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ORIGINAL PAPER

The population genetic structure of the urchin *Centrostephanus rodgersii* in New Zealand with links to Australia

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Abstract

The diadematid sea urchin *Centrostephanus rodgersii* occurs in Australia and New Zealand and has undergone recent southward range extension in Australia as a result of regional warming. Clarifying the population genetic structure of this species across its New Zealand range would allow a better understanding of recent and future mechanisms driving range changes in the species. Here, we use microsatellite DNA data to assess connectivity and genetic structure in 385 individuals from 14 locations across the Australian and New Zealand ranges of the species. We detected substantial genetic differentiation among *C. rodgersii* populations from Australia and New Zealand. However, the population from Port Stephens (located north of Newcastle), Australia, strongly clustered with New Zealand samples. This suggests that the New Zealand populations recently originated from this area, likely via larval transport in the Tasman Front flow that arises in this region. The weak population genetic structure and relatively low genetic diversity detected in New Zealand (global $F_{st} = 0.0021$) relative to Australia (global $F_{st} = 0.0339$) is consistent with the former population's inferred history of recent climate-driven expansion. Population-level inbreeding is low in most populations, but were higher in New Zealand (global $F_{is} = 0.0833$) than in Australia (global $F_{is} = 0.0202$), suggesting that self-recruitment is playing an increasingly important role in the New Zealand region. Our results suggest that *C. rodgersii* is likely to spread southwards as ocean temperatures increase; therefore, it is crucial that researchers develop a clearer understanding of how New Zealand ecosystems will be reshaped by this species (and others) under climate change.

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Introduction

Recent anthropogenic climate change has driven shifts in ocean currents, causing range shifts, novel introductions, and extinctions in marine communities (Poloczanska et al. 2013; IPCC 2019; Pinsky et al. 2020). Most marine species have indirect life cycles and responses in their free-living larval stages and can play a key role in climate-induced population responses and distributional shifts. The biological effects of recent marine climate change have been particularly prominent in temperate waters of southern Australia, with numerous species shifting poleward in response to warming (Ling et al. 2009; Pitt et al. 2010; Wernberg et al. 2011; Monaco et al. 2021). Currently, there are few studies of climate-driven range shifts in New Zealand marine ecosystems (although see Brooks 2020; Middleton et al. 2021).

One of the best-documented examples of range extension due to the interaction of ocean warming and larval ecology is seen in the warm-temperate diadematid sea urchin *Centrostephanus rodgersii* (Agassiz 1863). This relatively

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large sea urchin is found along the coasts of eastern Australia and northern Aotearoa New Zealand, as well as Lord Howe Island, Norfolk Island, and the Kermadec Islands (Byrne and Andrew 2020). The species has been found to spawn in the Austral winter from June to August (Byrne and Andrew 2020), meaning their larvae develop in the coldest months of the year. *C. rodgersii* has a long-lived larval stage, reaching competency from 40 days to > 3 months depending on temperature (Hugget et al. 2005; Soars et al. 2009; Hardy et al. 2014; Mos et al. 2020), and is capable of long-distance passive dispersal (Banks et al. 2007b). Evidence suggests the geographic distribution of this species is limited by sea temperatures, with larvae having a minimum thermal limit of 12 °C (Ling and Johnson 2009). Over the past 50 years, warming winter sea temperatures have facilitated range expansions of *C. rodgersii* across the Tasman Sea and the Bass Strait (Ling and Johnson 2009). These increased sea temperatures are influenced by the East Australian Current (EAC; Fig. 1), which has extended at least 350 km further south over the past 60 years, bringing with it an increase in temperature and salinity (Hill et al. 2011). In south-eastern Australia (and particularly Tasmania), thermally facilitated southward range extension of *C. rodgersii* (and reduced predation pressure) have led to kelp over-grazing by this species (Johnson et al. 2011). This range expansion has driven a regime shift from dense kelp beds to rocky barrens, reducing biodiversity and fisheries yields (Ling et al. 2009; Ling and Johnson 2009).

Centrostephanus rodgersii also occurs along coastal north-eastern New Zealand, as well as offshore islands including Rangitāhua (the Kermadec Archipelago, Fig. 1), Manawatāwhi (Three Kings Island, 34°9′S, 172°8′E) and Te Puia o Whakaari (White Island, 37°31′S, 177°11′E) within New Zealand's Exclusive Economic Zone (Pecorino et al. 2013, Byrne and Andrew 2020, Byrne and Gall 2017). In contrast to the Australian populations, New Zealand populations of *C. rodgersii* have been less well studied. Reproduction and growth parameters reported in New Zealand populations are similar to those reported in Australian populations (Agassiz 1863). In contrast, New Zealand population densities appear to be lower (Pecorino et al. 2013; Edgar et al. 2017), and the species is not associated with extensive urchin barrens. Currently, *C. rodgersii* populations appear to be restricted to north of New

