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RESEARCH ARTICLE

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Population connectivity across east Australia's bioregions and larval duration of the range-extending sea star *Meridiastra calcar*

O. Selma Klanten[1,2] | Mailie Gall[2] | Sergio S. Barbosa[2] | Michael W. Hart[3] | Carson C. Keever[3] | Jonathan B. Puritz[4] | Januar Harantio[2] | Robert J. Toonen[5] | Paulina Selvakumaraswamy[2] | Richard K. Grosberg[6] | Maria Byrne[2]

[1]School of Life Sciences, University of Technology Sydney, Sydney, New South Wales, Australia

[2]School of Life and Environmental Sciences, The University of Sydney, Sydney, New South Wales, Australia

[3]Department of Biology, Okanagan College, Kelowna, British Colombia, Canada

[4]Biological Sciences, College of the Environment and Life Sciences, The University of Rhode Island, Kingston, Rhode Island, USA

[5]Department of Biology, Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Honolulu, Hawaii, USA

[6]Coastal and Marine Sciences Institute, College of Biological Sciences, University of California Davis, Davis, California, USA

Correspondence
O. Selma Klanten, School of Life Sciences, University of Technology Sydney, Sydney 2007, NSW, Australia.
Email: osklanten@me.com

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Abstract

1. The diversity and distribution of marine species in eastern Australia is influenced by one of the world's strongest western boundary currents, the East Australia Current, which propels water and propagules poleward, a flow intensifying due to climate change.
2. Population genetic structure of the asterinid sea star *Meridiastra calcar* was investigated across its range in eastern Australia (12° of latitude, 2,500 km) from northern New South Wales to its poleward-extending range in Tasmania at the southern edge influence of the East Australia Current.
3. Population structure and connectivity of *M. calcar* were examined across six bioregions using six microsatellite loci (nuclear DNA) and the control region (mitochondrial DNA). The potential influence of the extent of *M. calcar*'s intertidal rock platform habitat was also assessed.
4. Genetic structure analysis indicated that the Hawkesbury Shelf contained distinct genetic clusters, whereas the two sites in the Batemans Shelf differed from each other, with Jervis Bay Marine Park having just one genetic cluster. The Manning Shelf, Twofold Shelf, and Bruny bioregions all had similar genetic composition.
5. Strong self-seeding (68–98%) was indicated by microsatellite loci for all bioregions, with lower (0.3–6.5%) migration between bioregions. Poleward (New South Wales to Tasmania) migration was low except from the Manning Shelf (30%).
6. Contemporary population connectivity and genetic structure of *M. calcar* appear to be influenced by ocean currents, habitat distribution, and its short planktonic larval duration, which was a minimum of 12–14 days, depending on availability of a settlement cue.
7. The dominance of unique genetic groups in the Hawkesbury bioregion shows the importance of this region for *M. calcar* and possibly a diversity of co-distributed

rock platform species. This highlights how important it is to have a large marine park in the Hawkesbury bioregion, which is presently lacking.

KEYWORDS

Asteroidea, East Australia Current, Echinodermata, marine conservation, planktonic duration, population genetics

1 | INTRODUCTION

In marine systems where many species have the biphasic bentho-pelagic life history, understanding the degree to which populations are connected by larval dispersal is crucial for biodiversity conservation, for management of marine resources, and for determination of the dynamics of climate-change-driven range shifts (Coleman et al., 2011a; Coleman et al., 2019). The interactions between oceanography, biology, ecology, and changing climate are generating location- and region-specific patterns in marine population connectivity (O'Connor et al., 2007; Munday et al., 2009; Teske et al., 2016; Teske et al., 2017) that can often be a challenge to understand.

Because most larvae cannot be followed in the plankton or tagged, data from genetic markers together with estimates of pelagic larval duration (PLD) and data from oceanography are used to model population structure and the movement of individuals among populations (Teske et al., 2016; Marko & Hart, 2018). Although the expectation that possession of dispersive propagules leads to genetic panmixia throughout species' ranges (Kinlan, Gaines & Lester, 2005; Coleman & Ayre, 2007; Addison et al., 2008; Shanks, 2009), a correlation between the PLD and population differentiation is often not realized (Weersing & Toonen, 2009; Selkoe & Toonen, 2011). Across a diversity of broadcast-spawning marine invertebrates, population genetic differentiation is influenced by historical phylogeography, coastal topography, availability of recruitment and adult habitat, ocean currents, and a suite of other biotic and abiotic factors (Keever et al., 2009; Weersing & Toonen, 2009; Hart & Marko, 2010; Selkoe et al., 2010; Puritz & Toonen, 2011; Sunday et al., 2014; Selkoe et al., 2016; Teske et al., 2016; Puritz et al., 2017; Teske et al., 2017; Marko & Hart, 2018; Sorte et al., 2018).

Among the most powerful drivers of marine biogeography and population connectivity are the fast-flowing western boundary currents that carry warm water and propagules from the tropics poleward and which generate complex eddy systems (Coleman et al., 2013; Coleman et al., 2017; Azis Ismail & Ribbe, 2019; Malan et al., 2020; Schilling et al., 2020). These currents, such as the Kuroshio Current along the western North Pacific coast and the East Australia Current (EAC; see Figure 1) have strongly influenced regional biodiversity for hundreds of thousands of years (Ridgway, 2007; Suthers et al., 2011; Cortese et al., 2013). They also determine the poleward limits of coral reefs and associated tropical biodiversity (Yamano, Sugihara & Nomura, 2011; Kim et al., 2019). Under the influence of climate change, the Kuroshio Current and EAC have increased in speed and poleward extent, driving species' range shifts and the tropicalization of temperate regions (Vergés et al., 2014; Pecl et al., 2017; Soler et al., 2022). Tropicalization of temperate habitats in the Pacific has been a strong trend. In contrast, poleward flow of the major Atlantic Ocean western boundary current, the Gulf Stream, has slowed due to the influence of Arctic meltwater (Boers, 2021). In eastern Australia, many species of echinoderms, molluscs, and fishes have extended their poleward range due to migration of their pelagic stages in the increased flow of the EAC with some extensions involving thousands of kilometres from larval source populations (Booth et al., 2007; Ling et al., 2009; Pitt, Poloczanska & Hobday, 2010; Ramos et al., 2018; Gervais, Champion & Pecl, 2021). This is also seen in the appearance of larvae of species that have not yet established (Woodings et al., 2019).

Environmental, biological, and geological features (Roy & Thorn, 1981; Last et al., 2010; Leaper et al., 2012) have informed the classification of Australia's provincial bioregions (Commonwealth of Australia, 2006). In the absence of empirical data on large-scale structure and biodiversity distribution, this bioregionalization scheme provides a framework to support management of marine biodiversity and development of marine protected areas to protect a comprehensive and representative suite of habitats and species. Most Australian bioregions have at least one large marine park (MP). Climate-change-driven alterations of larval trajectories have created the imperative to understand present-day and potential future changes in marine population connectivity in the context of the designated bioregions, especially among marine protected areas with respect to their role in safeguarding biodiversity and providing climate change resilience (Coleman et al., 2011a; Coleman et al., 2017; Balbar & Metaxas, 2019; Pena & Colgan, 2020).

The strong influence of the EAC on population genetic connectivity in south-east Australia is shown for many co-distributed species, including sea urchins, sea stars, gastropods, and macroalgae (Banks et al., 2007; Piggott et al., 2008; York, Blacket & Appleton, 2008; Ayre, Minchinton & Perrin, 2009; Banks et al., 2010; Coleman et al., 2011b; Puritz et al., 2017; Coleman et al., 2019). Many studies show population connectivity between the Australian mainland and Tasmania (Piggott et al., 2008; Coleman & Kelaher, 2009; Puritz et al., 2017), although the south-east corner of the Bass Strait region is a biogeographic break (Sherman, Hunt & Ayre, 2008; York, Blacket & Appleton, 2008; Aguilar et al., 2015). The poleward range extension of many species in the region over the last ≥50 years is testament to the strong influence of the EAC on marine connectivity (Poloczanska et al., 2013; Poloczanska et al., 2016; Soler et al., 2022). Although the dominant flow is

FIGURE 1 Map of Australia showing the flow (grey arrows) of the East Australia Current (EAC) (modified from Oke et al., 2019). Blue circles indicate local eddies. WA, Western Australia; NT, Northern Territory; SA: South Australia; QLD, Queensland; NSW: New South Wales; VIC, Victoria; TAS, Tasmania.

poleward, the influence of the EAC on near-shore connectivity is complex (Figure 1) due to flow field variations and local topography (e.g. eddies, counter currents) that also enhance local retention of propagules as well as equatorward dispersal (Coleman et al., 2013; Malan et al., 2020).

