We calculated the deviation of AR in the Tasmanian samples from the mean mainland population AR values [$(AR_{Tas} - AR_{Mainland})/AR_{Mainland}$] and determined where the observed values of this statistic fell on the distribution of simulated values. We used Meirmans (2006) standardization approach to compare mean pairwise Tasmanian—mainland Australian F_{ST} values (F'_{ST}) between the real and simulated datasets. While these models are a simplistic representation of *C. rodgersii* population processes and were not realistically analysable in some of the more complex methods outlined previously, they provided a basic assessment of our ability to distinguish a defined set of alternative demographic situations of very recent colonization using genetic diversity and differentiation data.

Results

Genetic diversity

Genetic diversity of the populations sampled in the range extension zone was similar to that of pre-extension established populations (Table 1). Analyses of F_{IS} revealed a heterozygote deficit in populations sampled in 2000 but not in 2005. Overall, 4.8% of locus pairs within populations showed significant evidence of linkage disequilibrium (LD) at the 5% significance level (Table 1). In 2000, all locus pairs in LD occurred in sites 1 and 2 (Bass Strait and Tasmania), but in 2005 this was not observed.

A GLM of per-locus H_E identified significant variation among loci, but site, year and sample size (n) had no significant effect (see online 'Supplementary Material 1' for full details of all GLM and GLMM results). We then fitted a GLM with locus and *Ext_Zone* as candidate explanatory variables and found no effect of the latter variable ($t = 0.21$, $P = 0.832$). The allelic diversity GLM revealed significant effects of locus, sample size (n: coefficient = 0.177, SE = 0.065, $t = 2.72$, $P = 0.008$) and site (site 1 vs. the reference category site 17: coefficient = 1.723, SE = 0.702, $t = 2.46$, $P = 0.016$). We then grouped the site data according to the *Ext_Zone* variable. However, after accounting for variation among loci and due to sample size, no significant effect of *Ext_Zone* was detected ($t = 1.52$, $P = 0.133$). The GLMM of observed heterozygosity identified significant effects of locus ($F = 46.43$, $P < 0.001$) and year ($F = 13.65$, $P < 0.001$), but not site ($F = 26.82$, $P = 0.062$). The probability of being heterozygous was lower in 2000, as also shown by the F_{IS} values. When the site data were represented by the *Ext_Zone* variable, no significant effect was detected ($F = 1.33$, $P = 0.250$). Thus, there was no evidence for changes in heterozygosity or allelic diversity associated with the range extension zone.

Table 2 Results summary of hierarchical analysis of molecular variance of *Centrostephanus rodgersii* genetic data collected in 2000 and 2005. Group structure corresponded to the recently colonized and historical pre-expansion zones of the species' range. Data presented include estimates of *F* statistics, their *P*-values (1000 permutations) and the estimates standardized by the maximum possible values, according to the method of Meirmans (2006)

Year	*F*-statistic	Estimate	*P*	Standardized estimate
2000	F_{ST}	0.0108	0.098	0.0269
	F_{SC}	0.0042	0.268	0.0104
	F_{CT}	0.0066	0.331	0.0166
2005	F_{ST}	0.0000	0.166	0.0000
	F_{SC}	0.0020	0.136	0.0050
	F_{CT}	0.0000	0.808	0.0000

Bottleneck tests

The heterozygosity excess test found no evidence for a population bottleneck. All *P*-values were considerably higher than 0.05. We found no evidence for significant differences among sites in the M-ratio statistic associated with the extension zone, year, locus or site (GLM: *Ext_Zone* $t = 0.420$, $P = 0.677$). The mean M-ratio statistics for the Tasmanian samples were well within the range of that observed at other sites (Table 1).

