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Mitochondrial DNA analyses of the red rock lobster *Jasus edwardsii* supports an apparent absence of population subdivision throughout Australasia

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Abstract. Nucleotide sequence polymorphism in the mitochondrial genomes of 132 adult lobsters (*Jasus edwardsii*) collected from widespread locales across southern Australia and from New Zealand (April 1989 to June 1990) was assayed, using six restriction endonucleases, to test the hypothesis of a lack of genetic subdivision in a marine species with a long-lived planktonic larva. The mean amount of mtDNA diversity among the 132 mitochondrial genomes was 0.77%. Phenetic clustering and gene-diversity analyses, as well as pairwise comparison of the genetics of specimens from each, or grouped, locales did not detect the presence of genetic subdivision across approx 4600 km of Southern Ocean habitats. The inability of this study to detect population subdivision does not preclude fortutitous, active or habitat-specific larval settlement from producing and maintaining hidden groupings. If genetic homogeneity is maintained in this species by larval dispersal in ocean currents flowing to the east, then westerly populations may deserve special conservation status.

Introduction

Animals and the genes that they carry are not evenly distributed in space. They occupy distinct habitats which are defined by unique combinations of physical, chemical and biological features. The clustering of animals and their genes into large and small populations, with different densities and rates of intergroup exchange, has profound implications not only for the evolution of the species, but for the management of the species as a commercial resource.

In the absence of obvious boundaries to populations, subdivision within a species can be detected with genetic analyses. Allozyme frequency variation, among representative samples of a species, can be used to detect the presence of partially, or fully, isolated groups of animals (Richardson et al. 1986). This approach is only possible, however, in species which have a measurable amount of allozyme frequency variation throughout their range. Population subdivision in red rock lobsters (*Jasus edwardsii*) cannot be measured in this way. Smith et al. (1980) found an average of only 1.22 alleles per locus for 141 individuals at 32 protein loci. The proportion of these loci that were polymorphic (0.95 criterion) was only 3% and the overall heterozygosity for this species was a low 1.5%. This is generally the case in marine decapods.

In species with low levels of allozyme heterozygosity, nucleotide sequence polymorphism in the mitochondrial genome provides an alternative system which can be used to measure population subdivision (Takahata and Palumbi 1985, Rand and Harrison 1989, Lynch and Crease 1990). An added advantage of the use of mitochondrial DNA (mtDNA) for the study of population subdivision is that if distinct populations are found, their phylogeny can be estimated, as the genome is inherited intact from generation to generation (Lansman et al. 1983, Avise and Vrijenhoek 1987). Using mtDNA analysis, Edwards and Skibinski (1987) demonstrated that the mussel *Mytilus edilus* from south-western England consists of a series of genetically distinct populations. Oysters, *Crassostrea virginica* (Reeb and Avise 1990), and horseshoe crabs, *Limulus polyphemus* (Saunders et al. 1986), have been found to have significantly different mitochondrial genomes on either side of a point bisecting their continuous distribution along the south-eastern American coastline, implying reproductive isolation.

Adult *Jasus edwardsii* are found on the continental shelf around southern Australia, including Tasmania, and in southern and eastern New Zealand (George and Main 1967). Each mature female produces 37 000 to 800 000 eggs each year (Booth et al. 1990). The eggs are brooded by the female for 5 to 6 mo prior to hatching. Larval development consists of numerous phases: naupliosoma, phyllosoma and puerulus. Like those of all palinurid lobsters, the larvae of *J. edwardsii* are capable of vertical movement and are assumed to be carried passively by wind-induced currents, displacements by upwellings, and eddy systems (Phillips and McWilliam 1986). At the end of the 6 to 23 mo larval life, pueruli actively swim

toward shallow, rocky reefs, where settlement and recruitment into the adult habitat occurs (Booth et al. 1990). In New Zealand, a small proportion of immature females and males of a similar size move 5 km or more along the coastline each year (Street 1969). Similar movements are undertaken by lobsters in Australia (Lewis 1983).

Red rock lobsters (*Jasus edwardsii*) previously consisted of two nominal species: *J. novaehollandiae* (Australia) and *J. edwardsii* (New Zealand). In an allozyme analysis of 33 loci, Smith et al. (1980) only found significantly different gene frequencies between Australian and New Zealand samples at the lactose dehydrogenase locus. Following a detailed analysis of morphology and larval distribution, and further allozyme results, Booth et al. (1990) suggested that the two species be synonomized. Most recently, Brasher et al. (1991) showed that the mitochondrial genomes of samples of lobsters from Australia and New Zealand are similar and that they constituted a closely related and major phylogenetic group within the genus.

The aim of this study was to use mtDNA nucleotide sequence polymophism to test for the presence of macro- and micro-scale population subdivision in the red rock lobster *Jasus edwardsii*. The results of this study are relevant to the management of the commercial lobster fishery in Australia and New Zealand as well as to the study of the process of evolution in marine species with teleplanic larvae.