The sea star *Meridiastra calcar*, a non-target species relatively free of direct human impact (e.g. fishing, shell collecting) and with a dispersive larva, was used as a model species to assess population genetic connectivity with respect to east Australia's provincial bioregions. This species is a member of a group of asterinids that have evolved non-feeding lecithotrophic larvae, along with many other marine invertebrates in the region, a shift that may have been influenced by the comparatively low ocean productivity of the region (Byrne, 2006; Marshall et al., 2012). *M. calcar* is an endemic species, and along the east coast of Australia it is a rocky intertidal specialist and an ecologically important omnivore (Arrontes & Underwood, 1991; Byrne & O'Hara, 2017; McLaren & Byrne, 2021). This sea star has increased its poleward range by 235 km along the east coast of Tasmania since the 1950s (Pitt, Poloczanska & Hobday, 2010). This trend is seen for many macroinvertebrate species and is being driven by the poleward extended flow of the EAC (Pitt, Poloczanska & Hobday, 2010; Soler et al., 2022). In its rocky shore habitat, *M. calcar* is associated with a distinct community of co-distributed species, including the alga *Hormosira banksii* and the sea star *Parvulastra exigua*, which due to their limited dispersal and the local oceanography tend to have highly structured population genetics (Barbosa et al., 2013; Puritz et al., 2017; Coleman et al., 2019; Clark et al., 2020). Other members of this community include overharvested abalone and sea urchin species and declining macroalgal species, which have high connectivity and are of conservation concern (Piggott et al., 2008; Coleman & Kelaher, 2009; Chick, 2020).

M. calcar has an extensive range along the east coast of Australia from southern Queensland to Tasmania (Dartnall, 1971). Its main distribution in eastern Australia is from the Coffs Harbour area in New South Wales (NSW) to Tasmania (Figure 2). In far northern NSW, the populations are small and fragmented due to vast expanses of unsuitable habitat (sandy beach) coastline. Along the south coast of Australia, the western limit of *M. calcar* is the Eyre Peninsula, South Australia (Dartnall, 1971; Ayre, Minchinton & Perrin, 2009; Puritz et al., 2017). Southern Tasmania is at the limit of the poleward distribution of *M. calcar* and is also at the end of available habitat. The population genetic structure of *M. calcar* was investigated along its main distribution in eastern Australia from northern NSW (26.3°S) to Tasmania (14.3°S), over 12° of latitude (~2,500 km), a distribution that overlaps with the trajectory of the EAC and encompasses the east Australia bioregions (Figure 2).

M. calcar were collected from 14 populations across the five NSW bioregions and one bioregion in Tasmania. The latter allowed for inferences to be made on connectivity at the southern influence of the EAC and recent range extension at the poleward limits of its distribution and habitat. Genetic structure and connectivity of *M. calcar* were characterized by sequencing the mitochondrial DNA (mtDNA) control region to explore influences of longer term processes and nuclear DNA (nDNA) microsatellite loci to assess the influence of contemporary processes. The data were used to determine migration patterns along the coast. As *M. calcar* is abundant on intertidal rock platform habitat (Arrontes & Underwood, 1991; McLaren & Byrne, 2021), the distribution of this intertidal landform class across bioregions was determined to consider the potential influence of habitat availability on population connectivity. The duration of the planktonic life stage of *M. calcar* has not been established and is determined here with respect to larval responses to a settlement cue and how this may influence dispersal time.

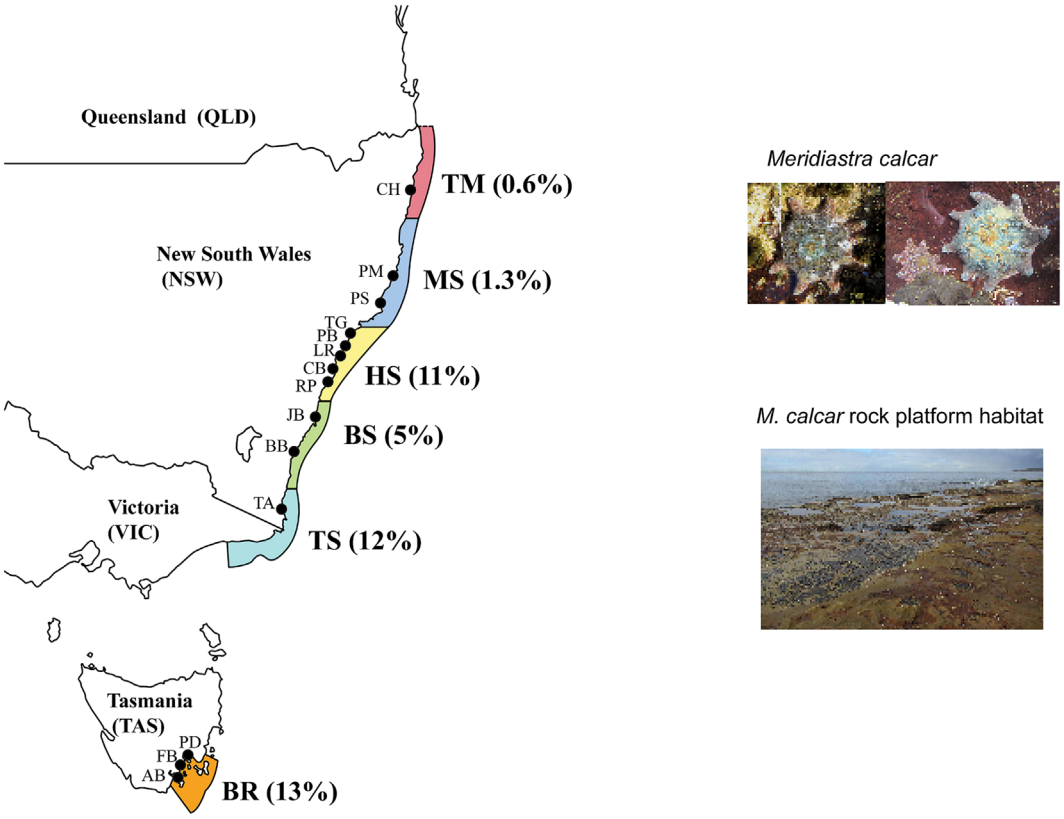

FIGURE 2 Map showing bioregions in New South Wales (NSW) to Tasmania (TAS) and collection sites. The bioregions are coloured to show boundaries: TM, Tweed–Moreton; MS, Manning Shelf; HS, Hawksbury Shelf; BS, Batemans Shelf; TS, Twofold Shelf; BR, Bruny region, Tasmania. Sites: CH, Coffs Harbour; PM, Port Macquarie; PS, Port Stephens; TG, Terrigal; PB, Pearl Beach; LR, Long Reef; CB, Cape Banks; RP, Royal National Park; JB, Jervis Bay; BB, Batemans Bay; TA, Tathra; PD, Primrose Sands; FB, Fortescue Bay; AB, Adventure Bay (see Table 1). The percentages in parentheses represent the amount of rock platform habitat along the total length of coastline for each bioregion. The inset photographs show an aggregation of *Meridiastra calcar* in the Hawkesbury region and its rock platform habitat.

There has been considerable interest in the phylogeography of *M. calcar* and other species in south-east Australia with respect to the formation of a major biogeographical barrier, the Bassian Isthmus, which is the historic Pleistocene Bass Strait land bridge that spanned between mainland Australia and Tasmania (Ayre, Minchinton & Perrin, 2009). Both the land bridge and expanse of sandy habitat at Ninety Mile Beach have curtailed or cut off gene flow between populations (Sherman, Hunt & Ayre, 2008; York, Blacket & Appleton, 2008; Ayre, Minchinton & Perrin, 2009; Puritz et al., 2017). For *M. calcar*, there remains a distinct regional genetic differentiation between populations reflecting the influence of Ninety Mile Beach and the land bridge (Ayre, Minchinton & Perrin, 2009; Puritz et al., 2017). During the Pleistocene, populations of *M. calcar* in NSW and eastern Tasmania were restricted to two refugia, with subsequent gene flow mediated by contemporary ocean currents (Puritz et al., 2017). There have been several studies of the population genetic structure in *M. calcar*, including a study using allozyme markers in populations spanning 2,500 km along the east coast of Australia to Tasmania that did not find significant population structure or influence of oceanographic processes (Sherman, Hunt & Ayre, 2008), whereas a study that used mtDNA in populations spanning ~700 km across the faunal break on either side of where the land bridge formed found significant structure (Ayre, Minchinton & Perrin, 2009). Though not designed from the bioregion perspective, the Puritz et al. (2017) study included populations from two NSW bioregions and one in Tasmania and showed that *M. calcar* has relatively high levels of regional genetic structure but little structure among sites. This study built on the previous research using a sampling design targeted to assess the population genetic structure and connectivity of *M. calcar* across the NSW bioregions and how these are connected to populations in Tasmania.

Given the strength of the EAC over ~100 ka, recent poleward range expansion, and possession of a planktonic larva, we hypothesized that poleward connectivity among *M. calcar* populations from NSW to Tasmania would be high. We also hypothesized that, among bioregions, population genetic connectivity would be influenced by the oceanography of the region, as well as habitat availability, as noted for associated species (Piggott et al., 2008; Coleman et al., 2011a). These factors, along with the length of the planktonic stage of *M. calcar*, are likely to promote genetic patchiness and potential self-seeding in some regions (Coleman et al., 2011a; Cetina-Heredia et al., 2015; Coleman et al., 2017; Pena &

Colgan, 2020). The Bass Strait biogeographic break between mainland Australia and Tasmania (Ayre, Minchinton & Perrin, 2009) was also expected to influence *M. calcar*'s population structure.

