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OCEANIC VARIABILITY AND COASTAL TOPOGRAPHY SHAPE GENETIC STRUCTURE IN A LONG-DISPERSING SEA URCHIN

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Abstract. Understanding the scale of marine population connectivity is critical for the conservation and sustainable management of marine resources. For many marine species adults are benthic and relatively immobile, so patterns of larval dispersal and recruitment provide the key to understanding marine population connectivity. Contrary to previous expectations, recent studies have often detected unexpectedly low dispersal and fine-scale population structure in the sea, leading to a paradigm shift in how marine systems are viewed. Nonetheless, the link between fine-scale marine population structure and the underlying physical and biological processes has not been made. Here we show that patterns of genetic structure and population connectivity in the broadcast-spawning and long-distance dispersing sea urchin *Centrostephanus rodgersii* are influenced by physical oceanographic and geographic variables. Despite weak genetic differentiation and no isolation-by-distance over thousands of kilometers among samples from eastern Australia and northern New Zealand, fine-scale genetic structure was associated with sea surface temperature (SST) variability and geography along the southeastern Australian coast. The zone of high SST variability is characterized by periodic shedding of eddies from the East Australian Current, and we suggest that ocean current circulation may, through its influence on larval transport and recruitment, interact with the genetic consequences of large variance in individual reproductive success to generate patterns of fine-scale patchy genetic structure. If proven consistent across species, our findings suggest that the optimal scale for fisheries management and reserve design should vary among localities in relation to regional oceanographic variability and coastal geography.

Key words: *Centrostephanus rodgersii*; connectivity; genetic patchiness; larval dispersal; microsatellite; multilocus spatial autocorrelation; oceanography; sea urchin.

INTRODUCTION

Understanding the scale of connectivity of marine populations is critical for sustainable fisheries management and reserve design (Palumbi 2004). Recent advances in population genetics and oceanographic particle transport modeling have provided new insights into the scale of larval dispersal and population connectivity in the marine environment (Jones et al. 1999, Swearer et al. 1999, Barber et al. 2002, Kinlan et al. 2005, Cowen et al. 2006). While some studies have confirmed expectations of lack of population structure in long-dispersing species (Kinlan et al. 2005), several others have revealed reduced or infrequent dispersal among marine populations, even over spatial scales of tens of kilometers. Subdivision of marine populations has been detected in the form of sharp breaks due to biogeographic barriers such as ocean currents or upwellings (Barber et al. 2000, Palumbi 2003, Perrin et al. 2004) and as isolation by distance resulting from local larval retention (Beheregaray and Sunnucks 2001,

Palumbi 2003, Taylor and Hellberg 2003, Palumbi 2004). However, while recent genetic studies have described patterns of marine population structure in diverse taxa, the link between the scaling of connectivity and the underlying physical and biological processes remains to be made.

Genetic population studies commonly assume that significant differentiation at neutral markers corresponds to restricted dispersal between geographic localities (Palumbi 2004). However, genetic differentiation in marine organisms has not only a spatial, but an important temporal component. Highly fecund broadcast-spawning species have large variance in reproductive success, resulting in a low effective vs. census population size ratio and genetic differentiation between generations (Hedgecock 1994, Moberg and Burton 2000, Flowers et al. 2002, Levitan 2005, Pujolar et al. 2006). If the rate of recruitment is spatially and temporally variable, fine-scale “patchy” genetic structure is possible even in the absence of restricted dispersal (Johnson et al. 1993). Larval settlement rates in intertidal invertebrates have been shown to be influenced by both the spatial and temporal variability of ocean currents (Connolly and Roughgarden 1999, Connolly et al. 2001, Broitman et al. 2005). Therefore, we hypothesize here that through

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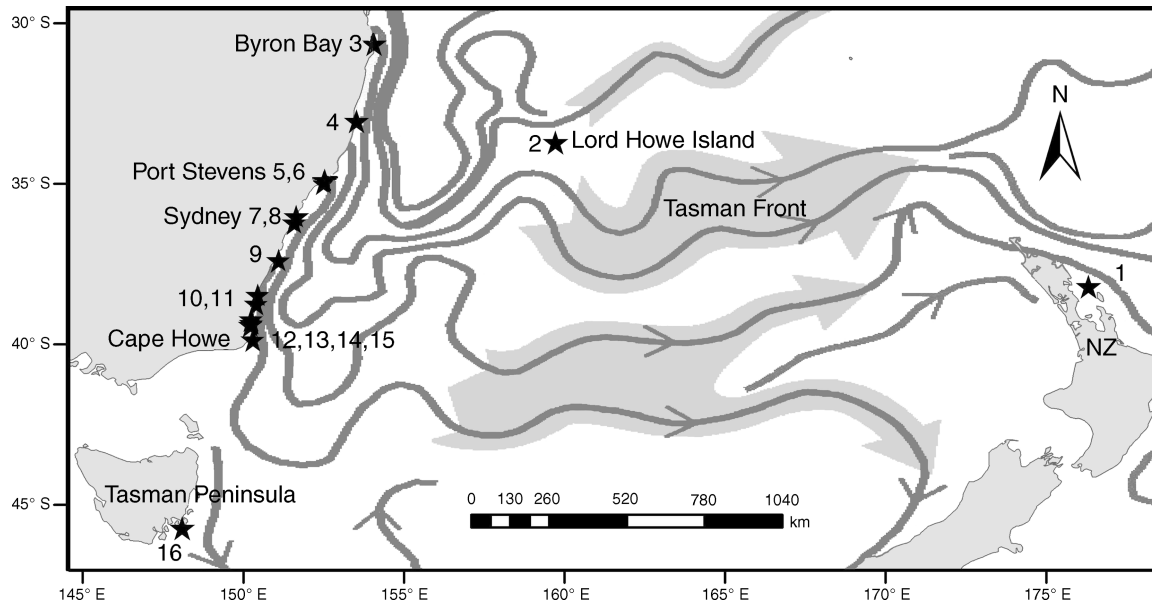