Materials and methods

Jasus edwardsii adults were sampled on a single occasion from 13 localities between April 1989 and June 1990 (Table 1). Nine localities were approximately equidistant along the southern Australian coastline from the state of South Australia to Victoria, including western Bass Strait, southern and eastern Tasmania and eastern Bass Strait. Samples were collected from one Western Australian and one New South Wales locality. New Zealand populations were sampled once from the east coast of the North Island and once from the east coast of the South Island (Fig. 1). Most individuals were caught in commercial lobster pots at 4 to 30 m; however, some individuals were captured by divers and some were collected at 70 m (Temma) and 120 m (Flying Cloud Point).

Antennal glands were stored in liquid nitrogen until required for mtDNA extraction. Mitochondrial DNA was recovered, cleaved with restriction endonucleases, and visualized by agarose electrophoresis as described by Brasher et al. (1991). The presence or absence of restriction sites recognized by *Afl*II (recognition site CTTAAG), *Ava*I (CPyCGPuG), *Ban*I (GGPyPuCC), *Bst*YI (PuGATCPy), *Eco*RV (GATATC) and *Hin*dIII (AAGCTT) was determined within the mtDNA from each lobster. To facilitate the scor-

Table 1. *Jasus edwardsii*. Collection location, sample size (*n*) and haplotype designations

Location	(*n*)	Haplotypes
Western Australia		
Esperance (34°00′S; 122°00′E)	(15)	AAAAAA (3), AAABAB (2), AAACAB (3), AAAEAA (1), AAAFAB (1), AAAMAB (1), AACAAA (1), AADAAA (1), ADABAH (1), CBANAN (1)
South Australia		
Bucks Bay (38°53′S; 140°23′E)	(8)	AAAAAA (1), AAAAAJ (1), AAALAB (1), AAGKAA (1), AAJAAA (1), BBAJJA (1), HAAAAA (1), IAABAB (1)
Port Lincoln (34°46′S; 135°52′E)	(10)	AAAAAA (2), AAABAA (1), AADAAA (1), AADCAG (1), AAEAAA (1), AAGAAA (1), ABAFAB (1), CAABAB (1), IAABAB (1)
Victoria		
Port Fairy (38°23′S; 142°18′E)	(10)	AAAAAM (1), AAACAB (1), AAAEAA (1), AAAIAB (1), AADAAA (1), AAGAAA (1), AAHCAB (1), ABAFAB (2), ABABAD (1)
Bass Strait		
King Island (39°52′S; 143°49′E)	(10)	AAAAAA (1), AAABAB (1), AAABAL (1), AAACAB (1), AAADAB (1), AAAMAB (1), AADAAA (1), AAFAAA (1), AAGAAA (1), CAACAB (1)
Flinders Island (40°00′S; 148°16′E)	(10)	AAAAAA (1), AAABAB (1), AAACAB (2), AAAEAA (1), AACAAA (1), AADDAB (1), AAEAAA (1), ADAAAA (1), BAFAAA (1)
Tasmania		
Temma (41°14′S; 144°35′E)	(11)	AAAAAA (2), AAAADA (1), AAACAB (1), AAAEAA (1), AADAAA (1), BAAAAA (1), BAABAB (1), CAADAB (1), DAAHBA (1), FCABEB (1)
Flying Cloud Point (43°31′S; 145°55′E)	(16)	AAAAAA (4), AAAACB (1), AAABAB (3), AAABAF (1), AAAEAG (1), AAAFAB (1), AAAIAB (1), AADAAE (1), AAGGAA (1), ADABAD (1), EBAFAC (1)
Sullivans Point (43°33′S; 146°55′E)	(13)	AAAAAA (2), AAACAB (1), AAAIAB (2), AABAAA (1), AACAAA (1), AAEAAA (1), ABAFAB (3), CAABAB (1), GCABAB (1)
Bicheno (41°57′S; 148°19′E)	(6)	AAABAA (1), AAACAB (1), AADAAA (1), ADABAD (1), ADABAH (1), JEABAB (1)
New South Wales		
Batemans Bay (35°45′S; 150°20′E)	(4)	AAAAAA (1), AAKCAB (1), AFABAB (1), IAABAB (1)
New Zealand		
Gisborne (38°37′S; 178°00′E)	(10)	AAAAAA (3), AAACAB (3), AADAAA (2), AAFAAA (1), AAFGAA (1)
Moeraki (45°31′S; 170°54′E)	(9)	AAAAAA (3), AAAAAE (1), AAABAB (1), AAACAB (1), AAGAAK (1), CAACAB (1), EAABAB (1)
Total	(132)	

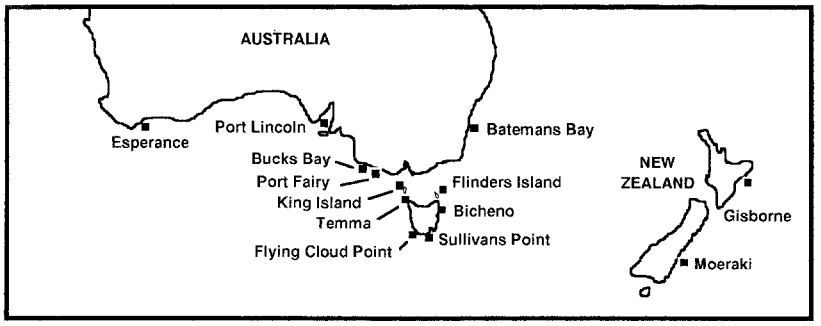

Fig. 1. Locations from which *Jasus edwardsii* were collected during study

ing of sites from restriction fragment profiles, a restriction map for the genome of a single individual was constructed for these six enzymes, as well as for *Pvu*II, *Nco*I and *Bg*II, using double-digestion techniques (Ovenden et al. 1991).

