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Geographic Differentiation of Eastern Australian Penaeid Prawn Populations

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Abstract

The geographic differentiation of *Metapenaeus bennettae*, *M. macleayi* and *Penaeus plebejus* has been examined by electrophoretic techniques. Differences between localities were detected in *M. bennettae* and *M. macleayi*, but not in *P. plebejus*. The observations for *M. bennettae* and *P. plebejus* are consistent with what has previously been revealed by ecological investigations. Despite the existence of detectable genetic heterogeneity in *M. bennettae* and *M. macleayi*, the differences in gene frequency are in almost all cases of a minor order, and the overall degree of divergence between populations is quite small. The comparative measures of geographic differentiation for the three species *M. bennettae*, *M. macleayi* and *P. plebejus* are $\phi^* = 0{\cdot}051$, $0{\cdot}014$, and $0{\cdot}007$ respectively.

Introduction

Penaeid prawns (Crustacea : Decapoda : Penaeidae) have been commercially exploited from eastern Australia for over 150 years (Ruello 1975*a*). In south-eastern Australia the eastern king prawn, *Penaeus plebejus*, is the most common species and yields an annual catch of about 3×10^6 kg (Ruello 1975*b*). Large populations of the school prawn, *Metapenaeus macleayi*, are found in the Noosa, Clarence, Manning, Hunter, Hawkesbury and Shoalhaven Rivers from each of which each year more than 4×10^4 kg are normally taken (Ruello 1977). Large numbers of the eastern greasyback or greentail prawn, *M. bennettae*, occur in Moreton Bay, Lake Macquarie and Lake Munmorah. All three species are endemic to eastern Australia.

A comprehensive investigation of the biology of these commercial species was undertaken by Racek (1959), followed by detailed stock investigations of *P. plebejus* and *M. macleayi* by Ruello (1975*b*, 1977). The adult population structure of all three species has been established (with the possible exception of *P. plebejus* south of Sydney and north of Tin Can Bay). Distances of larval dispersal are unknown, but for deepwater spawners such as *P. plebejus* the range may be considerable with the aid of the East Australian Current (Ruello 1975*b*).

Electrophoretically detectable variation is used in this investigation as an alternative approach to the determination of population structure. Previously, tagging experiments have been routinely used for the separation of contiguous stocks, which is the basic prerequisite for fisheries management. The sensitivity of biochemical polymorphisms for the detection of population subdivision may therefore be assessed by direct comparison with the results of the earlier ecological investigations.

Separate breeding populations are recognizable by geographic differences in allele frequencies caused by natural selection or genetic drift. Genetic differentiation has

previously been revealed in the decapod lobster *Homarus americanus* (Tracey *et al.* 1975), but not as yet among populations of penaeid prawns (Proctor *et al.* 1974; Marvin and Caillouet 1976; Lester 1979). The present study makes use of enzyme polymorphisms detected in an earlier investigation of the extent of genetic variation and evolutionary relationships within a group of Australian commercial species (Mulley and Latter 1980). Details of geographic differentiation within tropical Australian species are given in a separate paper (Mulley and Latter 1981).

Methods

Populations were sampled throughout south-eastern Australia from locations representative of the distribution of each species (Fig. 1). The sample preparation, electrophoresis and staining procedures are described by Mulley and Latter (1980). The genetic markers studied are listed for each species in Table 1, all representing loci with unambiguous genetic interpretations. At all loci, alleles are designated *a*, *b*, *c*, etc. in order of decreasing electrophoretic mobility. Genotypic frequencies at all sampled localities agreed closely with Hardy–Weinberg expectations, so that allele frequencies are adequate to describe the genetic differences observed.

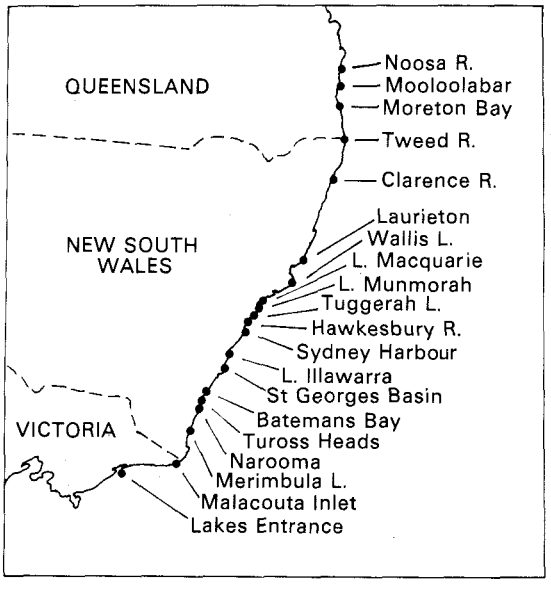

Fig. 1. Sampling locations in south-eastern Australia.