FIG. 1. Map showing *Centrostephanus rodgersii* sampling localities (stars) in relation to a schematic of the surface currents of the Tasman Sea (modified from Ridgway and Dunn [2003]). Numbers next to sampling sites are presented for reference with the F_{ST} matrix (Table 1).

its influence on larval supply and recruitment patterns, ocean current variability can influence the spatial genetic structure of marine populations.

We evaluated this hypothesis by relating the genetic population structure of a broadcast-spawning marine invertebrate against simple measures of ocean current variability, coastal topography, and benthic habitat distribution in southeastern Australian and New Zealand coastal waters. The dominant oceanographic feature of this region is the East Australian Current (EAC), a warm western boundary current that flows southward along the east coast of Australia (Fig. 1). At latitude of $\sim 32^\circ\text{S}$, the EAC turns eastward to flow as the Tasman Front toward New Zealand (Godfrey et al. 1980). This region of separation of the EAC from the Australian coast is characterized by periodic eddy formation (Nilsson and Cresswell 1981). Southward flowing currents may continue as far south as Tasmania, particularly in summer, but are highly variable in strength and direction (Roughan and Middleton 2004). Our target species is the sea urchin *Centrostephanus rodgersii* (see Plate 1), an ecologically important benthic herbivore common on subtidal rocky reefs throughout southeastern Australian and northern New Zealand coastal waters (Fletcher 1987). In New South Wales (NSW), *C. rodgersii* is the dominant benthic herbivore on subtidal rocky reefs. Following a spawning period that occurs in June in northerly populations, and may extend for another 5–6 months in southerly populations (Byrne et al. 1998), the species has a planktonic larval dispersal period of approximately four months and is thus expected to have a long dispersal capability (Huggett et al. 2005). We investigated the broadscale

genetic structure of *C. rodgersii* in relation to the major ocean current patterns in the region and used an information-theoretic approach to identify the physical oceanographic, coastal topographic, and habitat-related influences in fine-scale population structure.

METHODS

Sampling and genotyping

We sampled 16 sea urchin populations in southeastern Australia and northern New Zealand, a sampling effort that essentially covers the entire range of the species (Fig. 1). At each site we collected ~ 25 adult sea urchins (test diameter 50–100 mm) and stored gonad tissue in 95% ethanol (Appendix A). Collections were made between May 2005 and March 2006, a period covering one reproductive season. Therefore, comparisons of spatial patterns detected in different regions could not be biased by substantial recruitment between sampling events. We extracted DNA using a salting-out procedure (Sunnucks and Hales 1996) and genotyped all 413 samples at the six microsatellite loci CRO1-6, CRO2-9, CRO3-4, CRO3-10, CRO3-22, and CRO3-58 (Banks et al. 2007).

Genetic diversity and population structure

We tested for deviations in genotypic patterns from Hardy-Weinberg (H-W) and linkage equilibria using the software GENEPOP 3.4 (Raymond and Rousset 1995). We estimated the genetic diversity within each sampling locality as allelic diversity, allelic richness, and expected and observed heterozygosity using the software FSTAT 2.93 (Goudet 1995). Genetic differentiation among populations (F_{ST}) was estimated by the statistic θ and

tested for significance with 10000 permutations using the software ARLEQUIN 3.01 (Excoffier et al. 2005). To determine whether the level of genetic differentiation between populations followed an isolation by distance (IBD) pattern, we used FSTAT 2.93 (Goudet 1995) to analyze the relationship between pairwise θ and geographic distance, measured as the shortest distance between sites that could be traversed in the marine environment. To assess the robustness of the relationship between genetic differentiation and geographic distance over loci, we jackknifed over loci and populations by manually removing each locus or population sample from the data set and repeating this analysis.

Individual-based analyses of multilocus genotypic arrays from highly variable markers such as microsatellites are likely to be better indicators of fine-scale population structure resulting from contemporary processes than analyses based on allele frequency differentiation among populations (Sunnucks 2000). Therefore, we used multilocus spatial autocorrelation analysis (Smouse and Peakall 1999) to identify the scale of spatial genotypic structure in *C. rogersii* and to assess the influence of oceanographic and geographic variables on genetic structure. We calculated autocorrelation coefficients of multilocus microsatellite genotypes (r) among individuals sampled in the same locality (distance class 0) and among individuals separated by distances binned between the following intervals: 25, 50, 100, 250, 500, 750, 1000, 1500, and 4000 km. The significance of each autocorrelation coefficient was assessed by comparison to the 95% confidence interval of 1000 permutations of the data set involving randomization of the geographic distance matrices by the software GenAlEx 6 (Peakall and Smouse 2006).