The null hypothesis of the absence of genetic subdivision within *Jasus edwardsii* was tested in two ways. In the first test, nucleotide sequence diversity was calculated between each pair of mitochondrial genomes using the maximum likelihood method of Nei and Tajima (1983). Standard errors of the mean amount of mtDNA sequence divergence between pairs of populations were then calculated by the method of Nei and Jin (1989) using the unweighted pair group method with arithmetic means (UPGMA, Nei 1987, p. 293) to estimate genome phylogeny. If the mean amount of mtDNA sequence divergence between a pair of populations was larger than zero, as judged by the relative magnitude of the standard error, then genetic subdivision may be present. Secondly, the presence of genetic subdivision was tested by nucleotide (G_{ST}, Takahata and Palumbi 1985; N_{ST}, Lynch and Crease 1990) and haplotype diversity (G'_{ST}, Rand and Harrison 1989) analyses. A significantly large value of G_{ST}, N_{ST} or G'_{ST} would indicate that reproductively isolated lobster populations were represented among the samples. The significance of G_{ST} was estimated by bootstrapping (Palumbi and Wilson 1990). Jackknifed estimates of G'_{ST}, in which one sample population was omitted each time (Ovenden and White 1990), evaluated the significance of G'_{ST}.

For both tests of the presence of genetic subdivision, a sample of lobsters from a particular collection location was not necessarily assumed to represent a single population. Samples from collection locations were grouped together according to the presence of possible isolating mechanisms between hypothesized interbreeding populations. Two classes of location groupings were made (Table 2). The first assumed that populations may be reproductively isolated due to their presence in different current flows. Under this scenario, gene flow between adult populations may be curtailed due to the lack of exchange of larvae between water masses. The second type of locality grouping assumed that populations may be reproductively isolated due to their occurrence in physico-chemically different habitats.

The phylogeny for an alphabetic compilation of mtDNA haplotypes was estimated using the UPGMA. The validity of the topology of the UPGMA tree was assessed by the relative magnitude of standard errors on appropriate branch points (Nei et al. 1985).

Results

A total of 67 restriction sites (11 *Afl*II, 7 *Ava*I, 12 *Ban*I, 16 *Bst*YI, 9 *Eco*RV and 12 *Hin*dIII) were identified amongst the 132 *Jasus edwardsii* mitochondrial genomes (Table 3). The relative locations of 36 restriction sites in the genome of a representative lobster are shown in Fig. 2. The size (mean ± standard error) of the lobster genome was estimated to be 15966 ± 350 nucleotide pairs

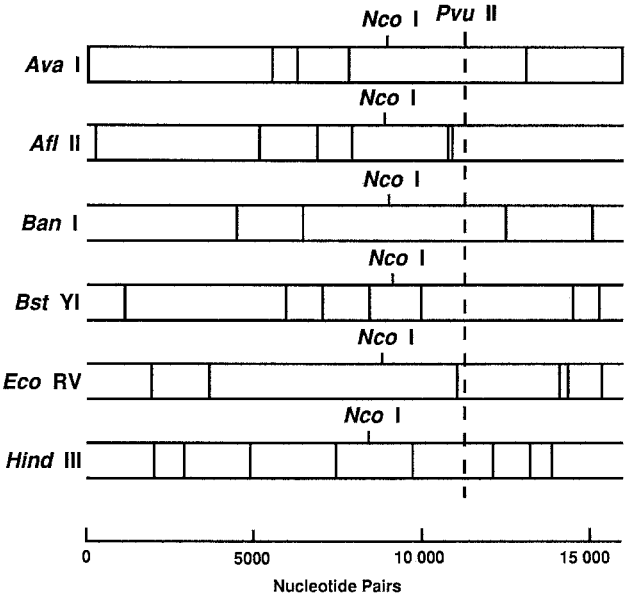

Fig. 2. *Jasus edwardsii*. Restriction endonuclease cleavage map (Haplotype AAAAAA). The single *Pvu*II restriction site, which was used in mapping experiments, is fixed. To illustrate error associated with mapping restriction sites, position of the single *Nco*I site is shown according to the results of double-digestion mapping experiments with each of the six restriction enzymes

from all successful endonuclease digests using only one representative morph from each gel.

