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Population Structure of the Sword Prawn (*Parapenaeopsis hardwickii*) (Decapoda: Penaeidae) in the East China Sea and Waters Adjacent to Taiwan Inferred from the Mitochondrial Control Region

Tzong-Der Tzeng*

College of Liberal Education, Shu-Te University, 59 Hun-Shan Rd., Hun Shan Village, Yen Chau, Kaohsiung County 824, Taiwan

Tzong-Der Tzeng (2007) Population structure of the sword prawn (*Parapenaeopsis hardwickii*) (Decapoda: Penaeidae) in the East China Sea and waters adjacent to Taiwan inferred from the mitochondrial control region. *Zoological Studies* **46**(5): 561-568. Sequence analyses on the complete mitochondrial control region (1048 bp in length) were conducted to elucidate the population genetic structure of the sword prawn (*Parapenaeopsis hardwickii*) (Decapoda: Penaeidae) in the East China Sea (ECS) and waters adjacent to Taiwan. Four samples including 171 individuals were separately collected from the ECS and waters off Ilan (IL, northeastern Taiwan), Taichung (TC, west-central Taiwan), and Cheding (CD, southwestern Taiwan), and 153 haplotypes were obtained. The haplotype diversity (*h*) was high for all samples (99.6%), with values from 99.2% (TC) to 99.8%. Nucleotide diversity (π) was low for all samples (0.77%), with values from 0.66% ± 0.12% (ECS) to 0.95% ± 0.11% (IL). Both Tajima's *D* and Fu and Li's *D* statistics suggested that this species in the studied waters has experienced population expansion since the last glacial maximum. Despite no phylogeographic structure in the haplotypes, F_{ST} values between IL and the rest of the samples indicated significant genetic differences. The UPGMA tree of the 4 samples showed 2 distinct clusters: the IL sample and the rest of the samples. The analysis of molecular variance (AMOVA) also showed significant genetic differences between IL and the rest of the samples. The results suggest that 2 distinct populations exist in the ECS and waters adjacent to Taiwan. The utility of the mitochondrial control region for discriminating stocks of sword prawn is herein demonstrated, but further verification of the population genetic structure is essential.
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Key words: Mitochondrial control region, *Parapenaeopsis hardwickii*, Population structure, Fishery management.

Understanding the population genetic structure is an important component of successful and sustainable long-term management of fishery resources (Hillis et al. 1996). Analyses of the population genetic structures of marine biota have frequently revealed that organisms with a high dispersal capacity have little genetic distinction over large geographic scales (Hellberg 1996). Such studies suggest that there are high levels of gene flow among 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, and historical events, and they may produce sufficient chances for genetic distinction (Palumbi 1994).

Sword prawn (*Parapenaeopsis hardwickii*) (Decapoda: Penaeidae) is distributed mainly in the Indo-West Pacific from Pakistan to Japan and lives at 5-90 m in depth in areas with a sandy bot-

tom. This is a very abundant and highly valued species in the East China Sea (ECS) and waters adjacent to Taiwan (Wu 1985, Song and Ding 1993). The life history of the sword prawn, with an offshore planktonic larval phase, estuarine post-larval and juvenile phases, and offshore adult and spawning phases (Dall et al. 1990), may allow moderate gene flow among populations.

Various approaches have been adopted to examine the population structure of marine organisms, including studies of the distribution and abundance of various life-history stages, marks and tags, morphological characters, allozymes, and DNA markers. Because each technique has its merits and disadvantages, integrating the result of several methods used in a multi-pronged approach to stock identification may maximize the likelihood of correctly defining stocks (Pawson and Jenning 1996). Several studies on the fishery biology of sword prawn in this area have been conducted (Wu 1985, Guo 1993, Tzeng and Yeh 2000, Li et al. 2000, Zheng and Li 2002), but only 1 paper analyzed morphological characters in an attempt to determine the stock structure of this species (Tzeng 2004). Two morphologically distinguishable populations of sword prawn in the ECS and Taiwan Strait were discriminated. However, variations in morphological characters can be affected by both genetic and environmental factors, so that discrimination of populations based on morphological variations must be verified by genetic evidence to confirm that the variations reflect the true degree of reproductive isolation rather than environmental isolation (Pepin and Carr 1992).