Environmental influences on genetic population structure

We used a model selection approach to identify the major oceanographic, coastal topographic, and habitat-related factors influencing the spatial variability of local genotypic autocorrelation values (referred to as “local r ” values: the autocorrelation coefficient at distance class 0 at each sampling site). The variables evaluated related to sea surface temperature (SST) variability, coastal geometry, subtidal habitat distribution, and latitude. The latter was incorporated to test for the presence of any unknown influences with a latitudinal gradient. The data sources and details of the variables are described next.

Sea surface temperature.—SST data were obtained from the 4-km AVHRR Pathfinder version 5.0 SST data set ([available online](#)).⁴ We used the mean monthly SST for July, August, and September from 1990 to 2004 calculated as the focal mean SST over the 4-km cell encompassing the sampling site and the immediately adjacent cells. We used data from July to September as these months are most likely to incorporate the larval

period following the major gamete release events in all populations for the 15 generations prior to sampling (Byrne et al. 1998). Spawning may continue later in more southerly regions (Byrne et al. 1998), so we also repeated the analysis with SST data from July to December. For each site we calculated the mean SST over this period in each year (SSTAV) and the interannual variability, estimated as the standard deviation among the mean values for each year (SSTSD) using GeoTiff files processed in ArcGIS 9 (ESRI, Redlands, California, USA).

Coastal topography.—Coastal topographic variables were measured in ArcGIS 9 from vector GIS layers including the Geodata Coast 100K 2004 data set (Geoscience, Australia; [available online](#)).⁵ The coastal topographic variables included the length of the coastline (CL₂₀) and the area of land (LA₂₀) within a 20 km radius of each sampling locality. The combination of these variables enabled a simplistic numerical representation of the geography of the coastline surrounding the sampling localities. Straight coastlines had low CL₂₀ values; promontories, headlands, or bays had higher values and were distinguished by the LA₂₀ variable, which was higher for enclosed bay sites and lower for promontories.

Benthic habitat distribution.—Benthic habitat distribution for *C. rogersii* was represented by the area of subtidal rocky reef within a 20 km radius (RR₂₀). While we do not have specific data on *C. rogersii* distribution and abundance throughout the sampling range, the species is very common on rocky reef habitat in this region. Therefore, at a very broad scale, we considered subtidal rocky reef data to be a reasonable proxy for *C. rogersii* habitat distribution. Subtidal reef habitat coverage was estimated from a variety of GIS sources including the NSW Nearreef V5 nearshore seabed mapping data set (NSW Department of Environment and Climate Change, *unpublished data*), aerial orthophotos of Lord Howe Island (NSW Department of Environment and Climate Change, *unpublished data*), and preliminary data from the SeaMap Tasmania project (Barrett et al. 2001; [available online](#)).⁶

For the model selection analysis, the CL₂₀ and RR₂₀ variables were log₁₀- and square-root transformed, respectively. All independent variables were standardized to a mean of zero and standard deviation of one. The log-likelihoods and R^2 values of the linear models containing all possible combinations of the oceanographic, topographic, and habitat-related variables to explain the observed variation in local r values were estimated using the all.regs function of the hier.part package implemented in the software R 2.3.1 ([available online](#)).⁷ The best models were selected according to Akaike's Information Criterion corrected for small

⁵ (<http://www.ga.gov.au/meta/ANZCW0703006621.html>)

⁶ (<http://www.utas.edu.au/tafi/seamap/>)

⁷ (cran.r-project.org)

⁴ (www.nodc.noaa.gov/sog/pathfinder4km)

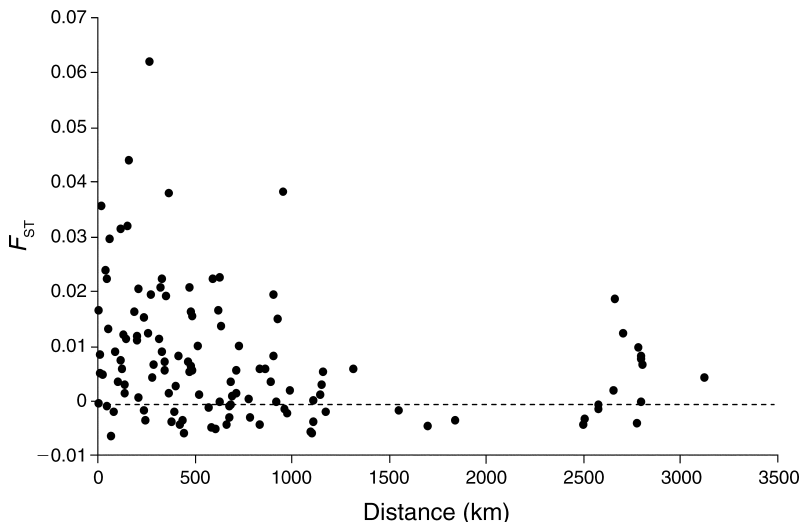


FIG. 2. Scatterplot showing the negative isolation by distance relationship between pairwise genetic differentiation (F_{ST}) and geographic distance (km) between *Centrostephanus rodgersii* sampling localities.

sample size (AIC_c; Burnham and Anderson 2002). The independent contribution of each variable to the variation in local r was estimated by hierarchical partitioning. Regression models were fitted in R 2.3.1 (see footnote 7).