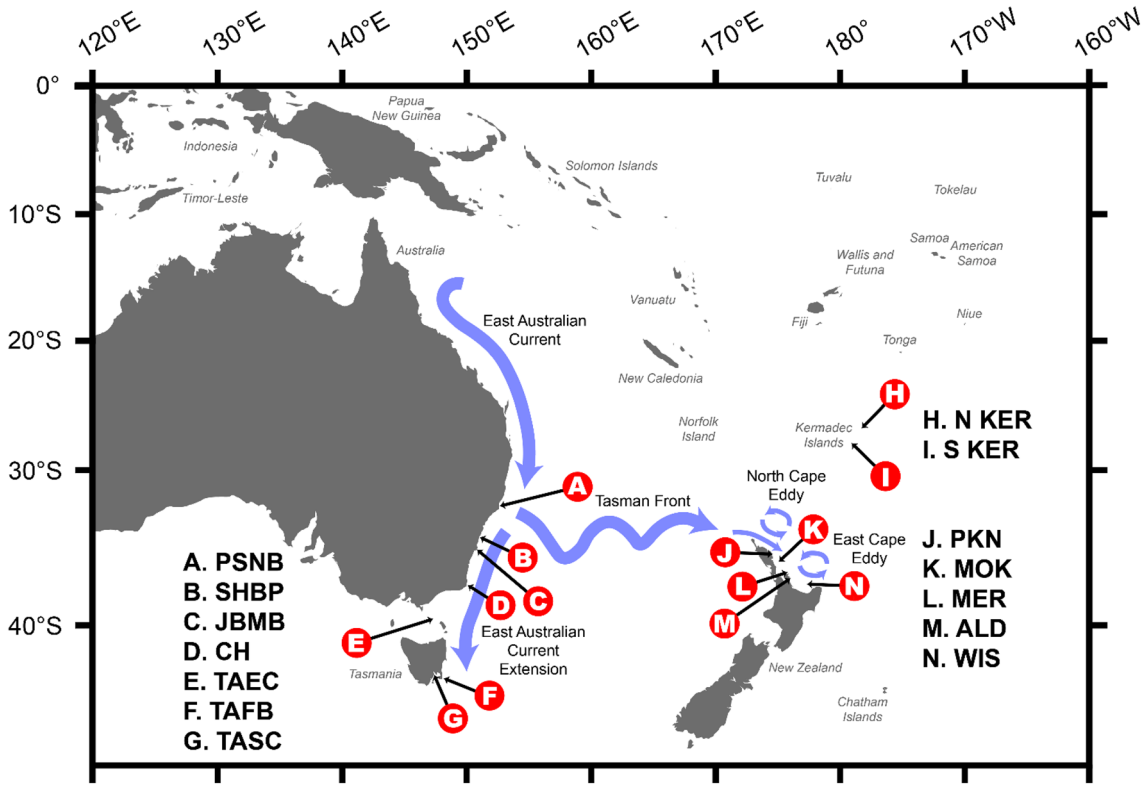

Fig. 1 Map of collection sites of *Centrostephanus rodgersii* along mainland Australia and Tasmania, the Kermadec Islands, and New Zealand. Approximate locations of oceanic currents are indicated with blue arrows (modified from Hill et al. 2011). *PSNB* Port Stephens Bay, *SHBP* Sydney Harbour, *TASC* Tasmania (Safety Cove), *TAFB* Tasmania (Fortescue Bay), *JBMB* Jervis Bay, *CH* Cape Howe, *TAEC* Tasmania (East Cape), *PKN* Poor Knights Island, *WIS* White Island, *ALD* Alderman Islands, *MOK* Mokohinau Island, *MER* Mercury Island, *NKER* northern Kermadec Islands, *SKER* southern Kermadec Islands

Zealand's East Cape (37.7°S), where winter sea temperatures are above 15 °C, consistent with experimentally assessed larval temperature thresholds (Pecorino et al. 2013). While there have been no reports of recent range shifts in New Zealand *C. rodgersii*, it seems likely that this urchin will increase in abundance and expand its distribution southward as sea temperatures continue to rise.

Previous studies examining the genetic structure of *C. rodgersii* populations using microsatellite markers included only a single New Zealand population (Mokohinau Islands) (Banks et al. 2007a, b, 2010). These studies suggested that genetic structure of this species in southeastern Australia is primarily constrained by the influence of regional oceanographic circulation on larval retention. Specifically, while these studies detected little or no large-scale genetic differentiation, they revealed fine-scale autocorrelation indicative of self-recruitment linked to sea surface temperature (SST) variability and coastal topology (Banks et al. 2007b), especially in southern New South Wales (NSW). Banks et al. (2010) further characterised the genetic structure of Australian *C. rodgersii* populations to better understand the process of range extension and connectivity in the region, with analyses supporting recent southward extension to Tasmania, and high ongoing connectivity between source (mainland) and founder (Tasmanian) populations. Banks et al. (2007b) detected little trans-Tasman genetic differentiation in *C. rodgersii*, suggesting the New Zealand populations arrived only recently. However, their sampling of New Zealand populations was insufficient to understand larval-mediated connectivity across the Tasman sea and within New Zealand, or an ongoing demographic response to regional climate change.

