Heredity (2013) 111, 345–354

www.nature.com/hdy

ORIGINAL ARTICLE

Testing the consistency of connectivity patterns for a widely dispersing marine species

L Thomas[1,2] and JJ Bell[1]

Connectivity is widely recognized as an important component in developing effective management and conservation strategies. Although managers are generally most interested in demographic, rather than genetic connectivity, new analytic approaches are able to provide estimates of both demographic and genetic connectivity measures from genetic data. Combining such genetic data with mathematical models represents a powerful approach for accurately determining patterns of population connectivity. Here, we use microsatellite markers to investigate the genetic population structure of the New Zealand Rock Lobster, *Jasus edwardsii*, which has one of the longest known larval durations of all marine species (>2 years), a very large geographic range (>5500 km), and has been the subject of extensive dispersal modeling. Despite earlier mitochondrial DNA studies finding homogeneous genetic structure, the mathematical model suggests that there are source-sink dynamics for this species. We found evidence of genetic structure in *J. edwardsii* populations with three distinct genetic groups across New Zealand and a further Australian group; these groups and patterns of gene flow were generally congruent with the earlier mathematical model. Of particular interest was the consistent identification of a self-recruiting population/region from both modeling and genetic approaches. Although there is the potential for selection and harvesting to influence the patterns we observed, we believe oceanographic processes are most likely responsible for the genetic structure observed in *J. edwardsii*. Our results, using a species at the extreme end of the dispersal spectrum, demonstrate that source-sink population dynamics may still exist for such species.
Heredity (2013) **111,** 345–354; doi:10.1038/hdy.2013.58; published online 3 July 2013

Keywords: connectivity; dispersal; rock lobster

INTRODUCTION

Connectivity is a broad term used to describe the extent to which populations in different parts of a species' range are linked by the exchange of larvae, recruits, juveniles or adults (Palumbi, 2003; Cowen and Sponaugle, 2009; Weersing and Toonen, 2009; Lowe and Allendorf, 2010), and it can be generally divided into genetic connectivity and demographic connectivity. Genetic connectivity refers to the degree to which gene flow affects evolutionary processes within populations, whereas demographic connectivity refers to the degree to which population growth and vital rates are affected by dispersal and recruitment (Lowe and Allendorf, 2010). Understanding connectivity is important because it controls the following: (1) a population's buffering potential from local catastrophes and therefore its extinction risk (Allison *et al.*, 2003); (2) a population's potential as a source of new individuals to other populations; (3) the level of genetic mixing between populations (Bell and Okamura, 2005; Bell, 2008); and (4) a population's susceptibility to disease or pollution, the so-called 'dark-side' of connectivity (Hughes *et al.*, 2010).

Although measuring genetic and demographic connectivity provides insights into patterns of dispersal in the marine environment, it is usually demographic connectivity that is of most use to resource managers, as it provides information relevant to the typically short time scales at which management operates (years to decades). This is particularly the case for spatially explicit management strategies such as protected areas networks, where protection success is usually dependent on whether the design accurately reflects ecologically relevant patterns of connectivity (Palumbi, 2003; Shanks *et al.*, 2003; Berumen *et al.*, 2012).

Despite the importance of connectivity in marine systems, it is poorly understood in most species, as it is difficult to estimate (Kinlan and Gaines, 2003; Cowen *et al.*, 2007; Selkoe and Toonen, 2011). Demographic connectivity is particularly difficult to measure directly because the majority of marine species (particularly invertebrates) have a bi-partite life cycle comprising a relatively sessile adult stage and a dispersing larval stage. The duration of the larval stage ranges from several hours to years, making dispersal technically and logistically challenging to track (Leis *et al.*, 2011; Selkoe and Toonen, 2011). Although genetic data are more easily collected, the nature of data often makes it difficult to interpret in a management context (Lowe and Allendorf, 2010; Selkoe and Toonen, 2011). A better approach to understanding connectivity patterns is to provide connectivity estimates using a combination of different approaches (Cowen *et al.*, 2007). Although a large number of population genetic studies have been conducted across the world for marine species to estimate genetic connectivity (see Kinlan and Gaines, 2003; Cowen *et al.*, 2006; Bradbury *et al.*, 2008; Gardner *et al.*, 2010; Kelly and Palumbi, 2010 who consider hundreds of species), there are far fewer estimates of demographic connectivity based on either direct or

[1]School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand and [2]The Oceans Institute, School of Plant Biology, The University of Western Australia, Crawley, Western Australia, Australia
Correspondence: Dr JJ Bell, School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand.
E-mail: james.bell@vuw.ac.nz
Received 21 February 2013; revised 3 May 2013; accepted 20 May 2013; published online 3 July 2013

indirect observation (but see Swearer *et al.*, 1999; Jones *et al.*, 2005; Becker *et al.*, 2007 for individual species studies). Further, there have been few studies that have validated connectivity models through complementary approaches (but see Thorrold *et al.*, 2002; Jones *et al.*, 2005).

Importantly, the development of new genetic tools and analysis methods, particularly highly polymorphic microsatellite markers (Selkoe and Toonen, 2006), is enabling genetic data to be used to estimate demographic connectivity, particularly through assignment testing (Berry *et al.*, 2004; Manel *et al.*, 2005; Underwood *et al.*, 2007; Saenz-Agudelo *et al.*, 2009; Polato *et al.*, 2010). These developments provide opportunities for using genetic tools to estimate both the genetic and demographic connectivity and present opportunities to compare such data with mathematical models.

Jasus edwardsii supports valuable commercial fisheries in both New Zealand (NZ) and Australia, worth over New Zealand Dollar (NZD) 230 million per annum to the New Zealand economy alone. It is a keystone predator of subtidal rocky reef systems (Shears and Babcock, 2003) with a range that encompasses 10 degrees of latitude and stretches over 5500 km from the Chatham Islands in New Zealand to Western Australia. Importantly, *J. edwardsii* is thought to have one of the longest pelagic larval durations of any marine species and can remain in offshore oceanic waters for up to 24 months, where it undergoes 11 developmental stages with 17 instars before developing into the nektonic puerulus that settles in coastal environments (Booth and Phillips, 1994).

Previous analysis of mitochondrial DNA has shown that *J. edwardsii* populations are genetically indistinguishable between and within Australia and New Zealand (Ovenden *et al.*, 1992). This suggests that populations were isolated too recently to allow genetic divergence, that there is sustained gene flow between Australia and New Zealand homogenizing populations or that it is the result of the conserved nature of mitochondrial DNA that may have prevented the identification of genetic structure (Selkoe and Toonen, 2006). However, although the existing genetic data suggest homogeneity, extensive oceanographic modeling studies for *J. edwardsii* suggest that some source-sink dynamics exist. These models have estimated New Zealand-scale patterns of connectivity (Chiswell and Booth, 2008) and also the supply of recruits from Australia to New Zealand (Chiswell *et al.*, 2003). Chiswell and Booth (2008) used a Lagrangian modeling approach, applying time varying ocean currents (1993–2003) derived from a satellite altimeter to track the paths of individual *J. edwardsii* larvae released from different locations around New Zealand. The aim of their study was to identify source-sink relationships between the different rock lobster management areas (CRA zones of which there are currently nine). The results from the model showed significant exchange among most regions, and the authors identified four major geographic areas associated with rock lobster larval dispersal around New Zealand: (1) the far north, (2) the east coast of the North Island, (3) the South Island and (4) the Chatham Islands. In addition to these four geographic regions, Chiswell and Booth (2008) identified high levels of local settlement at the bottom of the South Island and suggested that populations in this region are likely to be maintained by self-recruitment. Using a similar modeling approach, Chiswell *et al.* (2003) investigated trans-Tasman dispersal rates and estimated that 9–14% of *J. edwardsii* larvae originating from the south east coast of Australia would be able to reach the west coast of New Zealand, which was used to explain the genetic homogeneity for *J. edwardsii* on the basis of mitochondrial DNA data (Ovenden *et al.*, 1992).

