Spatial scales of genetic patchiness in the western rock lobster *Panulirus cygnus*

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ABSTRACT: In planktonic dispersers, impediments to dispersal, local selection or large variance in the reproductive success among individuals (sweepstakes reproductive success) can create genetic heterogeneity at local scales. While these processes are well recognized, relatively few studies have investigated the spatial scales over which genetic heterogeneity occurs and how it is distributed across species' ranges. We investigate population structure in the western rock lobster *Panulirus cygnus*, a commercially exploited species found in shallow and deep-water reef habitats along the Western Australia coastline. We screened 631 individuals from 9 locations across the species' range for genetic variation at 22 microsatellite loci. Consistent with expectations of extensive larval mixing during an extended planktonic stage, we found no significant genetic differentiation among locations ($F_{ST} = 0.003$, $G''_{ST} = 0.007$). Despite the lack of large-scale geographic structure, small but significant positive spatial autocorrelation (SA) was detected over distances up to 40 km. Two-dimensional local SA analysis confirmed that fine-scale genetic heterogeneity was common throughout the species' range. An intriguing aspect of these results is that SA was based on juvenile and adult lobsters, suggesting restricted movement or spatial cohesion of individuals after settlement.

KEY WORDS: Western rock lobster · Genetic variation · Microsatellites · Population structure · Sweepstakes reproductive success

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INTRODUCTION

The spatial extent of genetic structure is largely dependent on the dispersal capacity of individuals (Bohonak 1999). This is especially apparent in the marine environment, where species with planktotrophic larvae that spend months in the water column tend to maintain low levels of genetic structure across large geographic scales, while those with short planktotrophic larval phases or direct developers usually have much higher levels of subdivision (Waples 1987, Palumbi 1994). However, the role of dispersal capacity in structuring marine populations is complex, and can be strongly influenced by other factors. For example, in spiny lobsters, most species are characterized by a lack of genetic differentiation among localities, consistent with their high dispersal capability during an extended planktonic larval stage (e.g. Ovenden et al. 1992, Silberman et al. 1994, Tolley et al. 2005, García-Rodríguez & Perez-Enriquez 2008, Naro-Maciel et al. 2011). In contrast, barriers to dispersal created by topographic or oceanographic features can lead to moderate to high levels of population structure in some species (Perez-Enriquez et al. 2001, Gopal et al. 2006, Palero et al. 2008).

Impediments to dispersal are not always obvious. For example, Johnson & Black (2006) showed that over short distances (<2 km), genetic subdivision increased fivefold between populations on different islands compared to different populations on the same island in both a direct developing snail and a planktonic disperser. Such genetic heterogeneity at local scales can occur even when there is little genetic subdivision over large distances (e.g. Hedgecock 1986, Benzie & Stoddart 1992, Johnson et al. 1993, Ayre & Hughes 2000). Adaptation to local environments (e.g. low salinity or temperature) can also lead to genetic differentiation at loci under selection and linked neutral loci despite high levels of gene flow (see Nielsen et al. 2009). The extent of population structure can therefore vary considerably among species and is not always determined by life-history characteristics alone. For commercially exploited species, failure to detect underlying population structure is a concern, because it may result in over-exploitation and depletion of localized subpopulations with a corresponding loss of genetic variation (Carvalho & Hauser 1994, Begg et al. 1999).

The western rock lobster *Panulirus cygnus* (Decapoda: Palinuridae) is found in shallow and deep-water reef habitats along the Western Australia coastline from Cape Leeuwin (34° 22′ S) to North West Cape (21° 45′ S). It supports one of the most economically important single species fisheries in Australia, with an annual commercial catch of between 8000 and 14 500 t until recently (Fletcher et al. 2005). A key assumption underlying the management of *P. cygnus* is that the breeding stock comprises a single, demographically united population. This assumption is based on the extended pelagic larval stage of *P. cygnus*, which is thought to ensure high dispersal throughout the species' range. Larvae hatch in spring and early summer, and spend the next 9 to 11 mo in the plankton, with mid stages being found up to 1500 km offshore. The late-stage larvae metamorphose into pueruli and swim inshore to start the juvenile stage of their life-cycle (Phillips et al. 1979). Allozyme studies also suggest *P. cygnus* is a single panmictic population, but with ephemeral genetic patchiness (small-scale genetic heterogeneity among local populations) caused by temporal variation in allele frequencies of recruits (Thompson et al. 1996, Johnson & Wernham 1999). *P. cygnus* therefore represents an extreme model for testing for subtle fine-scale genetic structure over a large geographic range. The aim of this study was to investigate the spatial scale of genetic patchiness in juvenile and adult *P. cygnus* across the main geographic

distribution of the species. To achieve a resolution beyond previous genetic studies, we sampled at finer spatial scales, and used 22 microsatellite loci for our study. Microsatellites have proven to be a powerful tool for detecting genetic subdivision within marine species with high larval dispersal capabilities (e.g. Knutsen et al. 2003, Riccioni et al. 2010, White et al. 2010) and have revealed spatial genetic structure on finer scales than found with allozymes or mtDNA (e.g. Ruzzante et al. 1996, Jørgensen et al. 2005).