Here, we examine the population genetic structure of *C. rodgersii* in New Zealand. We combine the previously published data of Banks et al. (2007b) with new genotypic data from seven populations across the New Zealand range of *C. rodgersii*. Using these datasets, we: (1) assess the extent to which New Zealand populations are self-recruiting versus reliant on larvae from Australia; and (2) assess population genetic structure and genetic diversity across the range of *C. rodgersii* in New Zealand. Where the New Zealand populations rely on the Australian populations for larval delivery, we expected that the New Zealand populations would have little genetic differentiation with Australia, few private alleles, and little genetic diversity in New Zealand. In the case of no contemporary larval delivery, we expected genetic differentiation among Australia and New Zealand, with signals of reduced genetic diversity in New Zealand. However, under a hypothesis of self-recruitment within New Zealand, and an absence of larval delivery, we expected that there would be genetic differentiation from Australia, but with equivalent levels of genetic diversity.

Materials and methods

Centrostephanus rodgersii were collected from rocky subtidal reefs (5–30 m) throughout the species' New Zealand range (with appropriate consent and permissions, see "Acknowledgements"). The number of individuals sampled per location was relative to the local abundance to avoid interfering with the species' local demography.

DNA was extracted from 193 *C. rodgersii* specimens from seven New Zealand locations (Fig. 1; Table 1) using a chelex protocol (Casquet et al. 2012). Specimens were genotyped using six microsatellite loci [Supplementary Table 1, as described in Banks et al. (2007a)]. Amplified fragments were analysed on an ABI 3730xl using GeneScan 500 ROX. Fragment lengths were scored manually using Geneious R6 (Kearse et al. 2012; https://www.geneious.com) to avoid binning error. For quality control, and to ensure combinability of Australian and New Zealand data, a subset of Australian specimens used in a previous study of *C. rodgersii* (Banks et al. 2010) were re-genotyped in our laboratory and compared to the findings of Banks et al. (2010). These analyses yielded a combined dataset of 385 specimens from 14 locations across the Australian and New Zealand ranges of the species. The loci were tested for linkage disequilibrium and Hardy–Weinberg equilibrium (HWE) using the R package *pegas* (Paradis 2010). We tested for presence of null alleles and scoring using errors using MICROCHECKER (Oosterhout et al. 2004).

To estimate population genetic and demographic parameters of *C. rodgersii* in New Zealand, we used several population genetic indices and analyses, using package specific default settings, unless specified. Observed heterozygosity (H_o), expected (H_e) heterozygosity, inbreeding coefficient (F_{is}), and mean allelic richness (A_R) for all loci in all populations and F_{is} values for each loci were calculated using the R package *hierfstat* (Goudet 2005). Confidence intervals for population F_{is} with 1000 bootstrap replicates were calculated using the *boot.ppfis* function in *heirfstat*.

We assessed genetic differentiation among sampled locations by estimating pairwise F_{st} values in Arlequin ver 3.5.2.2 (Excoffier and Lischer 2010). The significance of these values was tested with 10,000 permutations. Hierarchical population genetic structure (analysis of molecular variance, AMOVA) was also assessed in Arlequin. As pairwise F_{st} values may not be appropriate for highly variable microsatellite data (see Jost 2008), we also calculated pairwise *JOST'S D* values. We calculated these values and 95% confidence intervals using 1,000 bootstrap replicates using the R package *diveRsity* (Keenan et al. 2013). Emergent genetic structuring across our 14 sampled locations was assessed using the Bayesian clustering algorithm in

Table 1 Location of *Centrostephanus rodgersii* sampling sites across New Zealand and Australia

Region	Pop	*N*	LAT	LONG	Mean H_o	Mean H_e	Private alleles	Mean rarefied allele count	Mean within pop F_{is} (min–max)
Australia	PSNB	17	− 32.718	152.142	0.648	0.613	0	4.081	− 0.0230 (− 0.2020 to 0.1150)
	SHBP	21	− 34.594	150.904	0.473	0.55	1	3.403	0.1689(− 0.0004 to 0.3282)
	TASC	26	− 43.167	147.85	0.642	0.605	3	4.059	− 0.0519 (− 0.2034 to 0.0492)
	TAFB	27	− 43.135	148	0.537	0.595	10	3.888	0.1165 (0.0354 to 0.2517)
	JBMB	29	− 35.126	150.752	0.668	0.602	2	3.858	− 0.1027 (− 0.1543 to − 0.0358)
	CH	30	− 37.504	149.983	0.627	0.577	2	3.801	− 0.1036 (− 0.2199 to 0.0496)
	TAEC	42	− 39.473	147.35	0.502	0.56	3	3.729	0.1066 (0.0830 to 0.1264)
									Overall F_{is} = 0.0202
									Overall F_{st} = 0.0339
New Zealand	PKN	30	− 35.47	174.74	0.543	0.573	0	3.838	0.0904 (− 0.0813 to 0.2213)
	WIS	30	− 37.53	177.17	0.58	0.607	9	4.134	0.0714 (− 0.1690 to 0.1829)
	ALD	30	− 36.96	176.07	0.55	0.612	0	3.947	0.0944 (− 0.0878 to 0.247)
	MOK	32	− 35.93	175.12	0.637	0.602	1	3.859	− 0.0431 (− 0.2139 to 0.108)
	MER	6	− 36.61	175.85	0.383	0.447	0	2.745	0.1977 (0.0252 to 0.4604)
									Overall F_{is} = 0.0833
									Overall F_{st} = 0.0021
Kermadecs	NKER	55	− 29.281	− 177.9	0.4763	0.63	1	3.986	0.2198 (0.0604 to 0.3123)
	SKER	10	− 31.347	− 179	0.528	0.676	0	3.964	0.2128 (− 0.4634 to 0.5645)
									Overall F_{is} = 0.2311
									Overall F_{st} = 0.0059