2 | METHODS

2.1 | Population sampling and habitat assessment

M. calcar specimens were collected from across its main distribution range in eastern Australia, with samples from five bioregions in NSW and one in Tasmania (Table 1, Figure 2). In NSW, the bioregions included Tweed–Moreton (TM, one population), Manning Shelf (MS, two populations), Hawkesbury Shelf (HS, five populations), Batemans Shelf (BS, two populations) and Twofold Shelf (TS, one population). Three populations were sampled in the Bruny (BR) Bioregion, Tasmania (Table 1, Figure 2). The population from Coffs Harbour in the TM bioregion is located at the northern end of the main distribution of *M. calcar*. In northern NSW, populations of this species are small and fragmented due to the prevalence of sandy shores. This constrained the sampling effort in the northern most bioregions. Where possible, samples were collected in protected areas in NSW with a focus on marine parks (Table 1). The bioregions investigated in NSW each have at least one large marine park, except the HS Bioregion, although there are aquatic reserves and intertidal protected regions with *M. calcar* populations in this region (Figure 2, Table 1).

Maps from OzCoasts' Smartline Map Database, which contains habitat map information (http://www.ozcoasts.gov.au/coastal/smartline.jsp) for all the beaches around Australia, were used to determine the distribution of the rock-platform-type habitat of *M. calcar* for the east coast of Australia (see Figure 2). For analysis, maps were stitched together using DoubleTake (http://echoone.com/doubletake) and then analysed using GraphClick (http://www.arizona-software.ch/graphclick/tour.html). The following attributes and their classifications, as described in the Smartline data dictionary (Sharples, Mount & Pedersen, 2009), were selected to identify rocky intertidal platform habitats: (1) intertidal landform (classes: rocky shore, rocky shore platform, sloping rocky shore, hard bedrock shore, and sloping hard rock shore), (2) substrate type (classes: hard lithic material, bedrock), (3) intertidal slope (class: flat to gently sloping <5°), and (4) stability (field name: stable hard rocky shore).

2.2 | Spawning and larval rearing

M. calcar has a 3-week spawning period in spring (Byrne, 1992), and mature animals were collected from Gordons Bay, Sydney, in October 2021 when the ambient sea-surface temperature was 19°C. The ovaries were dissected and placed in dishes of filtered sea water (FSW; 0.1 μm). Spawning was induced by using the ovulatory hormone 1-methyladenine (1 μM in FSW). Sperm were obtained

TABLE 1 Sampling locations of *Meridiastra calcar* along the east coast of Australia.

Bioregion	Location	Marine park (MP) Aquatic reserve (AR)	Gene region	*n* msat/CR	Latitude	Longitude
New South Wales						
Tweed–Moreton (TM)	Coffs Harbour (CH; Diggers Beach)	Solitary Islands MP	msat	50/0	30°48′18″S	153°48′79″E
Manning Shelf (MS)	Port Macquarie (PM; Towns Beach)	N/A	msat	50/0	31°25′80″S	152°55′39″E
	Port Stephens (PS; Fingal Bay)	Port Stephens Great Lakes MP	msat/CR	50/47	32°44′92″S	152°10′45″E
Hawksbury Shelf (HS)	Terrigal (TG)	N/A	msat/CR	50/46	33°27′01″S	151°27′11″E
	Pearl Beach (PB)	N/A	msat/CR	50/44	33°32′95″S	151°18′53″E
	Long Reef (LR)	Long Reef AR	msat/CR	50/46	33°44′25″S	151°18′29″E
	Cape Banks (CB)	Cape Banks AR	msat/CR	50/46	33°59′92″S	151°14′63″E
	Royal National Park (RP; Jibbons Beach)	Royal National Park AR	msat/CR	50/46	34°04′65″S	151°09′63″E
Batemans Shelf (BS)	Jervis Bay (JB; Chinamens Beach)	Jervis Bay MP	msat/CR	50/44	35°05′76″S	150°41′00″E
	Batemans Bay (BB; Malua Bay)	Batemans MP	msat/CR	50/46	35°46′67″S	150°14′12″E
Twofold Shelf (TS)	Tathra (TA; Baragoot Point)	N/A	msat/CR	50/46	36°41′39″S	149°59′49″E
Tasmania						
Bruny (BR)						
Hobart	Primrose Sands, Roches Bay (PD)	N/A	msat/CR	0/40	42°53′74″S	147°40′16″E
Port Arthur	Fortescue Bay, Pirates Bay (FB)	N/A	msat/CR	0/40	43°08′55″S	147°57′84″E
Bruny Island	Adventure Bay (AB)	N/A	msat	50/0	43°21′19″S	147°19′44″E
Total samples				600/491		

Note: Gene regions examined: five mitochondrial DNA control region (CR) loci and six nuclear DNA microsatellites (msat) loci; *n*, number of samples for each gene region msat/CR examined. N/A, not applicable.

directly from dissected testes. The gametes were checked for quality (e.g. egg shape, sperm motility), and gametes from two females and two males were used to generate larval cultures reared at 19–20°C. The larvae were reared in 200 mL glass dishes (one larva per millilitre) with the FSW renewed daily by reverse filtration. Their responses to the geniculate coralline alga *Amphiroa* sp., a metamorphic cue (Byrne, personal observation) common in near-shore rocky reefs and rock platform habitats, were investigated. Groups of larvae ($n = 20$) were placed in 10 mL dishes with a small piece of the alga on days 3, 5, 8, or 9, with three or four replicates per treatment, and the time to settlement determined. The water and algae were renewed every second day. There was also a control with a set of four replicates where larvae were not provided with *Amphiroa* sp. For larvae exposed to *Amphiroa* sp. from day 3, counts of attached and metamorphosing larvae and juveniles were carried out from when the first settlers were observed on day 7 and thereafter on days 8, 9, 12, and 14, with the latter used as the last time point because most larvae had settled by then. For the larvae exposed to *Amphiroa* sp. on day 5, these counts were carried out on days 7, 8, 9, 12, and 14. For the larvae exposed to *Amphiroa* sp. on day 8, counts were carried out on days 9, 12, and 14. For those exposed to *Amphiroa* sp. on day 9, counts were carried out on days 12 and 14. Though most larvae had settled by day 14, swimming larvae were present for another 3 days.

Data on the percentage settlement on day 14 were analysed by one-way analysis of variance with days of cue exposure (four treatments and no cue) as the factor. Normality and homoscedasticity assumptions were valid, as indicated by Shapiro and Levene tests after arcsine transformation of the data. Tukey honestly significant difference post hoc tests for significant pairwise comparisons were computed between levels of days of exposure to *Amphiroa*. Significance for all tests was accepted at $P < 0.05$. All analyses were performed in R (v1.2.1335) using RStudio (R Core Team, 2020).

2.3 | DNA extraction and amplification

A non-destructive sampling method was used by collecting tube foot tissue on site from 600 *M. calcar* from 12 populations ($n = 50$ per population) and placing them directly into tubes of 95% ethanol (Table 3). The animals were returned to the area of collection after sampling. Total DNA was extracted from ethanol-preserved tube foot tissue using the salt extraction protocol of Meeker et al. (2007). Six asterinid microsatellite loci (B202, C8, C112, C114, C204a, C232) were amplified for all 600 animals following the protocols of Keever et al. (2008, 2009). All six microsatellite loci were polymorphic for all *M. calcar* populations. Amplification of the putative control region (mtDNA) followed the protocol of Barbosa et al. (2013), resulting in a 586 bp alignment length, including gaps, which were treated as point mutations during analysis. For the control region (mtDNA), 491 *M. calcar* samples in 11 populations were examined (Table 1).

2.4 | Population genetic analysis

Microsatellite allele frequencies, the mean number of alleles per locus, expected heterozygosity H_E, observed heterozygosity H_O, and departure from Hardy–Weinberg equilibrium were estimated using Arlequin v. 3.5 (Excoffier & Lischer, 2010). The presence of null alleles was assessed using MICRO-CHECKER v. 2.2.3 (http://www.nrp.ac.uk/nrp-strategic-alliances/elsa/software/microchecker/) (van Oosterhout et al., 2004). Tests for linkage disequilibrium were performed using Genepop v. 4.2.1 with significance of the pairwise comparisons assessed after application of a Bonferroni correction.

Diversity indices (nucleotide π and haplotype h) of mtDNA control region were determined in FaBox (Villesen, 2007) and examined using Arlequin v. 3.5 (Excoffier & Lischer, 2010). In addition, two neutrality tests, Tajima's D (Tajima, 1989) and Fu's F_s (Fu & Li, 1993), were carried out to test for departures from neutral mtDNA sequence variation.