With each restriction enzyme, 5 to 14 restriction site morphs were detected (10 *Afl*II, 6 *Ava*I, 11 *Ban*I, 14 *Bst*YI, 5 *Eco*RV and 14 *Hin*dIII; Table 3). The pairwise difference among morphs was the simple gain or loss of one or more restriction sites. For example, *Afl*II morph B possessed 5 *Afl*II sites. *Afl*II morph A possessed these 5 sites and 1 other, *Afl*II Site #6.

There were 55 different haplotypes (Table 1). Of the 55 haplotypes, 36 were represented by only one specimen. Of the 55 haplotypes, 6 were found in two or three lobsters. Haplotypes AAAEAA and AAAIAB were represented by 4 individuals each, ABAFAB by 6 individuals, and AAABAB and AADAAA by 8 individuals each. The most frequently identified haplotypes were AAACAB (14) and AAAAAA (22).

The haplotypes were clustered by UPGMA (Fig. 3) into two major groups of 25 each. The standard errors on

Table 2. *Jasus edwardsii.* Collection locations grouped for detection of reproductive isolation between hypothesized populations. The two groupings in Class I are based on the assumption that larval dispersal is primarily determined by hydrological factors; within each group, collection locations have been pooled into possible populations based on (1) major oceanic currents or water masses, and (2) predominant coastal eddy systems. The three groupings in Class II assume that pueruli settle and survive only in habitat having same environmental parameters as that of their parent population; possible populations within each group are based on (1) coastal substrate and freshwater composition in the Australasian region, (2) geographically disjunct marine provinces, and (3) locally distinct parameters

Class I
- Grouping 1
  - Northern East Australian Current:
    Batemans Bay, New South Wales; Gisborne, New Zealand
  - Southern East Australian Current:
    Flinders Island, Bass Strait; Sullivans Point and Bicheno, Tasmania; Moeraki, New Zealand
  - Great Australian Bight:
    Port Lincoln and Bucks Bay, South Australia; Port Fairy, Victoria; King Island, Bass Strait; Temma and Flying Cloud Point, Tasmania
  - Western Australia:
    Esperance
- Grouping 2
  - New Zealand inshore eddies:
    Gisborne and Moeraki, New Zealand
  - Bass Strait inshore eddies:
    Bucks Bay, South Australia; Port Fairy, Victoria; King and Flinders Island, Bass Strait; Temma and Bicheno, Tasmania
  - Southern Tasmanian inshore eddies:
    Flying Cloud Point and Sullivans Point, Tasmania
  - South Australian inshore eddies:
    Port Lincoln
  - Western Australian inshore eddies:
    Esperance

Class II
- Grouping 1
  - Australian carbonate sands, low freshwater runoff:
    Esperance, Western Australia; Bucks Bay and Port Lincoln, South Australia; Port Fairy, Victoria; King Island, Bass Strait; Temma and Flying Cloud Point, Tasmania
  - Australian quartzose sands, high freshwater runoff:
    Flinders Island, Bass Strait; Batemans Bay, New South Wales; Sullivans Point and Bicheno, Tasmania
  - New Zealand, high freshwater runoff:
    Gisborne and Moeraki
- Grouping 2
  - Western:
    Esperance, Western Australia
  - Central:
    Bucks Bay and Port Lincoln, South Australia; Port Fairy, Victoria; King and Flinders Island, Bass Strait; Temma, Flying Cloud Point, Sullivans Point, and Bicheno, Tasmania; Batemans Bay, New South Wales
  - Eastern:
    Gisborne and Moeraki, New Zealand
- Grouping 3
  - All collection locations separate

Table 3. *Jasus edwardsii.* Restriction sites scored; presence (1) and absence (0) for *Afl* II, *Ava* I, *Ban* I, *Bst* YI, *Eco* RV and *Hind* III morphs identified amongst 132 individuals. –: sites not scored