F_{ST} and hierarchical analysis of molecular variance

Overall genetic differentiation among sites sampled in 2000 was estimated by $\theta_{RH'}$ at 0.022 ($P = 0.0068$) and in 2005 at 0.029 ($P = 0.0002$). Overall F_{IS} was higher in 2000 (0.114) than 2005 (0.025), a pattern consistent across populations in each year (Table 1). Hierarchical AMOVA revealed no significant variance explained by the group structure representing new (Tasmanian) and pre-expansion zones of the species' range (Table 2) in either 2000 or 2005.

Genetic distances and partial Mantel tests

Partial Mantel tests identified significant associations between ocean temperature variability (SST_{SD}), coastal topography (CL_{20}) and pairwise genetic distances between sites. No significant effect of year was detected, so the *Ext_Zone* variable was tested after fitting SST_{SD} and CL_{20}. The *Ext_Zone* variable explained no significant component of the variation in genetic distances (Table 3).

Further investigation of the genetic distance measures with specific reference to the Tasmanian sites provided evidence for an absence of population structure associated with the range expansion. On an individual level, the greatest multilocus likelihood for the genotypes of Tasmanian samples was rarely in the home Tasmanian site and the other sampled populations were almost never excluded as populations of origin with any acceptable threshold *P*-value for the simulation-based exclusion test in Geneclass 2 (Piry *et al.* 2004) (data not shown). Multilocus genotypic autocorrelation among individuals within sites found that individuals sampled in the extension zone sites were no more similar to individuals in the same site than to a random assortment from any of the sampled sites (all *P*-values > 0.05).

Table 3 Results of partial Mantel tests of the association between genetic distances and environmental variables. Genetic distance measures include $\theta_{RH'}$ [the F_{ST} estimator of Raufaste & Bonhomme (2000)], Jost's (2008) *D*, Paetkau *et al.*'s (1997) D_{LR} and Smouse & Peakall's (1999) spatial autocorrelation coefficient calculated using pairwise population comparisons as distance bins (r_{POP}). Environmental variables include interannual sea surface temperature variability (SST_{SD}, multiplied over pairs of sites), coastline complexity (CL_{20}: the length of coastline within a 20 km radius of each site, added across pairs of sites) and *Ext_Zone*, scored as '1' for pairwise comparisons between Bass Strait/Tasmanian and mainland Australian coastal populations

Response variable	Explanatory variable	Correlation (Partial)	Coefficient	*P*	R^2
$\theta_{RH'}$	SST_{SD}	0.268	0.070	0.003	0.179
	CL_{20}	0.281	0.022	0.002	
	Ext_Zone	−0.167	−0.035	0.080	
D	SST_{SD}	0.385	0.014	0.001	0.197
	CL_{20}	0.150	0.002	0.048	
	Ext_Zone	−0.164	−0.006	0.095	
D_{LR}	SST_{SD}	0.377	0.199	0.001	0.199
	CL_{20}	0.220	0.034	0.013	
	Ext_Zone	−0.090	−0.039	0.358	
r_{POP}	SST_{SD}	−0.366	−0.061	0.001	0.201
	CL_{20}	−0.293	−0.039	0.005	
	Ext_Zone	0.053	0.011	0.234	

Bayesian inference of population-specific F_{ST} and its environmental influences

The analysis implemented in GESTE 2 found strongest support for a model featuring the variable *Ext_Zone* to explain variation in population-specific F_{ST} (Table 4). The coefficient for *Ext_Zone* was negative, revealing a reduced population-specific F_{ST} in samples from the extension zone (*Ext_Zone*: −0.349, 95% HPDI −0.647 to −0.071; Constant: −3.39, HPDI −3.69 to −3.10; σ^2: 0.283 HPDI 0.104 to 0.511). The population-specific F_{ST} estimates presented in Table 1 reveal the estimate for the Tasmanian samples to be the lowest among all samples from that year.

