Vol. 532: 1–12, 2015
doi: 10.3354/meps11362

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 21

FEATURE ARTICLE

FREE ACCESS

On-shelf larval retention limits population connectivity in a coastal broadcast spawner

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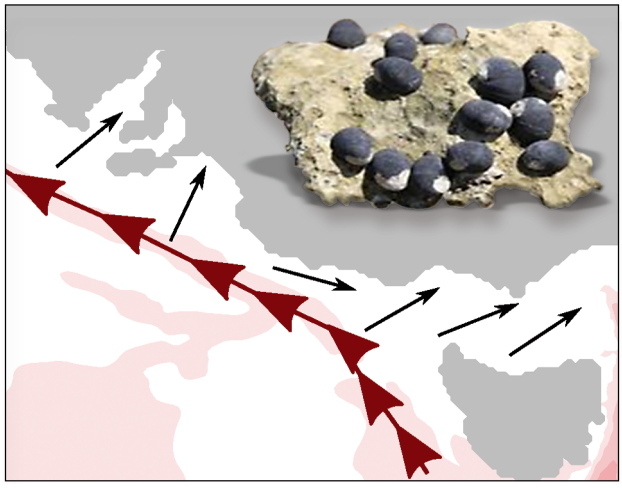
ABSTRACT: Broadcast-spawning marine organisms with long pelagic larval duration are often expected to be genetically homogeneous throughout their ranges. When genetic structure is found in such taxa, it may be in the form of chaotic genetic patchiness: i.e. patterns that might seem independent of any underlying environmental variation. The joint analysis of population genetic data and marine environmental data can elucidate factors driving such spatial genetic diversity patterns. Using meso-scale sampling (at a scale of 10s to 100s of km), microsatellite data and advection connectivity simulations, we studied the effect of temperate southern Australian ocean circulation on the genetic structure of the snail *Nerita atramentosa*. This species has a long pelagic larval duration and is represented as a single metapopulation throughout its ~3000 km range, but even so, we found that its dispersal potential is lower than expected. Connectivity simulations indicate that this is a result of the larvae that remain on the continental shelf (where currents are erratic and often shoreward) returning to the coast in much larger numbers than larvae that become entrained in the region's shelf-edge boundary currents. Our study contributes to the growing evidence that departures from the expectations of panmixia along continuous and environmentally homogeneous coastlines are not limited to low-dispersal species, and it identifies on-shelf larval retention as an important factor limiting dispersal.

KEY WORDS: Isolation by distance · IBD · Marine ecology · Marine protected areas · MPAs · Planktonic larval duration · Population genetic structure · Seascape genetics



A section of the coast of Australia where a seascape genetic analysis of the snail *Nerita atramentosa* revealed particularly strong on-shelf larval retention (red: boundary currents; black: on-shelf currents).

Image: L. Beheregaray, E. van Sebille, P. Teske

INTRODUCTION

The life history of many marine organisms includes a planktonic dispersal stage that theoretically allows even species whose adults are sessile or sedentary to maintain high levels of connectivity over vast distances (Siegel et al. 2003). Understanding the effects of ocean currents and other environmental factors on connectivity among populations of such organisms has important implications for improving our knowledge about marine ecology, including the management of exploited species and the design of marine reserves (Cowen et al. 2000). Numerous genetic

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studies have confirmed that in the absence of dispersal barriers, populations of planktonic dispersers often show low levels of genetic differentiation compared to species with lower dispersal potential, such as direct developers (e.g. Teske et al. 2007). However, high-dispersal species are often neither panmictic (i.e. freely interbreeding) throughout their ranges, nor is the amount of genetic structure inversely correlated with the time that larvae spend in the plankton (Palumbi 2004, Weersing & Toonen 2009). Instead, genetic structure often shows a pattern of seemingly 'chaotic genetic patchiness' (Johnson & Black 1984). This was traditionally attributed to variability in recruitment success (Hedgecock 1994), but a number of recent studies have shown that such complex genetic patterns could be explained by the structuring effects of environmental features such as coastal topography (Banks et al. 2007, Nicastro et al. 2008), ocean currents (Banks et al. 2007, Piggott et al. 2008, White et al. 2010) and the size of suitable habitats (Selkoe et al. 2010).

To understand population connectivity in broadcast spawners, one needs to take into consideration that the interactions between populations may be subject to a complex interplay of environmental and biological factors. Detailed assessments of the mechanisms involved in limiting larval dispersal have only recently become possible by jointly analysing population genetic and oceanographic data, an approach known as 'seascape genetics'. In the case of high-dispersal species with inherently high rates of migration, the genetic data on their own tend to lack sufficient genetic signal to calculate dispersal rates and directions, but they can be used to determine which of a number of oceanographic dispersal scenarios is most appropriate for the species under investigation (Selkoe et al. 2010).

Here, we present an in-depth seascape genetic analysis of the temperate Australian coastal snail *Nerita atramentosa*. This species' planktonic larvae settle after several months, which should theoretically allow it to maintain high levels of connectivity throughout its range. Using a combination of mesoscale sampling, population genetic data and advection connectivity simulations, we tested whether shallow genetic structure among sites could be explained by the region's oceanography. The finding that dispersal is limited because it is facilitated primarily by weak on-shelf currents rather than offshore boundary currents highlights the value of the seascape genetic approach in uncovering biologically meaningful patterns in species in which genetic structure, if present at all, was traditionally believed to be the result of random dispersal processes.