Esterase-3 is a locus not included in the overall survey of Australian species of *Metapenaeus* and *Penaeus* because it could not be scored satisfactorily in all species. It is, however, polymorphic in *M. bennettae* and *P. plebejus*, and provides useful information confirming conclusions based on the other genetic markers.

Results

M. bennettae

Gene frequency estimates for *M. bennettae* are presented in Table 2. No significant genetic differentiation was observed at the *Odh* locus, but the *Pgm* allele frequencies were heterogeneous over the four localities ($\chi^2_6 = 29{\cdot}98$, $P < 0{\cdot}001$), and the *Est-3* allele frequencies differed significantly at the two localities studied ($\chi^2_1 = 11{\cdot}95$, $P < 0{\cdot}001$). The *Pgm* allele frequencies at the two localities in Queensland were significantly different ($\chi^2_1 = 6{\cdot}41$, $P < 0{\cdot}02$), and the same is true of the comparison between Lake Macquarie and Lake Munmorah in N.S.W. ($\chi^2_1 = 8{\cdot}07$, $P < 0{\cdot}02$).

Despite the clear statistical evidence of heterogeneity, differences in gene frequency between localities were numerically small in all instances, apart from the difference for *Est-3*.

Table 1. Genetic markers in *M. bennettae*, *M. macleayi* and *P. plebejus*

Enzyme of prawn	EC No.	Locus	No. of populations	N^A	Het[B]
M. bennettae					
Octanol dehydrogenase	1.1.1.73	*Odh*	4	333	0·11
Phosphoglucomutase	2.7.5.1	*Pgm*	4	293	0·27
Arylesterase	3.1.1.2	*Est-3*	2	169	0·29
M. macleayi					
Mannosephosphate isomerase	5.3.1.8	*Mpi*	11	859	0·51
P. plebejus					
Mannosephosphate isomerase	5.3.1.8	*Mpi*	11	1043	0·52
Arylesterase	3.1.1.2	*Est-3*	8	891	0·61

[A]*N*, No. of individuals sampled. [B]Het, heterozygosity.

M. macleayi

The *Mpi* allele frequencies in *M. macleayi* are shown in Table 3. Genetic differentiation among localities was significant ($\chi^2_{10} = 19{\cdot}35$, $P < 0{\cdot}05$), with the greatest contribution to heterogeneity coming from the Noosa River and Tweed River samples. The Noosa River population did not differ significantly from that in the

Table 2. Gene frequencies at the *Odh*, *Pgm* and *Est*-3 loci in populations of *M. bennettae* (1975–1977)

Location	N^A	Alleles[B]			
		a	*b*	*c*	*d*
		Odh			
Noosa River	42	—	1·00	—	—
Moreton Bay	80	0·02	0·94	0·01	0·03
Lake Macquarie	69	0·02	0·95	0·01	0·02
Lake Munmorah	142	0·03	0·92	—	0·06
		Pgm			
Noosa River	42	0·01	0·14	0·82	0·02
Moreton Bay	80	—	0·05	0·91	0·04
Lake Macquarie	69	—	0·10	0·84	0·06
Lake Munmorah	102	—	0·05	0·80	0·14
		***Est*-3**			
Moreton Bay	80	0·01	0·22	0·74	0·03
Lake Macquarie	89	0·02	0·07	0·91	0·01

[A]*N*, No. of individuals assayed.
[B]—No record of the allele concerned.

Tweed River, but was significantly different from that of the Clarence River ($\chi^2_1 = 6{\cdot}68$, $P < 0{\cdot}01$) and from all locations further south. Allele frequencies at all locations other than the Noosa and Tweed Rivers were homogeneous, and were significantly different from the combined Noosa and Tweed Rivers samples ($\chi^2_1 = 14{\cdot}21$, $P < 0{\cdot}001$).