In this study, we reassessed the genetic structure of *J. edwardsii* using a recently developed panel of eight microsatellite markers (Thomas and Bell, 2011) to determine levels of genetic differentiation and gene flow between populations at the New Zealand scale and also the genetic relationships between Australia and New Zealand. Specifically, we used our genetic data to provide estimates of contemporary rates of gene flow and estimates of demographic connectivity to test the findings of the earlier oceanographic models that predicted dispersal patterns of *J. edwardsii* across the Tasman Sea (Chiswell *et al.*, 2003) and throughout New Zealand (Chiswell and Booth, 2008). Given that the results from the New Zealand scale model (Chiswell and Booth, 2008) revealed high levels of larval exchange between management areas throughout New Zealand, we hypothesized that the genetic structure of *J. edwardsii* would reflect those findings and reveal a relatively homogenous population. One possible exception to this might be found at the bottom of the South Island, for which there is evidence for high levels of self-recruitment. Furthermore, we propose that the resolving power of highly polymorphic microsatellites would identify a significant trans-Tasman genetic structure that has previously remained undetected using more conservative mDNA markers (Ovenden *et al.*, 1992).

MATERIALS AND METHODS

Sampling

A total of 336 adult lobsters from eight populations were collected by commercial fishers between January and November 2011. Sample sizes ranged from 45–48 individuals per population and were all from adult individuals of minimum legal size. Samples were collected from five of the nine management zones (termed 'CRA' zones) in New Zealand (CRA 2, 4, 5, 6 and 8), one population in the Southern Zone (SZRLF) of the South Australia Rock Lobster Fishery and one population from the Tasmania Fishery zone (Figure 1). Geographical coordinates and the corresponding management zone from where the samples were collected are provided in Table 1. Samples covered roughly 10 degrees of latitude and over 3500 km across the Tasman Sea to South Australia.

Laboratory protocol and PCR amplification

Tissue samples for DNA extraction were taken from the pereiopods and antennae preserved in 99% ethanol, and the remains were stored in 50 ml polypropylene test tubes at −80 °C. DNA for PCR amplification was extracted using a modified phenol–chloroform protocol and genotyped across eight microsatellite loci (for details see Thomas and Bell, 2011). Samples were screened using a Touchdown PCR protocol (Korbie and Mattick, 2008). Amplifications were performed on a GENEAMP 2700 (Applied Biosystems, Foster City, CA, USA) thermocycler in a final reaction volume of 12.5 µl, containing 6.75 µl MyTaq Red Mix 2X Bioline, 0.75 µl of the forward and reverse primers, 50–100 ng of DNA template and ddH_20 to reach the final volume. PCR products were viewed on a 2% agarose gel. Genotyping was conducted on an ABI 3730XLs sequencer (Applied Biosystems) and loci were scored by eye using 5′ fluorescent labels with a 500LIZ size standard in GENEMARKER v 1.97 (www.softgenetics.com).

Genetic analyses

MICRO CHECKER v 2.2.3 (van Oosterhout *et al.*, 2004) was used to identify deviations from Hardy–Weinberg equilibrium resulting from large-allele drop out, scoring errors due to stuttering or the presence of null alleles. Genetic diversity of sampling locations was quantified using the mean number of alleles per locus and total number of alleles by FSTAT v 2.9.3 (Goudet, 1995) and number of private alleles and Nei's unbiased heterozygosity (Nei, 1987) by GENEALEX 6.3 (Paekall and Smouse, 2006). We also preformed exact tests for deviations from Hardy–Weinberg equilibrium with GENEALEX v 6.3 and tested for any evidence of linkage equilibrium with ARLEQUIN v 3.5.1.2 (Excoffier *et al.*, 2005) *P*-values were adjusted for multiple comparisons using standard

Figure 1 Sampling locations for *J. edwardsii* throughout New Zealand and on the Australian coast.

Table 1 Sampling locations with standard genetic diversity indices: (N) number of individuals sampled; (N_A) mean number of alleles per locus; (H_O) observed and (H_E) expected heterozygosity; and (F_{IS}) inbreeding coefficients with corresponding significant values (P_{HWE})

Population	*MA*	*Coordinates*	*N*	N_A	H_O	H_E	F_{IS}	P_{HWE}
HG	CRAY2	36° 34′ S 174° 46′ E	48	16.75	0.781	0.859	0.092	0.001
SI	CRAY8	46° 38′ S 167° 37′ E	47	13.63	0.785	0.829	0.047	0.006
CHI	CRAY6	43° 55′ S 176° 43′ W	45	17.63	0.802	0.850	0.056	0.003
WEL	CRAY4	41° 20′ S 174° 48′ E	48	19.38	0.822	0.866	0.054	0.006
KAI	CRAY5	42° 24′ S 173° 40′ E	48	17.50	0.797	0.836	0.051	0.007
SWC	CRAY9	43° 53′ S 166° 09′ E	44	18.38	0.772	0.853	0.095	0.001
SA	SZRLF	36° 49′ S 139° 49′ E	48	19.63	0.789	0.877	0.101	0.001
TAS	TASI	43° 07′ S 148° 16′ E	48	20.13	0.810	0.876	0.088	0.001

Abbreviations: CHI, Chatham Islands; HG, Hauraki Gulf; KAI, Kaikoura; SA, South Australia; SI, Stewart Island; SWC, SouthWest Coast; TAS, Tasmania; WEL, Wellington.
The corresponding management areas (MA) are also shown.

Bonferroni corrections (Rice, 1989). Markov-chain parameters were 10 000 dememorization steps, 1000 batches and 10 000 iterations per batch.

Population genetic structure

To determine the proportion of genetic variation that could be attributed to differences between sampling sites, hierarchal analysis of molecular variance ($n = 10\,000$ permutations) was performed by GENEALEX v 6.3. Estimates of population differentiation (F_{ST}; Weir and Cockerham, 1984) were also measured across all loci with ARLEQUIN v 3.5.1.2 using sampling locations as population units. Significance values were based on 10 000 permutations. To account for the high levels of within-population diversity, values were standardized to a scale of 0-1 (F'_{ST}) according to the method described by Meirman (2006) using RECODEDATA (Meirman, 2006). There is much debate as to whether the stepwise mutation model and associated R_{ST} index are appropriate for population genetic studies using microsatellite loci (Meirmans and Hedrick, 2011); therefore, we avoided using the R_{ST} index as it is unlikely that the loci used in this analysis adhered to a strict stepwise mutation model, given the imperfect nature of the repeats (see Thomas and Bell, 2011). A Mantel test for isolation by distance was conducted using linearized values of F'_{ST} ($F'_{ST}/(1-F'_{ST})$) and oceanographic distance (km).

To visualize the genetic relationships between sampled populations, a principle coordinate analysis was conducted by GENEALEX 6.3 using the pairwise matrices of F_{ST}, F'_{ST}, and the genotype likelihood ratio distance, D_{LR}. This measurement of genetic distance (D_{LR}: Paetkau *et al.*, 1995) was developed from assignment tests in which the likelihood of complete multi-locus genotypes are compared across individuals from discrete populations and was determined to be a better predictor of statistical power than F_{ST} (Paetkau *et al.*, 1997).

Bayesian clustering analysis in STRUCTURE v 2.3.2 (Pritchard *et al.*, 2000) was used to infer population structure using the admixture model with correlated allele frequencies among clusters and informed priors with a burn-in period of 10^4 iterations and 10^5 Markov Chain Monte Carlo repetitions and with the K value ranging from 1–8. LOCPRIOR models (Hubisz *et al.*, 2009) consider sampling locations to be informative about ancestry and are best suited for instances when genetic structure is present but at relatively weak levels (Pritchard *et al.*, 2010). Each individual in the data set is represented by a single vertical line, which is partitioned into K segments that represent that individual's estimated membership fraction in each of the K-inferred clusters.