MATERIALS AND METHODS

Southern Australian ocean currents

The boundary currents of temperate southern Australia are unusual in 2 respects. First, the southern west coast is dominated by the Leeuwin Current (LC), which, unlike many cold eastern boundary currents elsewhere, is of tropical origin (Godfrey & Ridgway 1985) and flows in a poleward rather than equatorward direction (Fig. 1). Second, southern Australia has perhaps the longest zonal coastal boundary in the world (Ridgway & Condie 2004). As the LC passes Cape Leeuwin (CL) in south-western Australia, it turns eastwards towards the Great Australian Bight (GAB) (Cresswell & Golding 1980). From the eastern GAB, zonal current flow continues in what Ridgway & Condie (2004) consider to be a separate current, the South Australian Current (SAC), until the current flow becomes poleward again as the Zeehan Current (ZC) flows along the western Tasmanian coast. During the winter months, there is continuous warm west-to-east current flow (Ridgway & Condie 2004) that potentially connects the fauna of the entire region. In summer, there is an overall weakening of currents and a reversal of boundary flow along the eastern south coast (Vaux & Olsen 1961). The GAB has a shallow shelf region up to 100 km wide. The SAC flows along the continental slope, and at places is thus far away from the coastline.

Study species

The intertidal snail *Nerita atramentosa* is a particularly suitable study organism for investigating the effects of southern Australia's oceanography on coastal biota because it is represented on rocky shores throughout the temperate southern Australian region (Spencer et al. 2007). In south-eastern Australia, *N. atramentosa* occurs only sporadically beyond Wilson's Promontory (WP in Fig. 1) and on the Tasmanian east coast, where it is replaced by its sister species *N. melanotragus*, whose range is strongly linked to the region dominated by the East Australian Current (EAC) (Waters et al. 2005, 2014). Australian neritid snails have long spawning seasons of up to 9 mo, with peak spawning occurring throughout austral summer (Przeslawski 2008), and long larval durations of around 4 mo (Underwood 1975). Large geographic distances between suitable habitats, a feature that can affect genetic structure in low-dispersal species in the absence of any other explanations (e.g.