RESULTS

Genetic diversity and population structure

We detected no consistently significant patterns of linkage disequilibrium (LD) at any locus pairs across populations (2% of comparisons were significant at the 5% level). On average, no locus showed consistent deviations from H-W expected genotype frequencies across populations (average $F_{IS} = -0.022$). However, trends in heterozygote proportions were associated with population structure as discussed later. Summary statistics presented in Appendix A reveal similar levels of

genetic diversity throughout the sampled range of the species. As predicted by the species' long planktonic larval duration (Byrne et al. 1998, Huggett et al. 2005), genetic differentiation among populations was very weak but significant ($\theta [F_{ST}] = 0.008, P < 0.001$), even when the geographically isolated New Zealand sample was excluded ($\theta = 0.008, P < 0.001$). However, our analysis of the spatial pattern of genetic differentiation among *C. rodgersii* sampling localities revealed a highly unexpected result. There was a significant negative relationship ($R^2 = 0.07, P = 0.0051$) between genetic differentiation and marine geographic distance between sampling sites (Fig. 2). This means that neighboring populations are, on average, more genetically differentiated than geographically distant ones. Jackknifing over loci and populations revealed this pattern to be robust, and not driven by outlying samples or loci (Appendix B; Appendix C for Australian sites only). The negative correlation between θ

TABLE 1. Pairwise F_{ST} (θ) values among *Centrostephanus rodgersii* samples from 16 localities in southeastern Australia and northern New Zealand. The θ values marked * and ** are significant at the 5% and 1% levels, respectively.

	1 (NZ)	2 (Lord Howe)	3 (NSW)	4 (NSW)	5 (NSW)	6 (NSW)	7 (NSW)	8 (NSW)	9 (NSW)
2 (Lord Howe)	0.000								
3 (NSW)	0.000	0.000							
4 (NSW)	0.000	0.000	0.000						
5 (NSW)	0.000	0.000	0.000	0.022*					
6 (NSW)	0.000	0.000	0.000	0.001	0.000				
7 (NSW)	0.003	0.007	0.000	0.010	0.005	0.023			
8 (NSW)	0.037*	0.039**	0.042*	0.002	0.084**	0.059**	0.070**		
9 (NSW)	0.025*	0.003	0.011	0.011	0.008	0.037*	0.003	0.063**	
10 (NSW)	0.000	0.000	0.000	0.000	0.005	0.000	0.024*	0.030*	0.015
11 (NSW)	0.018	0.000	0.011	0.041**	0.000	0.015	0.012	0.114**	0.022*
12 (NSW)	0.015	0.002	0.015	0.000	0.039**	0.013	0.043**	0.022	0.032*
13 (NSW)	0.000	0.005	0.000	0.006	0.011	0.009	0.013	0.039**	0.022*
14 (NSW)	0.013	0.010	0.028*	0.001	0.030**	0.030*	0.036**	0.018	0.040**
15 (NSW)	0.016	0.000	0.000	0.019	0.001	0.019	0.000	0.074**	0.000
16 (TAS)	0.008	0.000	0.000	0.011	0.000	0.000	0.000	0.074**	0.011

Note: Sites 5 and 6 are in the vicinity of the East Australian Current (EAC) separation point and sites 7–16 are south of this point.

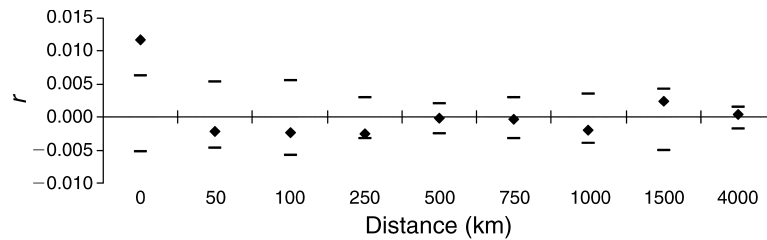


FIG. 3. Multilocus spatial autocorrelation analysis based on all 413 *Centrostephanus rodgersii* samples. Autocorrelation r values (diamonds) are presented in relation to the 95% confidence limits (horizontal lines) based on 999 random permutations of the data. Geographic distances presented are the maximum distance of each class.

and geographic distance is shaped by relatively high θ between neighboring populations along the Australian mainland coast south of the EAC separation point (Table 1). In fact, 23 of the 55 pairwise θ values among sites in this region revealed significant genetic differentiation, even among populations separated by as little as 8 km (mean $\theta = 0.025$). In contrast, no population pairs north of Port Stephens (latitude 32.7°S, close to the EAC separation point) and east to New Zealand showed significant genetic differentiation, even over geographic distances >3000 km (mean $\theta = 0.002$).

