Genetic and morphological differentiation in the Sakura shrimp (*Sergia lucens*) between Japanese and Taiwanese populations

Hideyuki Imai^{1,4}, Yukio Hanamura², Jin-Hua Cheng³

¹ Laboratory of Marine Biology and Coral Reef Studies, Faculty of Science, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan

² National Research Institute of Fisheries Science, Fisheries Research Agency, Kanazawa-ku, Yokohama 236-8648, Japan

³ Tungshang Biotechnology Research Center, Taiwan Fisheries Research Institute, Pingtung 928, Taiwan

⁴ E-mail: imai@sci.u-ryukyu.ac.jp

Keywords: gene flow, genetic diversification, morphology, stock identification

Abstract

The Sakura shrimp *Sergia lucens* is a remarkable meso-pelagic crustacean species, which is harvested for human consumption in restricted geographical areas of Taiwan and Japan in the northwestern Pacific. Nucleotide sequence analysis of the mitochondrial DNA control region was conducted to investigate the levels of genetic variability and differentiation between Japanese and Taiwanese populations of *S. lucens*. The latter half of the control region, which contained 589 nucleotide sites, was sequenced using DNA extracted from 178 individuals from the two geographical regions. Analyses yielded 162 haplotypes, and the amount of genetic variability within the populations as shown by the levels of haplotype and nucleotide diversity revealed that the two populations included in this study have higher levels of diversity than intraspecific variation previously reported in other crustaceans. Our AMOVA and pairwise *F_{st}* results indicated the existence of significant genetic differences between the Japanese and Taiwanese populations. Morphological analyses also revealed minor but notable differences between the two groups. These findings suggest that postulated gene flow of *S. lucens* is unlikely to occur across the isolated Japanese and Taiwanese populations, and that each population completes their life history in a restricted geographical area.

Introduction

The genetic population structures of aquatic animals are often correlated with varying levels of dispersal in their species, which are closely associated with swimming ability, type/duration of larval stages, or water currents. In the north Pacific region, from tropical to temperate areas, the Kuroshio Current plays an important role in the distribution of marine organisms. For example, the Japanese eel *Anguilla japonica* Temmink and Schlegel, 1847 does not show any genetic differentiation among Taiwanese, Chinese and Japanese populations (Taniguchi and Numachi, 1978; Minegishi *et al.*, 2012). On the other hand, some species, such as the Bowed fiddler crab *Uca arcuata* (De Haan, 1833), Bigfin reef squid *Sepioteuthis* spp. and Golden rabbitfish *Siganus guttatus* (Bloch, 1787), show genetic differences among populations (Aoki *et al.*, 2008a, b; Imai and Aoki, 2012; Iwamoto *et al.*, 2012).

The Sakura shrimp *Sergia lucens* (Hansen, 1922) is a commercially important species that is found in the same Kuroshio region. In the past, based on limited numbers of specimens, genetic differences were reported between Japanese and Taiwanese populations (Omori *et al.*, 1988), despite the two populations supposedly being connected by the Kuroshio Current. Recently, the number of Sakura shrimp caught in Japan has decreased. It is important to understand this species' population structure for appropriate resource management.

Further compounding potential management problems of this species, the species name for the Sakura

Contents

Introduction	123
Material and methods	124
Genetic analysis	124
Morphological analysis	125
Results	125
Discussion	127
Acknowledgements	128
References	128

shrimp has not yet been definitively decided. Article 15.1 of the International Code of Zoological Nomenclature (ICZN, 2000; see also Article 11.5.1 concerning “conditional proposals” made before 1961) gives priority to the designation *Sergia kishinouyei* (Nakazawa and Terao, 1915) over *S. lucens*, although the latter name has been popularly used by researchers since Gordon (1935), who provided a detailed account of the species (cf. Omori, 1969). *Sergestes phosphoreus* Kishinouye, 1928 has also been used to refer to the Sakura shrimp, but the validity of this name is questioned (see Vereshchaka, 2000). To avoid taxonomic confusion, herein we use *S. lucens* until the nomenclature issues of the Sakura shrimp are formally resolved.