Mitochondrial (mt)DNA 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 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 among prawn populations (Simon 1991). In this paper, sequence analyses of the complete mtDNA control region were conducted to elucidate the population genetic structure of sword prawn in the ECS and waters adjacent to Taiwan.

MATERIALS AND METHODS

Sampling

Four sword prawn samples including 171 specimens were collected from commercial shrimp trawlers during Oct. 2002 to Feb. 2003 (Fig. 1, Table 1). They were separately sampled from the ECS and waters off Ilan (IL, northeastern Taiwan), Taichung (TC, west-central Taiwan), and Cheding (CD, southwestern Taiwan). Specimens were iced or frozen immediately after capture and later kept at -75°C before DNA extraction.

DNA extraction, amplification, and sequencing

Total DNA was extracted from frozen muscle tissue using a standard DNA proteinase *K* digestion/phenol-chloroform extraction procedure. The complete control region was amplified using the primers P30 (5'-GATCTTTAGGGGAATGGTG TAATTCCATTG-3') and P24 (5'-GTGTAACA GGGTATCTAATCCTGG-3'), which bind to the tRNA^Met and 12S rRNA genes, respectively. A polymerase chain reaction (PCR) was conducted according to standard protocols (Kocher et al. 1989). Thermal cycling was performed in a GeneAmp 2400 thermal cycler (Perkin-Elmer,

Table 1. Sample code, sampling locality, sample size, gene diversity (*h*) with the standard deviation (SD), nucleotide diversity (π) with the SD, Tajima's *D*, and Fu and Li's *D* in 4 sword prawn samples in the East China Sea and waters adjacent to Taiwan

Sample code	Locality	Sampling size	*h* ± SD (%)	π ± SD (%)	Tajima's *D*	Fu and Li's *D*
ECS	East China Sea	29	99.8 ± 1.0	0.66 ± 0.12	-2.4586**	-3.8256**
IL	waters off Ilan	43	99.8 ± 0.6	0.95 ± 0.11	-2.4749**	-4.6889**
TC	waters off Taichung	48	99.2 ± 0.7	0.71 ± 0.09	-2.6121***	-4.5861**
CD	waters off Cheding	51	99.8 ± 0.4	0.69 ± 0.06	-2.6049***	-5.3151**
Total		171	99.6 ± 0.2	0.77 ± 0.05	-2.7858***	-9.0231**

** *p* < 0.01; *** *p* < 0.001.

Norwalk, CT, USA) and PCR conditions consisted of 39 cycles of denaturation at 95°C for 50 s, annealing at 50°C for 1 min, and extension at 72°C for 1.5 min. An initial denaturation step at 95°C for 5 min and a final extension holding at 72°C for 10 min were respectively included in the 1st and last cycles. Amplified DNA was separated through electrophoresis on 1.5% agarose gels and purified with the Gene Clean II kit (Bio101, Vista, CA, USA). Double-stranded DNA was sequenced on an ABI 377 DNA sequencer (Applied Biosystems, Inc.; Foster City, CA, USA) with the same primers used for amplification.