MATERIALS AND METHODS

Sample collection

In 2009, tissue samples were collected from juvenile and adult *Panulirus cygnus* (carapace length >45 mm) at 9 locations spanning nearly 660 km along the Western Australian coastline (Fig. 1). A total of 631 individuals were captured using commercial lobster pots set over distances up to 27.4 km apart within each location. Sample sizes at each location ranged between 19 and 64 individuals. To allow investigation of fine-scale patterns within the Houtman Abrolhos Islands, samples were collected from an additional 7 sites (HAI 2–HAI 8; i.e. 8 sites in total) between 4 and 82 km apart (sample sizes ranged between 40 and 68 ind.). The spatial coordinates for each individual were recorded at the time of capture.
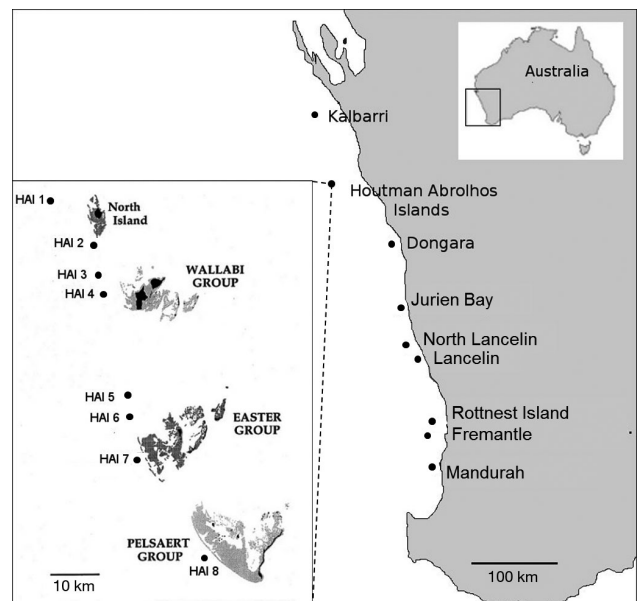

Fig. 1. *Panulirus cygnus*. Samples were collected at 9 locations along the south-west Australian coastline and 8 sites among the Houtman Abrolhos Islands

DNA extraction and microsatellite genotyping

DNA was extracted from the middle lobe of the tail fan stored in 100% ethanol, using a QIAGEN DNeasy Blood and Tissue kit, following the manufacturer's recommendations. After the DNA was extracted, each sample was analysed using a NanoDrop ND-1000 spectrophotometer to determine the concentration and quality of the DNA. All DNA samples were stored at –20°C until genotyping. Genotypes at 22 microsatellite loci (S3, S8, S28, S50, W25, Pcyg1–9 and Pcyg11–18) were determined for each individual using primers and PCR running conditions described in Groth et al. (2009) and Kennington et al. (2010). PCR products were analyzed on an ABI 3700 sequencer using a GeneScan-500 LIZ internal size standard and scored using GENEMARKER (SoftGenetics).

Data analysis

Microsatellite variation at each location was quantified by calculating allelic richness (a measure of the number of alleles weighted for sample size) and Nei's (1987) estimator of gene diversity. The presence of null alleles was tested for each population and locus using MICROCHECKER (van Oosterhout et al. 2004). Tests for a deficit or excess in heterozygotes at each location were carried out using randomisation tests, and the results were characterized using the F_{IS} statistic (inbreeding coefficient). Significantly positive F_{IS} values indicate a deficit of heterozygotes relative to random mating, and negative values indicate an excess of heterozygotes. The linkage disequilibrium between each pair of loci was assessed by testing the significance of the association between genotypes. Corrections for multiple comparisons were carried out using the sequential Bonferroni method (Rice 1989).

Genetic differentiation among locations was assessed by calculating Weir & Cockerham's (1984) estimator of F_{ST} and G''_{ST}, a version of Hedrick's (2005) standardized G_{ST} corrected for bias when the number of populations is small (Meirmans & Hedrick 2011). Microsatellite R_{ST} values (Slatkin 1995) were also calculated, but were qualitatively similar to F_{ST} values so are not reported. Tests for genetic differentiation were performed by permuting genotypes among samples. Estimates of allelic richness, gene diversity, F_{IS}, deficits in heterozygotes and linkage disequilibrium were calculated using FSTAT v. 2.9.3 (Goudet 2002). Estimates of F_{ST}, G''_{ST} and tests for genetic differentiation using were performed in GENALEX v. 6 (Peakall & Smouse 2005). Differences in

estimates of genetic variation and F_{IS} among locations were tested using Friedman's ANOVA. To test for a relationship between genetic and geographical distance, we compared a matrix of G''_{ST} with a matrix of geographical distance (ln km), using a Mantel test with 10 000 permutations.