Sergia lucens is found from Suruga Bay, Sagami Bay, and the mouth of Tokyo Bay in Japan, and the coastal waters of Tungkang as well as off the east coast of Taiwan (Omori, 1969, 1995; Holthuis, 1980; Omori *et al.*, 1988; Isshiki and Tajima, 1992; Lee *et al.*, 1996). Furthermore, Vereshchaka (2000) recorded this species from off Borneo and New Guinea. This shrimp has been commercially exploited in Suruga Bay and Tungkang, where the annual yields average around 2,000 and 100 tons, respectively (Omori, 1989; Fukui *et al.*, 2004). Several biological aspects of this shrimp, including the spawning activity, egg abundances, larval development, swimming behaviour, and population size fluctuation, have been reported in Suruga Bay (Huzita, 1959; Kosaka *et al.*, 1969; Omori, 1971; Omori and Ohta, 1981; Tsukui, 1987; Bishop *et al.*, 1989; Muranaka and Jo, 1990; Hirai *et al.*, 1992; Omori and Seino, 1993; Isshiki, 1996). In fact, more than 200 research articles, most of them in Japanese, dealing with this shrimp have been published over the last century (Kubota *et al.*, 1995). Omori *et al.* (1988) conducted a comparative taxonomic study on individuals collected from Suruga Bay and Tungkang waters. These authors did not find morphological differences discriminating the two populations, suggesting that they could be a single species, although they observed differences in spawning season and isoelectrophoretic patterns of water-soluble proteins. However, as this study examined only five individuals per population, no definitive conclusions could be reached in this study. Since this study, no further information regarding the population structure of *S. lucens* has become available.

Genetic markers such as the mitochondrial DNA control region sequence have been shown to be effective in identifying population structures, and therefore genetic data can contribute to resource management and conservation. As the validity of the research results

of Omori *et al.* (1988) are under question, in this study, the mitochondrial DNA of *S. lucens* collected from the Japanese and Taiwanese coastal waters were analyzed together with comparative morphology to more clearly understand the population structure of this commercially important species.

Material and methods

Genetic analysis

Samples were obtained by trawl fishing at three locations in Japan and Taiwan, which represent the main fishing grounds of *S. lucens* (Fig. 1). In total, 178 specimens were examined for sequence analysis of mitochondrial control region: 70 from Suruga Bay (35°06'N, 138°38'E) (collected in 1999), 61 from Tungkang (22°20'N, 120°20'E) and 47 from Gueishan Island waters (24°51'N, 121°55'E), Taiwan (collected in 2003 and 2010). All samples were stored at -40°C until use.

Total crude DNA was extracted from the pereopod muscle of the frozen specimens using proteinase K, phenol-chloroform, and TNES-8 M urea buffer (Imai *et al.*, 2004). The mitochondrial (mt) DNA control region was then amplified by polymerase chain reaction (PCR) using the designed primers shrimp-sPCR-f

Fig. 1. Sampling sites of *Sergia lucens* in Japan and Taiwan.

(5'-GAAATAGTAACTGTAAAGTT-3') and sakura-tRNA (5'-TCTATCCTATCAAGATAGCCC-3'). All reactions were carried out in a 50 μ l total volume containing 1 μ l of total crude DNA, 25 pM each primer, 2.5 U of ExTaq™ DNA polymerase (Takara Bio), 5 μ l of each dNTP, 1 $\times$ buffer, and dH₂O. A GeneAmp 9700 thermal cycler (Applied Biosystems) was used with the following parameters: 94°C (60 s) followed by 30 cycles of denaturation at 94.5°C (30 s), annealing at 40.5°C (30 s), and extension at 72°C (60 s). PCR products were purified with Exo-Sap-IT (Urb) and cycle-sequenced using a BigDye Terminator Kit and an ABI 3700 genetic analyzer (Applied Biosystems). The sequences obtained in this research were deposited in the DNA Data Bank of Japan (DDBJ) under Accession Numbers AB846666 to AB846827.