Sequence analyses

DNA sequences were aligned using the PILE-UP program in GCG (Genetics Computer Group, vers. 7.0; Devereux et al. 1991). The beginning and end of the control region were confirmed by comparing them with the complete published mtDNA sequence of *Penaeus monodon* (Wilson et al. 2000). Subsequent analyses were based on the complete control region sequence obtained from the 171 individuals. Nucleotide composition and numbers of variable sites were assessed with MEGA3 (Kumar et al. 2004). The genetic diversity
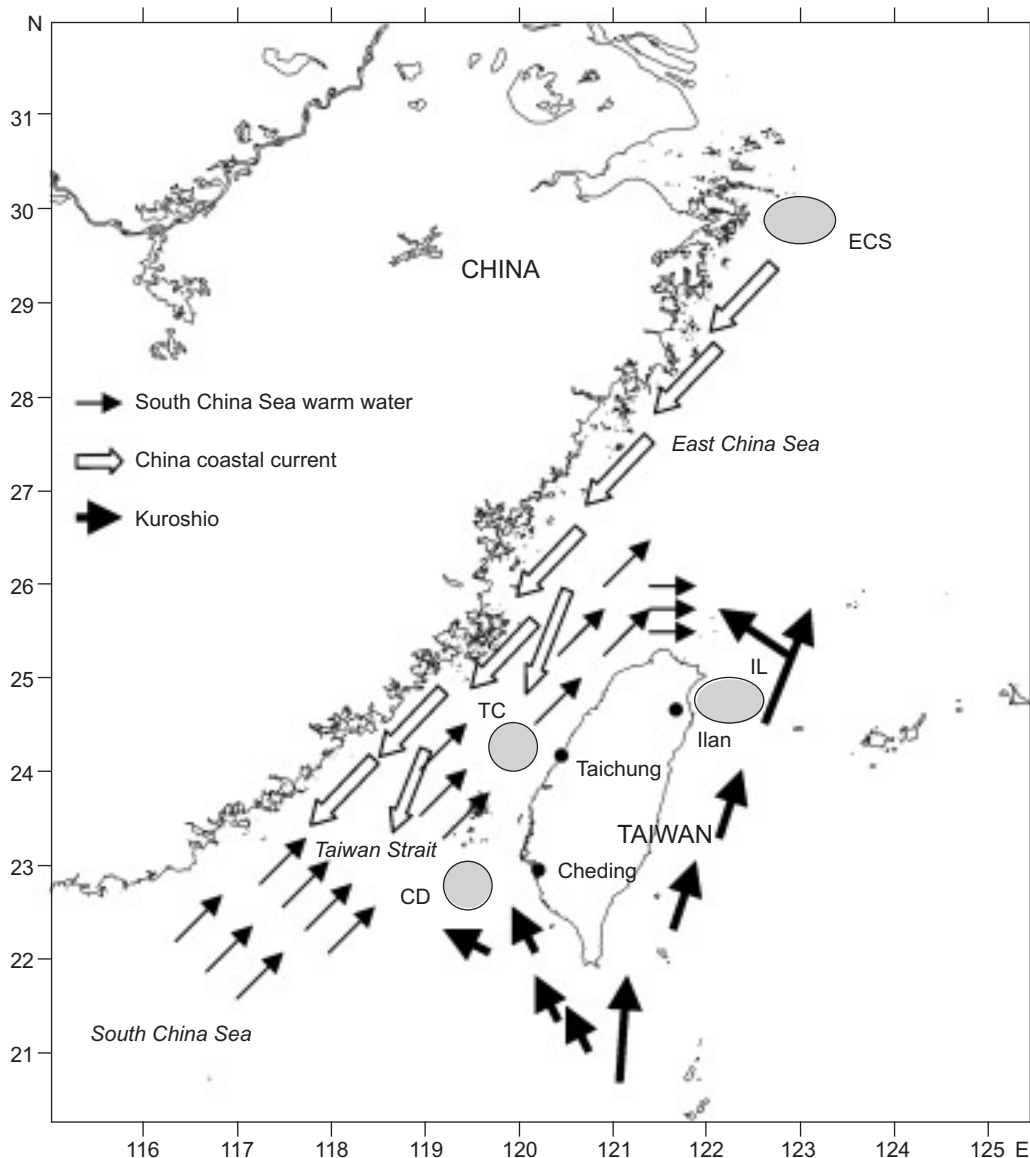

Fig. 1. Shaded areas indicating sampling areas in the East China Sea and waters adjacent to Taiwan.

(*h*) and nucleotide diversity (π) (Nei 1987) in each sample were calculated using DnaSP vers. 4.10 (Rozas et al. 2003). Genealogical relationships among mtDNA haplotypes were constructed with TCS (Clement et al. 2000) and the method described by Templeton et al. (1992).

To examine whether any two of the samples genetically differed from each other, pairwise FST statistics (Wright 1965) among the 4 samples were estimated and tested using the program, ProSeq (Filatov 2002). The statistical significance of the estimate was tested through 1000 permutations. The dendrogram of the 4 samples was constructed using the unweighted pair-group method with arithmetic means (UPGMA) based on F_{ST} values with MEGA3. Gene flow (N_m), was estimated using the relationship $N_m = ((1 / F_{ST}) - 1) / 2$ (Hudson et al. 1992).