Spatial genetic structure was also investigated using 2 Bayesian clustering methods, implemented in STRUCTURE (Pritchard et al. 2000) and GENELAND (Guillot et al. 2005). Both these programs group individuals into the most likely number of clusters (K) that maximizes the within-cluster Hardy-Weinberg and linkage equilibria. However, GENELAND differs from STRUCTURE in that geographical information can be incorporated to produce more accurate inferences of population structure based on the spatial distribution of individuals. Analyses involving STRUCTURE were based on an ancestry model that assumed admixture and correlated allele frequencies. No prior information about the origin of the samples was used. Ten independent runs were performed for each value of K (1–10), with a burn-in of 10 000 followed by 100 000 Markov chain Monte Carlo (MCMC) iterations. The most likely number of clusters was assessed by comparing the likelihood of the data for different values of K and using the ΔK method of Evanno et al. (2005). For the GENELAND analysis, the spatial coordinates (latitude and longitude) of each individual were used to run the spatial model. The uncertainty of coordinates was set at zero. Ten independent runs were performed for each value of K (1–10) using the uncorrelated and null allele models. Each run consisted of 100 000 MCMC iterations with a thinning of 100 and a burn-in of 200. The most likely number of clusters was chosen as the modal K (from each independent run) with the highest posterior probability.

We also carried out spatial autocorrelation (SA) analysis to evaluate the genetic similarity of individuals over varying spatial scales. We used GENALEX to calculate a spatial autocorrelation coefficient (r) for a range of distance classes. The results from the SA analysis were presented in 2 ways. Firstly, r was plotted as a function of distance class to produce a spatial genetic autocorrelogram. Secondly, because estimates of spatial autocorrelation are influenced by the size of distance classes (see Peakall et al. 2003), r was calculated for a series of increasing distance class sizes. When significant positive spatial structure is present, r will decrease with increasing distance class sizes. The distance class where r no longer differs significantly from zero provides an approximation of the extent of detectable positive spatial genetic

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structure (Peakall et al. 2003). Tests for statistical significance were performed by random permutation and calculating the bootstrap 95% confidence limits (CL) of r using 1000 replicates. We also performed a 2-dimensional local spatial autocorrelation analysis using GENALEX. With this analysis, the local autocorrelation (lr) is estimated by comparing an individual with its n nearest neighbours, allowing investigation of local patterns of spatial autocorrelation within the 2-dimensional landscape (Double et al. 2005). Calculations of lr were made using the nearest 5, 10, 20 and 50 individuals. As with the global autocorrelation analysis, statistical significance was determined using permutation tests.

Finally, tests for selection acting on marker loci were carried out using the F_{ST} outlier approach (Beaumont & Nichols 1996, Beaumont 2005), implemented in LOSITAN (Antao et al. 2008). The method evaluates the relationship between F_{ST} and expected heterozygosity in an island model of migration with neutral markers. This distribution is used to identify loci with excessively high (directional selection) or low (balancing selection) F_{ST} values compared to neutral expectations. Simulations were run using 10 000 replications, 99% confidence intervals and the neutral and forced mean options. For this analysis, individuals were grouped by location and both the stepwise and infinite allele mutation models were performed.

RESULTS

LOSITAN failed to detect any loci with higher than expected F_{ST} values, indicating that all 22 loci are likely selec-

tively neutral. However, MICROCHECKER identified thirteen loci (S3, S8, S50, Pcyg02, Pcyg04, Pcyg06, Pcyg07, Pcyg09, Pcyg12, Pcyg13, Pcyg14, Pcyg16 and Pcyg17) as having null alleles in at least one population and these loci were excluded from further analyses unless specified otherwise. The remaining loci showed high levels of genetic variation at each location (Table 1). There were no significant differences in allelic richness ($\chi^2 = 11.57$, p = 0.172), gene diversity ($\chi^2 = 6.89$, p = 0.548) or F_{IS} ($\chi^2 = 3.11$, p = 0.927) among locations, nor was there genotypic disequilibrium between pairs of loci after adjusting for multiple comparisons or deviations from Hardy-Weinberg equilibrium (HWE).

There was no significant genetic differentiation among the 9 sampling locations ($F_{ST} = 0.003$, $G''_{ST} = 0.007$, p = 0.249). Most tests of population differentiation between pairs of locations were non-significant (Table 2), and genetic differentiation between most locations were comparable to those observed between sampling sites within the Houtman Abrolhos Islands (pairwise G''_{ST} values ranged from −0.015

Table 1. *Panulirus cygnus*. Genetic variation at each location. Sample size (N), mean ± SE allelic richness based on a sample size of 14 individuals (A_R), gene diversity (H), and the inbreeding co-efficient (F_{IS}). No F_{IS} value significantly deviated from Hardy-Weinberg equilibrium. HAI 1 = Houtman Abrolhos Islands Site 1

Site	N	A_R	H	F_{IS}
Kalbarri	39.4 ± 0.3	7.1 ± 1.9	0.58 ± 0.11	−0.05
HAI 1	38.9 ± 0.4	7.8 ± 2.0	0.62 ± 0.10	0.01
Dongara	38.2 ± 0.7	7.2 ± 1.8	0.62 ± 0.10	−0.01
Jurien Bay	38.3 ± 0.6	7.3 ± 2.0	0.60 ± 0.10	−0.01
North Lancelin	17.7 ± 0.6	7.2 ± 2.0	0.56 ± 0.11	−0.04
Lancelin	35.9 ± 0.7	7.0 ± 1.8	0.59 ± 0.11	0.03
Rottnest Island	63.0 ± 0.2	7.5 ± 1.9	0.64 ± 0.11	−0.03
Fremantle	20.4 ± 0.2	6.8 ± 1.8	0.61 ± 0.10	−0.01
Mandurah	21.4 ± 0.2	7.3 ± 1.8	0.61 ± 0.10	0.00