The appropriate K value for the data set was determined by plotting the log probability (L(K)) and ΔK across multiple runs (Evanno *et al.*, 2005) as implemented in STRUCTURE HARVESTER (Earl and vonHoldt, 2012). Results from 10 runs were merged with CLUMPP (Jakobsson and Rosenberg, 2007) and visualized using DISTRUCT (Rosenberg, 2004). Analysis of molecular variance ($n = 10\,000$ permutations) was then used to test the results of STRUCTURE using GENEALEX v 6.3 and determine the proportion of genetic variation that was attributed to differences between clusters. In addition, standardized fixation indices were calculated between the clusters.

Trans-tasman dispersal

To investigate Trans-Tasman connectivity and determine the likely proportion of the New Zealand lobster to have originated in Australia, assignment tests were conducted using a Bayesian approach (Rannala and Mountain, 1997) in GENECLASS v 2.0 (Piry *et al.*, 2004) on the basis of the clustering scenario identified by STRUCTURE. An analysis of first generation migrants was conducted using an exclusion threshold approach where individuals were excluded from their corresponding sampling site when probability of assignment to the reference population was less than 0.05 (Type I error; Berry *et al.*, 2004). This exclusion approach is likely to be more accurate than the 'leave one out' methodology by Paetkau *et al.* (2004) because it does not require that all true source populations be sampled. Excluded individuals were then reassigned to a source population when the probability of assignment was greater than 10%. When an excluded individual was reassigned to more than one population ($P > 0.10$), it was left unassigned. Those individuals that could not be reassigned to any of the other populations were considered to have originated from a non-sampled location.

Trans-Tasman migration rates were determined using the coalescent approach implemented in MIGRATE v 3.2 (Beerli, 2010). Migration rates between clusters as well as effective population sizes were determined under the maximum likelihood strategy (Beerli and Felsenstein, 1999) with variable mutation rates using a Brownian motion model. Results are expressed as M (m/μ), which is the mutation-scaled immigration rate that represents the importance of variability brought into the population by immigration compared with the variability by mutation, and Θ ($4N_e\mu$), which is the mutation-scaled effective population size. The parameters were set as the following and averaged across two independent runs: 10 short chains with 1 000 000 genealogies sampled; 3 short chains with 10 000 000 genealogies sampled; and a burn-in of 10 000 genealogies for each chain. Results are presented with 95% confidence intervals.

Selection pressure and effective population sizes

Although it is generally assumed that microsatellite loci are selectively neutral, linkage to regions of the genome that are under selection can often lead to skewed estimates of connectivity (Selkoe and Toonen, 2006). As a result, screening markers to test for neutrality are important for any connectivity study. To identify any outlier loci that may be affected by selection, we applied the method by Beaumont and Nichols (1996) in the selection detection workbench LOSITAN (Antao *et al.*, 2008). This method plots F_{ST} values against heterozygosity and tests for conformity to the expected null distribution of Wrights (1951) Island Model. Analysis was performed with 50 000 simulations under both infinite allele and stepwise mutation models with a forced and 'neutral' mean F_{ST}.

RESULTS

Genetic diversity

MICRO CHECKER found no evidence of large-allele drop out and detected no evidence of scoring error due to stutter or the presence of null alleles. There was no evidence of linkage disequilibrium between any pair of loci across all sample sites following standard Bonferroni corrections. All populations exhibited a significant global heterozygote deficiency (Table 1) with inbreeding coefficients (F_{IS}) ranging from 0.047 to 0.101. Deviations from Hardy–Weinberg equilibrium at the locus level varied across sampling locations, although no population showed a significant deficiency at all loci (Table 1: Supplementary Material). The eight microsatellite loci exhibited a wide range of polymorphism: the number of alleles per locus ranged from 10 to 76 and the number of alleles per population ranged from 109 to 161 (Table 2). Genetic diversity was lowest at Stewart Island across all measures and showed significant heterozygote deficiencies at seven out of eight loci (Table 1; Supplementary Material) but did not exhibit a very strong overall heterozygote deficit relative to other populations. Heterozygosity can often be relatively insensitive to population bottlenecks and can remain high despite a significant loss of allelic diversity (Allendorf, 1986).

Population genetic structure

Our analysis revealed significant population structure of *J. edwardsii* stock across the Tasman Sea and within New Zealand (F_{ST} of 0.018, $P = 0.010$). Although analysis of molecular variance indicated that only a small proportion (2%) of genetic variation could be attributed to differences between sampling sites, significant F'_{ST} values were detected at 19 out of 26 (73%) pairwise comparisons following standard Bonferroni corrections (Table 3). Stewart Island and South Australia populations were significantly different from all other populations sampled. The highest values of genetic differentiation occurred between Kaikoura and South Australia ($F'_{ST} = 0.118$).

Table 2 Allele size variation (standardized allelic richness) and total number of alleles per locus (*N*) at 8 microsatellite loci

Locus	*HG*	*SI*	*CHI*	*WEL*	*KAI*	*SWC*	*SA*	*TAS*	*N*
je_17	10.91	10.83	10.96	9.00	10.99	10.00	9.90	14.58	17
je_40	18.65	19.40	16.91	10.00	16.57	17.00	21.31	20.47	30
je_107	4.92	5.83	5.98	4.87	5.92	8.00	6.83	6.83	10
je_NS	27.14	35.47	33.67	34.15	37.29	33.00	40.50	33.78	76
je_JM	14.83	13.90	21.82	16.74	15.66	20.00	19.64	19.33	31
je_O5	17.74	19.33	17.91	12.87	24.23	20.00	21.47	21.47	30
je_LZ	25.14	19.31	22.82	12.00	25.96	26.00	21.48	26.29	49
je_9M	11.74	11.82	9.98	8.00	13.49	13.00	11.74	14.41	19
Mean	16.75	13.63	17.63	19.38	17.50	18.38	19.63	20.25	32.75
Total	134	109	141	155	140	147	157	161	
UHe	0.86	0.83	0.85	0.87	0.84	0.85	0.88	0.88	
A_P	4	3	7	15	4	7	7	15	

Abbreviations: CHI, Chatham Islands; HG, Hauraki Gulf; KAI, Kaikoura; SA, South Australia; SI, Stewart Island; SWC, SouthWest Coast; TAS, Tasmania; WEL, Wellington.
Genetic diversity indices such as total number of alleles per population, mean number of alleles per loci, Nei's unbiased heterozygosity (Hue), and number of private alleles (A_P) and are also shown.

Table 3 Pairwise fixation index values F_{ST} (above diagonal) and standardized values F'_{ST} (below diagonal)

	HG	*SI*	*CHI*	*WEL*	*KAI*	*SWC*	*SA*	*TAS*
HG		**0.016**	**0.006**	**0.006**	**0.009**	**0.007**	**0.014**	**0.003**
SI	**0.106**		**0.013**	**0.017**	**0.015**	**0.016**	**0.016**	**0.014**
CHI	**0.044**	**0.082**		**0.007**	**0.007**	0.003	**0.015**	**0.004**
Well	**0.042**	**0.115**	**0.048**		**0.006**	0.004	**0.014**	**0.003**
KAI	**0.060**	**0.089**	**0.047**	0.040		0.004	**0.017**	0.008
SWC	**0.046**	**0.103**	0.022	0.026	0.024		**0.012**	0.004
SA	**0.106**	**0.107**	**0.108**	**0.109**	**0.118**	**0.093**		0.004
TAS	0.023	**0.096**	0.029	0.026	**0.059**	0.029	0.031	

Abbreviations: CHI, Chatham Islands; HG, Hauraki Gulf; KAI, Kaikoura; SA, South Australia; SI, Stewart Island; SWC, SouthWest Coast; TAS, Tasmania; WEL, Wellington.
Bold values indicate significance based on 10 000 permutations with a Bonferroni adjusted *P*-value of 0.002.

Pairwise comparisons between the SouthWest Coast, Wellington and Kaikoura were low and non-significant. Interestingly, only two of the sampled locations from New Zealand (Stewart Island and Kaikoura) were significantly different from the Tasmania sampling location. Isolation by distance plots (Figure 1: electronic Supplementary Material) showed a weak but significant positive correlation between F'_{ST} and oceanographic distance ($R^2 = 0.16$, $P = 0.037$). When the Stewart Island sampling location was excluded from the analysis, the isolation by distance plot showed a much stronger correlation ($R^2 = 0.480$, $P < 0.001$).