N sampling size, *LAT* latitude, *LONG* longitude, H_o observed heterozygosity, H_e expected heterozygosity. F_{is} inbreeding coefficient. *PSNB* Port Stephens Bay, *SHBP* Sydney Harbour, *TASC* Tasmania (Safety Cove), *TAFB* Tasmania (Fortescue Bay), *JBMB* Jervis Bay, *CH* Cape Howe, *TAEC* Tasmania (East Cape), *PKN* Poor Knights Island, *WIS* White Island, *ALD* Alderman Islands, *MOK* Mokohinau Island, *MER* Mercury Island, *NKER* northern Kermadec Islands, *SKER* southern Kermadec Islands

STRUCTURE 2.3.4 (Pritchard et al. 2000) as well as a k-means clustering algorithm using the R package *adegenet* (Jombart 2008). We initially ran the STRUCTURE analysis across the entire dataset, using the admixture model with allele frequencies correlated. Ten replicate analyses were conducted for each value of *K*, from $K = 1$ to $K = 15$, with each run using a different starting seed. Each run consisted of 200,000 burn-in iterations, followed by 2,000,000 iterations. We used CLUMPAK (Kopelman et al. 2015) to assess the most likely value of K (using the deltaK vs K method of Evanno et al. 2005), and to plot the results. We conducted additional STRUCTURE runs (using the parameters outlined above) to assess evidence of genetic structuring within New Zealand populations. For the k-means clustering, the optimal number of clusters was identified using the Bayesian Information Criterion (BIC). To describe the genetic groups identified using the k-means algorithm, we conducted a discriminant analysis of principal components (DAPC; Jombart 2008, 2010). To avoid overfitting, only the principal components that retain 90% of the variance were retained for the DAPC.

Contemporary migration and self-recruitment rates among the populations were estimated using BAYESASS v.3.0.1 (Wilson and Rannala 2003). Five independent Markov Chain Monte Carlo (MCMC) runs were performed, each with 10,000,000 reps and a burn-in of 1,000,000 steps, with sampling every 2000 steps. The reliability of migration rate estimates was assessed by checking for consistency among runs. For all BAYESASS runs, we followed the recommendations of Faubet et al. (2007) namely five independent runs with different random number seeds, and we used Bayesian deviance (using the *calculateDeviance.R* script from Meirmans 2014) to select the best run. Convergence of parameter estimates was also assessed by manual examination of the trace files.

Tests for recent population bottlenecks were performed using the program BOTTLENECK (Piry et al. 1999). A two-tailed Wilcoxon sign-rank test for heterozygosity excess (Luikart and Cornuet 1998) was applied to detect any recent bottlenecks. In non-bottlenecked populations, observed heterozygosity (H_o) is consistent with Hardy–Weinberg equilibrium heterozygosity (H_e), whereas in a population that has experienced a recent bottleneck the mutation-drift equilibrium is disrupted and H_o will be significantly greater than H_e (Luikart and Cornuet 1998). H_e values were calculated using the stepwise mutation model (SMM; Kimura and Ohta 1978) and the infinite allele model (IAM; Kimura and Crow 1964). We also tested for "mode-shift", to determine if allele

frequency distribution shifts have occurred in recently bottlenecked populations (Luikart and Cornuet 1998). Under HWE, the allele frequency distribution would exhibit an L-shaped distribution, recently bottlenecked populations would not exhibit this distribution.

Results

All the Australian samples genotyped were scored identically to those previously genotyped by Banks et al. (2010), justifying the subsequent combination of the datasets from Australia and New Zealand *C. rodgersii* populations. Deviations from HWE were detected for some loci/population combinations (Supplementary Table 2). However, these deviations were not consistently detected for a single population of *C. rodgersii* or locus, so all loci and populations were retained for further analysis. F_{is} values for individual loci ranged from − 0.1540 to 0.2740 (Supplementary Table 1). However, none of these values was significantly different from 0. When testing for null alleles using all of the populations, an excess of homozygotes was found for most of the loci (data not shown). However, the excess of homozygotes was not found when individual populations were tested, suggesting that these findings reflect incomplete mixing across sites, rather than null alleles. Scoring errors were not detected in the MICROCHECKER analysis.