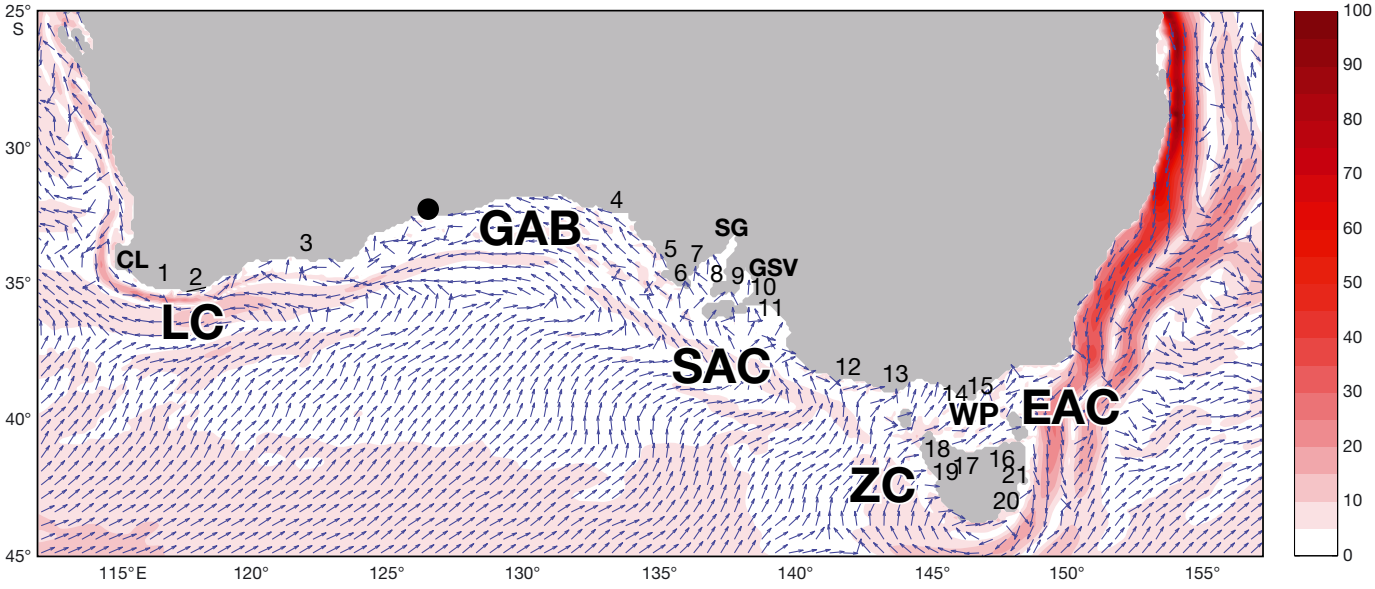

Fig. 1. Sampling localities (numbered 1–21, see Table 1) of *Nerita atramentosa* along the southern coast of Australia. Arrows and colours indicate the direction and magnitude (cm s^{-1}), respectively, of surface velocity in the Ocean General Circulation Model For the Earth Simulator (OFES) from 1 September to 31 January averaged over the years 1980 to 2010. The black circle between Sites 3 and 4 represents an inaccessible site that was not sampled, but for which oceanographic connectivity was simulated (see also Fig. 3 and Fig. S4 in Supplement 3 at www.int-res.com/articles/suppl/m532p001_supp.pdf). CL: Cape Leeuwin; EAC: East Australian Current; GAB: Great Australian Bight; GSV: Gulf St. Vincent; LC: Leeuwin Current; SAC: South Australian Current; SG: Spencer Gulf; WP: Wilson's Promontory; ZC: Zeehan Current

Table 1. Genetic diversity parameters of *Nerita atramentosa* from 21 sampling localities along the southern coast of Australia. N = sample size; NA = average number of alleles per locus; PA = private alleles; H_o = observed heterozygosity; H_e = expected heterozygosity

Site no.	Site name	N	NA	PA	H_o	H_e
1	Walpole	35	10.9	1	0.77	0.77
2	Albany	30	10.5	0	0.79	0.80
3	Esperance	50	11.4	0	0.78	0.78
4	Penong	35	10.3	0	0.80	0.77
5	Point Drummond	37	11.7	3	0.81	0.79
6	Fishery Bay	41	10.5	0	0.81	0.77
7	Peak Bay	35	10.6	1	0.78	0.78
8	Point Souttar	41	10.7	1	0.79	0.79
9	Edithburgh	45	11.7	4	0.82	0.78
10	Glenelg	44	11.6	0	0.84	0.79
11	Victor Harbor	48	11.3	0	0.80	0.78
12	Port Fairy	47	11.3	0	0.77	0.77
13	Marengo	48	11.1	0	0.77	0.77
14	Walkerville	48	11.9	0	0.74	0.78
15	Port Albert	47	11.8	0	0.74	0.77
16	Bridport	41	10.9	2	0.78	0.79
17	Penguin	40	11.2	2	0.83	0.79
18	Couta Rocks	38	11.2	1	0.74	0.80
19	Trial Harbour	40	11.0	0	0.80	0.79
20	Pirates Bay	42	12.2	3	0.79	0.81
21	Swansea	40	10.8	2	0.79	0.79

Hellberg 1996), are thus unlikely to impact on *N. atramentosa*. Also, unlike many other species that are represented in this region by highly divergent evolutionary lineages (e.g. Waters et al. 2004, York et al. 2008, Li et al. 2013), reflecting the effects of historical barriers on contemporary genetic structure, there is no evidence for any division other than the relatively recent evolutionary divergence between *N. atramentosa* and its sister species *N. melanotragus* (Waters et al. 2005). This suggests that any fine-scale genetic structure identified in this species is more likely to be the result of relatively recent events rather than historical oceanographic conditions.

Genetic data generation

During 2011 and 2012, tissue samples were excised from the foot of 870 snails from 21 localities (Fig. 1, Table 1) and preserved in 99% ethanol. Genomic DNA was extracted using a salting out protocol (Sunnucks & Hales 1996). Thirteen microsatellite loci (*Neat01*, *Neat02*, *Neat03*, *Neat04*, *Neat05*, *Neat07*, *Neat09*, *Neat10*, *Neat12*, *Neat14*, *Neat16*, *Neat18*, *Neat19*) were genotyped for all samples as described in Sandoval-Castillo et al. (2012), but 3 of these loci were excluded from the analyses because of high pro-

portions of non-amplification (*Neat02*) or departures from Hardy-Weinberg equilibrium (*Neat16* and *Neat18*, see Table S1 in Supplement 2 at www.int-res.com/articles/suppl/m532p001_supp.pdf). Data were generated for between 30 and 50 snails per locality (average of 41.5 across all localities).

Genetic diversity and differentiation

Observed and expected heterozygosity, and total number of alleles were calculated per microsatellite locus and location using ARLEQUIN 3.5 (Excoffier & Lischer 2010). We also calculated the number of private alleles using GENALEX 6.5 (Peakall & Smouse 2012). Pairwise values of F_{ST} (Wright 1965) and Jost's D_{est} (Jost 2008) were estimated between localities, and their significance at $\alpha = 0.05$ was assessed by running 999 permutations in GENALEX. To account for multiple comparisons, the B-Y false discovery rate method (Benjamini & Yekutieli 2001) was applied. Unlike Bonferroni correction (Rice 1989), this approach not only reduces Type I error but also Type II error, and is considered to be more suitable to provide critical values in biological systems (Narum 2006). To determine whether *Nerita atramentosa* comprises multiple regional populations, we used the Bayesian genetic clustering algorithm implemented in STRUCTURE 2.3 (Pritchard et al. 2000). We assumed admixture and that allele frequencies are correlated between populations, and used sampling locations as priors, as this can considerably improve the likelihood that genetic structure is identified when levels of genetic divergence are low (Hubisz et al. 2009). For each value of K (number of clusters, ranging from 1 to 21) we performed 10 independent runs, each with an initial burn-in of 100 000 steps followed by 1000000 Markov chain Monte Carlo iterations. The results of the 10 replicates were clustered using CLUMPP 1.1.2 (Jakobsson & Rosenberg 2007), and the most likely value of K was identified on the basis of having the highest probability (Pritchard et al. 2000).