2.5 | Population differentiation

The partitioning of genetic variation among sites within bioregions was determined using a hierarchical analysis of molecular variance (AMOVA) in GENALEX v. 6.501 (Peakall & Smouse, 2012). Two AMOVAs were performed using Arlequin v. 3.5 (Excoffier, Laval & Schneider, 2005) to test for partition of variation across the six bioregions and between NSW and Tasmania. To facilitate comparisons of the results obtained by the two genetic markers, two models were run on the microsatellite data. One model included all 12 locations and the second included only 11 locations (excluding Coffs Harbour) to match the populations sampled for mtDNA. The AMOVA results for the full and reduced models were found to be comparable, so only the full model (including Coffs Harbour) is described.

Population structure was characterized from microsatellite genotypes using an infinite allele model for *F*-statistics (Weir & Cockerham, 1984) using GenAlEx v. 6.2 (Peakall & Smouse, 2006). Significance values were based on 999 permutations of the data. In addition to standard *F*-statistics, we applied an alternative statistic, Jost's D_{EST}, using SMOGD v. 1.2.5 (Crawford, 2010). The bias-corrected estimator D_{EST} was applied as a measure of population differentiation, and we also used D_{EST} statistics to construct matrices of pairwise population comparisons. Pairwise D_{EST} was calculated with DEMEtics v. 0.8.7 (Gerlach et al., 2010; Jueterbock et al., 2011) running with R v.3.2 (R Core Team, 2018). Significance level was based on 1,000 bootstrap samples.

Population structure from mtDNA sequences was analysed by AMOVA (Excoffier, Smouse & Quattro, 1992) in Arlequin v. 3.5 as well as estimating pairwise F_{ST} of population comparisons. The model selected, using the Akaike information criterion implemented in jModelTest v. 0.1.1 (Posada, 2008), was Tamura and Nei corrected distances (Tamura & Nei, 1993) with a gamma correction of 0.01. In addition, population structure was assessed based on bioregions

and between NSW and Tasmania. A haplotype network for mtDNA was generated using the median-joining algorithm of Network v. 4.5.1.6 (http://www.fluxus-engineering.com) (Bandelt, Forster & Rohl, 1999).

2.6 | Population structure

STRUCTURE v. 2.3.4 (http://pritchardlab.stanford.edu/structure.html) (Pritchard, Stephens & Donnelly, 2000) was used to identify patterns of admixture in the populations according to the microsatellite data. An admixture model was used which allows connection among populations. A burn-in of 200,000 steps was set followed by 200,000 Markov chain Monte Carlo replicates, with 10 iterations and $k = 1$ to 12. The ΔK statistic of Evanno was applied (Evanno, Regnaut & Goudet, 2005) to get an indication of the best K with respect to the highest level of hierarchical genetic partitioning in the data. Since this method has been shown to underestimate subpopulation structure (Puechmaille, 2016; Janes et al., 2017), additional statistics were also calculated (MedMed, MedMean, MaxMed, and MaxMean) to account for unevenness of sampling in the data and because these are more sensitive in detecting subpopulation structure. Both approaches were used as implemented in StructureSelector (Li & Liu, 2018). Population and individual memberships from multiple runs were permuted using CLUMPP v. 1.1.2 (Jakobsson & Rosenberg, 2007). The output was visualized using DISTRUCT v. 1.1 (Rosenberg, 2004).

2.7 | Patterns of migration

To assess the influence of contemporary processes as indicated by microsatellite loci on patterns of migration, we used BayesAss v. 3.0.3 (Wilson & Rannala, 2003). The Markov chain Monte Carlo runs consisted of 50×10^6 steps with 1×10^6 burn-in, sampling every 2,000 steps, with prior values of migration rate (0.3), allele frequency (0.35), and inbreeding coefficient (0.85). These priors all returned an acceptance rate between 20% and 40% (Faubet, Waples & Gaggiotti, 2007). Convergence and effective sample size (ESS) of all best runs were checked with Tracer v. 1.6.1 (http://beast.bio.ed.ac.uk/Tracer) (Rambaut et al., 2014).

3 | RESULTS

3.1 | Provincial bioregions and habitat

The northernmost NSW bioregions, Tweed-Moreton (TM) and Manning (MS), have the longest coastlines (Table 2, Figure 2), but also have the lowest extent of the intertidal rock platform habitat for *M. calcar* (0.6% and 1.3% respectively; Table 2). These bioregions are dominated by a sandy or muddy coastline. In comparison, the central and southern NSW bioregions Hawkesbury Shelf (HS), Batemans Shelf (BS), and Twofold Shelf (TS) have 11%, 4.8%, and 12.2% of intertidal rock platform habitat respectively, with the latter bioregion having the shortest length of coastline (810 km). In Tasmania, the Bruny (BR) Bioregion has 12.7% of its coastline as rocky platform habitat (Table 2).

3.2 | Larval duration

By day 7 the larvae had a well-developed attachment complex. Once attached, the larvae took up to 3 days to metamorphose and transform to the sea star profile. Following introduction of *Amphiroa* sp. to the culture dishes on days 3 and 5, the number that settled were low (<10%) until days 12 (20%) and 14 (40–50%), indicating that competency to settle increased over time (Figure 3). In contrast, the larvae provided with the algal cue on days 8 and 9 had the most intense settlement response, indicating that most of them were competent to respond to the cue. Of those provided with the cue on day 8, 30% and 60% of larvae had settled by day 12 and day 14 respectively. The larvae provided with the cue on day 9 exhibited the strongest response, with 80% settled by day 14 (Figure 3). Few to no larvae settled in the control (no cue) treatment up to day 9. Thereafter, there was an increase in the number of spontaneously settled larvae in the no cue treatment to day 14 (15%). Overall, the percentage of larvae that settled by day 14 was influenced by the time of cue addition (or no cue) (analysis of variance: $F_{4,13} = 15.97$, $P < 0.001$; Table 3). Depending on the treatment, 15–80% of larvae had settled by day 14. Although the larval response was variable and depended on access to a metamorphic cue, it appears that the minimum planktonic duration is 2 weeks. Those larvae that did not settle were still swimming at the end of observations on day 17 and varied in appearance. In the no cue treatment the larvae that were

TABLE 2 Spatial extent of intertidal rock platform habitat as a percentage of the length of coastline for each of the six provincial bioregions.

Bioregion	Coast (km)	Hard rock platform (km)	Rock platform (%)
New South Wales			
Tweed–Moreton	5,736.681	35.228	0.61
Manning Shelf	4,660.556	61.532	1.32
Hawkesbury Shelf	3,696.780	405.979	10.98
Batemans Shelf	2,092.785	100.132	4.78
Twofold Shelf	810.267	99.067	12.23
Tasmania			
Bruny	1,864.648	237.368	12.73

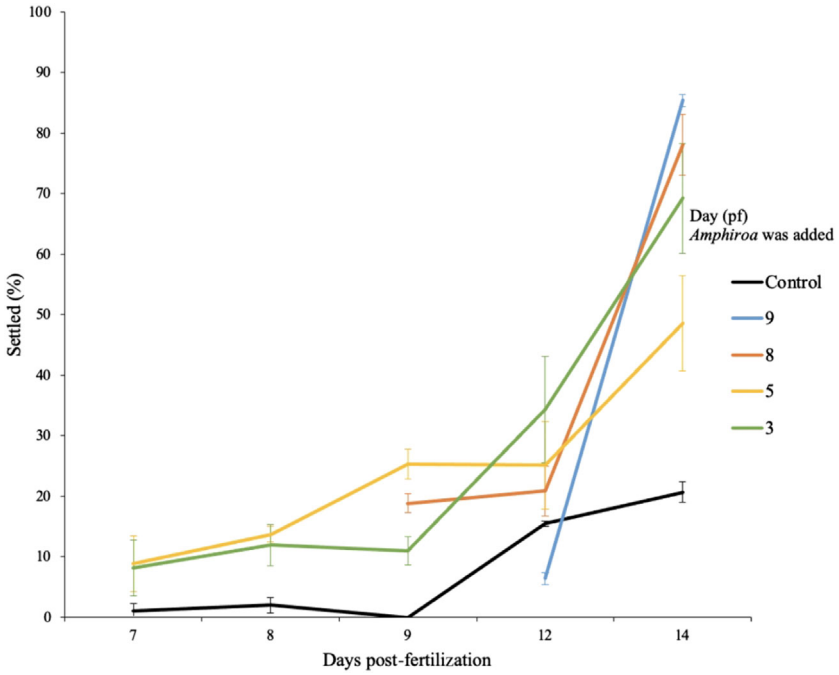

FIGURE 3 The percentage of *Meridiastra calcar* brachiolaria larvae settled (attached/metamorphosed) in response to the addition of a settlement cue (*Amphiroa*) on days 3, 5, 8, and 9 post-fertilization (pf) and for larvae that were not provided a cue. It appears that the larvae were most receptive when the cue was presented on days 8 and 9, resulting in high settlement.