Table 4 Model posterior probabilities and marginal probabilities for environmental factors for the GESTE 2 analysis of environmental associations with the genetic structure (population-specific F_{ST}) of *Centrostephanus rodgersii* populations

Model	Posterior probability
Constant	0.302
Constant + CL_{20}	0.017
Constant + SST_{SD}	0.016
Constant + SST_{SD} + CL_{20}	0.002
Constant + *Ext_Zone*	0.503
Constant + *Ext_Zone* + CL_{20}	0.067
Constant + *Ext_Zone* + SST_{SD}	0.021
Constant + *Ext_Zone* + SST_{SD} + CL_{20}	0.003
Constant + Year	0.030
Constant + Year + CL_{20}	0.002
Constant + Year + SST_{SD}	0.001
Constant + Year + SST_{SD} + CL_{20}	0.000
Constant + Year + *Ext_Zone*	0.028
Constant + Year + *Ext_Zone* + CL_{20}	0.005
Constant + Year + *Ext_Zone* + SST_{SD}	0.002
Constant + Year + *Ext_Zone* + SST_{SD} + CL_{20}	0.000
Environmental factor	**Marginal probability**
CL_{20}	0.097
SST_{SD}	0.046
Ext_Zone	0.631
Year	0.069

Structure analysis

We found no support for spatial genetic population structuring within the Australian distribution of *C. rodgersii* (Table 5). For the 2000 data, the admixture models provided no evidence for structure (the summed posterior probabilities of all $K > 1$ models was 1.14×10^{-12}). However, the no admixture models favoured a scenario of $K = 2$ in 2000 (Table 5). Under this model, 12 of 90 individuals were assigned to one of the two groups with at least 95% confidence and 23 of 90 were assigned with at least 90% confidence (Fig. 3). The distribution of Structure groups was roughly even across the three sites sampled in 2000, demonstrating that the apparent structure did not have a spatial component. No structure was evident among the genotypes collected in 2005, with the summed posterior probabilities of $K > 1$ = models was 4.56×10^{-84} for the admixture models and 2.02×10^{-39} for the no admixture models.

Modelling of alternative range expansion scenarios

The FE models predicted genetic results significantly different than observed (Table 6). The F'_{ST} data were inconsistent with FE models of 50–1000 founders, while the AR data rejected the FE scenarios with fewer founders (Table 6). Based on these findings, we rejected the FE model under these migration and growth rates. By contrast, we could not reject the OI scenarios with moderate to high migration rates. The low migration rate OI models, however, predicted F'_{ST} inconsistent with the observed values. This suggests that under scenarios of ongoing migration to Tasmania, we have the power to identify genetic structure associated with severely reduced migration to the range extension zone (i.e. 5% relative to among pre-expansion populations).

Discussion

Genetic diversity and structure of the C. rodgersii *range expansion*

The sea urchin *C. rodgersii* has undergone a rapid latitudinal range expansion coinciding with an increase in sea temperature off south-eastern Australia (Ridgway 2007; Ling *et al.* 2008, 2009). We found no reduction in genetic diversity in sites sampled in the range extension zone relative to the pre-extension range of the species and no spatial pattern of increased genetic population structure associated with the range expansion. The only distinctive genetic characteristic of the extension zone samples was reduced population-specific F_{ST}. To date, genetic documentations of contemporary range expansions on a comparable temporal and spatial scale have come predominantly from studies of biological invasions. These have commonly featured a genetic bottleneck associated with an initial anthropogenic introduction, with subsequent genetic structure in the colonized range dependent on human-mediated dispersal and the natural dispersal capabilities of the species (Darling & Folino-Rorem 2009; Excoffier *et al.* 2009; Tepolt *et al.* 2009). However, the processes of range expansion due to climate change are likely to be different to those facilitated by human-mediated dispersal (Hellmann *et al.* 2008). Two important aspects of this difference are the spatial nature of climate-change associated distributional changes in relation to the original range and the method of colonization and immigration to new habitats. In the case of *C. rodgersii*, the physical driver of range expansion (the extended EAC) leads to a prediction of high connectivity between the southern extension region and mainland coastal populations. The genetic results provide strong support for this, suggesting a poleward expansion of a continuous population. We discuss below the lines of evidence supporting this scenario.