Principle coordinate analysis plots (Figure 2) show the genetic relationships between the sampled locations, and results were largely consistent across the three measures of differentiation (F_{ST}, F'_{ST} and D_{LR}). All plots showed a close relationship among the New Zealand sample sites, except for Stewart Island, which was as different to the New Zealand grouping as South Australia. The Tasmania sample location appeared as an intermediate between the New Zealand and South Australia populations, which is consistent with its geographical location. The main discrepancy between the three measures was the level of separation within the New Zealand group, particularly relating to the Hauraki Gulf sample site. Principle coordinate analysis using standardized values revealed a more tightly clustered New Zealand group than produced by the F_{ST} matrix. The separation of the Hauraki Gulf population from the New Zealand cluster was most evident in the principle coordinate analysis based on the D_{LR} distance matrix.

The genetic divisions identified above were further supported by STRUCTURE. The optimal number of clusters according to Evanno *et al.* (2005) as implemented in STRUCTURE HARVESTER was determined to be $K = 4$ (Figure 3, Figure 2; electronic Supplementary Material): a central New Zealand cluster (Wellington, Kaikoura, Chatham Islands and SouthWest Coast), a northern New Zealand cluster (Hauraki Gulf), a southern New Zealand cluster (Stewart Island) and an Australian cluster (Tasmania, South Australia). Despite the evidence suggesting that the sampling locations represented four genetically discrete populations, analysis of molecular variance indicated that less than 2% of genetic variation could be partitioned between clusters using this scenario. Standardized fixation indices between clusters were all significant and ranged from 0.036 to 0.106 (Table 4).

Trans-Tasman dispersal

Assignment tests were performed by Geneclass v 2.0 to identify the relative contribution of the Australian stock to the New Zealand fishery. F_{ST} values, sample size and the number of markers can provide a measure of confidence to the results of assignment tests, particularly when marker variability is standardized (Cornuet *et al.*, 1999). Although population differentiation was relatively low between sample sites, we used the clustering scenario identified by STRUCTURE ($K = 4$, $F'_{ST} = 0.072$) for the assignment tests, increasing the likelihood of correct exclusion from groups of samples (Cornuet *et al.*, 1999; Berry *et al.*, 2004). As a result, we are confident that this analysis provided an accurate representation of immigration across the Tasman Sea.

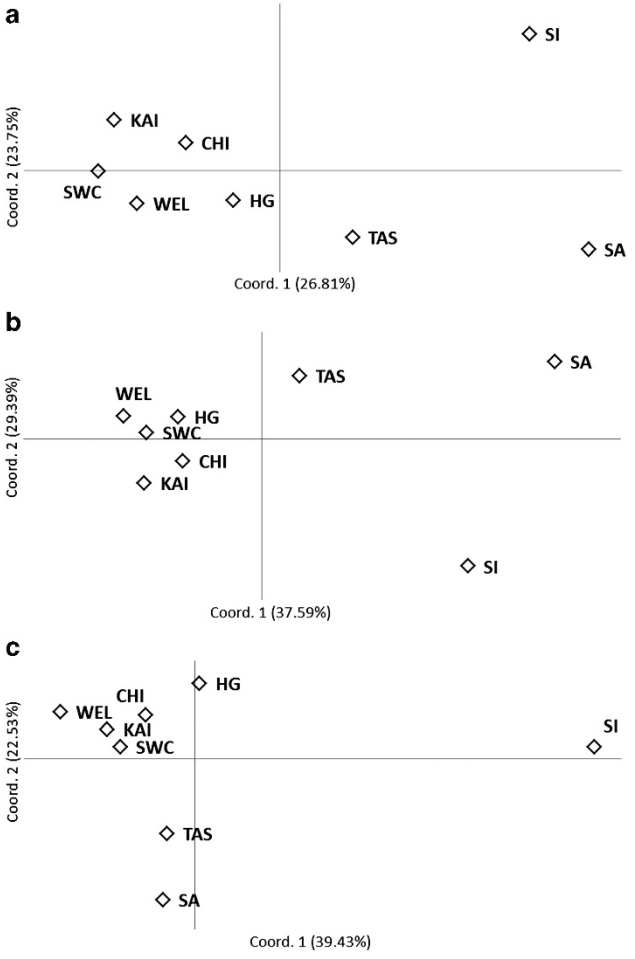

Figure 2 Principle coordinate analysis (PCA) implemented in GENEALEX v 6.3 of pairwise (**a**) F_{ST}, (**b**) F'_{ST} and (**c**) D_{LR} values between populations.

Under an exclusion approach, roughly nine percent of the lobster sampled from the central New Zealand locations (SouthWest Coast, Wellington, Kaikoura and Chatham Islands) were identified as *first generation migrants* on the basis of an a threshold of $P < 0.05$ (Table 5). Three of those individuals were determined to have originated from Australia and one individual near Stewart Island. The majority of excluded individuals, however, originated from non-sampled locations. Two individuals sampled in the far north of New Zealand (Hauraki Gulf) were also identified to have come from Australia. There was no evidence from assignment tests that the far north of New Zealand acts as a larval source for populations to the south.

Maximum likelihood trans-Tasman migration rates (M) determined in MIGRATE were low and ranged from 1.54 (to Stewart Island)