The mean number of private alleles per population was greater in Australia (three unique alleles per population) than in New Zealand (2.2 unique alleles per population) (Table 1). Population-level inbreeding was greater in New Zealand (global $F_{is} = 0.0833$) than Australia (global $F_{is} = 0.0202$). By contrast, the extent of population structuring is greater in Australia (global $F_{st} = 0.0339$) than in New Zealand (global $F_{st} = 0.0021$). Estimates of pairwise JOST'S D and F_{st} (Supplementary Table 3) show a similar pattern. Pairwise F_{st} values between New Zealand populations ranged from 0.0004 (between White Island, WIS and Mercury Island, MER) to 0.1434 (between MER and southern Kermadec Islands, SKER). Pairwise JOST'S D values ranged from 0.0003 (between WIS and MER) to 0.0236 (between MER and SKER). Comparisons between New Zealand and Australian populations yielded values F_{st} ranging from 0.0011 (JOST'S $D = 0.0329$) (between Port Stephens, PSNB and Mokohinau Island, MOK) to 0.2213 (JOST'S $D = 0.0428$) (between Tasmania East Cape, TAEC and SKER). F_{st} values between Australian populations ranged from 0.0012 (JOST'S $D = 0$) (between Tasmania Safety Cove, TASC and Tasmania Fortescue Bay, TAFB) to 0.1345 (JOST'S $D = 0.0281$) (PSNB and Sydney Harbour, SHBP). Hierarchical AMOVA analysis revealed that most of the variation (90.5%) was found within individuals, with 5.9% of the variation attributed to variation across the two regions [Australia and New Zealand (including the Kermadec Islands)], and 3.7% among populations within regions (Supplementary Table 4).

Bayesian clustering analyses indicated that the most likely number of populations (K) across the entire dataset was two (Figure S1). The seven New Zealand sites (including the two Kermadec Islands) and a single Australian site (PSNB) represented one population cluster, with the remaining six Australian sites forming the second cluster (Fig. 2a). No population structuring was evident when only the seven New Zealand populations were analysed (Fig. 2b). The optimal number of clusters with the lowest BIC using the k-means clustering algorithm was 10. The DAPC similarly indicates a genetic distinction between Australian and New Zealand *C. rodgersii*, but with the PSNB sample clustering with New

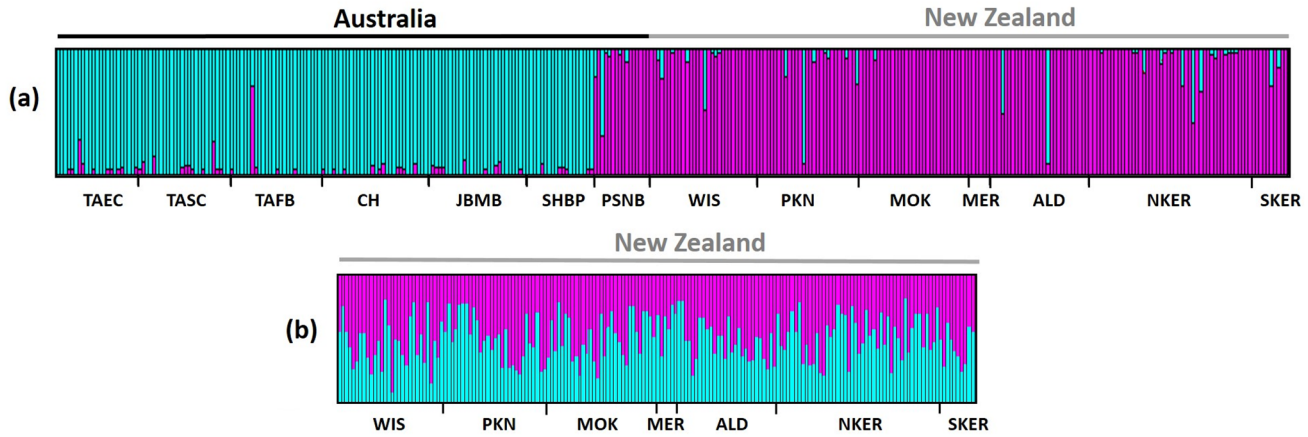

Fig. 2 Structure analyses ($K = 2$) for *Centrostephanus rodgersii* collected from (**a**) 14 sites across Australia and New Zealand, and (**b**) only the 7 New Zealand sites (including the Kermadec Islands). Each bar represents an individual sample, with the proportion of colour on each bar indicating the posterior probability of assignment of the individual to each of the two clusters