Table 5 Results of Structure 2.2 analysis of *Centrostephanus rodgersii* genotypes collected in 2000 and 2005. The estimated probability of the data [ln Pr (X|K)] and model posterior probabilities for different number of groups (*K*). Outputs are presented for admixture and no admixture models with correlated allele frequencies. Posterior probabilities of the best-supported models are rounded to 1, given the very small probabilities of the alternative models

		Admixture model		No admixture model	
Year	*K*	ln Pr (X|K)	Posterior probability	ln Pr (X|K)	Posterior probability
2000	1	−1932	1	−1933	5.07×10^{-9}
	2	−1960	1.14×10^{-12}	−1914	1
	3	−2144	1.40×10^{-92}	−1952	1.90×10^{-17}
	4	−2302	1.68×10^{-161}	−2003	1.82×10^{-39}
2005	1	−7183	1	−7183	1
	2	−7375	4.56×10^{-84}	−7272	2.02×10^{-39}
	3	−7898	0	−7355	2.21×10^{-75}
	4	−8415	0	−7647	2.28×10^{-202}
	5	−8863	0	−8001	0
	6	−9803	0	−8406	0
	7	−9718	0	−8619	0
	8	−9287	0	−8869	0
	9	−9597	0	−9058	0
	10	−9533	0	−9123	0
	11	−9946	0	−9532	0
	12	−9754	0	−9714	0
	13	−9398	0	−9392	0
	14	−9853	0	−10 097	0
	15	−9503	0	−9175	0
	16	−9497	0	−10 188	0

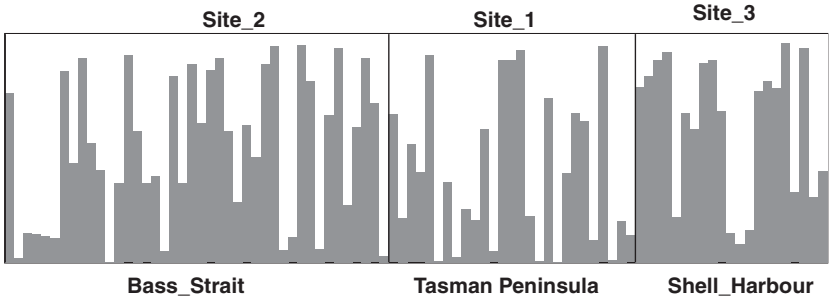

Fig. 3 Individual-level results of Structure analysis on 90 *C. rodgersii* sampled at sites 1, 2 and 3 in 2000. Each column represents a single individual from each of the sites labelled on the *X*-axis. The *Y*-axis represents the estimated proportion of ancestry in Group 1. This scenario was selected as most likely for the 2000 data under a no admixture model with correlated allele frequencies.

Genetic diversity

The finding that sites in the extension zone demonstrated no reduction in H_O, H_E, allelic diversity or the *M*-ratio statistic is contrary to the decrease in diversity expected when a small number of colonizers is at the forefront of a range extension, with little migration from the pre-extension zone (Excoffier *et al.* 2009). Our results are consistent with that expected under rapid range expansion with high migration, which is similar to that of a demographic expansion (Excoffier *et al.* 2009). The major variation in diversity that we detected was a rangewide change in H_o and F_{IS} from 2000 to 2005. This consistent trend across sites suggests non-independence of population processes across the pre- and post-extension zones.