All sequences were initially aligned using ClustalX ver.1.83.1 (Thompson *et al.*, 1997). A median-joining network of haplotypes was constructed using the Network ver. 4.6.1.1 (Bandelt *et al.*, 1999) including all individuals. All calculations [haplotype diversity (*h*; Nei, 1987), nucleotide diversity (π ; Tajima, 1983), *Fst* value and 10,000 times *Fst* permutation test (Reynolds *et al.*, 1983), an exact test based on 10,000 steps in a Markov chain (Raymond and Rousset, 1995), and the analysis of the molecular variance (AMOVA) (Excoffier *et al.*, 1992) were processed with Arlequin (Excoffier *et al.*, 2005). A sequential Bonferroni test (Rice, 1989) was used to correct multiple tests of the hypothesis, for which the pairwise *Fst* statistics did not differ from zero. Gene flow (N_m) was estimated using the relationship $N_m = [(1/Fst) - 1]/2$ (Hudson *et al.*, 1992). To investigate the population history of *S. lucens*, a mismatch distribution based on pairwise differences in the mtDNA control region sequences was conducted. In addition, to check for deviations from neutrality, two different *D* tests (Tajima, 1989; Fu and Li, 1993) were performed using Arlequin.

Morphological analysis

Thirty-seven specimens of both sexes (8.4–10.4 mm in carapace length) from the two aforementioned sites in Taiwan (Feb. 2003; July 2010) and 18 specimens (10.0–13.0 mm) from Suruga Bay (May 2003) were used for the examination of a relative distance of the photophores on the antennal scale (Fig. 2). The measurements were made using an ocular-micrometer mounted on a bi-ocular microscope. In addition, the structure of the petasma was examined for male specimens (16 individuals from Japan and 42 from Taiwan).

Results

In total, 589 base pairs (bp) from the control region were sequenced for 178 individuals from the three sampling locations. One hundred and sixty-two haplotypes and 149 variable sites were identified (On-line Supplementary Material, Table S1), and nearly all of the sequenced individuals had a unique haplotype (60 haplotypes from Suruga Bay, 40 haplotypes from Gueishan and 59 haplotypes from Tungkan). However, shared haplotypes were detected in four cases: haplotype 1, seven individuals from Suruga Bay and two from Gueishan; haplotype 2, one from Suruga Bay, three from Gueishan and one from Tungkan; haplotype 92, one from Suruga Bay and one from Gueishan and haplotype 122, one from Gueishan and one from Tungkan. Relationships between haplotypes were represented on a network tree, which did not show any geographical structuring (Fig. 3).

The haplotype and nucleotide diversities of the three geographical groups ranged from 0.991 to 1.000 and from 1.083% to 1.131%, respectively (Table 1). AMOVA in the three populations also showed a significant Φ value of 0.0126 ($P < 0.001$), indicating significant heterogeneity in at least one of the pairwise comparisons. The pairwise *Fst* value ranged from 0.0179 to 0.0205, differing significantly between Japan and Taiwan ($P < 0.001$); however, the values between Gueishan and Tungkan indicated no significant genetic differences. Significant population subdivisions were detected between the Japanese and Taiwanese groups (Suruga Bay vs. Gueishan, and Suruga Bay vs. Tungkan; $P < 0.05$, Bonferroni adjustment), while the N_m value between pairwise comparisons was 22.96 (Suruga Bay vs. Gueishan + Tungkan waters). Tajima's *D* and Fu and Li's *D* tests were also performed to determine neutrality. Significant negative values were obtained from all sampling sites by both tests (Table 1). The distribution of the pairwise number of differences in the control region haplotypes fits an expansion model, with a smooth wave predicted for each location that had undergone a demographic expansion (Fig. 4). The isolation time between the Japanese and Taiwanese populations was estimated to be 305,000 years, based on the observed nucleotide divergence between them and a mutation rate of 19%/MY, taken from the mtDNA control region of penaeid shrimps (McMillen-Jackson and Bert, 2003).

To support the differences observed in genetic analyses, some morphological features of *S. lucens* collected from Japan and Taiwan were examined (Fig. 5). These analyses showed that the relative distance of the three

Fig. 2. Antennal scale of *Sergia lucens* and measurement of photophore distance: male 10.3 mm in carapace length from Suruga Bay, Japan (A) and male 10.3 mm from off Gueishan, Taiwan (B).

