ICES Journal of Marine Science, 61: 913–920 (2004)
doi:10.1016/j.icesjms.2004.06.015

Short communication

Population genetic structure of the kuruma prawn (*Penaeus japonicus*) in East Asia inferred from mitochondrial DNA sequences

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Tzeng, T-D., Yeh, S-Y., and Hui, C-F. 2004. Population genetic structure of the kuruma prawn (*Penaeus japonicus*) in East Asia inferred from mitochondrial DNA sequences. – ICES Journal of Marine Science, 61: 913–920.

Sequence analyses on the complete mitochondrial DNA (mtDNA) control region (992 bp) were conducted to elucidate the population structure of kuruma prawns (*Penaeus japonicus*) in East Asia. Five populations including 95 individuals were collected. They are separated into the Japan Sea (JS), the north and south of the East China Sea (NECS and SECS), the Taiwan Strait (TS), and the north of the South China Sea (NSCS) populations. There are 292 variable sites without any insertions and deletions. Nucleotide diversity in the total populations is $2.51 \pm 0.07\%$, and the variations within populations ranged from $2.61 \pm 0.93\%$ (SECS) to $2.29 \pm 0.16\%$ (JS). F_{ST} values between the JS and the rest of the populations, between the NECS and NSCS populations, and between the SECS and NSCS populations show significant differences. The UPGMA tree of these five populations shows three distinct clusters; one includes the JS population; another includes the NECS population; the third includes populations from the rest of the areas. The analysis of molecular variance (AMOVA) shows clear genetic difference between the JS and the rest of the populations. Additional AMOVA analysis excluding the JS population indicates significant variation between the NECS population and the other three populations. We, therefore, conclude that three distinct populations exist in East Asia; one is in the JS; another is in the NECS; and the third is distributed in SECS, TS and NSCS.

Keywords: control region, East Asia, mtDNA, *Penaeus japonicus*, population structure.

Received 10 October 2003; accepted 15 June 2004.

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Introduction

A concrete understanding of population genetic structure is of primary importance for the management and conservation of genetic resources in exploited marine organisms (Hillis *et al.*, 1996). Studies on population genetic structure of marine biota have frequently indicated that organisms with high dispersal capacity would have little genetic distinction over large geographic scales (Hellberg, 1996). These studies suggest that there are high levels of gene flow between marine populations. However, there is growing evidence that widespread marine organisms are more genetically structured than expected given their high dispersal potential and apparent lack of barriers to dispersal in the ocean (Palumbi, 1997; Benzie, 1999; Briggs, 1999). Thus, there may be limits to the actual dispersal of marine organisms with high dispersal potential (Benzie and Williams, 1997). These limits vary widely with species, habitats, local ocean conditions, or historical events, and they may produce sufficient chances for genetic variation (Palumbi, 1994).

The kuruma prawn (*Penaeus japonicus*) is a widely distributed species throughout the Indo-west Pacific, ranging from eastern and southern Africa into the Red Sea through the entire Malay Archipelago to Taiwan, Korea, Japan, and Northern Australia, and they have moved through the Suez Canal into the Mediterranean (Hayashi, 1992). This species is one of the most important fishery animals in East Asia (particularly the East China Sea and the Taiwan Strait). The life history of the kuruma prawn,

1054-3139/$30.00

comprising an offshore planktonic larval phase, an estuarine post-larval and juvenile phase, and an offshore adult and spawning phase (Dall *et al.*, 1990), may allow moderate gene flow among populations.

Two morphologically distinguishable populations of kuruma prawn in the East China Sea and Taiwan Strait were discriminated by Tzeng and Yeh (1999). However, the variation of morphological characters could be affected by genetic and environmental factors, so discrimination of populations based on morphological variation must be verified by genetic evidence to confirm that the variation reflects the true degree of reproductive isolation rather than environmental isolation (Pepin and Carr, 1992).