Spatial autocorrelation analysis of individual microsatellite genotypes revealed significant positive autocorrelation (i.e., greater-than-random genetic similarity) among individuals sampled at the same locality (local $r = 0.012$, $P = 0.001$) but no spatial autocorrelation among individuals sampled in different localities, from 25 km to >3000 km apart (Fig. 3). However, there was variation between sites in the magnitude of local r values, which were not significant at all sites (Fig. 4). Greater-than-random genetic similarity among individuals within a site by default suggests differentiation from other sites, thereby explaining geographic concordance between the allelic (F_{ST}) and genotypic (spatial autocorrelation) results in that the location of significant genetic structure

among *C. rodgersii* samples along the Australian coast was restricted to the southernmost mainland sampling localities. We conducted linear regression analyses to determine whether the degree of positive genotypic autocorrelation among individuals within a site was associated with LD among loci or deviations from H-W expected genotype proportions. No relationship was detected for LD ($R^2 = 0.051$, $P = 0.392$). However, over five of the loci used (CRO1-6, CRO2-9, CRO3-4, CRO3-10, and CRO3-22) we detected an association between local r and heterozygote excess. The relationship between local r and average F_{IS} over these loci ($R^2 = 0.452$, $P = 0.004$) demonstrates an increase in the proportion of heterozygotes with positive local r (Appendix D).

Environmental influences on genetic population structure

The temporal analysis of satellite SST data revealed a zone of high interannual SST variability off the southern Australian coast, south of the point of separation of the EAC from the coastline (Figs. 4 and 5). Along with the measure of coastline complexity (CL_{20}), this interannual variability in SST (SSTSD) was a component of the best regression model to explain the strength of local genotypic autocorrelation throughout the species' range (Table 2). Local r values were stronger at sites with more interannual variability in SST and more complex surrounding coastlines (Table 2, Fig. 4). The support for the best model (SSTSD and CL_{20}) was only marginally stronger than that for the model incorporating SSTSD alone (evidence ratio calculated from AIC_c model weights = 1.2). However, support for subsequently ranked models was poorer, with the evidence ratio for the best model compared to the third (CL_{20}) and null models being 3.57 and 3.60, respectively. Hierarchical partitioning revealed that of the variance in r values explained by the models, SSTSD accounted for 61% and CL_{20} for 26%. The importance of ocean current variability as an influence on fine-scale genetic structure can be deduced from Fig. 4, which shows that the distribution of significant local r values coincides well with a region of extremely high SST variability along the far southeastern mainland Australian coast. The other variables evaluated, including the area of land surrounding the sampling site (LA_{20}), mean SST (SSTAV),

TABLE 1. Extended.

10 (NSW)	11 (NSW)	12 (NSW)	13 (NSW)	14 (NSW)	15 (NSW)
0.008					
0.000	0.041**				
0.000	0.024*	0.009			
0.016	0.054**	0.016	0.030*		
0.011	0.007	0.025*	0.000	0.045**	
0.002	0.000	0.026*	0.000	0.031*	0.000

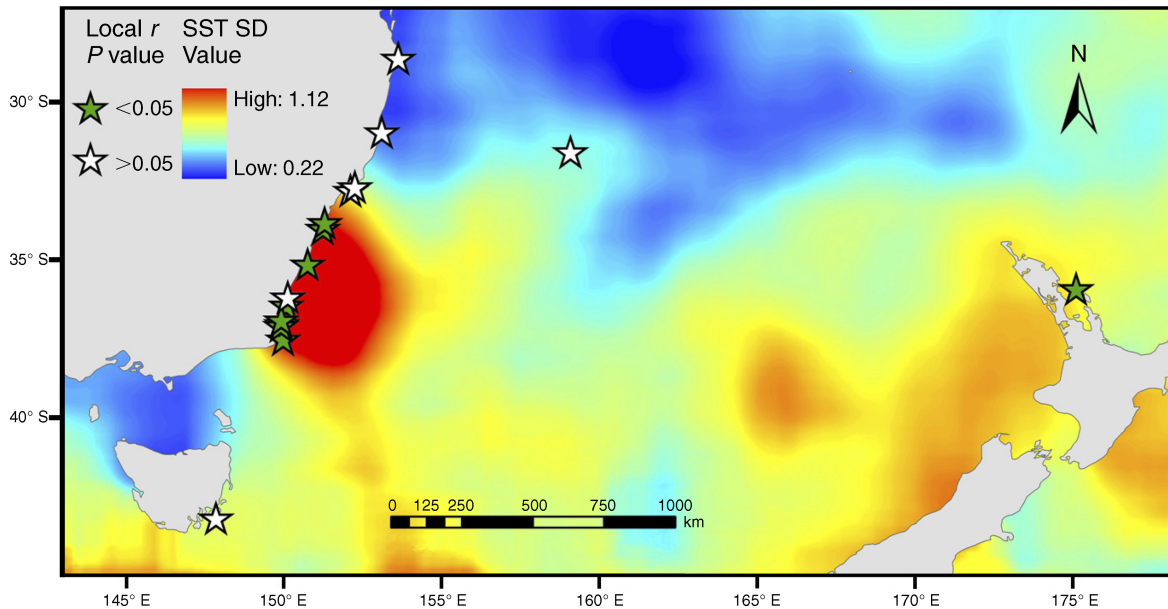


FIG. 4. Map showing the significance of local genotypic autocorrelation (local r : green, significant; white, nonsignificant) among microsatellite genotypes of *Centrostephanus rogersii* sampled in eastern Australia and northern New Zealand in relation to the oceanographic distribution of interannual sea surface temperature variability in degrees Celsius (SST SD) during the *C. rogersii* larval period (July–September) from 1990 to 2004.