Spatial analysis of genetic distances ('Seascape genetics')

There was no variation in pairwise population genetic distance/similarity explained by the range extension zone, indicating an absence of population structure across the transition from 'old' to 'new' populations. The spatial genetic data were analysed with a range of distance/similarity estimators that use the genetic data in

Table 6 Comparison of observed allelic richness (AR) and F'_{ST} data to distributions simulated from demographic and genetic models. The AR test statistic is the deviation of AR in Tasmanian 'extension zone' samples from the mean AR among mainland populations. The F'_{ST} test statistic is the mean pairwise Tasmania—mainland Australia F_{ST} value standardized according to Meirmans (2006). OI models feature continuous immigration and FE models a founder effect. Migration rates to the extension zone were high (100%), moderate (20%) and low (5%) relative to the rate among established demes. The table shows the percentage of simulated values smaller than the observed value. Asterisked values show that the observed data fell outside the 95% CI of the predictions of that model

Migration scheme	Migration rate	Population growth rate (%)	AR 2000	AR 2005	F'_{ST} 2000	F'_{ST} 2005
OI	High	10	63.6	58.6	61.8	38.0
OI	Moderate	10	80.6	66.4	31.4	17.6
OI	Low	10	87.6	83.6	2.8	**2.4***
OI	High	20	83.6	63.8	48.5	19.2
OI	Moderate	20	86.4	79.0	29.6	9.2
OI	Low	20	89.2	86.0	**2.0***	**1.6***
OI	High	40	87.6	79.4	31.6	12.0
OI	Moderate	40	97.0	88.4	23.8	5.4
OI	Low	40	97.4	96.4	**1.2***	**1.4***
FE	High	10	97.0	97.2	**1.4***	**1.2***
FE	Moderate	10	**98.0***	**98.2***	**1.2***	**0.6***
FE	Low	10	**99.0***	**99.4***	**0.4***	**0.0***
FE	High	20	94.6	95.0	**2.0***	**1.6***
FE	Moderate	20	96.0	96.4	**1.0***	**0.8***
FE	Low	20	**99.0***	**98.6***	**0.6***	**0.4***
FE	High	40	91.8	92.4	**2.4***	**2.0***
FE	Moderate	40	94.6	95.0	**1.6***	**1.4***
FE	Low	40	**99.0***	**98.2***	**1.0***	**0.8***

different ways, at the allelic level ($\theta_{RH'}$, D) the genotypic level (r) or both (D_{LR}), all of which yielded concordant results. The fine scale structure present in these data was explained by coastal topographic complexity and sea temperature variability. The role of coastline complexity in genetic structure is likely to be due to its effect of 'sheltering' populations in bays (or other complex coastal regions) from the currents that facilitate larval transport (Banks *et al.* 2007). The association between genetic structure and sea temperature variability is primarily driven by a region along the southern mainland Australian coast, south of the point of separation of the EAC, where sea temperature variability is indicative of temporal unpredictability of ocean circulation and hence larval transport (Banks *et al.* 2007). Our hypothesis is that where interannual variability in ocean circulation results in larval settlement being concentrated in different locations between years, genetic differentiation between yearly generations of larvae will lead to patchy genetic structure.

In contrast to the genetic distances, the GESTE analysis of population-specific F_{ST} supported an effect of the extension zone. However, this corresponded to reduced F_{ST}, or reduced genetic 'distinctiveness' of the extension zone populations. This is not expected under founder effect or low-migration scenarios (Excoffier *et al.* 2009), but is expected when the effect of genetic drift is greatly reduced due to increasing population size observed under rapid expansion and high connectivity (Foll & Gaggiotti 2006).

Structure analysis

The only structure supported by this analysis was an even spread of two genetic groups across pre- and post-extension zone sites in 2000 (Table 5; Fig. 3). The observation that Structure-inferred genetic grouping patterns changed consistently across sites from 2000 to 2005 in the pre- and post-range extension zones of the species' range is consistent with population processes in the range extension zone not being discrete from those occurring in mainland Australian coastal populations. Thus, the interpretation of the Structure results within and between years suggests that Tasmanian populations are not demographically discrete from those along the mainland Australian coast.