The fitting of a linear regression of allele frequency on latitude confirmed these conclusions. The effect of latitude was significant for both Mpi^b and Mpi^c ($t_9 = 4 \cdot 42$, $P < 0 \cdot 01$; $t_9 = 4 \cdot 68$, $P < 0 \cdot 01$, respectively), the correlation coefficient being numerically greater than $0 \cdot 8$ in both cases. No such association remained after the Noosa and Tweed Rivers data were omitted from the regression analysis. An analysis of standardized gene frequency deviations (Christiansen *et al.* 1976) led to the same conclusions.

Table 3. Gene frequencies at the *Mpi* locus in populations of *M. macleayi* (1975–1978)

Other polymorphic loci which showed no evidence of population differentiation were *Odh*, *Pgi*, *Pgm* and *Sdh* (Mulley and Latter 1980)

Location	*N*	Alleles			
		a	*b*	*c*	*d*
Noosa River	57	—	0·29	0·70	0·01
Tweed River	73	—	0·37	0·62	0·01
Clarence River	99	0·02	0·43	0·56	—
Laurieton	80	0·01	0·42	0·56	0·01
Wallis Lake	80	0·01	0·47	0·52	0·01
Tuggerah Lake	80	—	0·46	0·53	0·01
Hawkesbury River	100	0·01	0·48	0·52	—
Sydney Harbour	40	0·01	0·44	0·53	0·03
Lake Illawarra	72	—	0·48	0·52	—
Batemans Bay	78	0·01	0·43	0·55	0·01
Narooma	100	0·01	0·49	0·50	0·01

P. plebejus

Although *P. plebejus* was highly polymorphic at two loci (Table 4) no indication of genetic differentiation within the species was found. Allele frequencies at Moreton Bay were not significantly different from those at Lakes Entrance, at the other extreme of the distribution. Neither allele frequencies nor standardized gene frequency deviations were significantly associated with latitude. Sydney Harbour was sampled twice, without evidence of temporal changes in gene frequency during the 3-year interval.

Discussion

Life Cycles and Migrations

Data of adult and juvenile migrations indicate that the degree of isolation between populations is different for each of the three species investigated. *M. bennettae* reproduces and undergoes complete development within estuaries or tidal lakes, and normally does not undertake oceanic spawning migrations except in response to flooding (Racek 1959). *M. macleayi* undertakes seasonal spawning migrations in a northerly direction, to the relatively shallow inner littoral zone (Ruello 1977) where eggs are released into the sea immediately after fertilization. Larvae return to nearby river estuaries which are the preferred nursery grounds. Some mixing occurs among juvenile populations during the emigration from estuaries, and larvae do not necessarily return to the estuary where their parents originated. Seasonal migrations of *P. plebejus* are extensive, with spawning grounds located near the edge of the

continental shelf off northern New South Wales and southern Queensland (Ruello 1975*b*). Larvae return to the preferred nursery grounds of tidal lakes or inlets along the entire length of the distribution, with the species probably represented by a single breeding stock (Ruello 1975*b*). *M. macleayi* and *P. plebejus* differ in the preferred salinity tolerance of juveniles and in the length of oceanic spawning migrations and extent of subsequent larval dispersal. Whether juvenile *P. plebejus* from the southernmost regions contribute to the spawning of the next generation is not known.

Table 4. Gene frequencies at the *Mpi* and *Est*-3 loci in populations of *P. plebejus* (1976–1978)
Other polymorphic loci which showed no evidence of population differentiation were *Odh*, *6-Pgdh*, *Pgi* and *Pgm*. Blanks indicate that no data were available