benthic habitat variability (RR_{20}), and latitude, were not important predictors of local r values, accounting for a combined total of only 13% of the variance and not contributing to models highly ranked according to AIC_c . The results of the model selection analysis were identical when repeated with SST data collected over a longer duration within years (July to December): the same models were ranked highest by AIC_c and explained a similar proportion of the variance in the local r data [$R^2(\text{SSTSD} + CL_{20}) = 0.35$; $R^2(\text{SSTSD}) = 0.17$, $\Delta AIC_c = 0.78$].

DISCUSSION

Our results demonstrate an association between physical oceanography, coastal geography, and marine genetic population structure. The influence of these physical variables on fine-scale genetic structure in a species that can clearly disperse over great distances is a striking result. The lack of any significant allelic or genotypic structure over thousands of kilometers in populations north of the separation of the EAC from the Australian coast and east to New Zealand is consistent

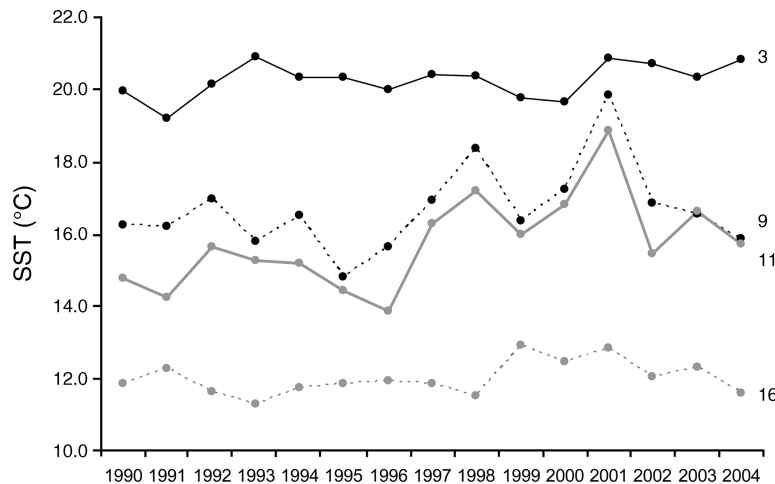


FIG. 5. Satellite sea surface temperature (SST) data averaged from July, August, and September from 1990 to 2004 at four of the *Centrostephanus rogersii* sampling sites along the east Australian coast: Byron Bay (3), Jervis Bay (9), Bermagui (11), and Tasman Peninsula (16). See Fig. 1 for site locations.

TABLE 2. Models of oceanographic, coastal topographic, and habitat-related variables to explain the spatial pattern of fine-scale genetic structure (local r values) among *Centrostephanus rodgersii* sampling sites.

Model rank	Variables							Log-likelihood	AIC _c	ΔAIC _c	R ²
	SSTSD	(log)CL ₂₀	$\sqrt{RR_{20}}$	LA ₂₀	SSTAV	Latitude	Intercept				
1	0.012	0.009					0.013	41.79	-75.59	0	0.370
2	0.011						0.013	40.09	-75.24	0.35	0.214
3		0.007					0.013	38.98	-73.04	2.55	0.099
4 (null)							0.013	37.65	-73.02	2.57	0
64 (full)	0.012	0.012	-0.001	-0.004	0.002	-0.001	0.013	41.97	-55.95	19.64	0.380
HP %IC	61.20	26.53	2.12	4.94	2.22	3.00					

Notes: Models are ranked by Akaike's Information Criterion corrected for small sample size (AIC_c) and the coefficients and R² values for the fitted models are presented. SSTAV and SSTSD represent the sea surface temperature (SST) average and interannual variability (standard deviation) for July–September from 1990 to 2004. CL₂₀, LA₂₀, and RR₂₀ are, respectively, the length of coastline, area of land, and area of subtidal rocky reef within a 20-km radius of each sampling site. All variables were standardized such that the mean and standard deviation equaled 0 and 1, respectively. The independent contribution of each variable to the variance in local r values explained by the models evaluated is presented as a percentage (HP %IC; "HP" denotes hierarchical partitioning).

with very long distance dispersal, as predicted by the species larval duration of at least three months (Huggett et al. 2005). This contrasts with the strong differentiation among local populations in a region of high interannual SST variability along the far southeastern Australian mainland coast. Jackknifing over loci and sampled populations revealed this pattern to be statistically robust and not driven by outlying loci or samples, thereby providing strong support for our results as a real biological phenomenon and not an artifact of sampling error in the data.