Mitochondrial DNA (mtDNA) has many attributes that make it particularly suitable for population genetic studies, including its rapid rate of evolution, lack of recombination, and maternal inheritance (Hoelzel *et al.*, 1991). Since the control region of the mtDNA has been shown to be the most variable region in both vertebrates and invertebrates, this region is an ideal marker for characterizing geographical patterns of genetic variation within and between prawn populations (Simon, 1991). In this paper, we amplified and sequenced the complete control region to elucidate the population genetic structure of the kuruma prawn in marginal seas of East Asia.

Material and methods

Collection of samples

Five putative kuruma prawn populations were collected during 1995 and 1996 (Figure 1 and Table 1). Specimens were iced or frozen immediately after capture and later kept at −75 °C until extracted, but specimens from the Japan Sea were stored in 95% ethanol. Total genomic DNA was extracted from muscle tissue by using a standard DNA extraction technique with proteinase K digestion followed by phenol/chloroform purification.

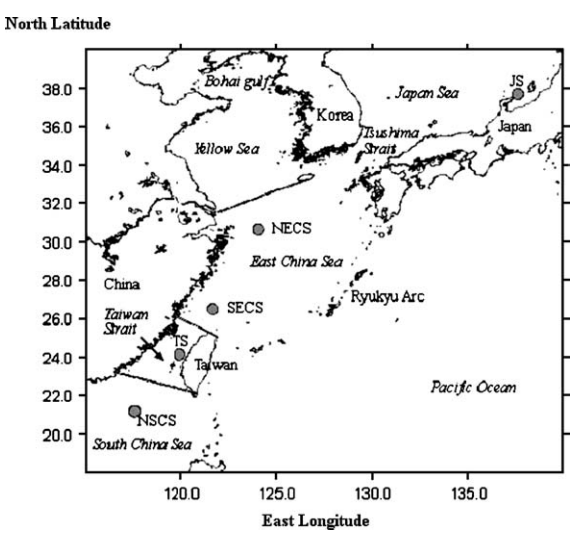

Figure 1. Five shaded areas showing the sampling locations of kuruma prawn in the Japan Sea (JS), the north (NECS) and south (SECS) of the East China Sea, the Taiwan Strait (TS), and the north of the South China Sea (NSCS).

Amplification and sequencing

A fragment of mtDNA was first amplified and sequenced for each specimen using primers P120-90 (5′-GATCTT-TAGGGGAATGGTGTAATTCCATTG-3′) and P14586-609 (5′-GTGTCTTCTTGAAGTCTG-3′). Then the primers P15764-47 (5′-GATAGCTTAAAGGTTTAACTAC-3′), P15481-60 (5′-GAGTCTTTAACTTTTAATGACCCC-3′), and P14857-80 (5′-GTGTAACAGGGTATCTAATCCT-GG-3′) were designed according to the nucleotide sequences of kuruma prawn obtained with primers P120-90 and P14586-609 and used for sequencing. Primer names indicate homologous positions on the *P. monodon* mitochondrial genome (Wilson *et al.*, 2000). The PCR protocol consisted of 39 cycles of denaturing at 95 °C for 50 s, annealing at 50 °C for 1 min, and extension at 72 °C for 1.5 min.

Dideoxy chain-termination DNA sequencing was performed (Sanger *et al.*, 1977) using Sequencing kit (version 2.0, United States Biochemical) with [α-^{35}S]-dATP as label. The DNA sequencing reaction was carried out using the following cycling parameters: 29 cycles of denaturation at 95 °C for 40 s, annealing at 50 °C for 40 s, and extension at 72 °C for 30 s. The sequencing reaction products were electrophoresed in a 6% polyacrylamide/7 M urea gel. The gel was fixed, dried, and visualized by autoradiography on a Kodak film for 24−72 h.