Table 2. *Panulirus cygnus*. Pairwise G''_{ST} estimates (below diagonal) and p-values from tests of differentiation (above diagonal) between geographic locations. The adjusted significance level for multiple comparisons is 0.0014. Significant values are highlighted in **bold**. HAI 1 = Houtman Abrolhos Islands Site 1

	Kalbarri	HAI 1	Dongara	Jurien Bay	N. Lancelin	Lancelin	Rottnest Is.	Fremantle	Mandurah
Kalbarri	–	**0.000**	0.005	0.157	0.065	0.120	0.845	0.176	0.308
HAI 1	**0.045**	–	0.128	0.137	0.252	0.205	0.002	0.022	0.099
Dongara	0.023	0.010	–	0.333	0.006	0.157	0.591	0.201	0.650
Jurien Bay	0.007	0.009	0.003	–	0.413	0.661	0.705	0.341	0.922
North Lancelin	0.017	0.007	0.037	0.002	–	0.431	0.025	0.352	0.251
Lancelin	0.009	0.006	0.008	−0.004	0.001	–	0.433	0.110	0.603
Rottnest Island	−0.005	0.026	−0.002	−0.003	0.023	0.001	–	0.278	0.789
Fremantle	0.009	0.026	0.009	0.004	0.005	0.015	0.005	–	0.888
Mandurah	0.004	0.015	−0.005	−0.013	0.008	−0.004	−0.007	−0.015	–

to 0.020), which were separated by much smaller geographical distances. There was no evidence for isolation-by-distance using pairwise G''_{ST} values calculated between locations (broad-scale) or between sampling sites within the Houtman Abrolhos Islands (local-scale) (Mantel tests, p = 0.170 and 0.111, respectively). No significant genetic divergences among locations were also found when analyses were performed using all 22 loci (F_{ST} = 0.000, G''_{ST} = 0.000, p = 0.595). We also failed to detect isolation-by-distance when analyses were performed using all 22 loci (Mantel tests, p = 0.170 and 0.453 for broad and local spatial scales, respectively).

No genetic subdivision was found using Bayesian clustering analysis. The STRUCTURE analysis revealed decreasing log probability estimates with increasing values of K and there were no large fluctuations in ΔK, suggesting that the probable number of genetic clusters was one. Further, when $K > 1$, the proportion of individuals assigned to each cluster was fairly even and most individuals were admixed, consistent with a lack of population structure (Pritchard et al. 2010). The analysis involving GENELAND gave a similar result, with posterior distributions of the estimated number of populations indicating a clear mode at $K = 1$ in 9 out of 10 replicates. Similar results were obtained when clustering analysis were performed using all 22 loci, as the STRUCTURE analysis revealed only slight increases in log probability estimates with increasing values of K and no large fluctuations in ΔK, and the GENELAND analysis also indicated a clear mode at $K = 1$ in all 10 replicates.

In contrast to the Mantel tests, spatial genetic structure was detected with the SA analyses. Significantly positive values of r were found within the first 4 distance classes (0–10, 11–20, 21–30 and 31–40 km), after which r decreased and oscillated between being non-significantly different from zero and significantly negative (Fig. 2A). This pattern is indicative of fine-scale spatial genetic structure generated by discrete patches of related multilocus genotypes (Smouse & Peakall 1999, Diniz-Filho & Telles 2002). Positive spatial genetic structure at local geographical scales was confirmed when estimates
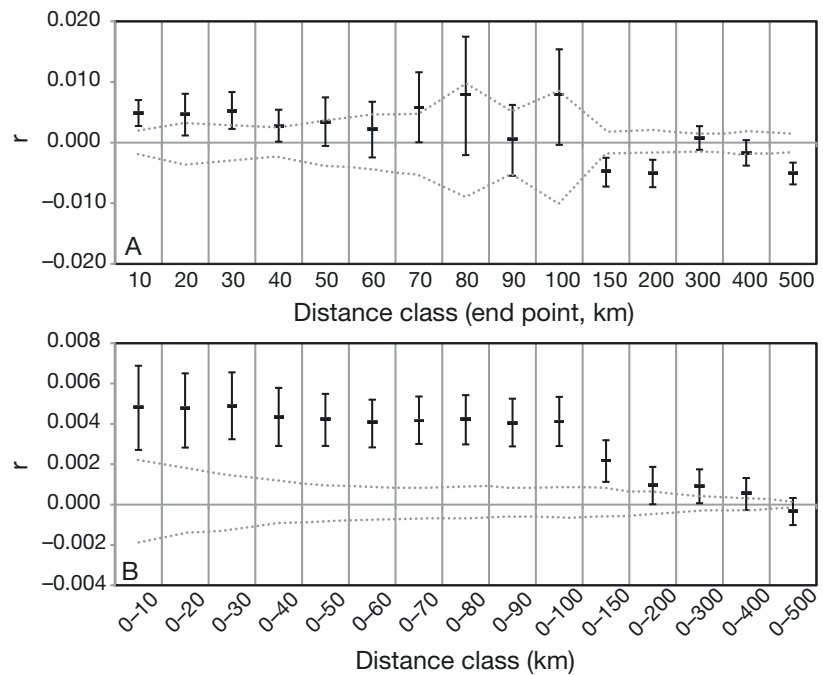