The first major question arising from our findings is how fine-scale genetic structure is generated in the absence of larger-scale differentiation. A common biological explanation for fine-scale genetic structure is restricted dispersal relative to the scale of sampling (Peakall et al. 2003). However, restricted dispersal is expected to result in a genetic isolation by distance pattern, or at least gradually weakening autocorrelation among neighboring samples (Bohonak 1999, Peakall et al. 2003). This was not observed in *C. rodgersii*. Similar patterns have previously been detected on a smaller scale in other marine invertebrates (Johnson and Black 1984, Johnson et al. 1993). These patterns are hypothesized to be due to large variance in individual reproductive success in highly fecund species, such that in any reproductive event only a small fraction of adults in a local population effectively contributes to the next generation (Hedgecock 1994). This can result in within-cohort spatial genetic patchiness, for instance due to cohesion of groups of genetically similar planktonic larvae (Johnson et al. 1993). Further, temporal variation in reproductive success among individuals may cause genetic differentiation among generations (Hedgecock 1994, Moberg and Burton 2000, Flowers et al. 2002, Levitan 2005, Pujolar et al. 2006), resulting in local patchy genetic structure if recruitment is spatially variable between locations. According to this hypothesis, we do not necessarily expect to observe stronger genetic structure over a larger scale (e.g., Johnson and Black 1984, Johnson et al. 1993) as

population connectivity may still be maintained by long-dispersing planktonic larvae. Our data are consistent with this "patchiness" hypothesis for two reasons. First, the significant association between positive local r and heterozygote excess suggests a very low effective (N_e) to census (N) population size ratio. Large variance in reproductive success among individuals can generate heterozygosity excess because allele frequencies differ between sperm and eggs when the effective number of breeders is small (Pudovkin et al. 1996, Luikart and Cornuet 1999, Addison and Hart 2005). The correlation between positive local r and heterozygote excess in *C. rodgersii* is consistent with this hypothesis in that where the N_e/N ratio within a population is small we expect the offspring generation to be characterized by increased genetic relatedness (measured as local r) among individuals and increased heterozygosity within genotypes. Second, where fine-scale structure was detected it was due to genetic similarity among individuals within sampling sites (significant positive local r) but showed no spatial pattern on a larger scale.

In *C. rodgersii* the pattern of fine-scale patchy genetic structure was unusual in being restricted to a specific region within the species' distribution. This allowed us to identify physical variables associated with this pattern. Our model selection analysis linked the presence of fine-scale genetic structure (local r : indicating genetic similarity among individuals within a sample) to coastal topography and interannual variability in SST. Of these physical factors, SST variability explained a greater proportion of the data. Because genetic structure is the end product of a range of interacting life history attributes and environmental factors, at this stage we cannot conclusively identify specific mechanisms by which SST variability, or its underlying causative factors, interacts with *C. rodgersii* larval ecology to produce the observed pattern of genetic structure. However, we propose the following hypothesis. First, the oceanographic influence on local genotypic structure relates to the temporal variability in SST, as opposed to absolute SST values or some other factor with a purely

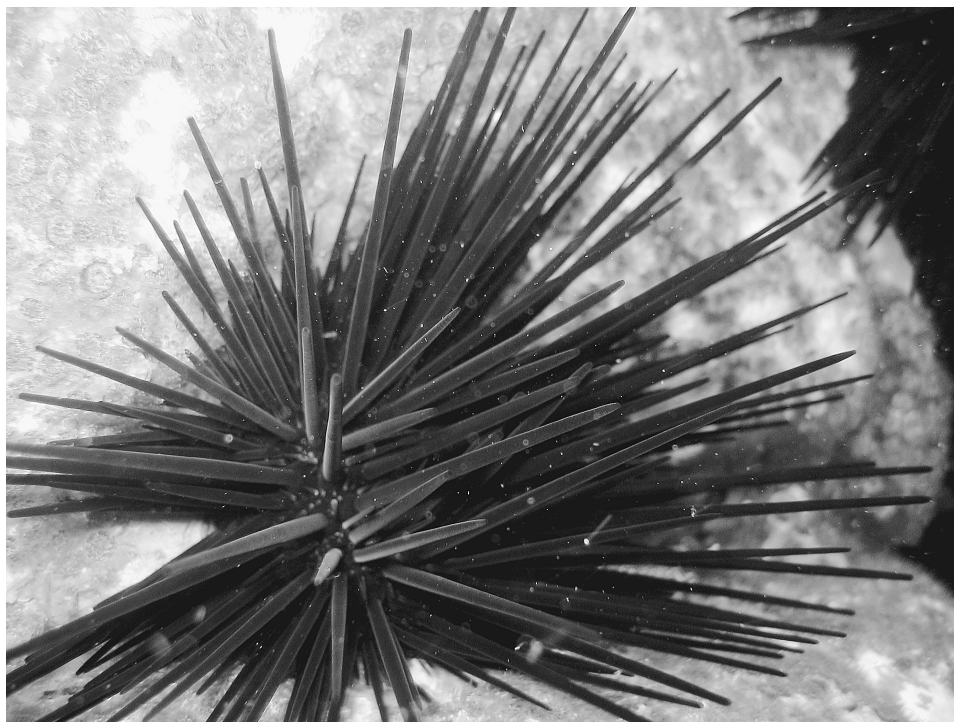


PLATE 1. *Centrostephanus rogersii* photographed near Eden, southern New South Wales, Australia. *C. rogersii* is the dominant benthic herbivore in shallow rocky reef habitat in this region. Photo credit: U. Bové.