Morph	Site No.:															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Afl II																
A	1	1	1	1	1	1	0	0	0	0	0	–	–	–	–	–
B	1	1	1	1	1	0	0	0	0	0	0	–	–	–	–	–
C	0	1	1	1	1	1	0	0	0	0	0	–	–	–	–	–
D	0	1	1	1	1	1	1	0	0	0	0	–	–	–	–	–
E	1	1	1	1	1	1	0	1	0	0	0	–	–	–	–	–
F	1	1	1	1	0	1	1	0	0	0	0	–	–	–	–	–
G	1	1	1	1	0	1	0	0	0	0	0	–	–	–	–	–
H	1	1	1	1	1	0	0	0	1	0	0	–	–	–	–	–
I	1	1	1	1	1	1	0	0	0	1	0	–	–	–	–	–
J	1	1	1	1	1	1	0	0	0	0	1	–	–	–	–	–
Ava I																
A	1	1	1	1	1	0	0	–	–	–	–	–	–	–	–	–
B	1	1	0	1	1	0	0	–	–	–	–	–	–	–	–	–
C	0	1	1	1	1	0	0	–	–	–	–	–	–	–	–	–
D	1	0	1	1	1	0	0	–	–	–	–	–	–	–	–	–
E	1	1	1	1	1	1	0	–	–	–	–	–	–	–	–	–
F	1	1	1	1	1	0	1	–	–	–	–	–	–	–	–	–
Ban I																
A	1	1	1	1	1	0	0	0	0	0	0	0	–	–	–	–
B	1	1	1	1	1	1	0	0	0	0	0	0	–	–	–	–
C	1	1	1	1	1	0	1	1	1	1	0	0	–	–	–	–
D	1	1	1	1	1	0	0	0	0	0	1	0	–	–	–	–
E	1	1	1	1	1	0	1	1	0	0	0	0	–	–	–	–
F	1	1	1	1	1	0	0	1	0	0	0	0	–	–	–	–
G	1	1	1	1	1	0	1	1	0	0	0	0	–	–	–	–
H	1	1	1	1	1	0	0	0	0	1	0	0	–	–	–	–
I	1	1	1	1	1	0	0	0	0	0	0	1	–	–	–	–
J	1	1	1	0	1	0	0	0	0	0	0	0	–	–	–	–
K	1	1	1	1	0	0	0	0	0	1	0	0	–	–	–	–
Bst YI																
A	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
B	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
C	1	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0
D	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
E	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0
F	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0
G	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
H	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0
I	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0
J	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0
K	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0
L	1	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0
M	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0
N	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
Eco RV																
A	1	1	1	1	1	1	0	0	0	–	–	–	–	–	–	–
B	1	1	1	1	0	1	0	0	0	–	–	–	–	–	–	–
C	1	1	1	1	1	1	1	0	0	–	–	–	–	–	–	–
D	1	1	1	1	1	1	0	1	0	–	–	–	–	–	–	–
E	1	1	1	1	1	1	0	0	1	–	–	–	–	–	–	–
Hind III																
A	1	1	1	1	1	1	1	1	1	0	0	0	–	–	–	–
B	1	1	1	0	1	1	1	1	1	0	0	0	–	–	–	–
C	1	1	1	0	1	1	1	1	1	1	0	0	–	–	–	–
D	1	1	1	0	1	0	1	1	1	0	0	0	–	–	–	–
E	1	1	0	1	1	1	1	1	1	0	0	0	–	–	–	–
F	1	1	0	0	1	1	1	1	1	0	0	0	–	–	–	–
G	0	1	1	1	1	1	1	1	1	0	0	0	–	–	–	–
H	0	1	1	0	1	1	1	1	1	0	0	0	–	–	–	–
I	1	1	1	1	1	1	1	1	1	0	1	0	–	–	–	–

Table 3 (continued)

Morph	Site No.:															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
J	1	1	1	1	1	1	1	0	1	0	0	0	–	–	–	–
K	1	1	1	1	1	1	1	1	1	0	0	0	–	–	–	–
L	1	0	1	0	1	1	1	1	1	0	0	0	–	–	–	–
M	1	0	1	1	1	1	1	1	1	1	0	0	–	–	–	–
N	1	1	1	0	1	1	1	1	1	0	0	1	–	–	–	–

Table 4. *Jasus edwardsii.* Intra-populational mean mtDNA nucleotide sequence diversity and standard errors (%) for 13 populations

Collection location	Diversity	SE
King Island, Bass Strait	0.6872	0.2497
Flying Cloud Point, Tasmania	0.7799	0.2363
Temma, Tasmania	0.8938	0.2486
Sullivans Point, Tasmania	0.9193	0.2605
Flinders Island, Bass Strait	0.7699	0.2462
Port Lincoln, South Australia	0.7334	0.2381
Gisborne, New Zealand	0.4382	0.2421
Moeraki, New Zealand	0.7114	0.2616
Bucks Bay, South Australia	0.8516	0.2235
Bicheno, Tasmania	0.8630	0.2865
Port Fairy, Victoria	0.9565	0.2486
Batemans Bay, New South Wales	0.8763	0.3309
Esperance, Western Australia	0.7681	0.2499