TABLE 3 Analysis of variance of the percentage settlement data showing the impact of time of introduction of the algal (*Amphiroa*) settlement cue (3, 5, 8, 9 days post-fertilization and no algae added) on settlement of *Meridiastra calcar* larvae by day 14. Tukey's honestly significant difference (HSD) post hoc test shows pairwise comparisons.

	df	Sum squares	Mean square	*F*	*P*	Tukey's HSD
Day 14	4	0.98	0.25	15.97	<0.001	No cue <9 d
	13	0.12	0.01			No cue <8 d = 5 d = 3 d
	17	1.18				9 d = 8 d
						9 d > 5 d
						9 d = 3 d

Abbreviation: d, days.

still swimming appeared normal with a well-formed attachment complex. By day 17, the larvae in the cue treatments that had not settled were starting to develop an abnormal appearance, indicating that they were beyond competence.

3.3 | Population genetic analyses

3.3.1 | Genetic diversity

All six microsatellite loci amplified in *M. calcar* were polymorphic, and the mean number of alleles per locus ranged from 6 to 16 summed across all samples (Supporting Information Table S1). The presence of null alleles was detected in 10 of 72 comparisons (13.9%). Deficit of heterozygotes is a known biological phenomenon associated with broadcast spawning of planktonic marine invertebrates (Addison & Hart, 2005). Null alleles were not consistently associated with a particular marker or population.

Of the 72 population–locus combinations for *M. calcar*, 33 deviated from Hardy–Weinberg equilibrium, and 25 of these were statistically significant after a Bonferroni correction for multiple tests. Significant deviations after Bonferroni correction were associated with 10 of the 12 locations (see Supporting Information Table S1), although the number of markers deviating ranged from one to five with no single marker found to consistently deviate across all sites. Observed heterozygosity H_O was smaller than expected heterozygosity H_E at all but two locations (Port Macquarie, Adventure Bay; Table 4), overall mean H_O (0.49) is smaller than mean H_E (0.54) for all loci across all sampled locations (Supporting Information Table S1).

A 586 bp alignment of the mtDNA was amplified for 491 individuals across 11 locations. Number of haplotypes per population ranged between 6 (Jervis Bay) and 18 (Batemans Bay), with unique haplotypes ranging from zero (Jervis Bay) to eight (Royal National Park, Port Stephens), resulting in a total of 88 haplotypes (Table 4). Overall haplotype diversity was high ($h = 0.853$), and the haplotype diversities for individual populations ranged from 0.734 (Jervis Bay) to 0.889 (Batemans Bay) and were similar across all sites sampled regardless of whether the *M. calcar* were collected from a protected area or not (Table 4). Nucleotide diversity π was low, ranging from 0.73% (Jervis Bay) to 2.2% (Primrose Sands) (Table 4). After correcting for simultaneous tests, the two neutrality analyses were not significantly different from zero for any of the populations,

TABLE 4 Population and genetic diversity measures of control region (mitochondrial DNA (mtDNA)) for 11 populations (five bioregions) and for six microsatellite loci in 12 populations within six bioregions[a].

		Control region (mtDNA)					Microsatellites			
Bioregion	**Population**	***n***	**Nh**	**Nuh**	***h***	***π* (%)**	***n***	H_O	H_E	R_S
New South Wales										
Tweed–Moreton (TM)	Coffs Harbour	–	–	–	–	–	50	0.48	0.56	5.33
Manning Shelf (MS)	Port Macquarie	–	–	–	–	–	50	0.50	0.48	5.50
	Port Stephens	47	16	5	0.869	1.27	50	0.46	0.47	5.83
Hawkesbury Shelf (HS)	Terrigal	46	17	7	0.872	1.31	50	0.57	0.61	7.67
	Pearl Beach	44	15	4	0.844	1.28	50	0.55	0.56	5.67
	Long Reef	46	16	6	0.872	0.92	50	0.52	0.52	6.67
	Cape Banks	46	14	6	0.858	1.18	50	0.44	0.58	6.83
	Royal National Park	46	17	8	0.873	1.37	50	0.47	0.59	7.17
	HS total	228	51	31	0.862	1.23				
Batemans Shelf (BS)	Jervis Bay	44	6	0	0.734	0.73	50	0.40	0.45	6.50
	Batemans Bay	46	18	7	0.889	1.41	50	0.51	0.67	6.67
	BS total	90	19	7	0.818	1.06				
Twofold Shelf (TS)	Tathra	46	10	3	0.772	1.01	50	0.45	0.50	5.50
Tasmania										
Bruny (BR)	Primrose Sands, Roches Bay	40	13	8	0.822	2.2	–	–	–	–
	Fortescue, Pirates Bay	40	12	7	0.744	0.9	–	–	–	–
	Adventure Bay	–	–	–	–	–	50	0.55	0.54	6.33
	BR total	80	23	15	0.795	1.62				
	TOTAL	491	88	61	0.853[a]	–	–	–	–	–

[a]For control region (mtDNA): number of individuals (*n*), number of haplotypes (Nh), number of unique haplotypes (Nuh), haplotype diversity (*h*), and nucleotide diversity (*π*) are indicated. Bioregions with several sites (three bioregions) for mtDNA total results are included. The overall (five bioregions, 11 populations) mtDNA results (TOTAL) are included with overall haplotype diversity *h* calculated following Nei (1983): $h = n\left(1 - \Sigma f_i^2\right)/(n-1)$. Mean results for six microsatellite loci: number of individuals (*n*), mean observed (H_O) and expected (H_E) heterozygosity, and mean allelic richness (R_S) averaged across all six loci (see also Supporting Information Table S1 for more detail). Dashes indicate no data.

suggesting neutral or random population expansion (Supporting Information Table S2).

3.3.2 | Population differentiation

Evidence of genetic structure was recorded for six microsatellite loci among *M. calcar* locations, with 17% of the variation allocated among populations for the infinite allele model ($F_{ST} = 0.169$, $P < 0.001$). Jost's *D* statistic ($D_{EST} = 0.163$) produced a similar measure to the F_{ST} value. Nearly all the pairwise F_{ST} comparisons between pairs of sites were significant ($P < 0.05$; heatmap for F_{ST}, Figure 4a; for all values, see Supporting Information Table S3A).

Tests for population differentiation revealed a significant and greater portion of the variation was partitioned among six bioregions ($F_{CT} = 0.124$, $P < 0.001$) than populations within regions ($F_{SC} = 0.074$, $P < 0.001$; Table 5). In contrast, when *M. calcar* populations were grouped by state (NSW vs Tasmania), no significant portion of variation was partitioned among states ($F_{CT} = -0.015$, $P > 0.05$). A significant and greater portion of the genetic variation was partitioned among populations within NSW and Tasmania ($F_{SC} = 0.172$, $P < 0.001$). For both bioregion and two-state comparisons ($F_{ST} = 0.189$ and 0.16 respectively, both $P < 0.001$) the variation was greatest within populations, supporting population structure (Table 5).

Overall, strong genetic structure was detected for the 11 *M. calcar* populations for control region (mtDNA) data ($\Phi_{ST} = 0.115$, $P < 0.001$, not shown). By grouping the 11 populations into the five marine bioregions, strong genetic partitioning was evident between individuals within populations ($\Phi_{ST} = 0.138$, $P < 0.001$). Moderate partitioning was seen among populations within bioregions ($\Phi_{SC} = 0.027$, $P < 0.05$). Low variation was explained by differences between populations grouped among bioregions ($\Phi_{CT} = 0.114$, $P = 0.09$; Table 6). In contrast, when grouped by state (NSW vs Tasmania), 27% of the total variance could be partitioned amongst states ($\Phi_{CT} = 0.269$, $P < 0.05$), 1% partitioned among populations within states ($\Phi_{SC} = 0.011$, $P < 0.05$), and 72% within populations ($\Phi_{ST} = 0.282$, $P < 0.001$) (Table 6). A genetic break between NSW and Tasmania was evident in the population pairwise F_{ST} comparisons between pairs of sites with significant genetic subdivision for all comparisons (except Royal National Park to Fortescue) between mainland Australian sites in NSW and Tasmania ($0.088 > \Phi_{ST} < 0.430$; heatmap, Figure 4b; values, Supporting Information Table S3B). Within NSW, only three of the 36 pairwise F_{ST}