latitudinal gradient. No other obvious influences on genetic structure, such as biogeographic barriers, are known in this region (Waters et al. 2005). The temporal SST variability associated with local genotypic structure in *C. rogersii* is most likely representative of frequent eddy formation at the EAC separation point at 32°S (Nilsson and Cresswell 1981). Feron (1995) identified a periodicity in eddy shedding in this region of ~130 days. These eddies generally coalesce with the EAC or move southward. High variability in SST, as well as oceanographic parameters relating to stirring and horizontal dispersal, has previously been identified in this region (Walker and Wilkin 1998, Waugh et al. 2006). Assuming that the temporal variability in SST is caused by ocean current variability due to the periodic shedding and southward movement of warm water eddies from the EAC separation point, it is plausible that patterns of larval transport and therefore recruitment in long-dispersing species are temporally and spatially variable in this region due to highly variable circulation. In this manner, ocean current circulation may interact with the genetic consequences of large variance in individual reproductive success to generate patterns of fine-scale genetic structure. Whether current variability directly affects the N_e/N ratio to produce the observed fine-scale structure and heterozygosity excess is unclear. However, the observed pattern could still be generated if the N_e/N ratio is consistently low throughout all populations but recruitment is more stochastic in areas of current

circulation variability. Populations in such areas may comprise fewer cohorts such that within-cohort patterns of heterozygote excess and elevated relatedness are more detectable over the sampled population than at sites where the population comprises a more even spread of generations due to more reliable recruitment patterns.

In addition to SST variability, we found that a measure of coastline geometry (the length of coastline within a 20 km radius) influenced fine-scale genetic structure. It is likely that this factor also affects local patterns of larval dispersal and settlement by influencing along-shore currents and local flushing times. In this study, the sites with the highest genotypic autocorrelation local r values were within relatively enclosed bays that may be relatively isolated in an oceanographic sense (Botany Bay in Sydney; Jervis Bay and Twofold Bay in southern New South Wales). Further, longer flushing times of such embayments may facilitate a higher degree of larval retention.

Our findings demonstrate that on a regional scale, what were previously considered random patterns of “chaotic genetic patchiness” of larval-dispersing marine organisms are influenced by underlying physical oceanographic and geographic processes. For *C. rogersii* we propose a biologically plausible mechanism for the interaction of these physical processes with reproductive ecology, larval dispersal, and recruitment. However, further comparative studies among taxa with common and contrasting life history strategies will be valuable in

resolving the importance of physical influences such as regional oceanography, coastal geography, and marine habitat distribution on life history attributes such as dispersal. With this aim we are currently conducting a comparative study of genetic structure in this region of a broad range of taxa with contrasting dispersal strategies.

If proven to be general, our findings have implications for marine community ecology, fisheries management, and marine reserve design strategies. Recruitment rates can influence marine community dynamics (Booth and Brosnan 1995), and our results show the potential for regional differences in population processes due to oceanographic variability. In relation to marine resource management, a "spatial bet-hedging" approach has been recommended where chaotic genetic patchiness exists as a result of stochastic recruitment (Larson and Julian 1999). In regions of spatially and temporally variable recruitment rates, management actions may need to be on a larger spatial scale to ensure reliable recruitment within the area. If similar patterns of spatial genetic structure are detected in other marine taxa in this region, it would suggest that the optimal scale for marine reserve design and fisheries management should vary along the coastline in relation to regional oceanographic variability. The approach we have used also holds promise for the incorporation of genetic considerations into marine reserve design strategies. Management criteria commonly incorporate genetic diversity and population connectivity (Australian and New Zealand Environment and Conservation Council Taskforce on Marine Protected Areas 1998); however, these are in practice rarely included in management decisions due to the data being unavailable or difficult to interpret. An improved understanding of how patterns of genetic structure and population connectivity are influenced by physical variables should enable model based predictions of regional population genetic patterns to inform management and conservation decisions.

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APPENDIX A

Centrostephanus rodgersii sampling site data and genetic summary statistics (*Ecological Archives* E088-190-A1).

APPENDIX B

Jackknifing over loci and populations to establish the robustness of the negative isolation-by-distance relationship between F_{ST} and geographic distance between *Centrostephanus rodgersii* samples (*Ecological Archives* E088-190-A2).

APPENDIX C

Scatterplot showing the negative relationship between pairwise genetic differentiation (F_{ST}) and geographic distance (km) between *Centrostephanus rodgersii* sampled in Australia (*Ecological Archives* E088-190-A3).

APPENDIX D

Scatterplot showing the significant negative relationship between local r values and F_{IS} within sampled populations of *Centrostephanus rodgersii* (*Ecological Archives* E088-190-A4).