The unusual pattern detected in 2000 may be due to genetic differentiation between cohorts, which has been detected in marine invertebrates and commonly explained by high variance in reproductive success among individuals (Hedgecock 1994; Levitan 2005). The sites sampled in 2000 were dominated by a large pro-

portion of juvenile *C. rodgersii*, suggesting that a large recruitment event prior to 2000 resulted in mainland and Tasmanian populations in that year being dominated by one or two discrete cohorts. Under this scenario, temporal differentiation between cohorts is expected to generate the observed pattern of structure (Moberg & Burton 2000). This interpretation is consistent with the homozygote excesses (positive F_{IS}) identified in each of the sites sampled in 2000 (Table 1), which would be generated by a 'temporal Wahlund effect' in sites dominated by a small number of genetically differentiated cohorts.

Predicted diversity and differentiation from simulation models

The analyses of genetic variation and structure were consistent with high connectivity between mainland coastal populations and those in the extension zone. However, the possibility remains of a massive founder event leading to a similar population genetic outcome (Roman 2006). In our analyses, the F'_{ST} data had more power to reject the 'large founder event' models than the AR data. However, genetic predictions of models of founder events of up to 1000 effective immigrants were not supported by the observed data. Given that N_e/N ratios in other marine species have ranged from 10^{-2} to 10^{-6} (Hauser & Carvalho 2008), this effective immigration rate is likely to represent a substantially larger number of 'real' immigrants. Even among the ongoing immigration models simulated, the data were consistent with those featuring moderate to high immigration and provided little support for a low immigration scenario. If *C. rodgersii* has a low N_e/N ratio, we would expect that rapid genetic drift would erode diversity in the extension zone populations if they were isolated from the rest of the species' range. That this was not observed lends credibility to our inference of high ongoing connectivity.

The demographic models we used in conjunction with coalescent simulations were a much-simplified representation of the population processes of this species. Several aspects of the species' population biology relevant to spatial patterns of genetic diversity, such as variation in individual reproductive success and N_e are poorly understood. Further, the stochastic nature of the processes generating the observed fine-scale patchy genetic structure limits the information that can be obtained from comparisons between simulations and observations. Thus, we did not attempt to more precisely estimate demographic parameters directly via simulation modelling, but can draw strong support for the conclusions of the other analyses presented in this study.

Physical processes driving range expansion in C. rodgersii

The inference of range extension through mass larval advection is concordant with conclusions drawn from analysis of *C. rodgersii* abundance and age distribution throughout the pre- and post-range extension regions (Ling *et al.* 2009). That study correlated *C. rodgersii* population patterns with the dynamics of the EAC to conclude that range expansion is driven by larval advection by this southward-flowing warm water current and that reproduction and further expansion within the extension region is also favoured by the EAC now maintaining a warmer coastal regime.

The combination of genetic, physiological, demographic and oceanographic evidence from across the range of *C. rodgersii* (Banks *et al.* 2007; Ling *et al.* 2008, 2009), identifies this sea urchin as a prime example of a species well-adapted to a rapid and opportunistic response to global warming. It has high dispersal potential, with a larval duration of approximately 4 months and demonstrated low genetic differentiation over thousands of kilometres (Huggett *et al.* 2005; Banks *et al.* 2007). It appears to have been limited from occupying otherwise suitable habitat only by a temperature threshold for development, as it has shown no capacity for adaptation to larval development at temperatures lower than this threshold (Ling *et al.* 2008). We do not expect to see temperature-related adaptation at the expanding range margin if a high proportion of recruits come from populations within the centre of the species range (that are well-adapted to warmer environmental conditions; Bridle & Vines 2006). Thus, the requirements to enable poleward range expansion by *C. rodgersii* are that its lower temperature threshold for development is exceeded and larval transport is facilitated by advection. These correspond to hypotheses 1 and 2 of the consequences of climate change for invasive species proposed by Hellmann *et al.* (2008), namely, that climate change alters transport mechanisms and climatic constraints.