Sequence analysis

DNA sequences were aligned by using the PILEUP program in GCG (Genetics Computer Group, version 7.0; Devereux *et al.*, 1991). The beginning and end of the control region were confirmed by comparing with the published sequence of *P. monodon* (Wilson *et al.*, 2000). Subsequent analyses were based on the complete control region sequence obtained from 95 individuals. The number of transitions (TS) and transversions (TV), and nucleotide diversities π (Nei, 1987) within populations were calculated by using ARLEQUIN 2.000 (Schneider *et al.*, 2000).

To examine whether two of the populations are genetically different from each other, the F_{ST} statistic (Wright, 1965) between five populations was estimated and tested using the program ProSeq (Filatov, 2002). The statistical significance of the estimate was tested through 1000 permutations. The dendrogram of five populations was constructed using the unweighted pair-group method with arithmetic means (UPGMA) based on the F_{ST} values. Gene flow (N_m), was estimated using the relationship $N_m = ((1/F_{ST}) - 1)/2$ (Hudson *et al.*, 1992).

Table 1. Sampling locality, sampling date, sample code, sample size, and nucleotide diversity (π) with standard deviation (s.d.) in five kuruma prawn populations in East Asia.

Locality	Sample code	Sampling date	Sampling size	$\pi \pm$ s.d. (%)
Japan Sea (37°N, 137°E)	JS	May 1996	14	2.29 ± 0.16
North of the East China Sea (30°−31°N, 123°−124°E)	NECS	Dec. 1995	12	2.54 ± 0.20
South of the East China Sea (26°−27°N, 122°−123°E)	SECS	Dec. 1995	23	2.61 ± 0.93
Taiwan Strait (24°−24°15′N, 119°36′−120°E)	TS	Dec. 1995	24	2.32 ± 0.84
North of the South China Sea (21°−21°30′N, 117°30′−118°E)	NSCS	Dec. 1995	22	2.43 ± 0.11
Total			95	2.51 ± 0.07

Relationships between haplotypes were determined with the Kimura two-parameter distance model by using the Neighbour-Joining method in MEGA 2.1 (Kumar *et al.*, 2001). Nucleotide diversities π (Nei, 1987) within populations were estimated by using ARLEQUIN.

Analyses of molecular variance (AMOVA) in ARLEQUIN were performed to test the geographic divisions among populations. This approach is a hierarchical approach analogous to analysis of variance (ANOVA) in which the correlations among haplotypes at various hierarchical levels are used as F-statistic analogs, designated as Φ-statistic. AMOVA computes the proportion of variation among groups (Φ_{CT}), the proportion of variation among populations within groups (Φ_{SC}), and the proportion of variation within populations (Φ_{ST}). The significance of these Φ-statistic analogs is evaluated by random permutations of sequences among populations. We experimented with various groupings of populations suggested by population trees, F_{ST} values, and ocean division. The groupings that maximize values of Φ_{CT} and are significantly different from random distributions of individuals are assumed to be the most probable geographic subdivisions.

Isolation by distance was assessed by a Mantel test in NTSYS (Rohlf, 1997). We used the pair-wise F_{ST} values and the corresponding pair-wise geographical distances as the input data and 1000 permutations were performed to determine the level of significance. The approximate geographic distances between sampling localities were taken as the minimum distance map.

Results

The control region of kuruma prawn mtDNA contains 992 bp. Among 95 haplotypes identified from 95 individual mtDNA sequenced, there are 292 variable sites without any insertions or deletions (Figure 2). The TS:TV rate is 2.34:1. Nucleotide diversity (π) in the total populations is 2.51 ± 0.07% but it varies within populations, ranging from 2.61 ± 0.93% in the SECS population to 2.29 ± 0.16% in the JS population (Table 1).