Spatial autocorrelation

Under dispersal models in which individuals separated by short geographic distances are more closely related to each other than they are to individuals at greater geographic distance, positive spatial autocorrelation should be evident at shorter distances (Peakall et al. 2003). We performed spatial autocorrelation analyses in GENALEX using genetic and geographic distance matrices. The detection of a positive spatial autocorrelation coefficient r (Smouse & Peakall 1999) that is significantly greater than expected under conditions of panmixia at the smallest distance classes is indicative of restricted dispersal (see Supplement 1 at www.int-res.com/articles/suppl/m532p001_supp.pdf for details).

Advection connectivity simulations

To estimate pairwise advection connectivity matrices between sites, we used the Connectivity Modelling System 1.1 (Paris et al. 2013) to integrate virtual Lagrangian particles within the Ocean General Circulation Model For the Earth Simulator (OFES; Masumoto et al. 2004) (see Supplement 1 for details). To visualise how the geographic position of larvae affected their arrival at the coast on a monthly basis, we generated an animation showing the movement of propagules throughout their larval periods. We generated 3 matrices: the first depicted pairwise connectivity among sites; the second depicted the percentage of propagules that remained on the continental shelf throughout their larval phases (i.e. that never reached water with depths of >100 m); and the third showed how many larvae released from a particular site arrived at the coast after completing larval development. Correlations between the latter 2 data sets were compared on a monthly basis by means of Spearman rank correlation tests (Spearman 1904) performed in SigmaStat 1.0 (Systat Software). To understand the role of ocean circulation in the inaccessible GAB, the simulations also included a site from which no samples could be collected (black circle in Fig. 1). The South Australian gulfs were each treated as a single location by merging sampling sites (SG: Sites 7 and 8; GSV: Sites 9 and 10).

Seascape genetics: genetic vs. environmental data

We determined the relative importance of 3 types of environmental parameters on genetic differentiation among sites: geographic distance, thermal gradients in sea surface temperature and ocean circulation. Mantel tests (Mantel 1967) and Multiple Regression on Distance Matrices (MRDM; Manly 1986, Legendre et al. 1994) in FSTAT 2.9.3.2 (Goudet 1995) were used to test for correlations between the environmental data and the genetic data. Mantel tests explore whether there is a correlation between a genetic dis-

tance matrix (in this case using pairwise F_{ST} values as a measure of genetic differentiation) and pairwise matrices of other parameters that may potentially explain genetic patterns. MRDM is a multivariate statistical extension of partial Mantel analyses (Smouse et al. 1986) that uses multiple regression to test for the correlation between a response variable (in this case F_{ST}) and 2 or more explanatory variables. This makes it possible to simultaneously determine statistical significance and to make inferences about the relative importance of each explanatory variable (Lichstein 2007). Oceanographic connectivity data simulated from 1 September to 30 January (austral summer; see Supplement 1) using data from the years 1980 to 2010 were transformed by taking the negative of the natural logarithm of the sum of migrants (i.e. immigrants and emigrants) for each pair of sites. As we generated multiple data sets for temperature and oceanographic connectivity (see previous paragraph), only those data sets were included in the MRDM analyses that explained most of the genetic variation in the Mantel tests. We also analysed correlations between F_{ST} and the explanatory variables for individual months, and performed Mantel tests between matrices of explanatory variables. Significance of all tests was based on 10 000 permutations.

RESULTS

Genetic diversity and differentiation

All microsatellites were polymorphic at all sampled localities. The number of alleles per locus was similar between sites, ranging from 10.3 at Site 4 to 12.2 at Site 20. Observed and expected heterozygosity were high at all sites, with an average of 0.786 and 0.774, respectively. While the number of private alleles (alleles present at a single sampling site) was low, such alleles were found at most of the sites (Table 1).

Overall genetic differentiation was low but significant across the species' range (F_{ST} = 0.006, p < 0.0001). For both F_{ST} and D_{est}, 68 out of 210 pairwise comparisons were significant after correction for multiple tests (Table S2 in Supplement 2 at www.int-res.com/articles/suppl/m532p001_supp.pdf). The majority of significant F_{ST} values involved Sites 1, 15 and 21, i.e. sites at the extremes of the sampling area (Fig. 1). As our results are primarily based on correlations between genetic and environmental data rather than the magnitude of the *F*-statistics themselves, we considered F_{ST} to be adequate for this purpose. STRUCTURE analyses identified $K = 1$ as the most likely number of clusters, even when using sampling location as a prior (Fig. S1 in Supplement 3 at www.int-res.com/articles/suppl/m532p001_supp.pdf), and there was also no support for a higher number of clusters on the basis of bar plots (Fig. S2 in Supplement 3).