Fig. 2. *Panulirus cygnus.* Spatial autocorrelation analyses. (A) Correlogram plot of the genetic correlation coefficient (r) as a function of distance. (B) Multiple distance class plot, showing the influence of different distance class sizes on genetic correlation. Permuted 95 % confidence interval (dashed lines) and the bootstrap 95 % confidence error bars are shown

of r were calculated with increasing distance class sizes. Fig. 2B shows little change in r between 10 and 100 km, after which r decreased, but remained significant until 150 km. It also appears that positive genetic structure was not confined to one geographical area. Two-dimensional local spatial autocorrelation analysis revealed clusters of positive lr at most sampling locations (Fig. 3). The close proximity of significantly positive and non-significant values suggests that local patches were not genetically uniform. A similar number and distribution of positive lr values were obtained when calculations were based on sampling the nearest 5, 10, 20 and 50 individuals, confirming the consistency of the result. Again, similar results to these were found when all 22 loci were used. The only exceptions were that in the SA analysis positive r values were found within the first 2 distance classes only, and none of the remaining distance classes were significantly negative.

DISCUSSION

The major finding of this study was the significant genetic heterogeneity among local populations in *Panulirus cygnus* over very short spatial scales with-
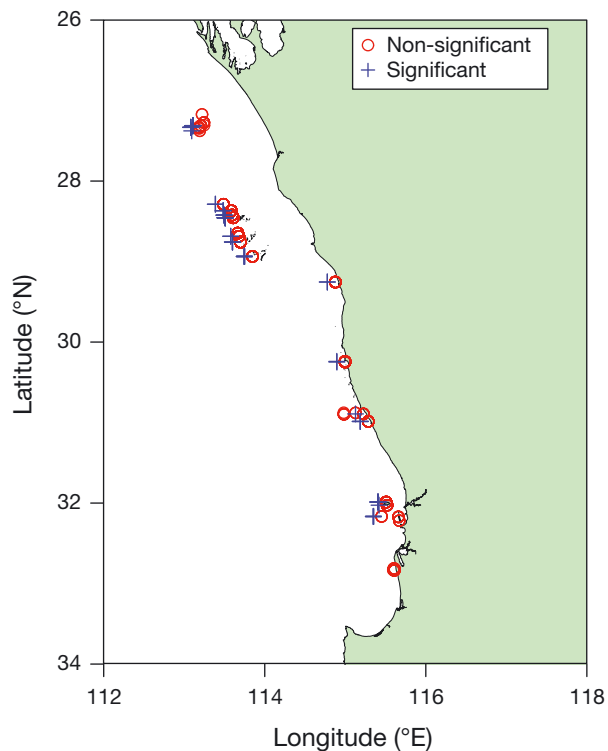
Fig. 3. *Panulirus cygnus*. Plot of 2-dimensional local spatial autocorrelation analyses. Symbols represent geographical coordinates of the local spatial autocorrelation (lr) analyses with significantly positive (blue crosses) or non-significant (red circles) values. Calculations of lr were based on sampling the nearest 20 individuals. Significantly positive values are offset by –0.1° longitude for clarity

out the presence of large-scale geographic structure. We found extremely low and non-significant differentiation among locations sampled across the species' range ($F_{ST} = 0.003$, $G''_{ST} = 0.007$), consistent with extensive gene flow over large geographic distances. The lack of geographic pattern was emphasized by genetic differentiation between locations (separated by distances >650 km) being no larger than the differentiation between sites at the Houtman Abrolhos Islands (separated by distances <85 km). We also found no evidence of isolation-by-distance using pairwise G''_{ST} estimates and no genetic subdivision using Bayesian clustering analyses. Our results, therefore, add weight to the findings of previous allozyme (Thompson et al. 1996, Johnson & Wernham 1999) and microsatellite studies (Kennington et al. 2013), which suggest that *P. cygnus* is a single, panmictic population.

Fine-scale population structure in *Panulirus cygnus* was most clearly evident with spatial autocorrelation analysis. Significant genetic structure was observed when lobsters were sampled over distances

up to 40 km, with detectable positive spatial genetic structure extending out to 150 km when distance classes were pooled. Further, 2-dimensional local SA analysis indicates that these patterns were not driven by the strong influence of one region alone, but were a common feature throughout the species' range. Such microgeographic genetic patchiness has been demonstrated in other marine species with planktonic larvae (e.g. Hedgecock 1994b, Knutsen et al. 2003, Pujolar et al. 2006), including several species along the Western Australian coast (Johnson & Black 1982, Watts et al. 1990, Johnson et al. 1993, Johnson et al. 2001). Genetic patchiness has also been observed in *P. cygnus*, using allozymes (Johnson & Wernham 1999), but the scale of the genetic heterogeneity reported here is much smaller than shown previously. This likely reflects the increased genetic sensitivity and fine-scale geographic information of this study.