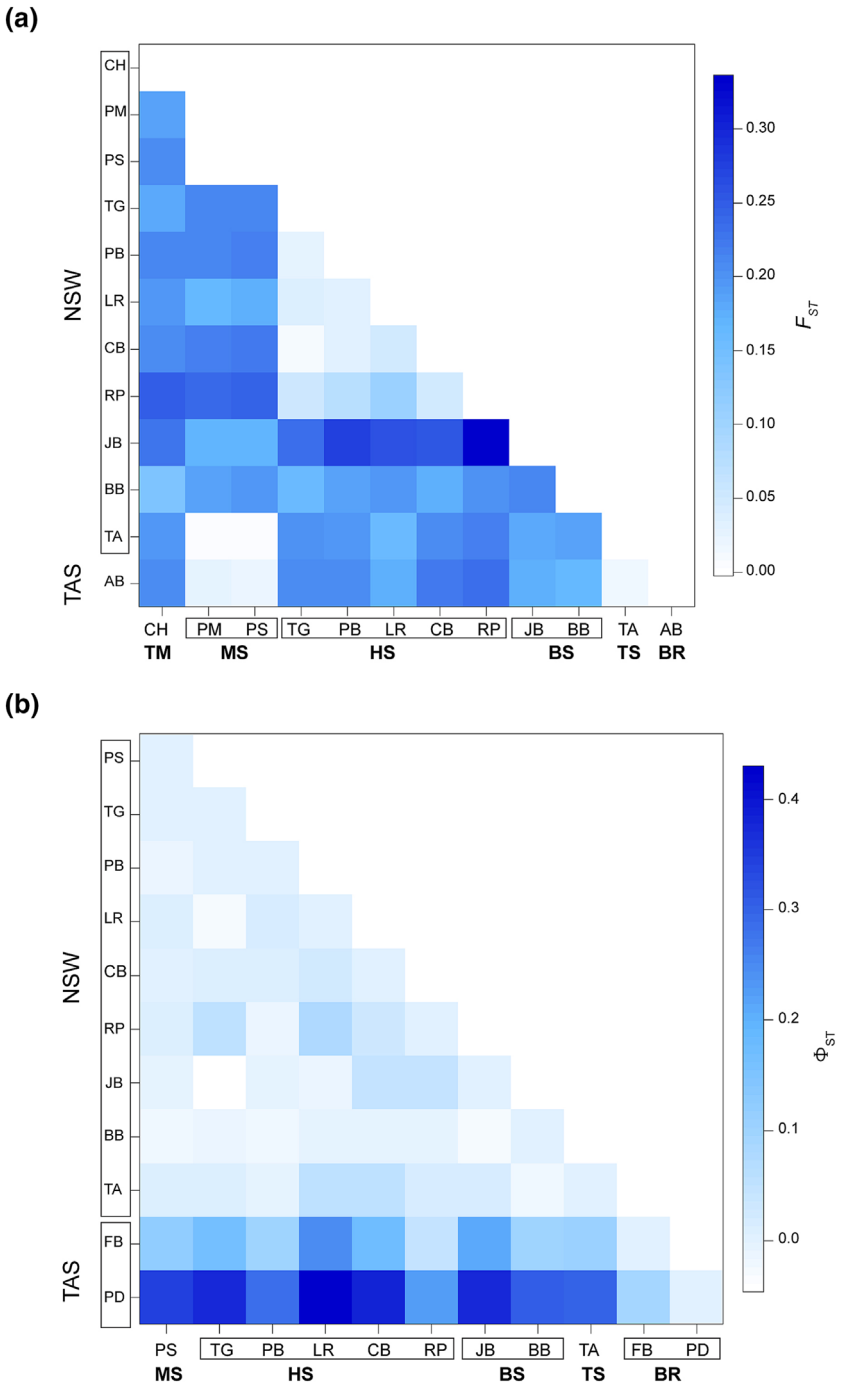

FIGURE 4 Heatmap of pairwise F_{ST} values. (a) Heatmap of six microsatellite loci (nuclear DNA) for 12 populations of *Meridiastra calcar* in six bioregions. (b) Heatmap of the control region (mitochondrial DNA) of 11 populations in five bioregions. Population locations are allocated to each bioregion (bold). TM, Tweed–Moreton; MS, Manning Shelf; HS, Hawksbury Shelf; BS, Batemans Shelf; TS, Twofold Shelf; BR, Bruny region, Tasmania; CH, Coffs Harbour; PM, Port Macquarie; PS, Port Stephens; TG, Terrigal; PB, Pearl Beach; LR, Long Reef; CB, Cape Banks; RP, Royal National Park; JB, Jervis Bay; BB, Batemans Bay; TA, Tathra; AB, Adventure Bay; FB, Fortescue Bay; PD, Primrose Sands (see Table 1).

TABLE 5 Microsatellite population comparisons of six loci among 12 populations grouped into six bioregions and by state (New South Wales and Tasmania).

	Marine bioregions			New South Wales–Tasmania		
Source of variation	**Variance (%)**	**Fixation index**	***P*-value**	**Variance (%)**	**Fixation index**	***P*-value**
Among regions	12	$F_{CT} = 0.124$	<0.001	0	$F_{CT} = -0.015$	ns
Among populations	6	$F_{SC} = 0.074$	<0.001	17	$F_{SC} = 0.172$	<0.001
Within populations	81	$F_{ST} = 0.189$	<0.001	83	$F_{ST} = 0.160$	<0.001

Note: *F*-statistics were compiled using infinite allele model.

TABLE 6 Population comparisons of mitochondrial DNA control region among 11 populations grouped into five bioregions, and by two states (New South Wales and Tasmania).

	Marine bioregions			New South Wales–Tasmania		
Source of variation	**Variance (%)**	**Fixation index**	***P*-value**	**Variance (%)**	**Fixation index**	***P*-value**
Among regions	12	$\Phi_{CT} = 0.114$	ns	27	$\Phi_{CT} = 0.269$	<0.05
Among populations	2	$\Phi_{SC} = 0.027$	<0.05	1	$\Phi_{SC} = 0.017$	<0.05
Within populations	86	$\Phi_{ST} = 0.138$	<0.001	72	$\Phi_{ST} = 0.282$	<0.001

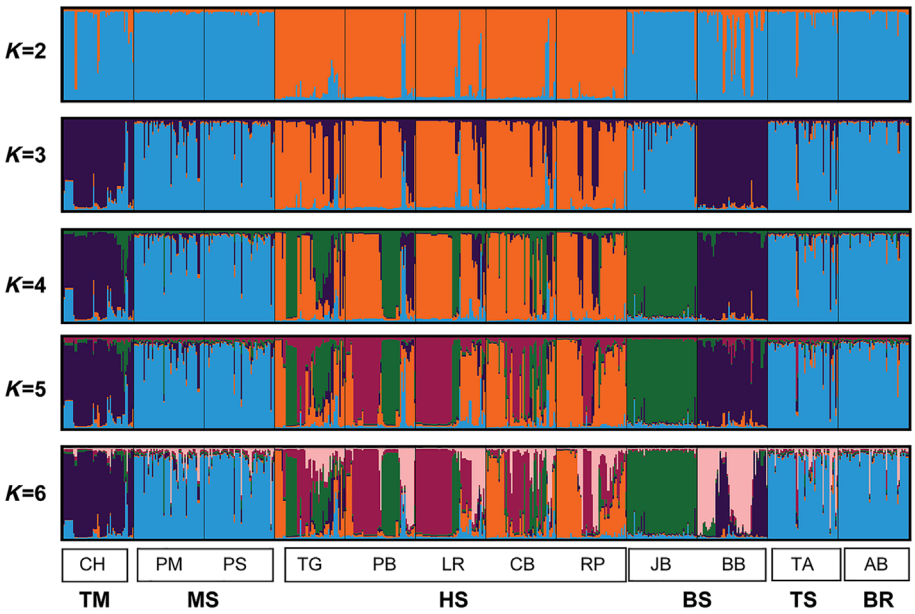

FIGURE 5 Population structure of *Meridiastra calcar* for microsatellites. Best fit determined by STRUCTURE is $K = 2$ for six microsatellite loci and $K = 6$ when including subpopulations. Patterns of admixture indicated two main groups identified among the 12 populations in six bioregions. Five of the six bioregions clustered together (blue): TM, Tweed–Moreton; MS, Manning Shelf; BS, Bateman Shelf; TS, Twofold Shelf; BR, Bruny. And a single bioregion, the Hawkesbury Shelf (HS), formed one cluster (orange). The 12 populations are displayed in squares and the six bioregions below are in bold; CH, Coffs Harbour; PM, Port Macquarie; PS, Port Stephens; TG, Terrigal; PB, Pearl Beach; LR, Long Reef; CB, Cape Banks; RP, Royal National Park; JB, Jervis Bay; BB, Batemans Bay; TA, Tathra; AB, Adventure Bay (see Table 1).

comparisons between pairs of sites were significant, but all within state comparisons for Tasmania were significant (Supporting Information Table S3B).

3.3.3 | Population structure

Bayesian clustering in STRUCTURE determined that the best fit using the method of Evanno, Regnaut & Goudet (2005) was $K = 2$ for the six microsatellite loci and identified two significant patterns of admixture among 12 populations (Figure 5). At $K = 2$, the Hawkesbury Shelf Bioregion had a different structure ('orange') relative to the other five bioregions ('blue') sampled. Applying the method of Puechmaille (2016) to detect finer subpopulation structure within these groupings, six patterns of admixture ($K = 6$) best fitted the data (Figure 5, Supporting Information Figure S1). The Manning Shelf, Twofold Shelf, and Bruny bioregions had a similar composition, with individuals showing a high probability of assignment to the 'blue' genetic group. Within the Hawkesbury Shelf Bioregion, there was diversity in patterns of admixture, some of which were shared with other regions (Tweed-Moreton, Batemans Shelf); but overall, the genetic patterns were largely unique to this bioregion. Sites in the Batemans Shelf Bioregion differed from each other. The Jervis Bay site had a single genetic group ('green'), and the Batemans Bay site contained a mix of genetic groups shared with the Tweed-Moreton ('black') and Hawkesbury Shelf ('pink') bioregions.