Spatial autocorrelation

In correlograms constructed for the entire distribution range of *Nerita atramentosa* using distance classes of 100 km and 1200 km (Fig. 2), we detected significant positive spatial autocorrelation at the lowest geographic distance category (*r* was greater than

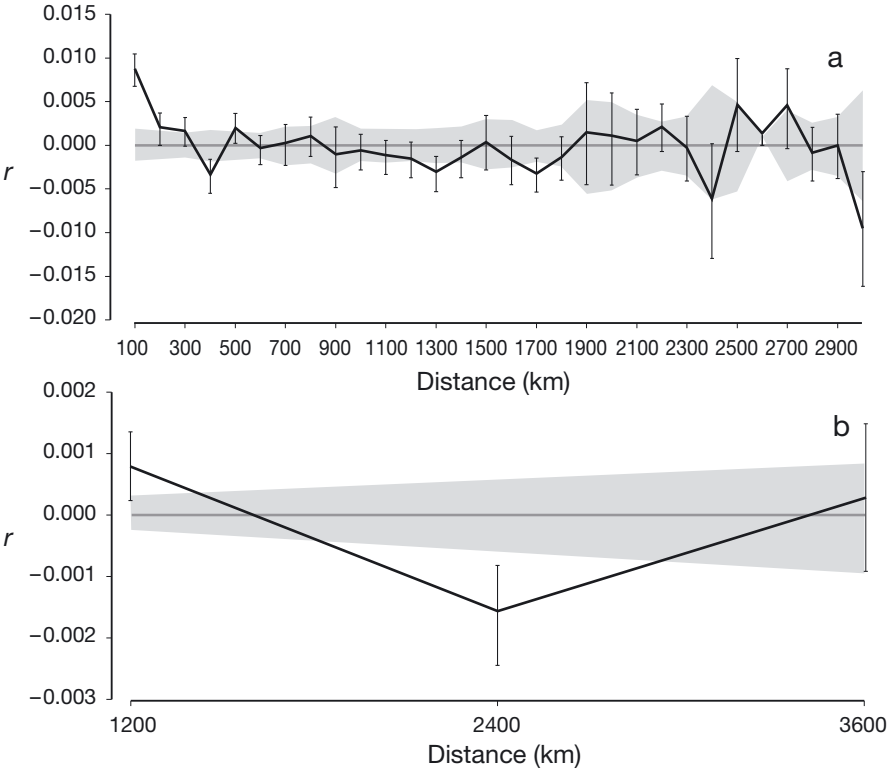

Fig. 2. Correlogram plots depicting the spatial autocorrelation coefficient (*r*) as a function of geographic distance along the entire range of *Nerita atramentosa*, with distance classes at (a) 100 km and (b) 1200 km intervals. The grey area represents 95% confidence intervals under the hypothesis of no autocorrelation, and whiskers represent standard errors of *r*

the upper bound of the null distribution of panmixia, and its 95% confidence intervals represented by error bars did not include zero). This indicates that despite the high dispersal potential of *N. atramentosa*, genetic variation was non-randomly distributed in geographic space at this spatial scale, and that the majority of larvae settled close to their spawning site. The autocorrelation coefficient *r* decreased with increasing distance class size (Fig. S3a in Supplement 3). As isolation by distance (IBD) predicts the presence of spatial autocorrelation (Epperson 1995, Legendre & Fortin 2010), the effect of geographic distance on genetic differentiation is most likely responsible for these departures from the expectations of panmixia. Moreover, *r* decreased rapidly for the smaller distance classes (0–100 to 0–400) and then changed more gradually, stressing the importance of limited dispersal at smaller geographic distances for the larvae. Autocorrelation plots constructed using regional data (Fig. S3b–f in Supplement 3) confirm that departures from the expectations of panmixia are important throughout the region, and thus not merely an artefact of sites that were comparatively distinct from most other sites (Sites 1 and 15; Table S2 in Supplement 2).

Advection connectivity simulations

A map depicting simulations of the direction and magnitude of surface velocity during the spawning season of *Nerita atramentosa* (Fig. 1) clearly depicts the westward boundary flow that characterises much of southern Australia during austral summer (Vaux & Olsen 1961). In addition to the seasonal current reversal from eastward to westward reported by those authors for the eastern south coast (north-westerly flow of the SAC towards the GAB), the model simulated a predominantly westward boundary flow of the LC from the GAB towards Cape Leeuwin, but with strong on-shelf current flow in an eastward direction at the western extreme of the sampled range. On-shelf currents in this region only showed a strong directional pattern in the GAB, where surface flow was westwards.

The advection connectivity model depicting particle dispersal between pairs of sites (Fig. S4 in Supplement 3) showed a pattern of IBD, with greater connectivity between adjacent sites than between more distant localities. Connectivity between sites increased considerably when multiple spawning cycles were considered. An animation of the particle advection simulations (www.int-res.com/articles/suppl/m532p001_supp/; for further information, see Supplement 4 at www.int-res.com/articles/suppl/m532p001_supp.pdf) showed that throughout much of the distribution range of *N. atramentosa*, and during most of austral summer, on-shelf circulation played a greater role in driving gene flow in southern Australia than did the boundary currents. In terms of the arrival of larvae at the coast, 2 major regions were identified. In the west (Sites 1–6), the number of larvae returning to the coast was very low, while at most sites east of Site 6 (with the exception of Sites 18 and 19), it was much higher, especially in South Australia (Fig. 3a). Larval arrival, particularly in the western and southern portions of the sampling range, was clearly linked to whether or not larvae remained on the continental shelf (Fig. 3b). Spearman rank correlation tests performed for monthly settlement success versus the number of larvae that remained on the shelf revealed that these variables were strongly correlated ($p < 0.01$, Table S3 in Supplement 2).