The F_{ST} and N_m values are shown in Table 2. The F_{ST} value across all populations shows a significant amount of genetic variation between five populations ($F_{ST} = 0.0434$, $p < 0.01$). F_{ST} values between the JS and the other populations, between the NECS and NSCS populations, and between the SECS and NSCS populations show significant genetic differences, but genetic variation between the other populations is not significant. The N_m values between all pairs of the five populations range from 0.0840 (JS−SECS populations) to 59.6404 (SECS−TS populations). N_m values between the JS and the rest of the four populations are relatively lower (from 0.0840 to 3.7203). The higher N_m values are found between the NECS and SECS populations (12.2787), and between the NECS and TS populations (12.1297).

The neighbour-joining tree of the 95 haplotypes shows little genealogical structuring and is characterized by shallow branching and nodes not well supported by bootstrap values (not shown).

The UPGMA tree of five sampling areas is shown in Figure 3. These five populations are clustered into two distinct groups; the first group includes the JS population; the second one includes the other four populations. The second group may be further divided into two subgroups; the first subgroup includes the NECS population; the second subgroup includes the SECS, TS, and NSCS populations.

The results of AMOVA for total populations are shown in Table 3. The AMOVA for five populations yields a small but significant Φ_{ST} value of 0.0362, indicating that at least one of the pair-wise populations reveals significant heterogeneity. Significant values of Φ_{CT} are observed in four of nine groupings. In four significant groupings, the division occurred in the JS population. The highest Φ_{CT} value (0.0542) is observed when the JS population and the rest are separately assigned into two groups (Table 3 and grouping 2). Significant Φ_{CT} values are also found in groupings 3 and 4, indicating that an additional genetic discontinuity may also have occurred in the NECS population.