Analyses of molecular variance (AMOVA) implemented in ARLEQUIN vers. 2.000 (Schneider et al. 2000) were performed to test the geographic divisions among samples. Various groupings of samples were suggested by (1) the UPGMA tree of sampling areas, (2) F_{ST} values between samples, and (3) the geographic distribution. The significant of these Φ statistics was evaluated by 1000 random permutations of sequences among samples. Groupings that maximized values of Φ_{CT} and significantly differed from random distributions of individuals were assumed to be the most probable geographic subdivisions.

To check for deviations from neutrality, Tajima's *D* statistical test (Tajima 1989) and Fu and Li's *D* statistical test (Fu and Li 1993) were carried out to assess evidence for population expansion using DnaSP (Rozas et al. 2003). Meanwhile, the concordance of data with the distribution underlying the expansion model was assessed. The population demographic history was examined by calculating mismatched distributions over all haplotypes with DnaSP. An estimate of the time since population expansion (τ) can be made from mismatched data. τ was calculated in units of 1/2μ generations with DnaSP, where μ is the mutation rate (μ) multiplied by the number of nucleotides in the sequence.

RESULTS

The target segment subjected to PCR using the P30 and P24 primers included a portion of tRNA[Met], tRNA[Gln], tRNA[Ile], the control region, and a portion of 12S rRNA. The 1048-bp-long control region was used for the following analyses. The nucleotide composition of the mitochondrial control region was obviously AT rich (85.9%). In total, 296 variable sites, including 203 singletons and 93 parsimoniously informative sites, were observed. The haplotype diversity (*h*) was high for all samples (99.6%), with values from 99.2% (TC) to 99.8%. Nucleotide diversity (π) was low for all samples (0.77%), with values from 0.66% ± 0.12% (ECS) to 0.95% ± 0.11% (IL) (Table 1).

Among the 171 individuals studied, 153 haplotypes were defined. Haplotype ECS12 was the most common one, being observed in all samples and shared by 9 individuals: 1 specimen was from ECS, 2 from IL, 4 from TC, and 2 from CD. The second most common haplotype was ECS25, and was observed in ECS, IL, and TC samples. Haplotype TS28 was shared by IL and TC samples. Haplotypes ECS21, IL14, TC14, TC23, and CD48 occurred twice in single samples. All others occurred in only 1 individual in single samples. The 95% parsimony network for the 153 haplotypes showed no geographical structuring (data not shown).

The F_{ST} and N_m values are shown in table 2. The F_{ST} value among all samples showed a significant amount of genetic variation ($F_{ST} = 0.0146$, *p* < 0.01). Pairwise F_{ST} values between IL and the rest of the samples revealed significant genetic differences, but the genetic variation among the other 3 samples was not significant. The N_m values between all pairwise comparisons ranged from 8.4135 (IL-CD) to 111.0035 (ECS-CD). The UPGMA tree of the 4 samples is shown in figure 2. The 4 samples were clustered into 2 distinct groups, with IL constituting the 1st group and the other 3 samples making up the 2nd group.

Various groupings of samples were tested using AMOVA, but only 2 groupings showed signif-

Table 2. F_{ST} (below the diagonal) and N_m values (above the diagonal) among 4 sword prawn samples in the East China Sea and waters adjacent to Taiwan. The abbreviations for the sampling locations are defined in table 1

	ECS	IL	TC	CD
ECS	-	14.5718	63.9440	111.0035
YL	0.0169**	-	11.5709	8.4135
TC	0.0039ns	0.0210**	-	49.7747
CD	0.0022ns	0.0289**	0.0050ns	-

** *p* < 0.01; ns, not significant.

icant variation (Table 3). In the 1st grouping, the AMOVA for the 4 samples yielded a small but significant Φ_{ST} value of 0.0153, indicating that at least one of the pair-wise comparisons revealed significant heterogeneity. In the 2nd grouping, the 4 samples were classified into 2 groups. One included IL, and the other included ECS, TC, and CD. A significant Φ_{CT} value of 0.025 was observed, indicating that genetic discontinuity occurred in the IL population.