Seascape genetics

By integrating stepping-stone theory (Model 2, Fig. S4 in Supplement 3), advection connectivity increased significantly, even between localities separated by more than 1500 km. For the complete data set, the advection connectivity matrix (number of particle migrants between localities) was significantly positively correlated with genetic differentiation, but so was geographic distance (Table 2). When these 2 variables were tested together using MRDM, neither was significantly correlated with genetic differentiation, a likely artefact of the strong correlation between them (Table S4 in Supplement 2), but this analysis nonetheless showed that at the range-wide scale, coastal distance explained genetic differentiation better than did oceanography.

Analyses of monthly advection connectivity data revealed temporal variability in the importance of oceanography, with the highest correlations between genetic structure and advection connectivity at the beginning and end of the spawning season, and correlations being non-significant during October and November (Table 2). MRDM analyses were congruent (significant correlations between genetic structure and advection connectivity were identified in all months except November). Temperature was a poor predictor of genetic structure, as none of the thermal data matrices were significantly correlated with the genetic data.

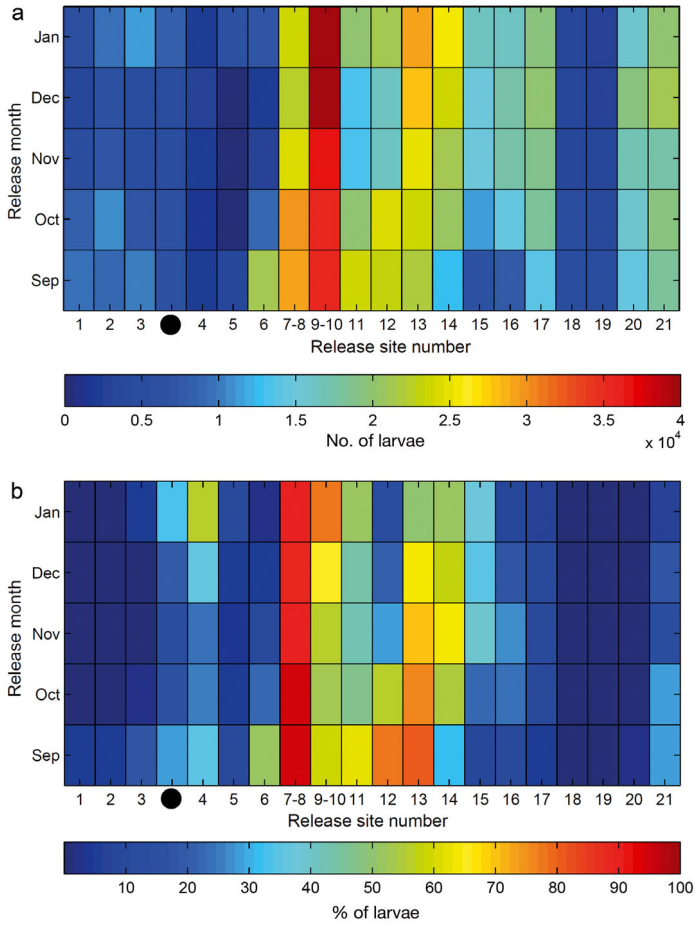

Fig. 3. Arrival of *Nerita atramentosa* propagules at the coast as a consequence of remaining on the continental shelf. (a) number of larvae released during a particular month and from a particular site that returned to the coast after completing larval development. (b) Percentage of larvae released that did not reach temperate Australia's boundary currents (i.e. that never reached water of depth >100 m). The black circle represents an inaccessible site from which no genetic samples were available (see Fig. 1)

DISCUSSION

Nerita atramentosa comprises a single metapopulation that is broadly connected over several previously reported biogeographic disjunctions in the area (Waters et al. 2005, Li et al. 2013). Despite this evidence for large-scale connectivity at evolutionary timescales, the species is not panmictic at ecological timescales. Pairwise genetic differentiation was significantly correlated with geographic distance, and positive spatial autocorrelation (indicating greater-than-random genetic similarity) was evident at shorter distance classes. Overall, these results suggest that many propagules ultimately settle at sites proximal to their natal origins. Limited dispersal of this nature has previously been identified in marine organisms with high dispersal potential (e.g. Pogson et al. 2001, York et al. 2008, Polato et al. 2010, Coleman et al. 2011), but adequate explanations for limited dispersal success in such species have proven elusive. We show that a detailed understanding of coastal oceanographic dynamics (see below) is key to explaining such findings. The understudied but general processes that have driven on-shelf dispersal in *N. atramentosa* are also expected to influence connectivity in other high-dispersal species with planktonic stages. As such, information derived not only from boundary currents but also from patterns of on-shelf circulation need to be considered in genetic studies of connectivity, marine community ecology, fisheries management, and marine reserve design.