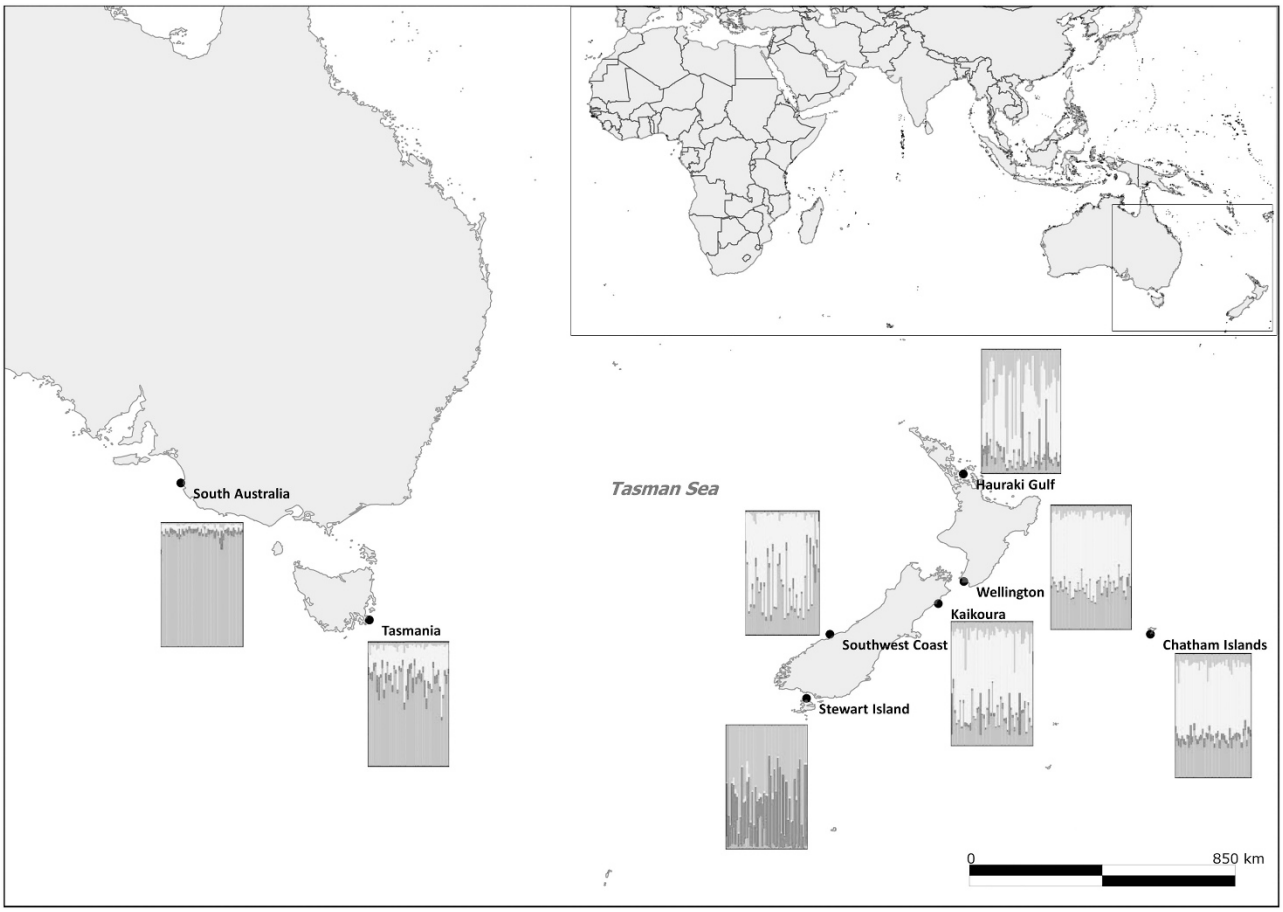

Figure 3 Bayesian clustering analysis using STRUCTURE 2.3.2 for *J. edwardsii* sample locations. Sampling locations are along the *x* axis and membership coefficient in each predefined cluster (*K*) is along the *y* axis. $K=4$ clustering scenario according to STRUCTURE HARVESTER. Results were averaged across 10 runs with CLUMP and visualized with DISTRUCT.

to 3.13 (to central New Zealand) (Table 6). Migration rates were consistent with results from assignment tests and showed that the central New Zealand cluster received relatively high amounts of gene flow from Australia compared with the other clusters; migration rates to New Zealand were more than two times higher than to Stewart Island. Estimates of the mutation scaled effective population size (Θ) were lowest for Stewart Island (4.76) and highest for Australia (10.87). Hauraki Gulf and the central New Zealand clusters showed similar values. Assuming a mutation rate of 10^{-4} (Gonzalez and Zardoya, 2007), we were able to translate these values into estimates of N_e that ranged from 1189 (Stewart Island) to 2717 (Australia).

Selection pressure and effective population sizes

In order to identify other evolutionary processes other than gene flow that could be influencing the patterns of population structure, an outlier loci analysis to test for selection pressure was conducted in LOSITAN. On the basis of the results from this analysis, there was no indication that any loci developed by Thomas and Bell (2011) were experiencing selection.

DISCUSSION

Despite *J. edwardsii* having one of the longest larval durations known of all marine species, having a wide distribution around New Zealand and Southern Australia, and being previously found to have genetic homogeneity throughout its range (Ovenden *et al.*, 1992), we found significant genetic structuring and evidence of restricted gene flow between certain regions, suggesting that *J. edwardsii* is not a single panmictic population. Although the levels of genetic differentiation were low, consistent patterns of differentiation were identified between Australia and New Zealand and also within New Zealand using multiple analysis methods. We also detected a strong pattern of isolation by distance, suggesting that distance is a barrier to gene flow, even though *J. edwardsii* has one of the longest known pelagic larval durations. Our analyses highlight the need to re-evaluate the management of *J. edwardsii* stocks and also the need to re-examine other species that are presumed to form panmictic populations on the basis of traditional molecular markers. The failure to accurately identify the biological boundaries of a harvested species can have dramatic effects on the sustainability of that resource (Allendorf *et al.*, 2008).

Consistency with oceanographic dispersal models in New Zealand

We aimed to use our genetic data to test the consistency between molecular and oceanographic modeling approaches for measuring connectivity. By comparing our results with an earlier study by Chiswell and Booth (2008), we are able to determine whether the prevailing current regimes in the region are likely to be the predominant forces driving the population structure and also explore the significance to the levels of genetic differentiation we reported.

Table 4 Hierarchal analysis of molecular variance was used to estimate levels of genetic differentiation between sampling sites ($n=8$) and clusters ($K=4$) identified by STRUCTURE

	Source	do	SS	MS	Est. var.	%
Sites	Among pops	7	94.718	13.531	0.131	2
	Within pops	368	2708.327	7.360	7.360	98
	Total	375	2803.045		7.491	100
Clusters	Among pops	3	52.870	17.623	0.124	2
	Within pops	372	2750.175	7.393	7.393	98
	Total	375	2803.045		7.516	100

	Stewart Island	Hauraki Gulf	New Zealand	Australia
Stewart Island	—	**0.106**	**0.084**	**0.094**
Hauraki Gulf	**0.016**	—	**0.036**	**0.057**
Central New Zealand	**0.013**	**0.005**	—	**0.052**
Australia	**0.013**	**0.007**	**0.007**	—

Abbreviations: do, degree of freedom; Est. vary, estimate variation; MS, mean square; pops, populations; SS, sample size.
Pairwise fixation index values between clusters (F_{ST}) below diagonal and standardized values (F'_{ST}) above diagonal. Bold values indicate significance on the basis of 10 000 permutations with a Bonferroni adjusted *P*-value of 0.01.

Table 5 Assignment tests conducted in GeneClass v. 2.0 to determine rates of trans-Tasman connectivity

Population	Excluded individuals	Per cent of population excluded	Assigned population				Not assigned
			SI	HG	CNZ	AUS	
Stewart Island	6	12.77	—	0	0	0	6
Hauraki Gulf	5	10.42	0	—	0	2	3
New Zealand	17	9.18	1	0	—	3	13

Abbreviations: AUS, Australia; CNZ, Central New Zealand; HG, Hauraki Gulf; SI, Stewart Island.
Tests were based on clustering scenario identified by STRUCTURE ($K=4$)). Detection of first-generation migrants was done using an exclusion threshold approach, where an individual was excluded from their corresponding sampling site when the probability of exclusion was >95%. Individuals that were excluded were assigned to another population when the probability of assignment was above a more conservative threshold of >0.10. Individuals that could not be reassigned to any of the sampled populations with a *P*-value >0.10 were considered to have originated from a non-sampled location.

Table 6 Effective population sizes and migration rates determined by MIGRATE

Group	Migrate				
	θ	95% CI	N_e	M	95% CI
Australia	10.87	10.64–11.85	2717.38	—	
Hauraki Gulf	9.21	8.99–9.87	2301.25	1.73	1.69–1.86
Stewart Island	4.76	4.64–5.08	1189.13	1.54	1.50–1.67
New Zealand	8.85	8.73–9.32	2213.50	3.13	3.07–3.29

Migrate results are presented as θ ($4N_e\mu$) and M (m/μ). In all, 95% confidence intervals are presented.
N_e was determined assuming a microsatellite mutation rate of 10^{-4}.

As we hypothesized, there is little evidence to suggest that the four geographic regions responsible for larval dispersal proposed by Chiswell and Booth (2008) represented genetically discrete stocks. Rather, our results provide genetic evidence for high levels of larval exchange among all regions across New Zealand (Table 2; electronic Supplementary Material). With the exception of sample sites in the far north and far south of the country, all of the sample locations showed high levels of genetic homogeneity. This includes sample sites on either side of the Cook Straight, as well as the geographically isolated Chatham Island location, of which we found no evidence to support genetic divergence from the mainland. These findings are consistent with the majority of genetic connectivity studies on marine species in New Zealand that have reported no genetic break between the North and South Island across the Cooke Strait, although other North-South breaks have been reported (see Gardner *et al.*, 2010 for a review).

Chiswell and Booth (2008) determined that nearly 95% of the larvae that recruit to CRA 8 are hatched within the CRA 8 boundary, and, although CRA 8 acts as a source of larvae to other areas around New Zealand, very few larvae that recruit to this region were determined by the model to have originated from CRA areas to the north. Our results support these findings with Stewart Island exhibiting signs of a self-recruiting population, as it had the lowest levels of genetic diversity (mean number of alleles, total alleles, private alleles and unbiased heterozygosity) and the smallest effective population size. Assignment tests also revealed that no individual sampled at Stewart Island was likely to have originated from northern sampling locations. On the basis of results from both studies, we propose that populations around Stewart Island (and likely other areas of CRA 8) are not reliant on outside larval sources, including recruits from Australia or Tasmania, to maintain healthy stock levels.