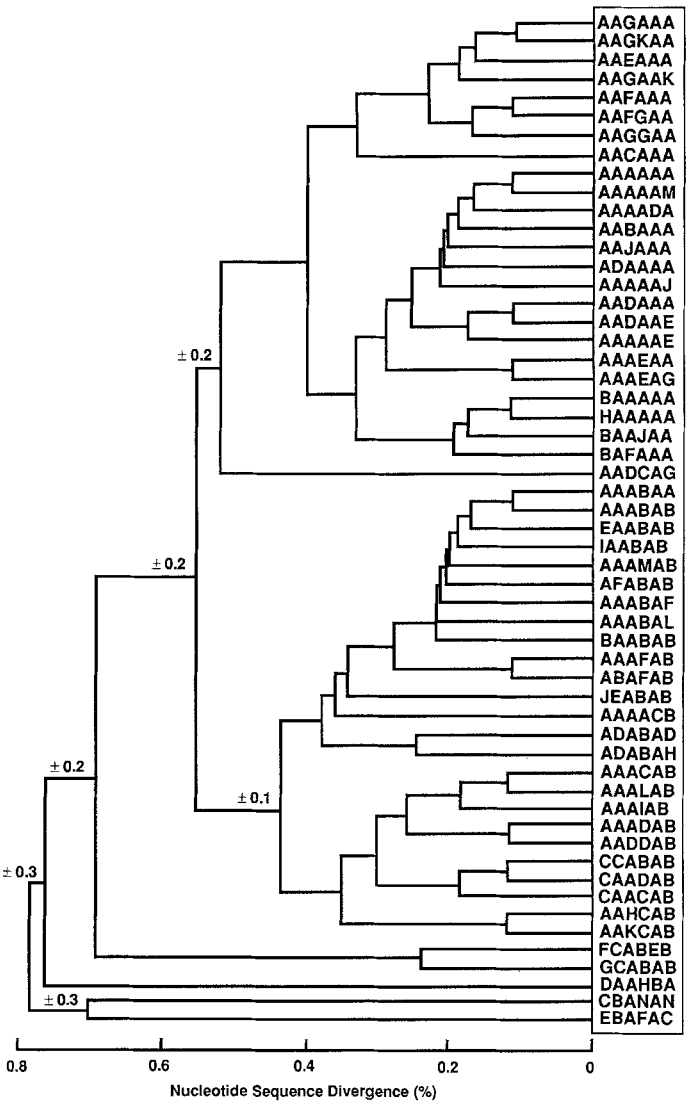

Fig. 3. *Jasus edwardsii.* UPGMA describing relationship between 55 haplotypes based on pairwise mtDNA nucleotide sequence divergence. Size of standard error for selected branch points is indicated

the branches leading to these groups were overlapping, so this grouping of haplotypes is not definitive. One haplotype group possessed predominantly A morphs for the restriction sites of *Bst*YI (18/25) and *Hin*dIII (18/25). Members of this haplotype group were found at each collection location (Esperance, 6/15; Bucks Bay, 6/8; Port Lincoln, 6/10; Port Fairy, 4/10; King Island, 4/10; Flinders Island, 6/10; Temma, 6/11; Flying Cloud Point, 7/16; Sullivans Point, 5/13; Bicheno, 1/6; Batemans Bay, 1/4; Gisborne, 7/10; Moeraki, 4/9). The haplotypes belonging to the other group possessed mostly B morphs for the *Bst*YI (12/25) and *Hin*dIII (20/25) restriction sites. Five haplotypes belonged to neither group. Two of these (FCABEB, DAAHBA) belonged to lobsters collected from north-western Tasmania (Temma, Table 1). Another two (EBAFAC, Flying Cloud Point; GCABAB, Sullivans Point) were from lobsters from southern Tasmania. The remaining haplotype (CBANAN) was identified once amongst the 15 lobsters collected from Esperance, Western Australia.

The mean number of base substitutions per nucleotide (mtDNA diversity) for the 132 lobster mitochondrial genomes was $0.78 \pm 0.19\%$ (mean $\pm$ standard error). A pair of lobsters, one from Flying Cloud Point, Tasmania (EBAFAC), and the other from Temma (DAAHBA) had the most different mitochondrial genomes ($2.41 \pm 0.82\%$). The locality with the most diverse set of mitochondrial genomes was Port Fairy, Victoria ($n = 10$, diversity $= 0.96 \pm 0.25\%$, Table 4). The 10 mitochondrial genomes sampled from lobsters at Gisborne, New Zealand, were the most similar ($0.44 \pm 0.24\%$).

The amount of nucleotide diversity between the mtDNA of lobsters from pairs of collection locations, corrected for intra-populational diversity, was less than or equal to zero for 51 of the 78 possible comparisons. The magnitude of the corrected inter-populational mtDNA diversities for the remaining pairs of collection locations ranged from 0.0016 to 0.1179%, with most values lying between 0.01 and 0.06% (Table 5). The size of the standard errors for some of these measurements were larger than the magnitude of the measurement itself. For example, the amount of inter-populational mtDNA nucleotide diversity between Flying Cloud Point, Tasmania and Flinders Island (Bass Strait), was 0.0016%. The standard error of this diversity was 0.0209%. Standard errors exceeded the inter-populational diversity measurements in 16 of the pairwise comparisons. For these comparisons, there is no evidence of historical or

Table 5. *Jasus edwardsii.* Inter-populational mean mitochondrial DNA nucleotide sequence diversity and standard errors (%) between samples collected from pairs of collection locations. Diversities between remaining pairs of locations were ≤0