Fig. 4. Observed pairwise differences (bars) and the expected mismatch distributions under the sudden expansion model (line) of haplotypes detected in the Japanese and Taiwanese populations of *Sergia lucens*.

Fig. 3. Haplotype network for 162 haplotypes of *Sergia lucens*. White, dark and black circles indicated haplotypes among localities. The size of the circles is proportional to the haplotype frequencies. Lengths of the line showed relative to the number of mutations between haplotypes.

Fig. 5. Comparison in relative distance between the photophores on the antennal scale of *Sergia lucens* in specimens collected from Japanese and Taiwanese waters.

photophores on the antennal scale differed significantly between the two populations (t -test = 2.414, $p < 0.05$), with the Japanese specimens having a mid-photophore placed more posteriorly than the Taiwanese ones.

The male petasma also showed minor variations in its form between the two groups, with approximately 21% of Taiwanese specimens having a small but distinct spine-like projection at the base of the lobus ter-

minalis as compared to less than 7% in the Japanese specimens (Fig. 6).

Discussion

Genetic diversity, as shown by haplotype diversity, was found to be very high in *S. lucens*. The values generated in this study are comparable with those derived from the mtDNA control region sequences for the crustaceans *Farfantepenaeus aztecus* (Ives, 1891), *Litopenaeus setiferus* (Linnaeus, 1767) and *Panulirus penicillatus* (Olivier, 1791) (McMillen-Jackson and Bert, 2003; Abdullah *et al.*, in press). The reported value for haplotype diversity of penaeid shrimp and spiny lobster were 0.996 and 1.000, respectively (Tzeng, 2007; Abdullah *et al.*, in press), which is almost same to our study (ranging from 0.991 to 1.000). The nucleotide diversity of penaeid shrimp (McMillen-Jackson and Bert, 2003) was higher than the value of 5.4% obtained in this study. A high level of genetic diversity in the mtDNA control region could be due to a large population size.

Omori *et al.* (1988) conducted a comparative genetic study of *S. lucens* for individuals collected from Suruga Bay, Japan and Tungkang waters, Taiwan, and found that the two populations differed in isoelectrophoretic patterns of water-soluble proteins, implying limited gene flow between them. The present study, based on the significance of isolation indicated by pairwise *Fst* statistical analysis by AMOVA, also suggested a clear isolation between the Japanese and Taiwanese populations.

A similar disjunctive distribution has been observed in other crustaceans: *i.e.*, *Portunus trituberculatus* (Miers, 1876) by Imai *et al.* (1999) and Imai and Numachi (2002), *Farfantepenaeus aztecus* by McMillen-Jackson and Bert (2003), *Alpheus djeddensis* (Coutiere, 1897) by Thompson *et al.* (2005), *Parapenaeopsis hardwickii* (Miers, 1878) by Tzeng (2007), and *Uca arcuata* by Aoki *et al.* (2008b). The Kuroshio Current runs along the eastern coasts of Taiwan and Japan at a rate of nearly 50 million m³/s (Taira, 1997; Ujiie *et al.*, 2003). This strong northward current seemingly enhances the larval transportation. However, for some previously studied species (*e.g.*, *Uca arcuata*, *Sepioteuthis* spp. and *Siganus guttatus*), no ongoing gene flow was found between the Japanese and Taiwanese populations (Aoki *et al.*, 2008a, b; Imai and Aoki, 2012; Iwamoto *et al.*, 2012). Additionally, the mtDNA data of this study clearly indi-

cate a lack of ongoing gene flow in *S. lucens*. Although Omori *et al.* (1988) mentioned that Japanese and Taiwanese *S. lucens* were morphologically indistinguishable, in our examination minor but appreciable differences were found in the relative distance of photophores on the antennal scale. The shape of the petasma also slightly differed between the two populations as the males from Taiwan had a tendency to have a developed projection at the base of the lobus terminalis of the petasma (Fig. 6; Table 2).