Location	*N*	Alleles							*N*	Alleles				
		a	*b*	*c*	*d*	*e*	*f*	*g*		*a*	*b*	*c*	*d*	*e*
					Mpi							***Est*-3**		
Mooloolabar	75	—	0·02	0·23	0·66	0·09	0·01	—	75	—	0·07	0·33	0·50	0·10
Moreton Bay	99	—	0·02	0·26	0·62	0·09	0·02	—	99	—	0·05	0·30	0·55	0·10
Wallis Lake	129	—	0·02	0·26	0·64	0·07	0·02	—						
Tuggerah Lake	80	—	0·01	0·24	0·67	0·06	0·02	—	80	—	0·06	0·29	0·48	0·18
Sydney Harbour														
A (March 1976)	80	—	0·01	0·31	0·63	0·04	0·01	—	79	—	0·06	0·21	0·63	0·09
B (March 1978)	80	—	0·01	0·32	0·61	0·05	0·01	—	80	0·01	0·04	0·33	0·56	0·07
Total	160	—	0·01	0·31	0·62	0·05	0·01	—	159	0·01	0·05	0·27	0·59	0·08
Lake Illawarra	80	—	0·04	0·28	0·61	0·06	0·01	—	80	—	0·04	0·34	0·52	0·10
St Georges Basin	80	0·01	—	0·27	0·63	0·07	0·01	0·01	59	—	0·02	0·31	0·58	0·10
Tuross Heads	80	—	0·01	0·26	0·58	0·13	0·03	—						
Merimbula Lake	80	—	0·03	0·24	0·65	0·06	0·01	—	80	—	0·06	0·36	0·49	0·08
Malacouta Inlet	80	—	0·01	0·24	0·67	0·07	0·01	—						
Lakes Entrance	100	—	0·01	0·24	0·66	0·09	0·01	—	100	—	0·05	0·37	0·48	0·11

Genetic Structure

The genetic differentiation observed in this study between populations of *M. bennettae* is readily explained by the known geographic isolation between populations at both larval and adult stages of development. All other Australian penaeid species either undergo oceanic spawning migrations or else the whole life cycle is completed in oceanic waters.

Some degree of genetic differentiation was also expected between populations of *M. macleayi* since tagging experiments indicated the existence of six breeding populations, and the maximum recorded migration is 120 km (Ruello 1977). The *Mpi* data detected a difference in gene frequency only at the northern extreme of the sampled distribution, all populations obtained from the New South Wales coast being homogeneous.

The electrophoretic data for *P. plebejus* is in complete agreement with what is known of the population biology of the species. Spawning migrations of juvenile *P. plebejus* originating from as far south as Sydney have been traced to the waters off southern Queensland (Ruello 1975*b*). The longest recorded migration was 930 km. Larvae repopulate the southern nursery grounds by dispersal, which presumably duplicates in reverse the adult migrations (Kirkegaard 1975; Ruello 1975*b*). Ruello

(1975*b*) concluded that a single adult population exists north of Sydney, but that 'there is a dearth of information on the migratory habits of *P. plebejus* emigrating from estuarine areas north of Tin Can Bay and south of Sydney'. Sampling for the present study was concentrated at locations south of Sydney where tagging would be of little value due to the lack of large offshore fishing fleets. Genetic markers revealed no evidence of regional differentiation. The origin of king prawns in southern New South Wales and Victoria remains unclear since females with ripe gonads have been collected as far south as Greenwell Point (Ruello 1975*b*). The southernmost limit of dispersal for larvae spawned in southern Queensland is unknown.

It may be concluded that a sample of *P. plebejus* from any location within the distribution is genetically representative of the species as judged by the available electrophoretic data at 38 loci. The genetic heterogeneity detected within *M. bennettae* and *M. macleayi*, on the other hand, is the outcome of either natural selection or genetic drift, and a sample from any one location cannot always be considered genetically representative of the species. However, in almost all instances the differences in gene frequency throughout the sampled range were of a minor nature.

A quantitative measure of genetic differentiation in each of the three species is provided by the parameter ϕ^* defined by Latter (1973, 1981), which relates the level of heterozygosity at polymorphic loci within populations, $\overline{H}_w$, to that which would be observed at the same loci in hybrids between populations, $\overline{H}_b$. The value of ϕ^* is given by

$$\phi^* = 1 - \overline{H}_w/\overline{H}_b,$$

with a possible range of values from zero to unity. The values of ϕ^* based on the data of Tables 2–4 for *M. bennettae*, *M. macleayi* and *P. plebejus* are 0·051, 0·014 and 0·007, respectively. All three values are quite small, and the overall degree of genetic isolation between the localities sampled for *M. bennettae* and *M. macleayi* is therefore of a minor nature. The most divergent populations of *M. macleayi*, originating from Noosa River in Queensland and Narooma in southern New South Wales, correspond to a ϕ^* value of 0·079, based on the data of Table 3 for *Mpi*.

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