Influence of boundary currents versus on-shelf circulation

Our advection connectivity simulations showed that particularly in South Australia, a large proportion of propagules remained on the continental shelf and often close to the coast, and boundary currents that flow along the shelf edge were comparatively less important in facilitating dispersal. Boundary currents are often considered to be key factors in determining the connectivity of coastal populations because of their effects on larval retention and dispersal (e.g. Mitarai et al. 2009, Coleman et al. 2013). However, instead of connecting coastal habitats, they may instead cause the loss of gametes and larvae due to offshore advection (e.g. Hutchings et al. 2002, Zardi et al. 2011, Jackson et al. 2012, Porri et al. 2014). Our simulations show that particularly in the western portion of temperate southern Australia, the fact that many larvae reach the boundary currents results in a drastic reduction in recruitment success, and the same is true off western Tasmania. In contrast, recruitment success is particularly high in South Australia, where most larvae remain on the continental shelf.

Particularly in genetic studies, the role of more variable and often erratic on-shelf transport is often not considered (e.g. Hoskin 2000, Hohenlohe 2004, Coleman et al. 2011, 2013), despite evidence that it is important in connecting coastal biota (Aiken et al. 2007, Teske et al. 2013). Given that the larvae of many coastal species have their highest concentrations within a few kilometres of the shoreline (Cockroft & Wooldridge 1987, Rothlisberg et al. 1995, Porri et al. 2014), meso-scale dispersal in shelf waters

Table 2. Mantel tests and Multiple Regression on Distance Matrices (MRDM) performed on data matrices from *Nerita atramentosa*. For the complete data set, Mantel tests are reported for the correlation between genetic distance (F_{ST}) and 1 of 5 environmental variables, including geographic distance among sites (Coastal distance), the negative ln of advection connectivity (Models 1 and 2), and thermal distance (Summer temperature and Delta temperature). For monthly data sets, only Advection connectivity (Model 2) are shown. MRDM analyses were performed using only the connectivity and thermal data sets that explained most of the genetic variation on the basis of the Mantel test for combined data. See Supplement 1 for details on model parameters. **Bold**: $p < 0.05$

Test Explanatory variable	Correlation	p	Variance explained (%)
September–January			
Mantel test			
Coastal Distance	0.24	**0.001**	5.9
Advection connectivity (Model 1)	0.12	0.133	1.3
Advection connectivity (Model 2)	0.22	**0.003**	4.7
Summer temperature	−0.09	0.245	0.8
Delta temperature	−0.12	0.106	1.5
MRDM			6.6
Coastal distance	0.24	0.160	
Advection connectivity (Model 2)	−0.02	0.722	
Delta temperature	−0.08	0.360	
September			
Mantel test			
Advection connectivity (Model 2)	0.23	**0.002**	5.4
MRDM			6.9
Coastal distance	−0.11	0.140	
Advection connectivity (Model 2)	0.23	**0.004**	
Delta temperature	−0.06	0.395	
October			
Mantel test			
Advection connectivity (Model 2)	0.19	**0.017**	3.5
MRDM			4.8
Coastal distance	−0.09	0.173	
Advection connectivity (Model 2)	0.19	**0.029**	
Delta temperature	−0.06	0.430	
November			
Mantel test			
Advection connectivity (Model 2)	0.16	0.068	3.9
MRDM			3.9
Coastal distance	−0.11	0.146	
Advection connectivity (Model 2)	0.16	0.068	
Delta temperature	−0.05	0.479	
December			
Mantel test			
Advection connectivity (Model 2)	0.22	0.070	4.8
MRDM			5.9
Coastal distance	−0.09	0.206	
Advection connectivity (Model 2)	0.22	**0.012**	
Delta temperature	−0.06	0.476	
January			
Mantel test			
Advection connectivity (Model 2)	0.26	**0.0005**	6.6
MRDM			8.1
Coastal distance	−0.01	0.155	
Advection connectivity (Model 2)	0.26	**0.002**	
Delta temperature	−0.07	0.366	

likely affects a greater proportion of planktonic propagules than do the boundary currents.

The low velocity of the southern Australian boundary currents compared to the EAC was interpreted as being the cause for lower population connectivity in this region, promoting a pattern of IBD as compared to a pattern of chaotic genetic patchiness on the east coast (Coleman et al. 2011, 2013). However, in addition to being weaker than the EAC, southern Australia's boundary currents flow at a considerably greater distance from the coast because in most of this region, the continental shelf is considerably wider than the shelf on the east coast (Fig. S5 in Supplement 3) (Porter-Smith et al. 2004). This suggests that a comparatively smaller proportion of propagules will ever reach the boundary currents, and that the few that do and are dispersed over greater distances may not reach the coast in time to complete larval development. We conclude that the larvae that remained on the continental shelf contributed a considerably greater number of gametes to the next generation, which strongly affected genetic estimates of connectivity.