Trans-Tasman connectivity

The SouthWest coast of New Zealand supports a productive *J. edwardsii* fishery with high levels of annual recruitment (Booth and Breen, 1992); however, there are no apparent oceanographic retention mechanisms in the region to trap larvae and facilitate self-recruitment (Heath, 1980; Chiswell *et al.*, 2003). This implies that the larvae recruiting to this coast are coming from another source. It has been previously suggested that because of the lack of genetic differentiation between New Zealand and Australian populations (Ovenden *et al.*, 1992), and the detection of mid-late stage phyllosoma larvae in Tasman Sea (Booth *et al.*, 1990; Booth and Ovenden, 2000), gene flow is occurring across the Tasman Sea at levels high enough to maintain west coast lobster populations in New Zealand.

The oceanographic model developed by Chiswell *et al.* (2003) tracking passive drifting particles across the Tasman Sea determined that dispersal from the west was 'likely to be a viable mechanism maintaining lobster populations in New Zealand.' The model showed that roughly 8–14% of *J. edwardsii* larvae released from southeast Australia can successfully arrive in New Zealand within the pelagic larval durations of the species. Despite identifying significant levels of genetic differentiation across the Tasman Sea, the results from our analyses are consistent with these findings and support the possibility of larval exchange between the two countries. In particular, our results revealed low levels of differentiation between Tasmania and the New Zealand populations, particularly the SouthWest Coast sample site, which is likely to be the main region of recruitment for Australian-derived larvae (Chiswell *et al.*, 2003). The high level of genetic differentiation between South Australia and New Zealand, however, suggests that populations from South Australia are unlikely contributors to the New Zealand fishery. Rather, trans-Tasman larvae

recruiting to New Zealand originate along the southeast coast of Australia and Tasmania.

Trans-Tasman migration rates from this analysis suggest that dispersal across the body of water occurs at low levels. Although the dispersal model indicated that ~9–14% of the larvae originating on the east coast of Australia could reach New Zealand, the true rate of demographic connectivity is likely to be much lower as a result of pre- and post-settlement mortality. According to the first-generation migrant analysis, less than 2% of adult rock lobster in New Zealand originates from Australia. We therefore conclude that Australian populations are likely only a small contributor to the New Zealand fishery.

Considering that recruitment patterns of marine species can be highly sporadic across time (for example, Wooster and Bailey, 1989), it is possible that dispersal across the Tasman Sea for *J. edwardsii* may occur during some years but not others. It is important to note that this study did not address temporal variation, and the data here possibly reflect only a single recruitment event (assuming that all sampled individuals are from the same cohort). Discrete cohorts often have markedly different genetic signatures (Planes and Lenfant, 2002) resulting from sweepstakes reproductive success, whereby a small proportion of adults account for the majority of the recruitment (Hedgecock *et al.*, 2007). Consequently, quantifying the dependence of the New Zealand rock lobster fishery on recruitment from Australia with the levels of accuracy needed to inform and benefit management practices would require further temporal sampling.

Population structure of *J. edwardsii* in New Zealand

Our microsatellite analysis revealed significant population structure within New Zealand and contrasts with a previous analysis by Ovenden *et al.* (1992), which found populations across New Zealand and Australia to be panmictic based on mitochondrial DNA data. The results from this analysis suggest that there are likely three genetically discrete populations throughout New Zealand: (1) the far north, (2) central (both islands) and (3) far south.

Despite identifying significant levels of differentiation between a number of New Zealand sample sites, results indicate that centrally located populations in New Zealand form a single-homogenous population characterized by high levels of gene flow between the regions. The consistencies with the oceanographic model developed by Chiswell and Booth (2008) suggest that the genetic homogeneity reflects contemporary patterns of connectivity and the exchange of larvae via coastal surface currents. The Westland Current flows north along the east coast of the South Island and eventually meets the D'Urville current that sweeps through the Cook Strait. The Straight was formed between 16 000 and 6000 years ago as a result of sea level rise (Lewis *et al.*, 1994), and a lack of any evidence for an east–west genetic break suggests that it has had a major role in homogenizing populations of this species on opposing coasts. Furthermore, the Waiarapa Eddy is the largest retentive mechanism along the east coast of New Zealand and is thought to be the most significant oceanographic feature influencing recruitment in the region (Lesser, 1978; Chiswell and Roemmich, 1998; Chiswell and Booth, 2008). It has been well documented that *J. edwardsii* larvae become entrapped in the Wairarapa Eddy along the east coast of New Zealand (Lewis *et al.*, 1994; Chiswell and Booth, 1999) and are kept within successful recruitment distance from the coastline for the duration of their pelagic larval stage. This oceanographic feature may not only be an important retention mechanism to maintain high levels of recruitment along the east coast of the North Island but also have an important role in maintaining genetic homogeneity for this species, by trapping phyllosoma larvae from a number of sources and providing a homogenized supply of recruits to east-coast populations, including the Chatham Islands.

One of the most consistent results from our analysis was the strong genetic break between Stewart Island and New Zealand populations to the north. Contrary to these findings, there appears to be no major oceanographic mechanisms near Stewart Island that would prevent gene flow to the north. However, Chiswell and Booth (2008) showed that although CRA 8 is largely self-seeding, 70% (data not shown) of larvae hatched in this region are widely distributed throughout the country, traveling up the west coast and through the Cook Straight, and also up the east coast of the South Island (Table 2: electronic Supplementary Material). These dispersal patterns, however, are based on the release of larvae across the entire CRA 8 region and because the prevailing current that flows through the Foveaux straight moves in an easterly direction, any larvae released near Stewart Island would likely be transported up the east coast of the South Island in the Southland Current (Heath, 1985). The Southland Current eventually hits the Chatham Rise at ~45 S and is diverted offshore. Any larvae trapped in this current would be removed from the system entirely, which would explain the levels of differentiation detected with other regions of New Zealand. Further sampling, particularly along the south east coast, would clarify this matter and determine whether restricted gene flow is the primary evolutionary force driving the patterns of differentiation.

Selection pressure and other considerations

The extremely long larval duration of *J. edwardsii* combined with the wide-spread dispersal of larvae, as determined by the oceanographic model (Chiswell and Booth, 2008), suggests that the population structure of this species in New Zealand may not be exclusively a product of restricted gene flow. *J. edwardsii's* range extends over 10 degrees of latitude and consequently across a gradient of environmental variables (for example, sea surface temperature; Chiswell, 1994). If loci were acting under selection for such traits, then local adaptation to abiotic factors would inflate measures of population differentiation (Whitlock and McCauley, 1999; Neilson *et al.*, 2006; Coyer *et al.*, 2011). Results from the outlier loci analysis, however, revealed no evidence of selection pressure on any of the markers used in this analysis, and therefore it is unlikely that the patterns we report are the result of local adaptation to environmental conditions.

Despite having a large census population size capable of supporting high catch levels for more than half a century (Table 3; National Rock Lobster Management Group, (2010)), *J. edwardsii* populations in the CRA 8 region are characterized by low levels of genetic diversity and a small effective population size relative to other regions in New Zealand. Although the model (Chiswell and Booth, 2008) indicated that these results are likely a product of self-recruitment and subsequent isolation from the larger gene pool, it is also possible that harvesting may be responsible for the patterns observed. The conventional wisdom that marine species with large census population sizes, high fecundity and pelagic larvae are safe from the effects of intensive fishing pressure (from a conservation genetic diversity perspective) has proven to be a coarse misconception. Recent studies have shown that fisheries exploitation can lead to marked declines in genetic diversity and effective population sizes of the stock (Hauser *et al.*, 2002; Hutchinson *et al.*, 2003), although the biological or ecological effects of these declines (if any) are poorly understood.