Following these findings, we presume the isolation time between the Japanese and Taiwanese populations to be 305,000 years (middle of the Pleistocene) based on nucleotide divergence estimation time (19%/MY) for penaeid shrimps (Kimura, 1996; McMillen-Jackson and Bert, 2003). The edge of the Chinese continent, which carries several large rivers, was once much closer to the Okinawa Trough. *Sergia lucens* may require large rivers and ridges on the deep sea floor to sustain a large-sized population (Omori *et al.*, 1988). Thus, it may be that there used to be several small populations along the continental shelf, among which gene flow most likely was maintained. However, now the main populations are distributed in central Japan and Taiwan at the edge of the continental shelf in isolation to each other.

The neutrality of mutations in the mtDNA control region was rejected on the basis of Tajima's *D* and Fu and Li's *D* tests. The significant negative values obtained using these tests suggest that the Japanese and Taiwanese populations have experienced a population expansion during their geographic history. The observed unimodal mismatched frequency distribution pattern also matched the predicted distribution under a model of population expansion. This unimodal pattern has also been observed in other crustaceans, including *Euphausia superba* Dana, 1850, *F. aztecus*, *F. duorarum* (Burkenroad, 1939), and *P. hardwickii* (see Zane *et al.*, 1998; McMillen-Jackson and Bert, 2003; Tzeng, 2007).

Recently, Vereshchaka (2000) recorded a small number of *S. lucens* from off Borneo and New Guinea, which notably expanded the known geographical range of this species. Due to the disjunctive distribution of this species, coupled with the genetic differences observed in this study between the Japanese and Taiwanese populations, *S. lucens* is likely to be formed by several small breeding units implying high genetic variability. Further research into the relationships between these units is needed for effective conservation of this commercially important species.

Fig. 6. Variation in form of petasma of *Sergia lucens* as indicated in the part of circle: male (10.3 mm in carapace length) from Suruga Bay, Japan, with no additional projection at the basal part of the lobus terminalis showing a typical form (entire part of left petasma, posterior view) (A); and male (10.0 mm) with a carinate swelling (distal part of right petasma, posterior view) (B); male from Taiwan (10.3 mm) with a distinct projection (entire part of right petasma, posterior view) (C): a, pars astringens; e, pars externa; lc, lobus connectens; pv, processus ventralis. Male with each form of petasma (A, B, C) was categorized as to III, I, and II in Table 2.

Table 1. Sampling locality, haplotype diversity (h), nucleotide diversity (π), and Tajima's D and Fu and Li's D test results for the Japanese and Taiwanese populations. * $P < 0.005$.

sample locality	sampling size	$h \pm SD$	$\pi \pm SD$	Tajima's D	Fu and Li's D
Suruga Bay, Japan	70	0.991 ± 0.01	1.096 ± 0.58	-2.40*	-11.30*
Gueishan waters, N Taiwan	47	0.995 ± 0.01	1.331 ± 0.70	-2.03*	-2.38*
Tungkang waters, S Taiwan	61	1.000 ± 0.00	1.299 ± 0.68	-2.31*	-11.32*

Table 2. Percentage occurrence of males with an additional projection at the base of the lobus terminals of the petasma. Basal part of lobus terminals (encircled part): I, smooth (typical form); II, carinate swelling; III, distinct projection.

category	Suruga Bay	Taiwan
I	50.0	39.4
II	43.7	39.4
III	6.3	21.2
total N	16	33

tute for help in sampling at the Tungkang fish market; Ms. Kaori Hirouchi for her assistance in preparing the manuscript and Mr. Abdullah Fadry Muhamad for his research assistance. We specially thank Asst. Prof. Tetsuo Yoshino of the University of the Ryukyus and Dr. Makoto Omori of the Akajima Marine Science Laboratory for some suggestions on species nomenclature. We also specially thank Asst. Prof. James Davis Reimer of the University of the Ryukyus for checking the manuscript's English. We thank two anonymous reviewers for their critical and editorial comments. This study was partially supported by a Grant-in-Aid for Young Scientists (B15780136) and the 21st Century COE program at the University of the Ryukyus from the Ministry of Education, Culture, Sports, Science and Technology, Japan.