Recent ocean circulation changes appear to have matched these requirements. Increasing summertime sea temperature off the Tasmanian east coast over the latter half of the 20th century suggests an increase in the frequency and intensity of the southward EAC extension (Holbrook & Bindoff 1997; Ridgway 2007). This potentially increases southward larval transport from Australian mainland coastal habitats, particularly from southern mainland populations closest to the extension zone, where the extended spawning period (Byrne *et al.* 1998) overlaps with the summertime EAC extension. The colonization of Tasmanian coastal waters has likely been facilitated by ocean current-mediated transport of heat and larvae from within the previous

range of the species (Ling *et al.* 2009), thus enabling both immigration and development.

Will high dispersal capability be advantageous under climate change?

Our results raise the question of whether high dispersal capability predisposes species to rapid geographical shifts in response to climate change (Vittoz *et al.* 2009). We expect that it will be advantageous in circumstances where there is a major geographical shift in the distribution of environmental suitability for that species. However, other factors, such as geographic or oceanographic features that either facilitate or act as barriers to successful dispersal will be important influences on future distribution al changes (Zacherl *et al.* 2003; Aronson *et al.* 2007; Tepolt *et al.* 2009). In the case of the poleward EAC extension, pelagic species or those with long pelagic larval durations, are likely to have range expansions assisted by changed ocean circulation patterns. Other species to show similar range expansions as *C. rodgersii* include a number of warmer water fish and zooplankton species associated with the EAC water mass (Poloczanska *et al.* 2007). In another oceanic region, Aronson *et al.* (2007) predicted rapid colonisation of the Antarctic benthos by taxa for which the only barrier has been a physiological temperature threshold. In such instances, long-distance dispersers are likely to predominate the first wave of colonizers.

In the case of *C. rodgersii* the spatial shift in the climate-related physiological threshold for development has been a latitudinal one driven by a large-scale oceanic phenomenon to which its pelagic larvae are subjected. Such latitudinal changes in the distribution of physiological rates or thresholds have been implicated in other climate-related range shifts (Harley 2006). However, recent evidence suggests that even in the marine environment, climate-related physical changes affecting physiological and ecological processes may not necessarily lead to simple latitudinal changes in climate envelopes. This is particularly true for nearshore or intertidal populations where habitat-level climatic conditions are not strongly associated with latitude, but rather with other processes such as fine-scale habitat selection, thermal niches and temporal variability in physical conditions (Sagarin & Gaines 2002; Helmuth *et al.* 2006; Broitman *et al.* 2009). High dispersal capability is likely to be less important in such cases, where large-scale geographic range shifts are not required.

Conclusion

Global warming is expected to result in a change in the geographical distribution of climatically-suitable habitat for biodiversity worldwide (Bakkenes *et al.* 2002; Beaumont & Hughes 2002). However, the demographic processes by which species respond to changing climate conditions and the resulting distribution of genetic diversity, remain unclear (Thomas *et al.* 2004). Here, multilocus microsatellite data revealed no loss of genetic diversity or increased differentiation during a poleward range expansion by the highly dispersive sea urchin *C. rodgersii*. This suggests a demographic scenario of ongoing immigration and recruitment from the pre-expansion source population. It appears that one of the major influences on the regional sea temperature increase, the southward extension of the EAC, drives both the geographic expansion of climatically-suitable conditions and larval transport to the newly suitable habitat.

In south-east Australian waters, the trend of altered temperature and ocean circulation conditions is predicted to continue, increasing the likelihood of further range extension by *C. rodgersii* (Cai *et al.* 2005; Ling *et al.* 2008). Given that Tasmanian rocky reef communities cannot track a poleward-shifting climate envelope due to the lack of any suitable habitat at higher latitudes, the ecological impacts of invasion by warmer water species such as *C. rodgersii* may constitute a major threat to the persistence of such ecosystems (Ling 2008).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Material S1 Genetic diversity regression analyses

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