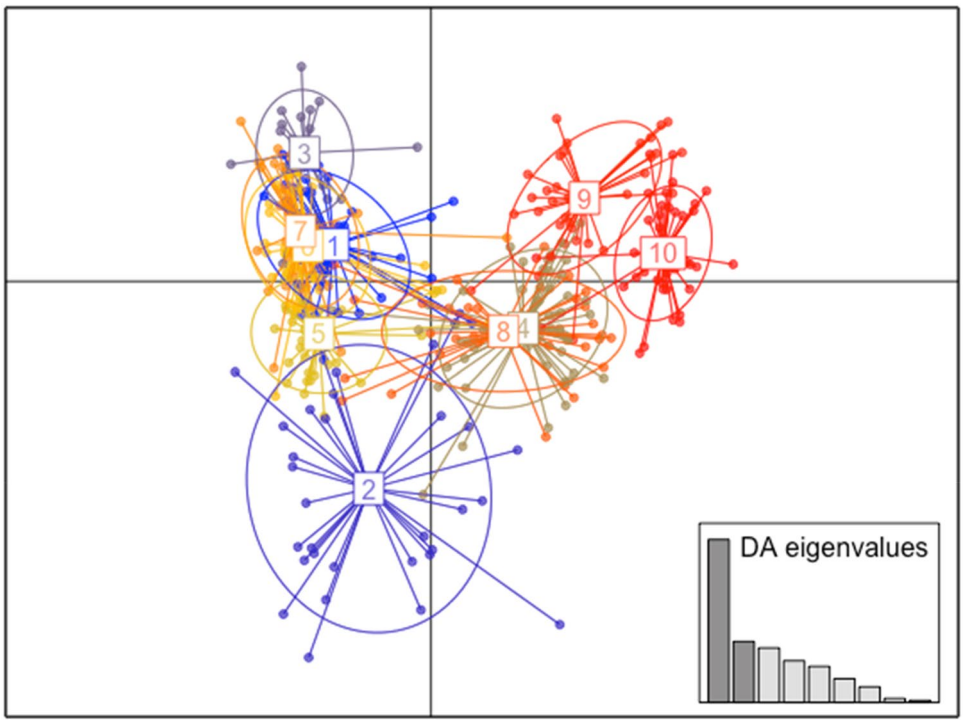

Fig. 3 Discriminant analysis of principal components for 385 *Centrostephanus rodgersii* individuals collected from 14 sites across Australia and New Zealand. Each small circle represents an individual. Individuals are grouped by k-means clustering, represented as inertia ellipses. Individuals from the Australian populations were mainly assigned to clusters 5, 6, 7, 9 and 10, apart from individuals from PSNB, which were mainly assigned to clusters 1, 2, 3, 4, and 8 with the New Zealand and Kermadec Islands individuals. This indicates that there is genetic differentiation among the Australian and New Zealand populations, and suggests the New Zealand populations came from PSNB. The *X*- and *Y*-axes indicate the 1st (explaining 40.6% of genetic variation) and 2nd (explaining 15.2% of genetic variation) linear discriminant axes. For detailed information on how individuals from each population are assigned to each cluster, see Table S5

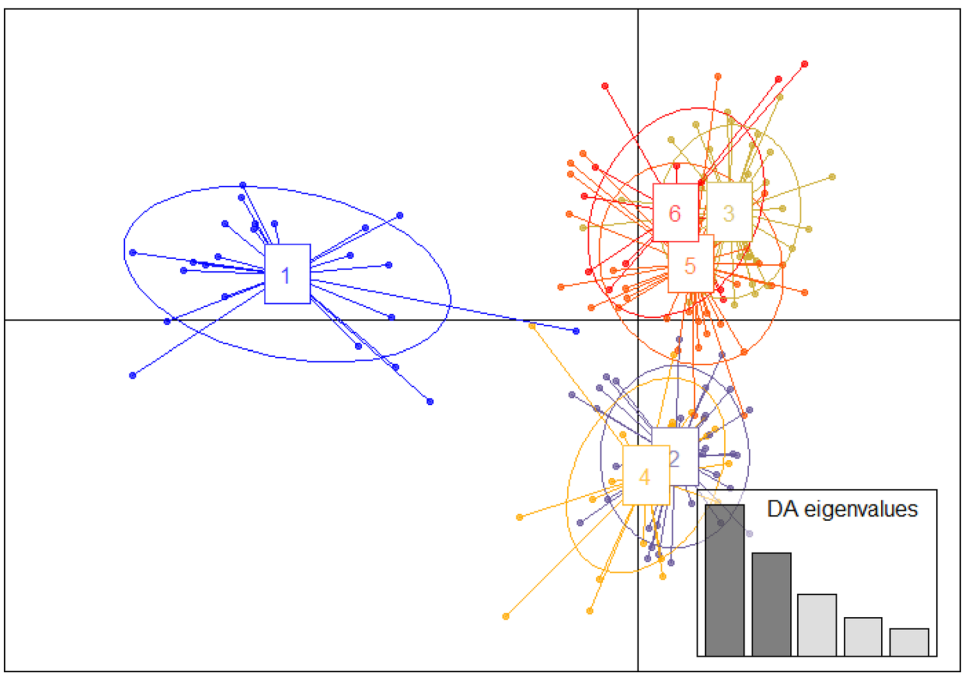

Fig. 4 Discriminant analysis of principal components for 193 *Centrostephanus rodgersii* individuals collected from seven sites across New Zealand and the Kermadec Islands. Each small circle represents an individual. Individuals are grouped by k-means clustering, represented as inertia ellipses. Individuals from the New Zealand and Kermadec populations were assigned relatively evenly across all clusters, suggesting there is very little genetic structure across this region. The *X*- and *Y*-axes indicate the 1st (explaining 35.4% of genetic variation) and 2nd (explaining 25.4% of genetic variation) linear discriminant axes. For detailed information on how individuals from each population are assigned to each cluster, see Table S6