Construction of a median-joining network revealed mostly shared haplotypes amongst NSW populations, whereas a few Tasmanian individuals shared haplotypes with NSW populations (Supporting Information Figure S2).

3.3.4 | Patterns of migration

Migration patterns using six microsatellite loci among six bioregions in BayesAss shows that *M. calcar* populations have high levels (68–98%,

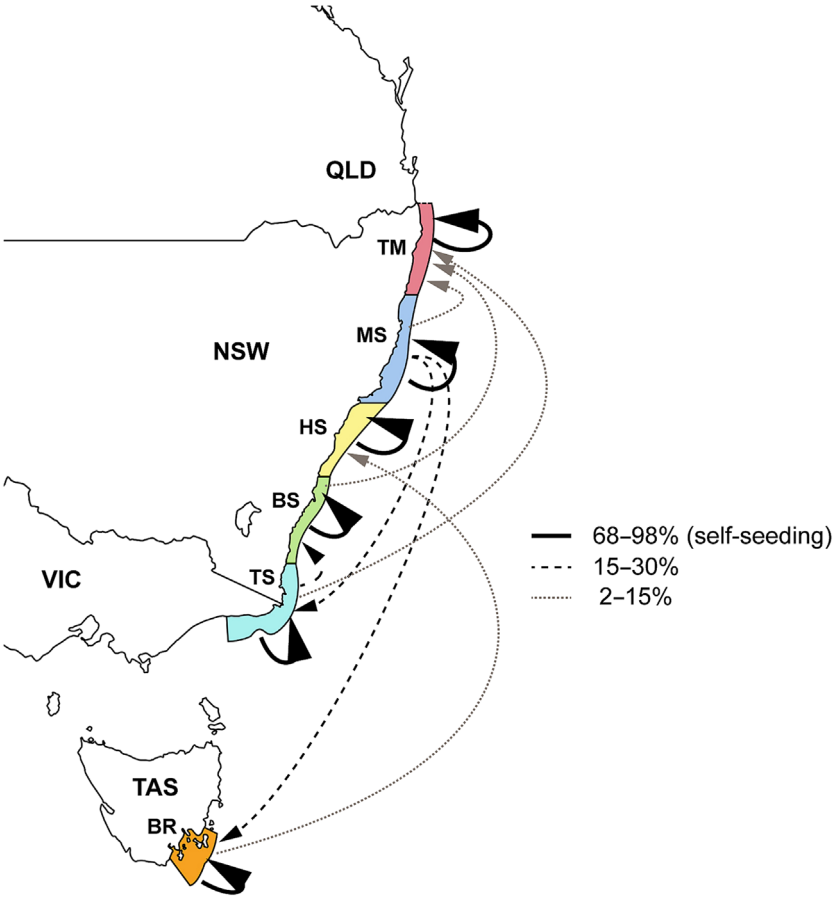

FIGURE 6 Map showing results of BayesAss migration and self-seeding of *Meridiastra calcar*. Microsatellite results of self-seeding and migration among the six bioregions. Black arrows indicate self-seeding of propagules (68–98%), dashed black lines represent 15–30% migration among bioregions, and grey dashed lines display 2–15% migration of propagules between bioregions. See also Supporting Information Table S4 for values. QLD, Queensland; NSW, New South Wales; VIC, Victoria; TAS, Tasmania; TM, Tweed–Moreton; MS, Manning Shelf; HS, Hawksbury Shelf; BS, Batemans Shelf; TS, Twofold Shelf; BR, Bruny (see Table 1).

Figure 6, Supporting Information Table S4) of self-seeding propagules. Low to mid levels (0.3–6.5%) of migration among the six bioregions were also evident (Table S4). Poleward migration (NSW to Tasmania) was trivial (~0.6%) with one exception, where 29.5% of individuals were the result of migration from Manning Shelf (NSW) to Tasmania over a few recent generations. That high migration rate was unexpected because it is not consistent with the pattern of differentiation between those two bioregions in mtDNA (Figure 4b), or with the pattern of differentiation between Tasmania and other mainland bioregions in the microsatellite data (Figure 4a). The unexpected microsatellite (but not mtDNA) similarity between those two bioregions (but not other pairs of bioregions) could reflect unexpectedly high gene flow by larval dispersal, or some other feature of microsatellite genetics (including high mutation rates and an unusual pattern of homoplasy of allele sizes in one of those two samples).

Furthermore, there was minimal migration (0.3–0.8%) of propagules moving northwards from Tasmania to NSW, and a 2.1% migration into the Hawkesbury Shelf. Within NSW, 4.7% of propagules migrated from Batemans Shelf north into the Tweed-Moreton Shelf, and 6.5% migrated into Tweed-Moreton from the adjacent Manning Shelf region. From the most southern bioregion sampled on the Australian mainland, Twofold Shelf, 5.8% of propagules migrated north to Tweed-Moreton (Supporting Information Table S4). Curiously, low (0.3–0.9%) migration was recorded from the Hawkesbury Shelf into the other NSW bioregions (Supporting Information Table S4).

4 | DISCUSSION

For *M. calcar*, a non-target species relatively free of human disturbance, the populations along the east coast of Australia have distinct structures, especially for microsatellite data. The Hawkesbury Shelf Bioregion is composed of genetic groups that are largely unique to this bioregion, whereas similarity was observed between the Manning Shelf, Twofold Shelf, and Bruny bioregions, despite their large geographical separation. Importantly, the strong genetic structure observed suggests self-seeding is a major feature of the population genetics of *M. calcar*. There was some gene flow among bioregions, with a poleward connectivity reflecting the flow of the EAC, as well as some migration from south to north. Contemporary connectivity of *M. calcar* populations along the east coast of Australia appears to be strongly influenced by ocean currents, by the distribution of intertidal rock platform habitat, and PLD, which was determined to be a minimum of 12–14 days with a peak receptivity to the metamorphic cue on day 9. This PLD depended on access to a cue. It appears that larvae that do not have access to a metamorphic cue during their early competent phase may disperse for some time. Eventual settlement would likely depend on access to cue/habitat and larval receptivity.

Migration analysis showed an overall trend of self-seeding. This is likely to be influenced by the relatively short PLD of *M. calcar*; and, in some locations, EAC eddies may promote propagule

retention. Self-seeding was highest in the Hawkesbury Shelf Bioregion, which may be facilitated by entrainment of larvae in the strong eddy–gyre system that characterizes the region where the EAC is close to the coast (Cetina-Heredia et al., 2015; Coleman et al., 2017). Propagule retention of *M. calcar*, its affinity for rock platform intertidal habitat, and high local spawner density may be influential in driving the distinct features of populations of this species in the Hawkesbury Bioregion. This region has a high proportion of rock platform habitat, and aggregations of *M. calcar* are a prominent feature of the intertidal fauna of the Hawkesbury Bioregion (Arrontes & Underwood, 1991; McLaren & Byrne, 2021).

The abiotic factors driving self-seeding in *M. calcar* populations are likely to be complex. For instance, high self-seeding in the Manning Shelf runs counter to expectations with respect to EAC flow. The sites where *M. calcar* were sampled in this region are close to a separation zone where the EAC departs from the coast and would be expected to promote offshore larval dispersal (Cetina-Heredia et al., 2015; Coleman et al., 2017). For the Twofold Shelf Bioregion, with relatively high suitable habitat (12% rock platform), self-seeding is low. In this region, the EAC eddy field is not strong and may not promote propagule retention. For the Bruny Bioregion, with the highest proportion (~13%) of rock platform habitat, larvae that do not self-seed could migrate north or west or may be lost, as this is the southern limit of habitat for *M. calcar*.

Persistence of *M. calcar* populations will be facilitated by self-recruitment (68–98% self-seeding) on a local scale together with connectivity with other populations (15–30%) on a regional scale. Local recruitment is also suggested to be important for a co-occurring abalone species, which has a larva similar to that of *M. calcar*, and an octopus species (Piggott et al., 2008; Ramos et al., 2018; Pena & Colgan, 2020). Though *M. calcar* is not a species of conservation concern, other co-occurring endemic species do need protection. These include the abalone *Haliotis rubra* and the sea urchin *Heliocidaris tuberculata*, which have been overharvested and are also prone to poaching (DAFF, 2005; O'Hara & Byrne, 2017; Chick, 2020). Strong self-seeding in *M. calcar* and other species in the region (Piggott et al., 2008; Ramos et al., 2018; Pena & Colgan, 2020) emphasizes the importance of protected areas to help conserve genetic diversity (Coleman et al., 2011a; Coleman et al., 2017) as well as the enforcement of protection.