Acknowledgements

We thank the late Capt. Yoshiaki Ichikawa (No. 2 *Kyousei-Mar*), Capt. Masanori Jitsuishi (*Myoujin-Mar*), Capt. Junichi Miyahara (*Takayoshi-Mar*), and *Futoi-Mar* of the "Sakura-ebi" Fisheries Cooperative Association for help in sampling at Suruga Bay; Prof. Shozo Sawamoto of Tokai University for providing some specimens from Suruga Bay; Director Dr. Tzyy-Ing Chen of the Taiwan Fisheries Research Insti-

References

- Abdullah FM, Chow S, Sakai M, Cheng JH, Imai H. In press. Genetic diversity and population structure of pronghorn spiny lobster *Panulirus penicillatus* in the Pacific region. *Pacific Science* 68.
- Aoki M, Imai H, Naruse T, Ikeda Y. 2008a. Low genetic diversity of oval squid *Sepioteuthis* cf. *lessoniana* (Cephalopoda: Loliginidae) in Japanese waters inferred from mitochondri-

- al DNA non-coding region. *Pacific Science* 62: 403-411.
- Aoki M, Naruse T, Cheng JH, Suzuki S, Imai H. 2008b. Low genetic variability in an endangered population of fiddler crab *Uca arcuata* on Okinawajima Island: analysis of mitochondrial DNA. *Fisheries Science* 74: 330-340.
- Bandelt HJ, Forster P, Rohl A. 1999. Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* 16: 37-48.
- Bishop GH, Omori M, Muranaka F. 1989. Temporal and spatial variations in the spawning activity of the micronektonic shrimp, *Sergia lucens* (Hansen) in Suruga Bay, Japan. *Journal of the Oceanographical Society of Japan* 45: 243-250.
- Excoffier L, Smouse PE, Quattro JM. 1992. Analysis of molecular variance inferred from metric distance among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* 131: 479-491.
- Excoffier L, Laval G, Schneider S. 2005. ARLEQUIN ver. 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* 1: 47-50.
- Fu YX, Li WH. 1993. Statistical tests of neutrality of mutations. *Genetics* 133: 693-709.
- Fukui A, Hara T, Ito D, Hoshio T, Uotani I. 2004. Abundance estimation of sergestid shrimp *Sergia lucens* in Suruga Bay. *Nippon Suisan Gakkaishi* 70: 592-597. (in Japanese, English abstract)
- Gordon I. 1935. On new or imperfectly known species of Crustacea Macrura. *Zoological Journal of the Linnean Society* 39: 307-351.
- Hansen HJ. 1922. Crustacés décapodes (Sergestidae) provenant des Campagnes des yachts Hironnelle et Princesse-Alice (1885-1915). Résultats Campagnes Scientifiques accomplies sur son yacht par Albert Ier prince souverain de Monaco, 64: 20-39.
- Hirai K, Kitano T, Saitou M. 1992. Preliminary investigation on distribution and survival of eggs and early larvae (developmental stages) of sergestid shrimp, *Sergia lucens* (Hansen), in 1990. *Bulletin of the Shizuoka Prefectural Fisheries Experiment Station* 27: 1-7. (in Japanese)
- Holthuis LB. 1980. *FAO species catalogue: vol. 1 — shrimps and prawns of the world*. FAO Fisheries Synopsis 125, Food and Agriculture Organization of the United Nations, Rome, Italy.
- Hudson RR, Slankin M, Maddison WP. 1992. Estimation of levels of gene flow from DNA sequence data. *Genetics* 132: 583-589.
- Huzita S. 1959. Ecological investigation of *Sergestes lucens* Hansen in Suruga Bay. *Bulletin of the Educational Faculty, Shizuoka University* 10: 235-244. (in Japanese, English summary).
- ICZN (International Commission of Zoological Nomenclature) (2000): *International code of zoological nomenclature*, 4th edition, adopted by the Union of Japanese Societies for Systematic Zoology. International Trust for Zoological Nomenclature, Hokkaido University, Sapporo, Japan (in Japanese).