Spatial genetic patchiness in some species is due to temporal variation in the genetic composition of recruits (Johnson & Black 1984, Watts et al. 1990, Hedgecock 1994a, Pujolar et al. 2006). This also seems to be the case for *Panulirus cygnus*, in which a combination of temporal variation in allele frequencies and contrasting patterns of recruitment resulted in genetically different cohorts of *P. cygnus* at 2 sites (Johnson & Wernham 1999). Furthermore, this pattern was ephemeral, as it was not repeated in the subsequent 2 years. Under the 'sweepstakes reproductive success' hypothesis (Hedgecock 1994a), temporal genetic variance in recruits might be a byproduct of large variance in the reproductive success of individuals, owing to chance matching of reproductive activity with oceanographic conditions conducive for larval survival. Other possible explanations for temporal genetic variation in *P. cygnus* recruits are (1) origin from different source populations, (2) limited mixing of larvae in the plankton, or (3) natural selection on larvae prior to settlement. Given the low geographic structure in *P. cygnus*, it is unlikely that temporal genetic variation arises from different source populations. The finding that *P. cygnus* larvae settling at the same time at locations 350 km apart shared the same allele frequencies (Johnson & Wernham 1999) also argues against temporal genetic variation being due to the cohesion of larvae in the plankton, though this result was based on only 3 allozyme loci.

If a combination of temporal variation in allele frequencies and contrasting patterns of recruitment is responsible for the genetic patchiness observed in this study, it would require juvenile *Panulirus cygnus*

to be relatively sedentary. Independent evidence supports this theory: studies on foraging movements suggest juvenile *P. cygnus* forage over relatively small areas (~150 m radius), though the extent of movement is variable (Jernakoff et al. 1987, Jernakoff & Phillips 1988). The life-cycle of *P. cygnus* also includes a migratory phase, which occurs between 4 and 6 years of age, just after many lobsters undergo a synchronised moult that changes their normal red shell to a paler colour (Morgan et al. 1982). During this migration, lobsters leave the coastal reefs and move into deeper water breeding grounds, where they become sedentary again on deeper reefs. Because the lobsters we collected were predominantly from shallow water locations, it is unlikely that they had undertaken these migratory movements. Nevertheless, tag and release experiments have shown that while large movements (>200 km) do occur, most lobsters (>87%) are recaptured within 10 km of their release site (Chubb et al. 1999). This spatial scale is within the distance range we detected positive population structure. More recently, a study using acoustic telemetry found that only a small proportion (13.6%) of migratory phase lobsters emigrated from their resident reef, suggesting that a mass offshore migration may not hold for all inshore reefs (MacArthur et al. 2008).

Another explanation for spatial genetic patchiness is natural selection acting after settlement (Larson & Julian 1999). Given the broad latitudinal range of *Panulirus cygnus* (>1200 km), local populations are likely to experience highly varied environmental conditions, providing the opportunity for local adaptations to develop across populations (Kawecki & Ebert 2004). Indeed, several studies have found evidence for local adaptation in widely distributed marine fish (see Nielsen et al. 2009). While we found no clear evidence of directional selection using outlier analysis, genome scans involving many more neutral markers, candidate genes or population transcriptomics would be needed to confidently exclude this possibility. A study monitoring the genetic composition of cohorts of recruits as they develop into adults would also yield valuable insights on post-settlement processes.

The implications of genetic patchiness for fisheries management have been discussed by Larson & Julian (1999). If genetic patchiness is due to selection after settlement, they suggest that the implications for fisheries management are minor, unless a fishery is concentrated on one particular habitat or location, which might disproportionately affect a certain portion of the gene pool. By contrast, factors affecting the genetic composition of recruits prior to settlement may have greater consequences. The most relevant of these to *Panulirus cygnus* is the effect of stochastic spatial variation in the sources of successful larvae (sweepstakes reproductive success). This effect implies that the sources of successful larvae vary unpredictably over time. Fisheries management should therefore ensure that both the distribution as well as the total spawning potential of the exploited population is protected. Further, spatial stochasticity of successful spawning argues for either the spatial dispersion of reserves (if they are involved in managing the exploitation), or suitably low exploitation rates across the fishery, thereby increasing the chance that at least some larvae will be released into conditions favourable for their survival. Local genetic patchiness also suggests juvenile and adult lobsters are comparatively sedentary, so they may be more susceptible to environmental or anthropogenic impacts at a finer scale than previously thought.