Comparisons of genetic and environmental data

Seascape genetic approaches represent a way to determine whether low but significant structure among sites along a species' range may be driven by environmental conditions, rather than merely being the result of stochastic processes. For *Nerita atramentosa*, we found that advection connectivity and geographic distance were both strongly correlated with genetic structure (and with each other) when analysing the complete data set, with the MRDM analysis identifying geographic distance as the most important explanatory variable. Monthly data seem contradictory in that they often identified advection connectivity as being more important than genetic distance. It is possible that our models described gene flow poorly when it was mostly facilitated by weak nearshore circulation (particularly during November, the likely peak spawning month), resulting in less support for advection connectivity during this time and, by extension, the whole data set. We used a global scale model that accurately represents the ocean circulation and hence movement of propagules in the open ocean and on the continental slope, but performs more poorly when the propagules stay within the 20 km closest to the coast. To simulate larval movement in this near-shore region and thereby somewhat mitigate the lack of resolution there, we

have used an additional sub-grid scale random-walk diffusion for the particles (e.g. Wood et al. 2013). Given that accurate dynamics close to the shoreline are particularly relevant when studying the settlement of particles at the same site at which they were spawned (which was not done in the present study), the effect of limited resolution in this area is likely minimal.

The assumption that *N. atramentosa* spawns throughout the austral summer is a likely simplification, as spawning in marine organisms typically peaks during some months and is much lower during the remainder of the spawning season (Zastrow et al. 1991). No such data are available for *N. atramentosa*. However, the fact that recruitment success remains fairly constant throughout the spawning season when comparing different sites, as well as the fact that spawning patterns may differ between years (Coombs et al. 2006), suggests that our assumption that spawning occurs throughout summer is reasonable. Our advection connectivity simulations further assumed that the larvae of *N. atramentosa* disperse like passive particles, which at large geographical scales is often an acceptable assumption (McQuaid & Phillips 2000); nonetheless it is possible that incorporating larval behaviour (such as diel vertical migrations, Barile et al. 1994) into the model would result in even stronger correlations between oceanographic and genetic data. However, since so little is known about larval behaviour for *Nerita* spp., it is impossible to incorporate any meaningful behaviour. Furthermore, the most relevant behaviour (for connectivity) happens on small scales near shores (see e.g. Staaterman et al. 2012), while in this model we are dealing with offshore, large-scale dispersion of larvae.

Water temperature is considered to be very important in shaping marine biogeography (Murawski 1993) and, by extension, genetic structure (Briggs & Bowen 2012), but we found no clear evidence for thermal selection playing a role in driving genetic structure along the range inhabited by *N. atramentosa*. Thermal gradients along the temperate southern Australian coast are minimal when compared to conditions in adjacent regions (Wernberg et al. 2013), and the areas dominated by the LC, SAC and ZC are sufficiently connected and homogeneous to be considered a single biogeographic province (Waters et al. 2010).

Implications for MPA design

Marine protected areas are an important tool for limiting the negative effects of anthropogenic activities on the ecological functioning of coastal biotas (Lubchenco et al. 2003, Edgar et al. 2014). Networks of marine reserves rather than large, single reserves are considered to be particularly important for ensuring the long-term persistence of marine communities (Lubchenco et al. 2003). Even though IBD was found in *N. atramentosa*, this species is likely able to maintain a single metapopulation by means of meso-scale dispersal over several spawning cycles. However, the finding that the region's boundary currents contribute comparatively little to dispersing propagules, particularly in South Australia, suggests that population persistence in species with smaller population sizes and lower dispersal potential could be jeopardised when reserves are spaced too far apart. The government of South Australia is currently establishing a network of 19 marine parks, but only 6% of coastal South Australian waters have been proposed as 'sanctuaries' (Government of South Australia 2012). Based on a recent meta-analysis of key features to be considered during marine reserve design (Edgar et al. 2014), it appears that many South Australian sanctuary zones are too small to achieve their desired conservation value. Nonetheless, given that dispersal distances of coastal species in this region can be expected to be comparatively small, the closely spaced proposed sanctuary zones probably represent a reasonable starting point to maintain population connectivity.

CONCLUSIONS

Studies of genetic population structure in coastal organisms often attribute genetic connectivity to dispersal driven by boundary currents (Hoskin 2000, Neethling et al. 2008), with stronger boundary currents having a greater potential of homogenising genetic structure than weaker currents (Coleman et al. 2011). Here, we show that genetic connectivity in a coastal broadcast disperser in much of southern Australia is primarily influenced by on-shelf current flow. A large proportion of planktonic propagules do not reach the region's boundary currents during their spawning season, and many of those that become entrained in the boundary currents do not return to the coast to settle. This demonstrates that a detailed understanding of current flows in the hydrodynamically complex coastal and shelf regions is needed to explain the dispersal of planktonic propagules along continuous coastlines.

Data accessibility. Microsatellite data: Dryad, doi: 10.5061/dryad.n9v91

Acknowledgements. This study was funded by the Australian Research Council (DP110101275 to L.B.B, J.W. and Luciana Möller and DE130101336 to E.v.S). The present article is publication no. 53 of the Molecular Ecology Group for Marine Research (MEGMAR).

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Editorial responsibility: Christine Paetzold, Oldendorf/Luhe, Germany

Submitted: January 8, 2015; Accepted: May 20, 2015
Proofs received from author(s): June 18, 2015