Tajima's *D* and Fu and Li's *D* statistical tests were performed to determine departure from neutrality. Significant negative values were obtained in all sampling regions by both of these tests (Table 1). The model of population expansion also could not be rejected when all samples were combined (Table 1). The distribution of the pairwise number of differences in the control region haplotypes well fit an expansion model, showing a smooth wave predicted for a population that had undergone a demographic expansion (Fig. 3). This outcome was also supported by the low Harpending's raggedness index ($r = 0.0046$, $p = 0.6712$). The estimated time since population expansion, τ, was $4.55/2\mu$ generations. McMillen-Jackon and Bert (2003) roughly estimated a mutation rate of 19%/MY for the mtDNA control region of brown shrimp *Farfantepenaeus*

aztecus and white shrimp *Litopenaeus setiferus*. Using this rate, the sword prawn population experienced a period of rapid growth approximately 11,400 yr ago.

DISCUSSION

Although the parsimony network for the 153 haplotypes revealed no genealogical branches or geographic clusters, results of the cluster analysis, sequence statistic (F_{ST}), and AMOVA indicated significant genetic division among the 4 samples. The cluster analysis indicated that the 4 samples could be clustered into 2 groups: the IL sample, and the other 3 samples (Fig. 2). F_{ST} values between IL and the other 3 samples showed significant genetic differences (Table 2), indicating that at least 2 isolated populations exist in the study area. Results of the AMOVA revealed 2 different populations in the ECS and waters adjacent to Taiwan (Table 3). Based on the above analyses, the sword prawn in the ECS and waters adjacent to Taiwan can be discriminated into 2 distinct populations. The first population is in waters adjacent to Ilan (IL), and the 2nd one in the ECS and Taiwan Strait (TC and CD). The present results that the sword prawns in the ECS and Taiwan
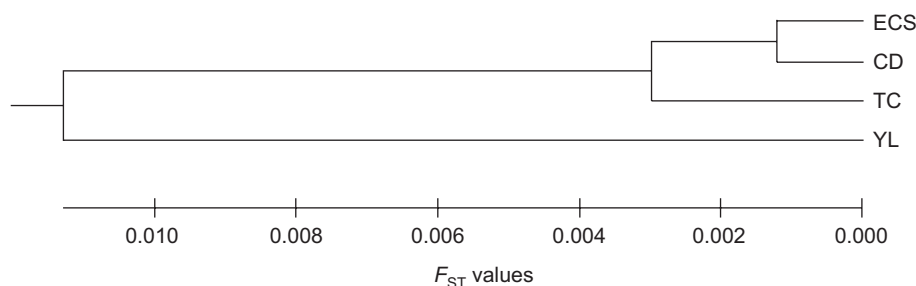

Fig. 2. UPGMA dendrogram illustrating the genetic relationships among sword prawn samples from the East China Sea and waters adjacent to Taiwan based on F_{ST} values. Abbreviations for the sampling locations are given in table 1.

Table 3. Results of AMOVA. Abbreviations for sampling locations are given in table 1

Groupings	Source of variation	Percentage of variation	Φ-statistics	*p*
One group for all locations				
1. Group 1{ECS, IL, TC, CD}	Among locations	1.53	$\Phi_{ST} = 0.0153$	< 0.0001
Two groups				
2. Group 1 {ECS, TC, CD} Group 2 {IL}	Among groups	2.50	$\Phi_{CT} = 0.0250$	< 0.0001

Strait share a single gene pool is not in agreement with a previous outcome that 2 morphologically distinguishable stocks separately exist in the ECS and the Taiwan Strait (Tzeng 2004). Gene flow in these waters may play an important role in the discrepancy.