- Imai H, Aoki M. 2012. Genetic diversity and genetic heterogeneity of bigfin reef squid, “*Sepioteuthis lessoniana*” species complex in northwestern Pacific Ocean. Pp. 151-166 in: Caliskan M., ed., *Analysis of Genetic Variation in Animals*. Rijela: InTech.
- Imai H, Numachi K. 2002. Genetic variability of swimming crab based on PCR-RFLP analysis of mitochondrial DNA D-loop region. *Suisanzoshoku* 50: 1-7. (in Japanese, English abstract)
- Imai H, Fujii Y, Karakawa J, Yamamoto S, Numachi K. 1999. Analysis of the population structure of the swimming crab, *Portunus trituberculatus* in the coastal waters of Okayama Prefecture, by RFLPs in the whole region of mitochondrial DNA. *Fisheries Science* 65: 655-656.
- Imai H, Cheng JH, Hamasaki K, Numachi K. 2004. Identification of four mud crab species (genus *Scylla*) using ITS-1 and 16S rDNA markers. *Aquatic Living Resources* 17: 31-34.
- Isshiki T. 1996. Population density of the sergestid shrimp *Sergia lucens* in Tokyo Bay with special reference to predation by the blackthroat seaperch *Doederleinia berycoides*. *Bulletin of the Kanagawa Prefectural Fisheries Research Institute* 1: 21-25. (in Japanese, English abstract)
- Isshiki T, Tajima Y. 1992. The research of a sergestid shrimp, *Sergia lucens* (Hansen) in the mouth of Tokyo Bay I. The seasonal distribution of adult and the distribution of eggs. *Bulletin of the Kanagawa Prefectural Fisheries Experiment Station* 13: 73-78 (in Japanese, English summary)
- Iwamoto K, Chang C, Takemura A, Imai H. 2012. Genetically structured population and demographic history of the gold-lined spinefoot *Siganus guttatus* in the northwestern Pacific. *Fisheries Science* 78: 249-257.
- Kimura M. 1996. Quaternary paleogeography of the Ryukyu Arc. *Journal of Geography* 105: 259-285. (in Japanese, English abstract)
- Kosaka M, Kubota T, Ogura M, Oda T, Nakai Z. 1969. Studies of the predatory species on the shrimp, *Sergestes lucens* in Suruga Bay. *Journal of the College of Marine Science and Technology, Tokai University* 3: 87-101. (in Japanese, English abstract)
- Kubota T, Ikematsu M, Amano R. 1995. Bibliography on a sergestid shrimp (*Sergia lucens*) from Suruga Bay, central Japan (Further note). *Bulletin of Institute of Oceanic Research and Development, Tokai University* 16: 59-65. (in Japanese, English abstract)
- Lee DA, Wu SH, Liao IC, Yu HP. 1996. On three species of commercially important sergestid shrimps (Decapoda: Sergestidae) in the coastal waters of Taiwan. *Journal of Taiwan Fisheries Research* 4: 1-19. (in Chinese, English abstract)
- McMillen-Jackson AL, Bert TM. 2003. Disparate patterns of population genetic structure and population history in two sympatric penaeid shrimp species (*Farfantepenaeus aztecus* and *Litopenaeus setiferus*) in the eastern United States. *Molecular Ecology* 12: 2895-2905.
- Minegishi Y, Aoyama J, Tsukamoto K. 2012. Lack of genetic heterogeneity in the Japanese eel based on a spatiotemporal sampling. *Coastal Marine Science* 35: 269-276.
- Muranaka F, Jo SG. 1990. Small-scale distribution of eggs and early larvae of sergestid shrimp, *Sergia lucens* (Hansen), at the main spawning ground in Suruga Bay. *Bulletin of the Shizuoka Prefectural Fisheries Experiment Station* 25: 1-9. (in Japanese)
- Nakazawa K. 1932. On three species of genus *Sergestes* found in Suruga Bay. *Zoological Magazine, Tokyo* 44: 31-32. (in Japanese)
- Nakazawa K, Terao A. 1915. Studies on sakura shrimp. *Zoological Magazine, Tokyo* 27: 622-630. (in Japanese)
- Nei M. 1987. *Molecular evolutionary genetics*. New York: Columbia University Press.