Zealand populations (Figs. 3, 4). The percentage contribution of the individuals assigned to each of the clusters estimated by the STRUCTURE and DAPC analysis are shown in Supplementary Tables 5 and 6. With the exception of PSNB, most of the Australian individuals are assigned to clusters 5, 6, 7, 9, and 10 of the DAPC analysis. By contrast, most of the New Zealand individuals, along with individuals from PSNB, are assigned primarily to clusters 1, 2, 3, 4, and 8 (Supplementary Table 5). Estimates of self-recruitment were high for all populations, being highest in NKER population (0.9285 ± 0.0170) (Supplementary Table 7). Across all runs, the highest estimates of trans-Tasman migration parameters were found for PSNB to NKER (0.1767 ± 0.0309).

Heterozygosity excess (an indication of a genetic bottleneck) was found in all of the Australian populations under the Stepwise Mutation Model (SMM) (Supplementary Table 8). Heterozygosity excess was also found in the New Zealand populations from MER and MOK. Tests of mode-shift likewise detected a bottleneck in the MER population.

Discussion

Marine climate change is driving species distributional shifts in many regions of the globe (Perry et al. 2005; Monaco et al. 2021), and the urchin *C. rodgersii* presents one of the most dramatic examples of such climate-driven ecosystem change (Ling et al. 2009). Consistent with the expectations of a climate-driven range shift (Banks et al. 2010), our study detected very weak population structure among New Zealand populations of this recently expanded species. In addition, while our study detected substantial genetic differentiation between New Zealand and most Australian *C. rodgersii* populations, the finding that a single Australian population (PSNB) clustered tightly with New Zealand samples suggests that this region has been the source for larvae arriving in New Zealand via the Tasman Front flow. This potential source for trans-Tasman connectivity is also supported by oceanographic circulation patterns, where the Tasman Front develops as a flow from the EAC along the NSW coast at around 34°S in the region north of Newcastle (Ridgway and Dunn 2003) and meets north-eastern New Zealand as the East Auckland Current (Stanton 1979). These results thus appear to highlight the crucial interplay between physical and biological marine processes, and specifically the importance of key oceanographic features in mediating marine biological dispersal and connectivity (Wolanski and Hamner 1988; Gaylord and Gaines 2000; Banks 2007b, 2010).

A previous study found little genetic differentiation between Australian populations and a single New Zealand population (from MOK; Banks et al. 2007b), suggesting *C. rodgersii* larvae are readily transported within the Tasman Front. Indeed, Banks et al. (2007b) found pairwise F_{st} values between the MOK population and Australian populations north of about 34°S were 0. By contrast, some populations south of PSNB had notably higher pairwise F_{st} values (0–0.37), indicating greater isolation from the New Zealand population. These patterns are consistent with our observations, suggesting a strong connectivity among New Zealand with Australian populations from regions linked via the Tasman Front.

Centrostephanus rodgersii has increased its range and abundance in southern Australia markedly over the past 60 years (Ling et al. 2009), mirroring southward range expansions detected in a host of additional temperate Australian marine taxa (Pitt et al. 2010; Last et al. 2011; Wernberg et al. 2011). Oceanographic data suggest that strengthening of the southerly EAC-extension along the Australian coastline is responsible for these changes in Australian *C. rodgersii* populations. In contrast, the offshoot of the EAC that crosses the Tasman Sea to New Zealand has weakened over recent decades (observed post-1980s; Sloyan and O'Kane 2015). Such weakening would presumably reduce transport of larvae from Australia to New Zealand, resulting in recent reductions of gene flow. As a consequence, established populations of *C. rodgersii* in New Zealand have the potential to become more genetically isolated and more reliant on local larval supply as this weakening continues.

Other sea urchin species in the region also appear to be strongly influenced by the EAC and the Tasman Front. The ranges of *Tripneustes kermadecensis* and *Heliocidaris tuberculata* extend from eastern Australia to the Kermadec Islands, and also locations within north-eastern New Zealand (Bronstein et al. 2017, 2019; Byrne and Gall 2017). Both species have planktotrophic larvae that are thought to be advected from Australia to the Kermadec Islands and New Zealand via the Tasman Front (Bronstein et al. 2019). Transport of larvae from Australia and New Zealand is also reflected in the genetic structure found in other coastal marine taxa around the Tasman Sea. For example, the gastropod mollusc *Nerita melanotragus,* a species with a pelagic larvae duration of 5–6 months, shows little or no mtDNA differentiation among eastern Australian and New Zealand populations (Waters et al., 2005; Spencer et al. 2007).