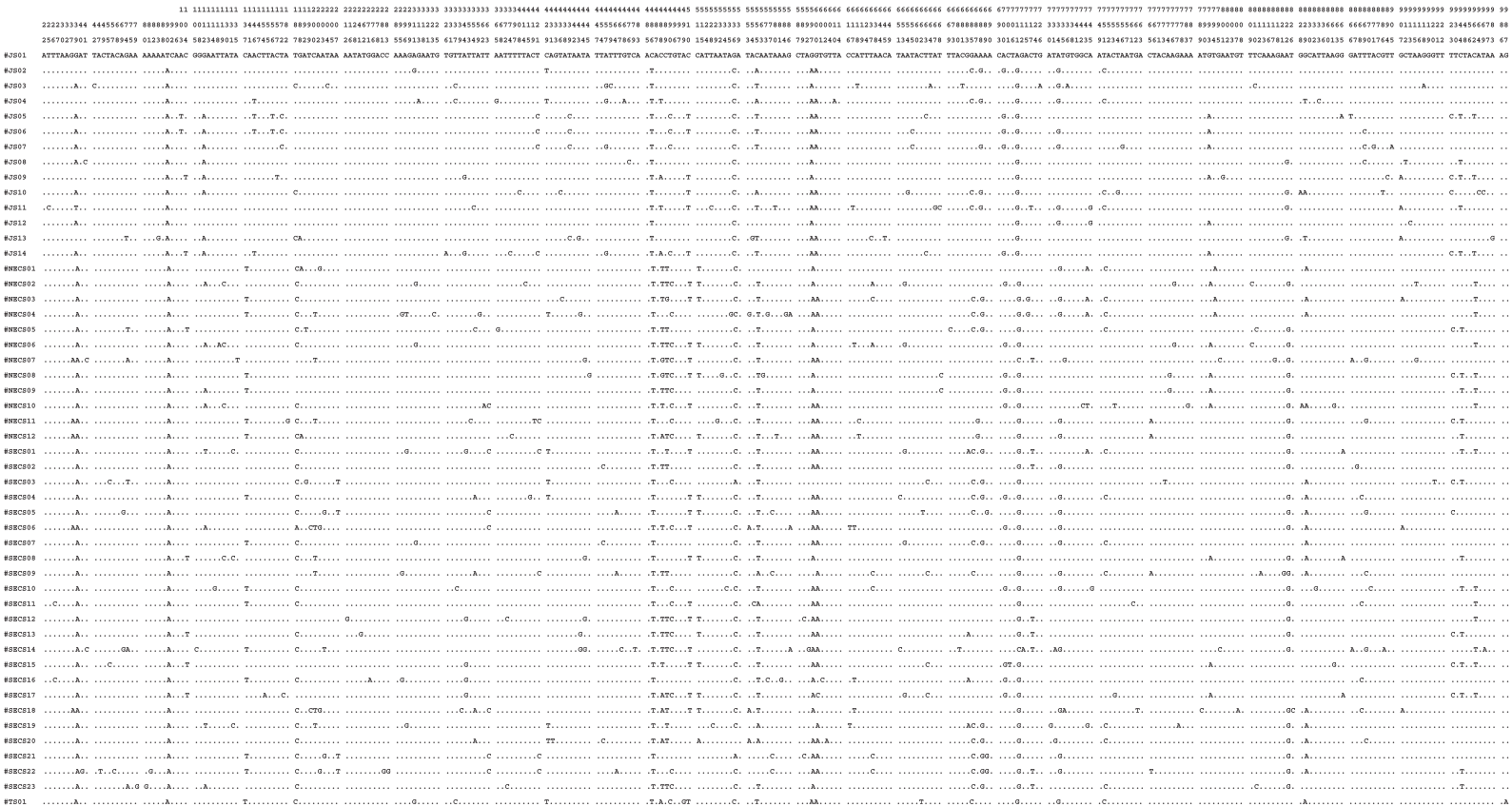

Figure 2. Variable sites in the 95 haplotypes found in the control region (992 bp) of 95 kuruma prawn individuals from five sampling localities. The numbers above the sequences correspond to the positions of the polymorphic sites. Dots indicate an identical nucleotide at the position relative to haplotype JS01.