- Omori M. 1969. The biology of a sergestid shrimp *Sergestes lucens* Hansen. *Bulletin of the Ocean Research Institute, University of Tokyo* 4: 1-83.
- Omori M. 1971. Preliminary rearing experiments on the larvae of *Sergestes lucens* (Penaeidae, Natantia, Decapoda). *Marine Biology* 9: 228-234.
- Omori M. 1989. Fishery of a sergestid shrimp *Sergia lucens* (Hansen) at Tung-kang, Taiwan. *Bulletin of the Japanese Society of Fisheries Oceanography* 53: 108-110. (in Japanese)
- Omori M. 1995. Biology of sakura shrimp. "Sakura-ebi"-History of one hundred years of the sergestid shrimp fishing industry. Pp. 64-74 in: Omori M and Shida K, eds. Shizuoka: Shizuoka Shinbunsha. (in Japanese)
- Omori M, Ohta S. 1981. The use of underwater camera in studies of vertical distribution and swimming behavior of a sergestid shrimp *Sergia lucens*. *Journal of Plankton Research* 3: 107-121.
- Omori M, Seino Y. 1993. Feeding reference of the hairtail *Trichilurus lepturus* Linnaeus in and neighboring the waters where *Sergia lucens* swarms in Suruga Bay. *Bulletin of the Japanese Society of Fisheries Oceanography* 57: 15-23. (in Japanese, English abstract)
- Omori M, Ukishima Y, Muranaka F. 1988. New record of occurrence of *Sergia lucens* (Hansen) (Crustacea, Sergestidae) off Tung-kang, Taiwan, with special reference to phylogeny and distribution of the species. *Journal of the Oceanographical Society of Japan* 44: 261-267. (in Japanese, English abstract)
- Raymond M, Roussett F. 1995. Genepop (Ver.1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86: 248-249.
- Reynolds J, Weir BS, Cockerham CC. 1983. Estimation for the coancestry coefficient: basis for a short-term genetic distance. *Genetics* 105: 767-779.
- Rice WR. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.
- Taira K. 1997. Sea as a fluid. Pp. 61-87 in: The Ocean Research Institute, University of Tokyo eds, *System of ocean*. Nippon Jitsugyo Publishing, Tokyo. (in Japanese)
- Tajima F. 1983. Evolutionary relationship of DNA sequences in finite populations. *Genetics* 105: 437-460.
- Tajima F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* 123: 585-595.
- Taniguchi N, Numachi K. 1978. Genetic variation of 6-phosphogluconate dehydrogenase, isocitrate dehydrogenase, and glutamic-oxaloacetic transaminase in the liver of Japanese eel. *Bulletin of the Japanese Society of Scientific Fisheries* 44: 1351-1355.
- Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The CLUSTAL-X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 25: 4876-4882.
- Thompson AR, Thacker CE, Shaw E. 2005. Phylogeography of marine mutualists: parallel patterns of genetic structure between obligate goby and shrimp partners. *Molecular Ecology* 14: 3557-3572.
- Tsukui F. 1987. Relationship between reproduction of a sergestid shrimp *Sergia lucens* (Hansen) and water temperature during the spawning season. *Bulletin of the Shizuoka Prefectural Fisheries Experiment Station* 22: 1-11. (in Japanese)
- Tzeng TD. 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: 561-568.
- Ujiié Y, Ujiié H, Taira A, Nakamura T, Oguri K. 2003. Spatial and temporal variability of surface water in the Kuroshio source region, Pacific Ocean, over the past 21,000 years: evidence from planktonic foraminifera. *Marine and Micro-paleontology* 49: 335-364.
- Vereshchaka AL. 2000. Revision of the genus *Sergia* (Decapoda: Dendrobranchiata: Sergestidae): taxonomy and distribution. *Galathea Report* 18: 69-207.
- Zane L, Ostellari L, Maccatrozzo L, Bargelloni L, Battaglia B, Patarnello T. 1998. Molecular evidence for genetic subdivision of Antarctic krill (*Euphausia superba* Dana) populations. *Proceeding of the Royal Society of London B* 265: 2387-2391.

Received: 23 November 2012
 Revised and accepted: 9 August 2013
 Published online: 27 September 2013
 Editor: R. Vonk

On-line Supplementary Information (SI)

SI. Variable sites in the 162 haplotypes found in mtDNA control region of 178 *Sergia lucens*. The numbers above sequences correspond to the positions of the polymorphic sites. Dots indicate an identical nucleotide at the position relative to haplotype 1.