Despite the high potential for long-distance dispersal in *C. rodgersii*, our analyses suggested that self-recruitment may be important in maintaining some populations (see Burgess et al. 2014). The northern Kermadec Island population (Raoul Island) has the highest levels of self-recruitment (0.9285 ± 0.0170), perhaps a reflection of its geographic isolation. Notably, these islands sit outside of the dominant flow of the Tasman Front and origin of the East Auckland Current in a region of weak and fluctuating eddy systems (Sutton et al. 2012). Self-recruitment at Raoul Island (NKER) has similarly been surmised as important in maintaining populations of crown-of-thorns

sea stars (Liggins et al. 2014), despite this species having a planktonic larval dispersal. By contrast, Reisser et al. (2014) noted an absence of genetic structure between populations of *Nerita melanotragus*, perhaps a reflection of this species' relatively extensive larval dispersal capacity. Our results here similarly suggest that migration of *C. rodgersii* larvae from New Zealand to the northern Kermadec population may be substantial (0.1767 ± 0.0309). Although not surprising based on previous larval dispersal modelling [estimated dispersal time for planktonic larvae was 20–50 days; (Sutton et al. 2012)], population densities of *C. rodgersii* at the Kermadec Islands are much higher than around mainland New Zealand (Edgar and Stuart-Smith 2017). In contrast, most of the inferred migrants arriving in New Zealand came from PSNB, supporting the results of the DAPC and STRUCTURE analyses.

Although the expansion of the Australian *C. rodgersii* populations over the past 60 years is well documented (Ling et al. 2009), previous analyses of Tasmanian populations imply that ongoing gene flow may mitigate the effects of genetic bottlenecks at the front of southward expanding populations (Banks et al. 2010). By contrast, higher levels of population-level inbreeding and lower levels of genetic structuring in New Zealand suggest higher levels of self-recruitment, and the likely influence of complex oceanographic conditions off north-eastern New Zealand as key drivers of genetic structure (see Ross et al. 2009; Gardner et al. 2010). These features include the persistent mesoscale East Cape Eddy and North Cape Eddy systems that are capable of retaining long-lived oceanic larvae, with retention of nearshore also likely enhanced through wind driven upwelling and ageostrophic secondary circulation (Chiswell and Roemmich 1998).

Species such as *C. rodgersii* with long-lived dispersive phases (1–3 months) that are temperature-limited will likely undergo ongoing range extensions under global warming (Banks et al. 2010). Such climate-driven shifts are increasingly evident for a broad range of coastal marine species in Australasia (Last et al. 2011; Wernberg et al. 2011; Monaco et al. 2021; Middleton et al. 2021) and globally (Perry et al. 2005; Poloczanska et al. 2013; Pinsky et al. 2020). Winter sea temperatures and warming has been an important control of *C. rodgersii* in Australia, with populations establishing in regions where at least one-in-three winters are warmer than 12 °C (the larval thermal threshold; Ling et al. 2009). In New Zealand, the larval thermal threshold appears to be around 15 °C, corresponding with the present distribution of the species (Pecorino et al. 2013). SSTs on average are increasing in the region and marine heatwaves are becoming more frequent (IPCC 2019; Misra et al. 2021). Law et al. (2018) modelled a predicted increase in SSTs of between 1 and 3 °C under RCP8.5 by 2100 across the current New Zealand range of *C. rodgersii*.

If populations of *C. rodgersii* in New Zealand respond to warming in the same way as Australian populations, we expect increases in population sizes and an expansion southwards.

Based on present-day New Zealand sea surface temperatures in the winter, a 3 °C of ocean warming would result in all of coastal North Island having winter sea temperatures 15 °C or warmer, equating to 400 km expansion south in the species' potential range. Changes in *C. rodgersii* distributions are driven by favourable currents (such as the EAC driving the southward expansion in Australia), and any changes in the New Zealand population would also be influenced by regional currents. Importantly, the southern-most reported distribution of New Zealand populations near East Cape not only coincides with the 15 °C winter isotherm, but is also within the south-flowing coastal East Cape Current that could facilitate the transport of larvae south and potentially population expansion. Given the well-documented biodiversity and socio-economic impacts that *C. rodgersii* can have (Johnson et al. 2011; Pecl et al. 2017), if there is such a southern expansion of the species' range, it is essential to develop a clearer understanding of how New Zealand ecosystems may be reshaped by this species and others under climate change.

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Availability of data and materials All voucher specimens are stored at the Department of Zoology, University of Otago and tissue collections held at Massey University are findable via the Genomics Observatories Metadatabase (GEOME). All genotype files and sample metadata are deposited in appropriate repositories (genotype files are available at https://doi.org/10.6084/m9.figshare.14450163.v1; sample metadata are available at GEOME [GUID https://n2t.net/ark:/21547/DpW2] as part of the Ira Moana Project, https://sites.massey.ac.nz/iramoana/). These samples and derived data have a Biocultural (BC) Notice attached. The BC Notice is a visible notification that there are accompanying cultural rights and responsibilities that need further attention for any future sharing and use of this material or data. The BC Notice recognises the rights of Indigenous peoples to permission the use of information, collections, data and digital sequence information generated from the biodiversity or genetic resources associated with traditional lands, waters, and territories. The BC Notice may indicate that BC (Biocultural) Labels are in development and their implementation is being negotiated. For more information about the BC Notices, visit https://localcontexts.org/notice/bc-notice/.

Code availability N/A.

Declarations

Conflict of interests The authors have no conflicts of interest to declare.

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The population genetic structure of the urchin Centrostephanus rodgersii in New Zealand with links to Australia

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