Collection locations			Diversity	SE
King Island, Bass Strait	vs	Gisborne, New Zealand	0.0177	0.0277
King Island, Bass Strait	vs	Bucks Bay, South Australia	0.0214	0.0229
Flying Cloud Point, Tasmania	vs	Temma, Tasmania	0.0083	0.0158
Flying Cloud Point, Tasmania	vs	Flinders Island, Bass Strait	0.0016	0.0209
Flying Cloud Point, Tasmania	vs	Gisborne, New Zealand	0.0552	0.0432*
Flying Cloud Point, Tasmania	vs	Bucks Bay, South Australia	0.0315	0.0219*
Temma, Tasmania	vs	Sullivans Point, Tasmania	0.0163	0.0185
Temma, Tasmania	vs	Gisborne, New Zealand	0.0125	0.0215
Temma, Tasmania	vs	Bicheno, Tasmania	0.0421	0.0264*
Temma, Tasmania	vs	Port Fairy, Victoria	0.0017	0.0180
Sullivans Point, Tasmania	vs	Gisborne, New Zealand	0.0632	0.0386*
Sullivans Point, Tasmania	vs	Bucks Bay, South Australia	0.0466	0.0333*
Sullivans Point, Tasmania	vs	Bicheno, Tasmania	0.0213	0.0298
Flinders Island, Bass Strait	vs	Bicheno, Tasmania	0.0336	0.0302*
Port Lincoln, South Australia	vs	Gisborne, New Zealand	0.0158	0.0325
Port Lincoln, South Australia	vs	Bicheno, Tasmania	0.0122	0.0239
Gisborne, New Zealand	vs	Moeraki, New Zealand	0.0021	0.0213
Gisborne, New Zealand	vs	Bicheno, Tasmania	0.1179	0.0480*
Gisborne, New Zealand	vs	Port Fairy, Victoria	0.0161	0.0254
Gisborne, New Zealand	vs	Batemans Bay, New South Wales	0.0565	0.0644
Gisborne, New Zealand	vs	Esperance, Western Australia	0.0386	0.0356*
Moeraki, New Zealand	vs	Bucks Bay, South Australia	0.0068	0.0203
Moeraki, New Zealand	vs	Bicheno, Tasmania	0.0379	0.0289*
Bucks Bay, South Australia	vs	Bicheno, Tasmania	0.1011	0.0343*
Bucks Bay, South Australia	vs	Port Fairy, Victoria	0.0228	0.0214*
Bucks Bay, South Australia	vs	Batemans Bay, New South Wales	0.0298	0.0423
Bucks Bay, South Australia	vs	Esperance, Western Australia	0.0270	0.0287

* Comparisons in which magnitude of standard error was less than that of diversity

contemporary restrictions in gene flow between populations. However, for 11 measurements of pairwise mtDNA diversity between collection locations the standard error of the measurement was smaller than the measurement itself (Table 5). In four of these comparisons, the inter-populational diversity may be larger than zero ($0.0421 \pm 0.0264\%$, Temma, Tasmania vs Bicheno, Tasmania; $0.0632 \pm 0.0386\%$, Sullivans Point, Tasmania vs Gisborne, New Zealand; $0.1011 \pm 0.0343\%$, Bucks Bay, South Australia vs Bicheno, Tasmania; $0.1179 \pm 0.0480\%$, Gisborne, New Zealand vs Bicheno, Tasmania) suggesting that gene flow may be restricted between these locations.

Large geographical distances between collection locations was not reflected by the amount of mtDNA sequence divergence. The lobster specimens collected in south-eastern Australian waters were separated by ~2000 km from the Western Australian specimens and by ~2600 km from the New Zealand specimens. The net amount of sequence diversity between Western Australian lobster genomes and those from south-eastern Australia was zero. That between genomes from New Zealand and south-eastern Australia was also close to zero (0.0129%).

None of the gene-diversity analyses on groups of collection locations (Table 2), based either on water-current patterns or environmental parameters of the adult habitats, yielded a result which was indicative of subdivision. For example, when lobster collection locations were grouped according to their occurrence in either the northern East Australian Current, the southern East Australian Current, the Great Australian Bight or in southern Western Australian waters (Table 2), the calculated nucleotide ($N_{ST} = -0.012$; $G_{ST} = 0.168$, range 0.138 to 0.232) and haplotype ($G'_{ST} = 0.009$, range 0.003 to 0.011) diversities (Table 6) indicated that adult lobster populations were unlikely to be fully or partially reproductively isolated.

Table 6. *Jasus edwardsii.* Nucleotide (N_{ST}, G_{ST}) and haplotype subdivision (G'_{ST}) between regional populations. Population groupings as in Table 2

Grouping type	Nucleotide			Haplotype	
	N_{ST}	G_{ST}	Range[a]	G'_{ST}	Range[b]
Current flow					
1	−0.012	0.168	0.138–0.232	0.009	0.003–0.011
2	−0.004	0.188	0.164–0.246	0.016	0.012–0.016
Environmental					
1	0.009	0.190	0.127–0.222	0.009	0.001–0.005
2	0.001	0.193	0.135–0.250	0.004	−0.001–0.007
3	−0.007	0.238	0.212–0.279	0.005	0.004–0.005

[a] Range of 1000 bootstrapped estimates of G_{ST}
[b] Range of jackknifed estimates of G'_{ST}

Discussion

The dominant feature of the biology of *Jasus edwardsii* which would be expected to curtail intraspecific subdivision is the long duration of the larval phase (6 to 23 mo.