Sword prawns migrate from inshore to offshore as they grow to a specific size or life stage, 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. Two spawning areas were found in the Taiwan Strait and ECS. One is located in the middle and northern portions of the Taiwan Strait (Guo 1993), but the other is located in the northern ECS (Zheng and Li 2002). In the northern ECS, the spawning season lasts from May to Sept., with the peak usually occurring in June and July (Zheng and Li 2002). Along the eastern coast of China, sword prawn larvae from the northern ECS may be transported to the Taiwan Strait by the China Coastal Current (Fig. 1). During the spawning season of the population in the ECS, the China Coastal Current can spread to the Taiwan Strait (Wu 1982). Higher levels of gene flow between the ECS and CD samples (N_m = 111.0), and between the ECS and TC samples (N_m = 63.9) were observed, but a lower N_m (14.6) value between the ECS and IL samples was found (Table 2). This mixing of sword prawn larvae results in homogeneity among the ECS, CD, and TC samples, but might not be large enough to eliminate the genetic difference between the ECS and IL samples (Table 2). In the Taiwan Strait, 2 peaks of spawning were found (Guo 1993): one in Feb. to Apr., and the other in Oct. and Nov. During the late spring, warm water from the South China Sea dominates the Taiwan Strait (Wang and Chern 1989). High gene flow between CD and TC (N_m = 49.8) was observed, and this prevents population differentiation between these 2 localities (Table 2). The main stream of the Kuroshio Current flows steadily northward along the eastern coast of Taiwan, and the Kuroshio enters Ilan Bay between November and March. Warm water of the South China Sea flows through the Taiwan Strait and a little water mass flushes into Ilan Bay between Apr. and Oct. (Wang and Chern 1989). There were lower gene flows detected between CD and IL (N_m = 11.6) and between TC and IL (N_m = 8.4) (Table 2). Therefore, this genetic difference between the IL and CD/TC samples may have resulted from recruitment of larvae from the ECS.

On the whole, in contrast to the high haplotype diversity (0.997), the lower nucleotide diversity (0.77%) suggests that sword prawn in the region studied has undergone population expansion (Avise 2000). The neutrality of mtDNA control region mutations was rejected on the basis of Tajima's *D* and Fu and Li's *D* tests (Table 1). These 2 statistics are sensitive to factors such as bottlenecks and population expansions which tend to drive the values of Tajima's *D* and Fu and Li's *D*
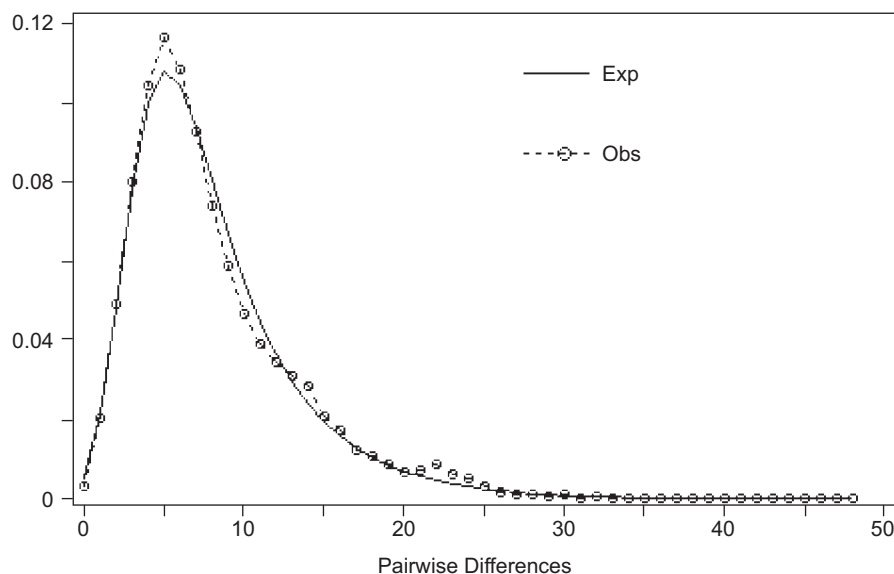

Fig. 3. Mismatched distribution constructed using pairwise differences among complete mitochondrial control region sequences of the sword prawn in the East China Sea and waters adjacent to Taiwan.