LITERATURE CITED

Antao T, Lopes A, Lopes RJ, Beja-Pereira A, Luikart G (2008) LOSITAN: a workbench to detect molecular adaptation based on a F_{ST}-outlier method. BMC Bioinformatics 9:323

Ayre DJ, Hughes TP (2000) Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. Evolution 54:1590–1605

Beaumont MA (2005) Adaptation and speciation: what can F_{ST} tell us? Trends Ecol Evol 20:435–440

Beaumont MA, Nichols RA (1996) Evaluating loci for use in the genetic analysis of population structure. Proc R Soc Lond B 263:1619–1626

Begg GA, Friedland KD, Pearce JB (1999) Stock identification and its role in stock assessment and fisheries management: an overview. Fish Res 43:1–8

Benzie JH, Stoddart JA (1992) Genetic structure of outbreaking and non-outbreaking crown-of-thorns starfish (*Acanthaster planci*) populations on the Great Barrier Reef. Mar Biol 112:119–130

Bohonak AJ (1999) Dispersal, gene flow and population structure. Q Rev Biol 74:21–45

Carvalho GR, Hauser L (1994) Molecular genetics and the stock concept in fisheries. Rev Fish Biol Fish 4:326–350

Chubb CF, Rossbach M, Melville-Smith R, Cheng YW (1999) Mortality, growth and movement of the western rock lobster (*Panulirus cygnus*). Final Report FRDC Project No. 95/020. Fisheries Western Australia, North Beach, Perth

Diniz-Filho JAF, Telles MPC (2002) Spatial autocorrelation analysis and the identification of operational units for conservation in continuous populations. Conserv Biol 16: 924–935

Double MC, Peakall R, Beck NR, Cockburn A (2005) Dispersal, philopatry, and infidelity: dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). Evolution 59:625–635

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14:2611–2620

Fletcher W, Chubb C, McCrea J, Caputi N, Webster F, Gould R, Bray T (2005) Western rock lobster fishery. ESD Report Series, No. 4. Dept of Fisheries, North Beach, Perth

García-Rodríguez FJ, Perez-Enriquez R (2008) Lack of genetic differentiation of blue spiny lobster *Panulirus inflatus* along the Pacific coast of Mexico inferred from mtDNA sequences. Mar Ecol Prog Ser 361:203–212

Gopal K, Tolley KA, Groeneveld JC, Matthee CA (2006) Mitochondrial DNA variation in spiny lobster *Palinurus delagoae* suggests genetically structured populations in the south-western Indian Ocean. Mar Ecol Prog Ser 319: 191–198

Goudet J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3.2 Available at www.unil.ch/Jahia/site/dee/op/edit/pid/36921)

Groth DM, Lim F, de Lestang SN, Beale N, Melville-Smith R (2009) Characterization of polymorphic microsatellite loci in the western rock lobster (*Panulirus cygnus*). Conserv Genet Resour 1:163–166

Guillot G, Mortier F, Estoup A (2005) GENELAND: a computer package for landscape genetics. Mol Ecol Notes 5: 712–715

Hedgecock D (1986) Is gene flow from pelagic larval dispersal important in the adaptation and evolution of marine invertebrates? Bull Mar Sci 39:550–564

Hedgecock D (1994a) Does variance in reproductive success limit effective population sizes of marine organisms. In: Beaumont AR (ed) Genetics and evolution of aquatic organisms. Chapman & Hall, London, p 122-134

Hedgecock D (1994b) Spatial and temporal genetic structure of marine animal populations in the California current. CALCOFI Rep 35:73–81

Hedrick PW (2005) A standardized genetic differentiation measure. Evolution 59:1633–1638

Jernakoff P, Phillips BF (1988) Effect of a baited trap on the foraging movements of juvenile western rock lobsters, *Panulirus cygnus* George. Aust J Mar Freshw Res 39: 185–192

Jernakoff P, Phillips BF, Maller RA (1987) A quantitative study of nocturnal foraging distances of the western rock lobster *Panulirus cygnus* George. J Exp Mar Biol Ecol 113:9–21

Johnson MS, Black R (1982) Chaotic genetic patchiness in an intertidal limpet, *Siphonaria* sp. Mar Biol 70:157–164

Johnson MS, Black R (1984) Pattern beneath the chaos: the effect of recruitment on genetic patchiness in an intertidal limpet. Evolution 38:1371–1383

Johnson MS, Black R (2006) Islands increase genetic subdivision and disrupt patterns of connectivity of intertidal snails in a complex archipelago. Evolution 60:2498–2506

Johnson MS, Wernham J (1999) Temporal variation of recruits as a basis of ephemeral genetic heterogeneity in the western rock lobster *Panulirus cygnus.* Mar Biol 135: 133–139

Johnson MS, Holborn K, Black R (1993) Fine-scale patchiness and genetic heterogeneity of recruits of the corallivorous gastropod *Drupella cornus.* Mar Biol 117:91–96

Johnson MS, Bentley SL, Ford SS, Ladyman MT, Lambert GJ (2001) Effects of a complex archipelago on genetic subdivision of the intertidal limpet *Siphonaria kurracheensis.* Mar Biol 139:1087–1094

Jørgensen HBH, Hansen MM, Bekkevold D, Ruzzante DE, Loeschcke V (2005) Marine landscapes and population genetic structure of herring (*Clupea harengus* L.) in the Baltic Sea. Mol Ecol 14:3219–3234

Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. Ecol Lett 7:1225–1241

Kennington WJ, Levy E, Berry O, Groth DM, Waite AM, Johnson MS, Melville-Smith R (2010) Characterization of 18 polymorphic microsatellite loci for the western rock lobster *Panulirus cygnus.* Conserv Genet Resour 2: 389–391