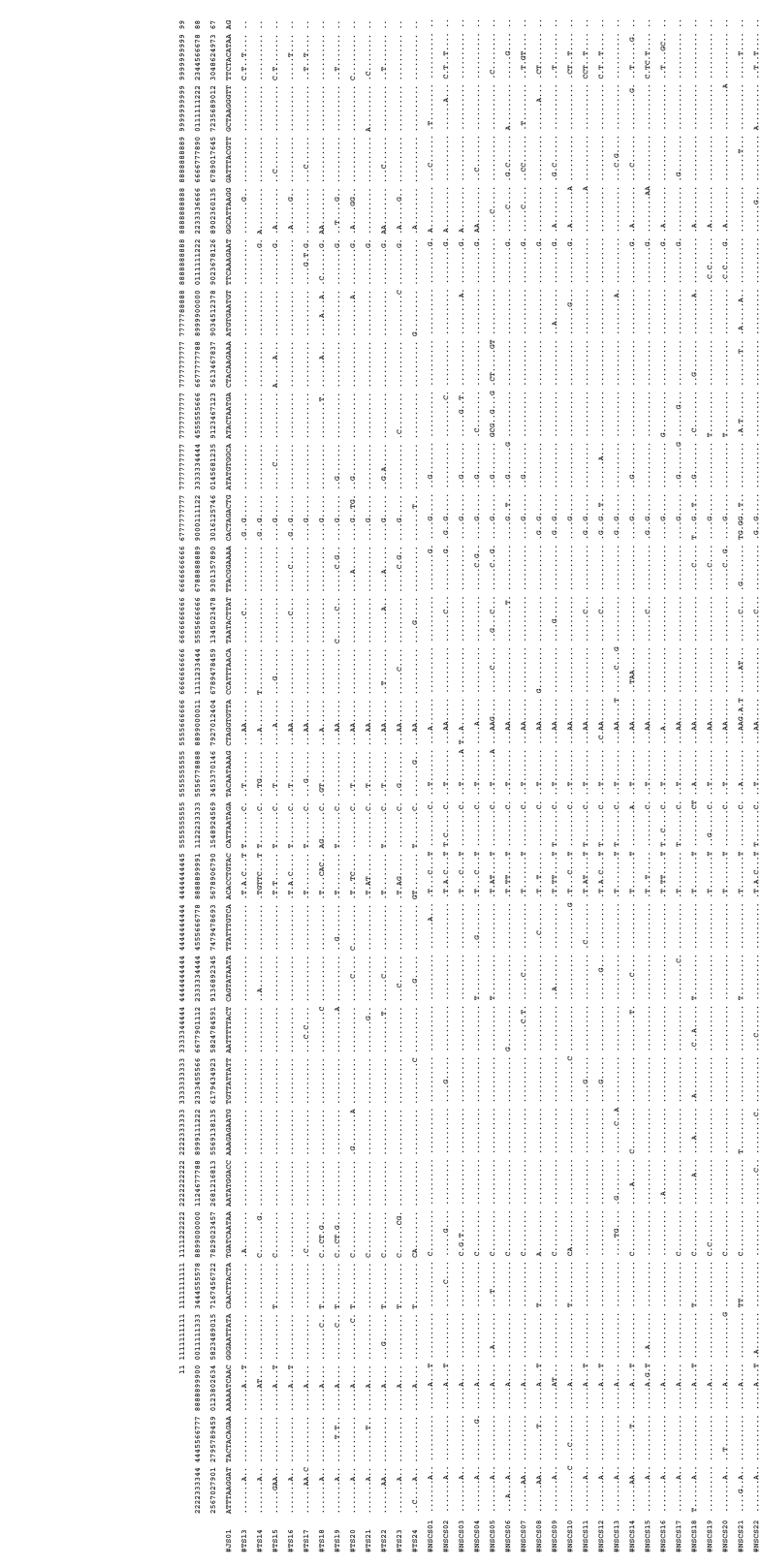

Figure 2. (*continued*)

Table 2. F_{ST} (above diagonal) and N_m (below diagonal) values between five kuruma prawn populations in East Asia. Abbreviations for populations are defined in Table 1.

	JS	NECS	SECS	TS	NSCS
JS		0.0845**	0.0735**	0.0840**	0.0630**
NECS	2.71		0.0200 n.s.	0.0202 n.s.	0.0457**
SECS	0.0840	12.2787		0.0042 n.s.	0.0024*
TS	2.7254	12.1297	59.6408		0.0093 n.s.
NSCS	3.7203	4.9285	9.9741	26.5970	

*$p < 0.05$, **$p < 0.01$, n.s. = not significant ($p > 0.05$).

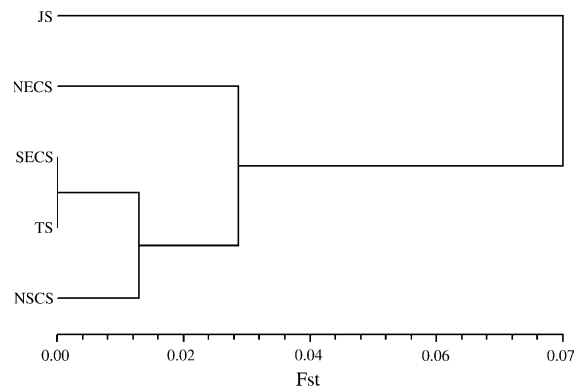

Figure 3. UPGMA tree showing relationships among five populations.

Table 3. The results of AMOVA for all five populations. Abbreviations for populations are defined in Table 1.