Harvest levels for *J. edwardsii* across New Zealand have been variable across regions historically, but more consistent in recent years since the implementation of the Quota Management System. Fishing

pressure in CRA 8 over the last 20 years (since the implementation of the Quota Management System) has been more intensive than anywhere else in New Zealand. From 1990–2010, CRA 8 has made up 30% (+/−4.6% s.d.) of the total national catch each year with average annual landings of 776 tonnes (+/−140 s.d.), exceeding all other regions by at least 50% (Table 3: electronic Supplementary material). Historical catch data show that harvest pressure before the 1990s was well above these levels, peaking at 4500 tonnes in the early 1950s and slowly declining to roughly 900 tonnes by 1990 (National Rock Lobster Management Group, (2010)). Further, the region that extends from the Banks Peninsula through to western Foveaux Straight (CRA 7 and part of CRA 8) is the only part of the country where female size at maturity is greater than the minimum legal size (National Rock Lobster Management Group, (2010)), meaning that lobsters are likely to have been removed from the system before reaching reproductive maturity.

The degree to which intensive fishing pressure has influenced the genetic diversity and effective population size of lobster stock in this region remains unknown given that there are no historic samples from which we could directly compare our results. Nevertheless, these results add to the cumulating evidence that exploited marine species with large populations sizes may be in danger of losing genetic diversity as a result of harvesting (Hauser *et al.*, 2002). Given the economic importance of this species, this should be a focus of future research.

CONCLUSIONS

Applying the results of genetic connectivity studies to the management actions can be problematic for widely dispersing marine species, as it is often difficult to interpret the ecological importance of low levels of genetic differentiation (Lowe and Allendorf, 2010; Hedgecock *et al.*, 2007). However, by combining our genetic data with earlier modeling approaches, we have been able to considerably increase our confidence in the demographic connectivity patterns for *J. edwardsii* throughout New Zealand and southern Australia, an approach we advocate for other commercial and ecologically important species. Although it is possible that selection and harvesting may have influenced the genetic patterns that we have reported, it is likely that oceanographic processes have the most influence in determining genetic structure in *J. edwardsii*. Finally, we examined the genetic structure of a species at the extreme end of the dispersal spectrum and found genetic structure and evidence for source-sink dynamics, which demonstrate that homogenous genetic structure cannot be assumed for species with a long-lived planktonic phase.

DATA ARCHIVING

Data can be obtained from the Dryad repository doi:10.5061/dryad.3639h. Data files: *Jasus edwardsii* microsatellite analysis.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ACKNOWLEDGEMENTS

We thank commercial fishermen who provided the samples used in this study and the New Zealand Rock Lobster Industry Council, particularly Daryl Sykes and Malcolm Lawson. Funding for this study was provided by the Victoria University of Wellington Research Fund (URF), the NZ Rock Lobster Industry Council and Grow Wellington. We also thank Dr Peter Ritchie, Dr Shane Lavery and several other anonymous reviewers for their useful discussions and comments.

Allendorf FW (1986). Genetic drift and the loss of alleles versus heterozygosity. *Zool Biol* **5**: 181–190.
Allison GW, Gaines SD, Lubchenco J, Possingham HP (2003). Ensuring persistence of marine reserves: Catastrophes require adopting an insurance factor. *Ecol Appl* **13**: 8–24.
Antao T, Lopes A, Lopes RJ, Beia-Pereira A, Luikart G (2008). LOSITAN: a workbench to detect molecular adaptation based on a Fst-outlier method. *BMC Bioinformatics* **9**: 323.
Beaumont MA, Nichols RA (1996). Evaluating loci for use in the genetic analysis of population structure. *Proc Royal Soc B* **263**: 1619–1626.
Becker BJ, Levin LA, Fodrie FJ, McMillan PA (2007). Complex larval connectivity patterns among marine invertebrate populations. *Proc Natl Acad Sci USA* **104**: 3267–3272.
Beerli P (2010). *MIGRATE Documentation Version 3.2*. Florida State University: Tallahassee, FL, USA.
Beerli P, Felsenstein J (1999). Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. *Genetics* **152**: 763–773.
Bell JJ (2008). Connectivity between island marine protected areas and the mainland. *Biol Conservation* **141**: 2870–2820.
Bell JJ, Okamura B (2005). Low genetic diversity in a marine nature reserve: re-evaluating diversity criteria in reserve design. *Proc R Soc* **272**: 1067–1074.
Berry O, Tocher MD, Sarre SD (2004). Can assignment tests measure dispersal? *Mol Ecol* **13**: 551–561.
Berumen ML, Almany GR, Planes S, Jones GP, Saenz-Agudelo P, Thorrold SR (2012). Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. *Ecol Evol* **2**: 444–452.
Booth JD, Breen PA (1992). *Stock structure in the New Zealand red rock lobster, Jasus edwardsii*. Report No. 92/20 Ministry of Agriculture and Fisheries: Wellington, New Zealand.
Booth JD, Ovenden JR (2000). Distribution of *Jasus* spp (Decapoda: Palinuridae) phyllosomas in southern waters: implications for larval recruitment. *Mar Ecol Prog Ser* **200**: 241–255.
Booth JD, Phillips BF (1994). Early life history of spiny lobster. Proceedings from the fourth international workshop on lobster biology and management. *Crustaceana* **66**: 271–294.
Booth JD, Street RJ, Smith PJ (1990). Systematic status of the rock lobsters *Jasus edwardsii* from New Zealand and *J. novaehollandiae* from Australia. *NZ J Mar Freshw Res* **24**: 239–249.
Bradbury IR, Laurel B, Snelgrove PV, Bentzen P, Campana SE (2008). Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proc Royal Soc B* **275**: 1803–1809.
Chiswell S, Booth JD (1999). Rock lobster Jasus edwardsii larval retention by the Wairarapa Eddy off New Zealand. *Mar Ecol Prog Ser* **183**: 227–2440.
Chiswell S, Roemmich D (1998). The East Cape Current and two eddies: a mechanism for larval retention? *NZ J Mar Freshw Res* **32**: 385–397.
Chiswell SM (1994). Variability in sea surface temperature around New Zealand from AVHRR images. *NZ J Mar Freshw Res* **28**: 179–192.
Chiswell SM, Booth JD (2008). Sources and sinks of larval settlement in Jasus edwardsii around New Zealand: where do larvae come from and where do they go? *Mar Ecol Prog Ser* **354**: 201–217.
Chiswell SM, Wilkin J, Booth JD, Stanton B (2003). Trans-Tasman Sea larval transport: Is Australia a source for New Zealand rock lobsters? *Mar Ecol Prog Ser* **247**: 173–182.
Cornuet JM, Piry S, Luikart G, Estoup A, Solignac M (1999). New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics* **153**: 1989–2000.
Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner F (2007). Population connectivity in marine systems: an overview. *Oceanography* **20**: 14–21.
Cowen RK, Paris CB, Srinivasan A (2006). Scaling of connectivity in marine populations. *Science* **311**: 522–527.
Cowen RK, Sponaugle S (2009). Larval Dispersal and marine population connectivity. *Ann Rev Mar Sci* **1**: 443–466.
Coyer J, Hoarau G, Pearson G, Mota C, Jüterbock A, Alpermann T *et al.* (2011). Genomic scans detect signatures of selection along a salinity gradient in populations of the intertidal seaweed *Fucus serratus* on a 12 km scale. *Mar Genomics* **4**: 41–49.
Earl DA, VonHoldt BM (2011). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conserv Genet Res* **4**: 359–361.
Evano 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.
Excoffier L, Laval G, Schneider S (2005). *Arlequin* ver. 3.0: an integrated software package for population genetics data analysis. *Evol Biol Online* **1**: 47–50.
Gardner JPA, Bell JJ, Constable HB, Ritchie PA, Zuccarello GC (2010). Multi-species coastal marine connectivity: a literature review with recommendations for further research. *NZ Aquatic Environment Biodiversity Report* **58**: 1–47.
Gonzalez EG, Zardoya R (2007). Relative role of life-history traits and historical factors in shaping genetic population structure of sardines (*Sardina pilchardus*). *BMC Evolutionary Biology* **7**: 197–209.
Goudet J (1995). FSTAT (version 1.2): a computer program to calculate F-statistics. *Heredity* **86**: 485–486.