Comparisons among and within populations and pairwise F_{ST} values for microsatellites showed that *M. calcar* was structured among bioregions and between NSW and Tasmania. Structure analysis revealed that the Hawkesbury Shelf Bioregion has distinct genetic structure in both the overall ($K = 2$) and subpopulation ($K = 6$) analyses. This is likely influenced by self-seeding due to local oceanography, as well as the prevalence of the Hawkesbury sandstone rock platform habitat. It is remarkable that the *M. calcar* populations in the Hawakesbury are largely differentiated from the other regions despite their abundance, spatial extent, and likely high propagule production. In contrast, the northern Tweed-Moreton and Manning Shelf, the southern Twofold Shelf, and Tasmania's Bruny bioregions shared alleles across large distances (NSW to Tasmania, ~2,500 km) and within NSW. The distinct genetic cluster in the Batemans Shelf Jervis Bay site is an important finding, as this is a major marine park centred around a large embayment where populations are likely isolated from the main flow of the EAC by protruding headlands (Coleman et al., 2011a).

For the mtDNA data, stronger differentiation was seen between states (NSW vs Tasmania) and less among the five bioregions, which was also supported by pairwise F_{ST} values. However, among and within population structure was equally strong for both bioregions and states. Though the median network for haplotypes suggested that *M. calcar* was mostly panmictic, a small subpopulation made of individuals from the Bruny Bioregion was evident. These specimens may have been the driving force to distinguish populations among the two states (NSW vs Tasmania). This distinction may reflect the location of *M. calcar* in Bruny as being near the edge of its EAC-driven range extension as well as connectivity with populations in western Tasmania, where *M. calcar* is known to have been common but transient for some time (Guiler, 1960) and is likely connected to genetically distinct South Australia populations (Puritz et al., 2017). The presence of a distinct mtDNA haplotype cluster from the Bruny location points to the need for further population genetic studies of this species around Tasmania, which is poorly known.

The diverse life history traits of sea stars in the family Asterinidae, with a range of dispersal abilities (long, short, none; see Byrne, 2006), have been used as a model system to test whether population genetic structure meets expectations based on life history (Supporting Information Table S5). For instance, comparison of *M. calcar* with a dispersive (weeks) lecithotrophic larva with that of the benthic egg layer *P. exigua* with a non-dispersive benthic larva from the same locations showed that populations of the benthic developer have much stronger genetic partitioning (Sherman, Hunt & Ayre, 2008; Barbosa et al., 2013; Puritz et al., 2017). Asterinids that have planktotrophic larvae with long PLDs (~2–3 months), including *Patiria miniata* and *Patiriella regularis*, have high genetic diversity (Table S5) across their range (Waters & Roy, 2004; Keever et al., 2009; Puritz & Toonen, 2011). These species, however, do show regional population structure, such as between the northern (Alaska) and southern (Vancouver Island to California) populations of *P. miniata*, suggested to be due to oceanographic circulation and the North Pacific Current (Keever et al., 2009; Sunday et al., 2014). Populations of *P. regularis* exhibit structure between the North and South Islands of New Zealand, suggested to be due to upwelling between the two islands (Waters & Roy, 2004). These studies show, as here for *M. calcar*, the importance of contemporary oceanography in population connectivity. In contrast, hermaphroditic viviparous asterinids that give birth directly to juveniles (Supporting Information Table S5) are inbred and have low genetic diversity and strong population structure (Keever et al., 2013).

It appears that whereas the minimum PLD of most *M. calcar* larvae approximates 2 weeks, which may promote self-seeding, some larvae may disperse for much longer, potentially for a month or more (Byrne, personal observation). Early exposure to the settlement cue (from day 3) increased the number of settling larvae, but most intense

settlement response was in larvae introduced to the cue from day 8 or 9. This indicates that there may be a window of time/age when the larvae are most receptive to the cue and thus are most competent to settle. The presence of early settling larvae as well as prolonged dispersal has been observed in other marine species (Marko & Hart, 2018). This may be a bet hedging strategy to ensure local recruitment and greater dispersal. With a PLD of ≥2 weeks, *M. calcar* larvae are likely to disperse widely. Poleward connectivity was highest between northern NSW (Manning Shelf) and the south-east corner of the continent (Twofold Shelf) and Tasmania (Bruny). Separation of the EAC in the Manning Shelf region, which connects with the offshore southerly flow, may promote connectivity between NSW and Tasmania, as suggested for other species, and is a major driver of poleward range extension (Cetina-Heredia et al., 2015; Coleman et al., 2017).

Population genetic connectivity of many shallow water and intertidal marine species in south-east Australia, including macroalgae and invertebrates, is strongly influenced by the southerly flow of the EAC (Banks et al., 2007; Piggott et al., 2008; Coleman et al., 2011a; Puritz et al., 2017). That the EAC is a major driver of population connectivity, despite the Bass Strait biogeographic break (York, Blacket & Appleton, 2008; Aguilar et al., 2015), is well evidenced by the range extension of many species from mainland Australia to Tasmania through migration of their pelagic propagules and post-larval success associated with warming of the region (Banks et al., 2007; Ling et al., 2009; Pitt, Poloczanska & Hobday, 2010; Ramos et al., 2018; Gervais, Champion & Pecl, 2021; Byrne et al., 2022). For *M. calcar*, the poleward increase in its distribution in Tasmania would have been facilitated by the seasonal (summer) strengthening of the EAC when the larvae would be in the plankton, as suggested for other species (Schilling et al., 2020).

The Hawkesbury Shelf Bioregion is particularly important for *M. calcar* in supporting a population with distinct and high genetic diversity. This region also has a large extent of rock platform habitat for *M. calcar*, where it is one of the most abundant intertidal species. The sandstone rock platform habitat in the Hawkesbury Bioregion supports a rich biodiversity, including *H. banksii*, a common fucoid seaweed and ecosystem engineer (Coleman et al., 2019) that forms the '*Hormosira*' flats assemblage (Underwood, 1998; Mueller, Wright & Bolch, 2018). This species has highly restricted dispersal ability and limited gene flow, as does the co-occurring sea star *P. exigua* (Barbosa et al., 2013; Puritz et al., 2017), highlighting the importance of protecting local genetic diversity (Coleman et al., 2011a; Coleman et al., 2019) *M. calcar* and the *Hormosira* species assemblages are co-distributed and are likely to have high habitat dependence. This points to the importance of geomorphology in understanding population connectivity.

Overall, the genetic diversity of *M. calcar* across the populations investigated was similar, regardless of whether the site was in a protected area or not. This was expected, as this species is not targeted and would not have a history of anthropogenic physical disturbance. However, *M. calcar* and co-distributed intertidal species are living in a climate change hotspot where warming is well above the global average and where they are vulnerable to acute marine and terrestrial heatwaves (Oliver et al., 2018). Studies of *M. calcar*, *P. exigua*, and *H. banksii* show their sensitivity to warming (Nguyen et al., 2012; Balogh & Byrne, 2020; Clark et al., 2020). Heatwave conditions in the intertidal region cause mortality of juvenile *P. exigua* and reduced growth of *H. banksii*, and warm conditions impair development in *M. calcar* (Nguyen et al., 2012; Balogh & Byrne, 2020; Clark et al., 2020). In the absence of adaptation, contraction at the warm, northern range edge of these species is likely to occur (Nguyen et al., 2012; Clark et al., 2020), with consequent impacts on genetic diversity. In addition to warming, the rock platform intertidal assemblage is vulnerable to storm water run-off, which kills *M. calcar* (Byrne, personal observation), as well as sea-level rise, especially in areas where the platforms abut coastal cliffs.

Though aquatic reserves and intertidal protected areas in the Hawkesbury Shelf Bioregion are important in conservation of *M. calcar* and co-distributed species, this is the only coastal bioregion in south-east Australia that lacks a major MP. Considering that the Hawkesbury Bioregion is highly urbanized with the pressures of a large city (Sydney) and increasing urbanization of the entire bioregion, a large MP is needed to protect local and regional species and genetic diversity in the face of changing climate and other threatening processes (Coleman et al., 2011b; Coleman et al., 2017). This is especially true for *M. calcar* and co-distributed intertidal species (e.g. *H. banksii*), where dominant unique genetic groups are localized to the region (Coleman et al., 2011b; Coleman et al., 2017). Ocean warming, sea-level rise, changes to currents and upwelling systems, altered larval physiology with warming reducing PLD, and habitat modification and urbanization pressures (e.g. stormwater and pollution) that occurs in the absence of protection all have the potential to impact species' population dynamics, survival, and range shifts (Gibson, 2011; Nguyen et al., 2012; Kendall, Poti & Karnauskas, 2016; Byrne et al., 2022). For *M. calcar* and co-distributed species, how these changes will unfold in the future and modify population connectivity is important for conservation planning but remain uncertain. Refugia within protected areas could be important in preserving genetic diversity in the face of deleterious impacts from climate change (Oliver et al., 2018; Coleman et al., 2019).

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest associated with this work.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available as files in Supporting Information of article (Mcalcar CR.fas; Mcalcar msat.xlsx).

DATA AVAILABILITY STATEMENT

Data available under Supporting Information; microsatellite data file as 'Mcalcar msat.xlsx' (Data S2) and control region mtDNA file as 'Mcalcar CR.fas' (Data S1).

ORCID

O. Selma Klanten https://orcid.org/0000-0001-6296-4225

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SUPPORTING INFORMATION

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