Kennington WJ, Cadee SA, Berry O, Groth DM, Johnson MS, Melville-Smith R (2013) Maintenance of genetic variation and panmixia in the commercially exploited western rock lobster (*Panulirus cygnus*). Conserv Genet 14:115–124

Knutsen H, Jorde PE, André C, Stenseth NC (2003) Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. Mol Ecol 12: 385–394

Larson RJ, Julian RM (1999) Spatial and temporal genetic patchiness in marine populations and their implications for fisheries management. CALCOFI Rep 40:94–99

MacArthur LD, Babcock RC, Hyndes GA (2008) Movements of the western rock lobster (*Panulirus cygnus*) within shallow coastal waters using acoustic telemetry. Mar Freshw Res 59:603–613

Meirmans PG, Hedrick PW (2011) Assessing population structure: F_{ST} and related measures. Mol Ecol Resour 11: 5–18

Morgan GR, Phillips BF, Joll LM (1982) Stock recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of Western Australia. Fish Bull 80:475–486

Naro-Maciel E, Reid B, Holmes K, Brumbaugh D, Martin M, DeSalle R (2011) Mitochondrial DNA sequence variation in spiny lobsters: population expansion, panmixia, and divergence. Mar Biol 158:2027–2041

Nei M (1987) Molecular evolutionary genetics. Columbia University Press, New York, NY

Nielsen EE, Hemmer-Hansen J, Larsen PF, Bekkevold D (2009) Population genomics of marine fishes: identifying adaptive variation in space and time. Mol Ecol 18: 3128–3150

Ovenden JR, Brasher DJ, White RWG (1992) Mitochondrial DNA analyses of the red rock lobster J*asus edwardsii* supports an apparent absence of population subdivision throughout Australasia. Mar Biol 112:319–326

Palero F, Abellób P, Macpherson E, Gristinad M, Pascual M (2008) Phylogeography of the European spiny lobster (*Palinurus elephas*): influence of current oceanographical features and historical processes. Mol Phylogenet Evol 48:708–717

Palumbi SR (1994) Genetic divergence, reproductive isolation, and marine speciation. Annu Rev Ecol Syst 25: 547–572

Peakall R, Smouse PE (2005) GenAlEx v. 6: genetic analysis in Excel. Population genetic software for teaching and research. Australian National University, Canberra.

Available at http://biology.anu.edu.au/GenAlEx/Welcome .html

Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial auto-correlation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes.* Evolution 57: 1182–1195

Perez-Enriquez R, Vega A, Avila S, Sandoval JL (2001) Population genetics of red spiny lobster (*Panulirus interruptus*) along the Baja California Peninsula, Mexico. Mar Freshw Res 52:1541–1549

Phillips BF, Brown PA, Rimmev DW, Reid DD (1979) Distribution and dispersal of the phyllosoma larvae of the western rock lobster, *Panulivus cygnus*, in the south-eastern Indian Ocean. Aust J Mar Freshw Res 30:773–783

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

Pritchard JK, Wen X, Falush D (2010) Documentation for *structure* software: version 2.3. Available at http:// pritch.bsd.uchicago.edu/structure.html

Pujolar JM, Maes GE, Volckaert FAM (2006) Genetic patchiness among recruits in the European eel *Anguilla anguilla.* Mar Ecol Prog Ser 307:209–217

Riccioni G, Landi M, Ferrara G, Milano I and others (2010) Spatio-temporal population structuring and genetic diversity retention in depleted Atlantic Bluefin tuna of the Mediterranean Sea. Proc Natl Acad Sci USA 107: 2102–2107

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Ruzzante DE, Taggart CT, Cook D, Goddard S (1996) Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: micro-

satellite DNA variation and antifreeze level. Can J Fish Aquat Sci 53:634–645

Silberman JD, Sarver SK, Walsh PJ (1994) Mitochondrial DNA variation and population structure in the spiny lobster *Panulirus argus.* Mar Biol 120:601–608

Slatkin M (1995) A measure of population subdivision based on microsatellite allele frequencies. Genetics 139:457–462

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. Heredity 82:561–573

Thompson AP, Hanley JR, Johnson MS (1996) Genetic structure of the western rock lobster, *Panulirus cygnus*, with the benefit of hindsight. Mar Freshw Res 47:889-896

Tolley KA, Groeneveld JC, Gopal K, Matthee CA (2005) Mitochondrial DNA panmixia in spiny lobster *Palinurus gilchristi* suggests a population expansion. Mar Ecol Prog Ser 297:225–231

van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICROCHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538

Waples RS (1987) A multispecies approach to the analysis of gene flow in marine shore fishes. Evolution 41:385–400

Watts RJ, Johnson MS, Black R (1990) Effects of recruitment on genetic patchiness in the urchin *Echinometra mathaei* in Western Australia. Mar Biol 105:145–151

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38: 1358–1370

White TA, Stamford J, Hoelzel AR (2010) Local selection and population structure in a deep-sea fish, the roundnose grenadier (*Coryphaenoides rupestris*). Mol Ecol 19: 216–226