Hauser L, Adcock GJ, Smith PJ, Ramiréz JHB, Carvalho GR (2002). Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (Pagrus auratus). *Proc Nat Acad Sci USA* **99**: 11742–11747.

Heath R (1985). A review of the physical oceanography of the seas around New Zealand—1982. *New Zeal J Mar Freshwater Res* **19**: 79–124.

Heath RA (1980). Eastward oceanic flow past northern New Zealand. *NZ J Mar Freshwa Res* **14**: 169–182.

Hedgecock D, Barber PH, Edmands S (2007). Genetic approaches to measuring connectivity. *Oceanography* **20**: 70–79.

Hubisz M, Falush D, Stephens M, Pritchard J (2009). Inferring weak population structure with the assistance of sample group information. *Mol Ecol Resour* **9**: 1322–1332.

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010). Rising to the challenge of sustaining coral reef resilience. *Trends Ecol Evol* **25**: 633–642.

Hutchinson WF, Carvalho GR, Rogers S (2001). Marked genetic structuring in localized spawning populations of cod Gadus morhua in the North Sea and adjoining waters as revealed by microsatellites. *Mar Ecol Prog Series* **223**: 251–260.

Jakobsson M, Rosenberg NA (2007). CLUMPP: a cluster match- ing and permutation program for dealing with label switch- ing and multimodality in analysis of population structure. *Bioinformatics* **23**: 1801.

Jones GP, Planes S, Thorrold SR (2005). Coral reef fish larvae settle close to home. *Curr Biol* **15**: 1314–1318.

Kelly RP, Palumbi S (2010). Genetic structure among 50 species of the northeastern Pacific rocky intertidal community. *PLoS One* **5**: 1–13.

Kinlan BP, Gaines SD (2003). Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* **84**: 2007–2020.

Korbie DJ, Mattick JS (2008). Touchdown PCR for increased specificity and sensitivity in PCR amplification. *Nat Protoc* **3**: 1452–1456.

Lesser JHR (1978). Phyllosoma larvae of *Jasus edwardsii* (Hutton) (Crustacea: Decapoda: Palinuridae) and their distribution off the east coast of the North Island, New Zealand. *NZ J Mar Freshwa Res* **12**: 357–370.

Leis JM, van Herwerden L, Patterson HM (2011). Estimating connectivity in marine fish populations: what works best? *Oceanogr Mar Biol* **49**: 193–234.

Lewis KB, Carter L, Davey FJ (1994). The opening of the Cook Straight: interglacial tidal scour and aligning basins at a subduction to transform plate edge. *Mar Geol* **116**: 293–312.

Lowe WH, Allendorf FW (2010). What can genetics tell us about population connectivity? *Mol Ecol* **19**: 3038–3051.

Manel S, Gaggiotti OE, Waples RS (2005). Assignment methods:matching biological questions with appropriate techniques. *Trends Ecol Evol* **20**: 136–142.

Meirmans P (2006). Using the AMOVA framework to estimate a standardized genetic differentiation measure. *Evolution* **60**: 2399–2402.

Meirmans PG, Hedrick PW (2011). Assessing population structure: F(ST) and related measures. *Mol EcolResources* **11**: 5–18.

National Rock Lobster Management Group (2010) NRLMG (2010). Annual Report. http://www.fish.govt.nz/

Nei M. (1987). *Molecular Evolutionary Genetics*. Columbia Univ. Press: New York, NY, USA.

Nielsen EE, Hansen MM, Meldrup D (2006). Evidence of microsatellite hitch-hiking selection in Atlantic cod (*Gadus morhua L.*): implications for inferring population structure in nonmodel organisms. *Mol Ecol* **15**: 3219–3229.

Ovenden JR, Brasher DJ, White RWG (1992). mDNA analysis of the red rock lobster *Jasus edwardsii* shows an apparent absence of population subdivisions throughout Australasia. *Mar Biol* **326**: 319–326.

Paetkau D, Calvert W, Stirling I, Strobeck C (1995). Microsatellite analysis of population structure in Canadian polar bears. *Mol Ecol* **4**: 347–354.

Paetkau D, Slade R, Burden M, Estoup A (2004). Direct, real-time estimation of migration rate using assignment methods: a simulation-based exploration of accuracy and power. *Mol Ecol* **13**: 55–65.

Paetkau D, Waits LP, Clarkson PL, Craigheadg L (1997). An empirical evaluation of genetic distance statistics using microsatellite data from Bear (Ursidae) populations. *Genet Soc Am* **147**: 1943–1957.

Palumbi SR (2003). Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* **13**: 146–158.

Peakall R, Smouse PE (2006). GenAlEx 6: genetic analy- sis in Excel. Population genetic software for teaching and research. *Mol Ecol Notes* **6**: 288–295.

Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A (2004). GeneClass2: a software for genetic assignment and first-generation migrant detection. *Heredity* **95**: 536–539.

Planes S, Lenfant. P (2002). Temporal change in the genetic structure between and within cohorts of a marine fish, *Diplodus sargus,* induced by a large variance in individual reproductive success. *Mol Ecol* **11**: 1515–1524.

Polato NR, Concepcion GT, Toonen RJ, Baums IB (2010). Isolation by distance across the Hawaiian Archipelago in the reef-building coral Porites lobata. *Mol Ecol* **19**: 4661–4677.

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

Pritchard J (2010). Structure (Online). Website last modified in 2010 (accessed January 20 2012). Available at http://pritch.bsd.uchicago.edu/software/install_v.2.3.1.html

Rannala B, Mountain JL (1997). Detecting immigration by using multilocus genotypes. *Proc Natl Acad Sci* **94**: 9197–9201.

Rice WR (1989). Analyzing tables of statistical tests. *Evolution* **43**: 223–235.

Rosenberg NA (2004). DISTRUCT: a program for the graphical dis- play of population structure. *Mol Ecol Notes* **4**: 137–138.

Saenz-Agudelo P, Jones GP, Thorrold SR, Planes S. (2009). Estimating connectivity in marine populations: an empirical evaluation of assignment tests and parentage analysis under different gene flow scenarios. *Mol Ecol* **18**: 1765–1776.

Selkoe KA, Toonen RJ (2006). Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. *Ecol Lett* **9**: 615–629.

Selkoe KA, Toonen RJ (2011). Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. *Mar Ecol Prog Ser* **436**: 291–305.

Shanks AL, Grantham BA, Carr MH (2003). Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* **13**: 159–169.

Shears N, Babcock R (2003). Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Mar Ecol Prog Ser* **246**: 1–16.

Swearer SE, Caselle JE, Lea DW, Warner RR (1999). Larval retention and recruitment in an island population of a coral-reef fish. *Nature* **402**: 799–802.

Thomas L, Bell JJ (2011). Characterization of polymorphic microsatellite markers for the red rock lobster, *Jasus edwardsii* (Hutton 1875). *Conservation Genet Resour* **4**: 319–321.

Thorrold SR, Jones GP, Hellberg ME, Burton RS, Swearer SE, Neigel JE *et al.* (2002). Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *Bulletin of Marine Science* **70**: 291–308.

Underwood J N, Smith L D, Van Oppen M J H, Gilmour J P (2007). Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Mol Ecol* **16**: 771–784.

van Oosterhout C, Hutchinson W, Wills D, Shipley P (2004). MICRO- CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Mol Ecol Notes* **4**: 535–538.

Weersing KA, Toonen RJ (2009). Population genetics, larval dispersal, and demographic connectivity in marine systems. *Mar Ecol Prog Ser* **393**: 1–12.

Whitlock M C, McCauley D E (1999). Indirect measures of gene flow and migration: FST not equal to 1/(4Nm + 1). *Heredity* **82**: 117–125.

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

Wooster WS, Bailey KM (1989). Recruitment of marine fishes revisited. *In Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models*Beamish RJ, McFarlane. GA (Eds). Canadian Special Publication of Fisheries and Aquatic Science **108**: 153–159.

Wright S. (1951). The genetical structure of populations. *Ann. Eugethcs* **15**: 323–354.

Supplementary Information accompanies this paper on Heredity website (http://www.nature.com/hdy)