towards more-negative values (Tajima 1996, Martel et al. 2004). Indeed, significant negative values of these 2 indices in this study indicated that sword prawn in the ECS and waters adjacent to Taiwan have experienced population expansion. The unimodel mismatched frequency distribution pattern based on the mtDNA sequence accorded well with the predicted distribution under a model of population expansion (Fig. 3, Rogers and Harpending 1992). This unimodel pattern has also been observed for other shrimp species, such as *Farfantepenaeus aztecus* and *Farfantepenaeus duorarum* (McMillen-Jackson and Bert 2003 2004). Past geological and climatic events undoubtedly played major roles in terrestrial biogeography. During the last glacial maximum (LGM, about 20,000-15,000 yr ago), the sea level was 130-150 m lower than the present level in the ECS and 100-120 m lower in the South China Sea. Consequently, the entire Yellow Sea and Taiwan Strait were exposed, and the ECS was reduced to an elongated trough during the LGM (Wang and Sun 1994). The disappearance of habitat restricted marine species to relatively limited areas and caused mixing among populations, reducing genetic variations between populations (Benzie and Williams 1997). After the LGM, the sea level of the ECS and Taiwan Strait gradually rose and reached a climax about 5000-6000 yr ago, when the exposed benthal areas of the Taiwan Strait and ECS were again covered by seawater (Zhao 1982). An estimate of the time since the sword prawn population expansion was approximately 11,400 yr ago, in agreement with the extension of the distribution of sword prawns following the rise in the sea level of the ECS and Taiwan Strait.

REFERENCES

Avise JC. 2000. Phylogeography: the history and formation of species. Cambridge, MA: Harvard Univ. Press.

Benzie JAH. 1999. Genetic structure of coral reef organisms–ghosts of dispersal past. Am. Zool. **39:** 131-145.

Benzie JAH, ST Williams. 1997. Genetic structure of giant clam (*Tridacna maxima*) populations in the West Pacific is not consistent with dispersal by present-day ocean currents. Evolution **51:** 768-783.

Briggs JS. 1999. Coincident biogeographic patterns: Indo-West Pacific Ocean. Evolution **53:** 326-335.

Clement M, D Posada, KA Crandall. 2000. TCS: a computer program to estimate 6 genealogies. Mol. Ecol. **9:** 1657-1659.

Dall W, BJ Hill, PC Rothlisberg, DJ Sharples. 1990. The biology of the Penaeidae. London: Academic Press.

Devereux J, P Haeberli, P Marquess. 1991. Genetic Computer Group Manual, vers. 7.0. Madison, WI: Univ. of Wisconsin.

Filatov DA. 2002. ProSeq: a software for preparation and evolutionary analysis of DNA sequence data sets. Mol. Ecol. Notes **2:** 621-624.

Fu YX, WH Li. 1993. Statistical tests of neutrality of mutations. Genetics **133:** 693-709.

Guo SY. 1993. Growth study of sword prawn (*Parapenaeopsis hardwickii*) in the southwestern coast of Taiwan. Master's thesis, National Sun Yat-sen University, Kaohsiung, Taiwan. (in Chinese with English abstract)

Hellberg ME. 1996. Dependence of gene flow on geographic distance in two solitary corals with different larval dispersal capabilities. Evolution **50:** 1167-1175.

Hillis DM, BK Mable, C Moritz. 1996. Molecular Systematics. Sunderland, MA: Sinauer Associates.

Hoelzel AR, JM Hancock, GA Dover. 1991. Evolution of the cetacean mitochondrial D-loop region. Mol. Biol. Evol. **8:** 475-493.

Hudson RR, M Slatkin, WP Maddison. 1992. Estimation of levels of gene flow from DNA sequence data. Genetics **132:** 583-589.

Kocher TD, WK Thomas, A Meyer, SV Edwards, S Paabo, SX Villablanca, AC Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proc. Natl. Acad. Sci. USA **86:** 6196-6200.

Kumar S, K Tamura, M Nei. 2004. MEGA3: integrated software for Molecular Evolutionary Genetics Analysis and sequence alignment. Brief Bioinform. **5:** 150-163.

Li M, HE Ni, JQ Zhu, HT Song, CG Yu. 2000. Population dynamics and estimation of maximum sustaining yield for *Parapenaeopsis hardwickii* in the northern area of East China Sea. J. Fish. China **24:** 364-369.