Booth et al. 1990) and the concomitant potential for dispersal. Yet, scenarios can be envisaged in which complete or partial barriers to larval exchange between populations exist. For example, pueruli which subsequently contribute to adult populations, may have metamorphosed from late-stage phyllosomas which were part of the small number of larvae not swept away from suitable habitat by prevailing currents (Phillips and McWilliam 1986). Larvae which have been reported far away from adult habitats, in the Tasman Sea for example (Booth et al. 1990), may be permanently lost to the population (Smith et al. 1980), although the maximum duration of larval existence and the nature of settlement cues are unknown. As well as fortuitous survival, *J. edwardsii* larvae may be able to regulate their dispersal to a limited extent, in the same way that *Panulirus cygnus* larvae control their distribution on the Western Australian coastline through the judicious choice of water masses by vertical movements (Phillips and McWilliam 1986).

Adaptation to local habitats is another factor which may promote population subdivision in *Jasus edwardsii*. In the marine environment, the potential for adaptation via natural selection is as great as in terrestrial environments, as physico-chemical and biological features vary widely between marine habitats (George 1969). Adaptation to specific habitats could develop, and be maintained by selective mortality amongst juveniles. The potential for habitat-specific settlement is a cornerstone of theories describing the process of speciation in this genus (Pollock 1990). Pollock suggested that lobster larvae have the ability to detect minute changes in the water composition and to metamorphose into the puerulus stage adjacent to an appropriate habitat. Habitat-specific larval recruitment may be responsible for the lack of *Panulirus cygnus* populations in the north of Western Australia despite the presence of late-stage larvae in surrounding waters (Phillips and McWilliam 1986).

In the present analysis of mtDNA nucleotide sequence polymorphism in southern Australian and New Zealand populations of *Jasus edwardsii*, subdivision was not detected. Lobster haplotypes were shown not to be geographically partitioned, and measurements of gene diversity between various groups of samples did not imply subdivision. The inability of restriction enzyme analysis of lobster mtDNA to detect population subdivision does not test the hypotheses of fortuitous, active or habitat-specific settlement from the larval to adult phases. One or other of these mechanisms may be operating within this species, and producing a degree of population subdivision, but the magnitude of the resultant pattern is below the degree of resolution of this analytic technique. The technique is one of the most sensitive available for stock assessment, but a refinement of mtDNA analysis, polymerase-mediated DNA amplification (Erlich 1989) followed by nucleotide sequence determination, may increase the resolution of similar studies in the future (Ovenden 1990).

Since the degree of genetic subdivision in Australian and New Zealand rock lobster populations cannot be measured by mtDNA analysis, the populations are most probably exchanging more than one reproductively successful migrant per generation (Avise et al. 1987). If this is the case, and as the prevailing Southern Ocean currents would move planktonic phyllosoma from west to east, Australian lobster populations may be a major source of recruits for the lobster fishery in New Zealand. Water currents would sweep the majority of larvae from New Zealand populations to the east. They would need to complete a global or Pacific circumnavigation before encountering a habitat suitable for settlement. For the same reasons, adult lobsters on the south-western Australian coastline may be major contributors to the south-eastern populations. If future studies confirm the one-way flow of *Jasus edwardsii* larvae across southern Australia and New Zealand, then the western populations may deserve special conservation status.

One of the approaches used here to test the null hypothesis of the absence of genetic subdivision is novel. A statistically significant large mtDNA sequence divergence between a pair of populations would have been accepted as evidence that gene flow between them was restricted. The sampling variance used in this test is that associated with the assay of a subset of nucleotides between pairs of genomes, one genome from each of two populations (Nei and Jin 1989). As a large number of pairwise comparisons between populations (78) were made, and the level of statistical significance used was 5%, 1 in 20 tests would have been expected to yield a significant result by chance. The significantly large inter-populational mtDNA sequence divergences involving lobsters collected from Bicheno, on the eastern coast of Tasmania (3/12 comparisons), and Gisborne, on the eastern coast of the North Island of New Zealand (2/12 comparisons), may be examples of this kind of error. The same type of error may have been associated with the low intra-populational mtDNA sequence divergence for the 10 individuals sampled from Gisborne, New Zealand. The relative magnitude of the intra-populational diversity of the Gisborne sample was taken by Brasher et al. (1991) to suggest subdivision across the Tasman Sea; however, analysis of a second New Zealand sample in this study failed to confirm this.

The lack of a detectable amount of genetic subdivision among populations of *Jasus edwardsii* across about 4600 km of the southern hemisphere and two continents, suggests that the mitochondrial genome may not differ significantly between other species of the genus (*J. tristani*, *J. lalandii*, *J. frontalis*, *J. paulensis* and *J. verreauxi*). If this were the case, and as most of the species (excluding *J. verreauxi*) are morphologically similar (George and Kensler 1970), possibly share the same oceanic pool of larvae (Pollock 1990), and have allopatric distributions (George and Main 1967), their specific status may be in doubt. However, Brasher et al. (1991) have shown that the mean pairwise amount of mtDNA sequence divergence between *J. lalandii*, *J. tristani* and *J. edwardsii* was 6.2%, and that the genome of *J. verreauxi* differs from them by 14.9 to 16.7%. The magnitude of these pairwise mtDNA divergences for species of *Jasus* is similar to that found in other congeneric species comparisons (Avise et al. 1987), which supports the current taxonomy of the genus.

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