Groupings		Variance component	% Total variance	Φ-statistics	p
For all populations					
1	Group 1 {JS, NECS, SECS, TS, NSCS}	AG	3.62	$\Phi_{ST} = 0.0362$	<0.0001
Based on UPGMA tree of five populations					
2	Group 1 {JS} Group 2 {NECS, SECS, TS, NSCS}	AG	5.43	$\Phi_{CT} = 0.0542$	<0.0001
3	Group 1 {JS} Group 2 {NECS} Group 3 {SECS, TS, NSCS}	AG	4.38	$\Phi_{CT} = 0.0437$	<0.0001
4	Group 1 {JS} Group 2 {NECS} Group 3 {SECS, TS} Group 4 {NSCS}	AG	3.94	$\Phi_{CT} = 0.0394$	<0.0001
Based on the significance of F_{ST}s					
5	Group 1 {JS} Group 2 {NECS, SECS, TS} Group 3 {NSCS}	AG	3.55	$\Phi_{CT} = 0.0354$	=0.0517
6	Group 1 {JS} Group 2 {NECS, SECS} Group 3 {TS, NSCS}	AG	2.71	$\Phi_{CT} = 0.0270$	<0.0001
Based on ocean divisions and others					
7	Group 1 {JS} Group 2 {NECS, SECS} Group 3 {TS} Group 4 {NSCS}	AG	1.38	$\Phi_{CT} = 0.0138$	<0.3994
8	Group 1{JS, NECS} Group 2{SECS, TS, NSCS}	AG	1.24	$\Phi_{CT} = 0.0124$	=0.0982
9	Group 1{JS, NECS, SECS} Group 2{TS, NSCS}	AG	−0.36	$\Phi_{CT} = -0.0035$	=0.5958

AG is the among-groups component of variance. The best groupings have maximal values of AG. Note that the Φ-statistic estimators in the AMOVA are random variables and can take either positive or negative values, negative values indicating excess of heterozygotes. Such negative estimates should be interpreted as zero in the AMOVA (Schneider *et al.*, 2000).

Table 4. The results of AMOVA for the NECS, SECS, TS, and NSCS populations. Abbreviations for populations are defined in Table 1.

Groupings		Variance component	% Total variance	Φ-statistics	p
1	Group 1 {NECS, SECS, TS, NSCS}	AG	1.79	$\Phi_{ST} = 0.0178$	=0.0047
2	Group 1 {NECS} Group 2 {SECS, TS, NSCS}	AG	1.92	$\Phi_{CT} = 0.0191$	<0.0001
3	Group 1 {NECS} Group 2 {SECS, TS} Group 3 {NSCS}	AG	2.01	$\Phi_{CT} = 0.0200$	<0.0001
4	Group 1 {NECS, SECS, TS} Group 2 {NSCS}	AG	1.23	$\Phi_{CT} = 0.0123$	<0.2442
5	Group 1 {NECS, SECS} Group 2 {TS, NSCS}	AG	−0.74	$\Phi_{CT} = -0.0073$	=0.6727
6	Group 1 {NECS, SECS} Group 2 {TS} Group 3 {NSCS}	AG	−0.58	$\Phi_{CT} = -0.0058$	<0.4977

AG is the among-groups component of variance. The best groupings have maximal values of AG. Note that the Φ-statistic estimators in the AMOVA are random variables and can take either positive or negative values, negative values indicating excess of heterozygotes. Such negative estimates should be interpreted as zero in the AMOVA (Schneider *et al.*, 2000).

Additional AMOVA excluding the JS population was also performed. The results are shown in Table 4. The AMOVA for all four populations yields a significant Φ_{ST} value of 0.0178, indicating significant genetic division among these four populations. Significant values of Φ_{CT} are observed in two of the five groupings. In two significant groupings, the division occurs in the NECS population, and indicates that the NECS population is an independent population. Genetic differentiation between populations is observed to be positively correlated with the distance of geographical separation between populations, which indicates that kuruma prawns conform to an isolation-by-distance model of maternal gene flow ($r = 0.83693$, $p = 0.037$).