Martel C, F Viardb, D Bourguetc, P Garcia-Meuniera. 2004. Invasion by the marine gastropod *Ocinebrellus inornatus* in France. 1. Scenario for the source of introduction. J. Exp. Mar. Biol. Ecol. **305:** 155-170.

McMillen-Jackson AL, TM Bert. 2003. Disparate patterns of population genetic structure and population history in two sympatric penaeid species in the southeastern United States. Mol. Ecol. **12:** 2895-2905.

McMillen-Jackson AL, TM Bert. 2004. Genetic diversity in the mtDNA control region and population structure in the pink shrimp *Farfantepenaeus duorarum*. J. Crustacean. Biol. **24:** 101-109.

Nei M. 1987. Molecular evolutionary genetics. New York: Columbia Univ. Press.

Palumbi SR. 1994. Genetic divergence, reproductive isolation, and marine speciation. Annu. Rev. Ecol. Evol. S. **25:** 547-572.

Palumbi SR. 1997. Molecular biogeography of the Pacific. Coral Reefs **16:** 47-52.

Pawson MG, S Jennings. 1996. A critique of methods for stock identification in marine captured fisheries. Fish. Res. **25:** 203-217.

Pepin P, SM Carr. 1992. Morphological, meristic, and genetic

analysis of stock structure in juvenile Atlantic cod (*Gadus morhua*) from the Newfoundland shelf. Can. J. Fish. Aquat. Sci. **52:** 1924-1933.

Rogers AR, H Harpending. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Mol. Biol. Evol. **9:** 552-569.

Rozas J, JC Sanchez-DelBarrio, X Messeguer, R Rozas. 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics **19:** 2496-2497.

Schneider S, D Roessli, L Excoffier. 2000. ARLEQUIN vers. 2.000: a software for population genetics data analysis. Geneva, Switzerland: Genetics and Biometry Laboratory, Univ. of Geneva.

Simon C. 1991. Molecular systematics at the species boundary: exploiting conserved and variable regions of the mitochondrial genome of animals via direct sequencing from amplified DNA. *In* GM Hewitt, AWB Johnston, JP Young, eds. Molecular techniques in taxonomy. New York: Springer-Verlag.

Song HT, TM Ding. 1993. A comparative study on fishery biology of main economic shrimps in the north of East China Sea. J. Zhejiang Coll. Fish. **12:** 240-248.

Tajima F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics **123:** 585-595.

Tajima F. 1996. The amount of DNA phylogeography: methods of evaluating and minimizing inference errors. Genetics **143:** 1457-1465.

Templeton AR, KA Crandall, CF Sing. 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. Genetics **132:** 619-633.

Tzeng TD. 2004. Stock identification of sword prawn (*Parapenaeopsis hardwickii*) in the East China Sea and Taiwan Strait inferred by morphometric variation. Fish. Sci. **70:** 758-764.

Tzeng TD, SY Yeh. 2000. Estimates of biological parameters of sword prawn (*Parapenaeopsis hardwickii*) in the adjacent waters off Taichung Harbor. J. Fish. Soc. Taiwan **27:** 241-251.

Wang J, CS Chern. 1989. On the Kuroshio branch in the Taiwan Strait during wintertime. Prog. Oceanogr. **21:** 469-491.

Wang P, X Sun. 1994. Last glacial maximum in China: comparison between land and sea. Catena **23:** 341-353.

Wilson K, V Cahill, E Ballment, J Benzie. 2000. The complete sequence of the mitochondrial genome of the crustacean *Penaeus monodon*: Are malacostracan crustaceans more closely related to insects than to branchiopods? Mol. Biol. Evol. **17:** 863-874.

Wright S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution **19:** 395-420.

Wu B. 1982. Some problems on circulation study in Taiwan Strait. Taiwan Strait **1:** 1-7.

Wu CC. 1985. Studies on the shrimp fishery and their fishing ground in Taiwan. Bull. Taiwan. Fish. Res. Inst. **39:** 169-197.

Zhao Z. 1982. A preliminary study on the evolution of Taiwan Strait. Taiwan Strait **1:** 21-24.

Zheng ZM, MY Li. 2002. Morphological and histological studies on the ovary development in *Parapenaeopsis hardwickii*. J. Fish. China **26:** 105-109.