Discussion

Although the neighbour-joining tree of the 95 haplotypes reveals few genealogical branches or geographic clusters, the results of cluster analysis, sequence statistic (F_{ST}), and AMOVA indicate significant genetic division between these five populations. The cluster analysis indicates that these five populations can be clustered into three groups. One includes the JS population, the second includes the NECS population, and the third includes the rest of the populations (Figure 3). F_{ST} values between the JS population and the rest, between the NECS and NSCS populations, and between the SECS and NSCS populations show significant genetic differences (Table 2), indicating that at least three isolated populations exist in these waters. Results of the AMOVA reveal three different populations in marginal seas of East Asia (Tables 3 and 4). Based on the above analyses, kuruma prawns in East Asia can be discriminated into three distinct populations. The first population is in the Japan Sea, the second in the north of the East China Sea, and the third in the south of the East China Sea, the Taiwan Strait, and the north of the South China Sea. The genetic divisions between the populations in SECS, TS, and NECS are in agreement with the previous morphological study by Tzeng and Yeh (1999).

Kuruma prawns migrate from inshore to offshore as they grow, but the migratory distance is limited (Dall *et al.*, 1990). Thus, the dispersal of larvae is the primary source of gene flow, and ocean currents play a major role in the dispersal of this species. The spawning season lasts from April until October in the NECS population (Yamada *et al.*, 1986). Along the eastern coast of China, kuruma prawn larvae from the north of the East China Sea may be transported to the Taiwan Strait by the China coastal current. However, during the spawning season of the NECS population, the China coastal current is not strong enough to flow through the Taiwan Strait, and only spreads to the north of Taiwan and to the middle of the Taiwan Strait (Wu, 1982). Higher levels of gene flow between the NECS and SECS populations ($N_m = 12.2787$), and between the NECS and TS populations ($N_m = 12.1297$) have been observed, but lower N_m (4.9285) between the NECS and NSCS populations has been found (Table 2). This occurrence of kuruma prawn larvae mixed results in homogeneity among the NECS, SECS, and TS populations, but may not be large enough to eliminate the genetic difference between the NECS and NSCS populations (Table 2).

In the NSCS and TS populations, the main spawning season is from late spring to summer. During the main spawning season, the South China Sea warm water dominates the Taiwan Strait (Wang and Chern, 1989) and

provides a northbound gene flow from the north of South China Sea to the south of East China Sea. Very high gene flow between the TS and NSCS populations ($N_m = 26.5970$) is observed and prevents population differentiation between these two populations (Table 2). In general, if the N_m value is greater than about 5, the gene flow is considered sufficient to maintain a relatively homogeneous gene pool (Slatkin, 1987). There is a high gene flow ($N_m = 9.9741$) between the NSCS and SECS populations, but significant genetic difference is still observed (Table 2). This genetic difference between the NSCS and SECS populations may result from the recruitment of larvae from the NECS population.

During the last glacial maximum (LGM), the sea level was 130−150 m lower than the present level in the East China Sea and 100−120 m lower in the South China Sea. Consequently, the entire Bohai gulf, the Yellow Sea, and the Tsushima and Taiwan Straits were exposed, and the East China Sea was reduced into an elongated trough during LGM (Wang and Sun, 1994). As the Tsushima Strait was exposed during LGM, the Japan Sea and East China Sea were completely separated from each other. Therefore, gene flow between the two waters was completely suspended, explaining why F_{ST} values between the JS and the rest of the populations are at least twice the ones obtained between other populations. The disappearance of habitat had restricted marine species to the relatively limited areas and caused the mixing among populations and reduced the genetic variation between populations (Benzie and Williams, 1997). After LGM, the distribution of kuruma prawns gradually extended corresponding to the rise of the sea level of the East China Sea. The similar magnitude of nucleotide diversity in each population provides part of the evidence that four populations may share common ancestry (Table 1).

Acknowledgements

We thank Dr Y. Uozumi, National Research Institute of Far Sea Fishery, Dr T. Minami, and H. Mastusato, Japan Sea National Research Institute in Niigata City, for kindly providing kuruma prawn samples from the Japan Sea.

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