



Short Communication

Comparative phylogeography of two marine species of crustacean: Recent divergence and expansion due to environmental changes



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ABSTRACT

Environmental changes, such as changes in the coastal topography due to Eurasian plate movements, climate oscillation during the Pleistocene, and alteration of ocean currents, have complicated the geographical structure of marine species and deepened their divergence between populations. As two widely distributed species of crustacean (*Oratosquilla oratoria* and *Eriocheir japonica*), weak differences were expected due to their high dispersal potential of planktonic larvae with ocean currents. However, results showed a significant genetic divergence between north of China and south of China in the study. In addition, the estimated north–south divergence time (27–30.5 Myr) of mantis shrimp was near the time of the Himalayan movement, and the China–Japan clade divergence time (10.5–11.9 Myr) of mitten crabs was also coincident with the time of the opening of the Sea of Japan. Thus, we hypothesized that environmental changes in the coastal topography contributed to the marine species divergence. Furthermore, based on phylogenetic analysis, network analysis and haplotype distribution, we surmised that mitten crabs originated from a population with the oldest haplotype (H6) and then divided into the north and south populations due to the recent Eurasian plate movements and ocean currents. And lineage of Japan originated from the north population for the opening of the Sea of Japan. While *O. oratoria* was guessed to originate from two separate populations in the China Sea. The results of “star-like” network, negative values in neutral test, and Tajima's D statistics of two marine species supported a recent rapid population expansion event after the Pleistocene glaciations.

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1. Introduction

Vagarious climate fluctuations during the Pleistocene have caused alterations of dramatic temperature, ocean currents and coastal topography (Clark et al., 1999; Hewitt, 1996, 2000). To elude the dramatic changes during the Pleistocene glaciations, marine organisms were forced into a repeated cycle of glacial retreat and interglacial expansion. The ranges of some faunal distributions have exhibited markedly altered contraction or expansion (Avice, 2000; Hewitt, 2000; Xu et al., 2009). Such historical events have led to species extinction and have also acted as the drivers of subspeciation for local adaptation and adaptive radiation (Crowley and North, 1988; Gillespie, 2004; Mayhew et al., 2008). The relative influence of environmental changes on marine organisms could best explain the patterns over a longer evolutionary time frame (Benton, 2009). Moreover, during the Pleistocene glacial cycles, the formation of land bridges due to the lowered sea level between islands and Asian continent might act as the barriers for marine organisms and potentially aid allopatric diversification (Kimura, 2000;

McManus, 1985; Tamaki and Honza, 1991; Voris, 2000; Wang, 1999). Furthermore, the dispersal of the pelagic larvae for ocean currents also played a fundamental role in ecology and evolution (Caley et al., 1996; Strathmann et al., 2002). These physical and environmental attributes as the potential mechanisms have shaped patterns of marine species divergence and population expansion by the occupation of newly formed habitats or adaptation to changing environments (Richardson, 2012).

Northwest pacific marginal seas connecting the mainland and deep oceans were regarded as the most suitable areas to understand the past global climate and oceanographic changes. The phylogeographic structure of marine species living in marginal seas was the typical representative of the intertidal invertebrate affected by historical climate, ocean currents and coastal topography. As the representative marine species, mantis shrimps *Oratosquilla* were widely distributed along the northwest pacific marginal seas, and mitten crabs *Eriocheir* were also distributed from China and Japan to Korea. Previous studies have indicated that *Eriocheir japonica* was divided into three geographic subspecies, namely *E. j. japonica*, *E. j. sinensis* and *E. j. hepuensis* (Tang et al., 2003). Thereinto *E. j. japonica* was distributed in Japan, and the 26°N latitude was considered the boundary between *E. j. sinensis* and *E. j. hepuensis* in China (Cohen and Carlton, 1997; Ingle and Andrews, 1976; Tang et al., 2003; Zhao et al., 1988). Subspeciation required the

Abbreviations: mt, mitochondria(l); nt, nucleotide(s); Myr, million years.

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termination of gene flow for geographic barrier or population isolation. It was understandable that subspeciation of *E. j. japonica* might be a result of the isolation between China and Japan. However, it was unacceptable that 26°N latitude was the unambiguous boundary between *E. j. sinensis* and *E. j. hepuensis*. So the subspeciation of *Eriocheir* still remains a controversial topic at present (Tang et al., 2003; Wang et al., 2008; Xu et al., 2009; Zhang et al., 2012), and additional data are needed to reveal the phylogeographic structure and to clarify the relationship between phylogeographic structure and environmental changes.

In this study, through a comparative phylogeography study of two marine species (*Oratosquilla oratoria* and *E. japonica*) of crustacean, we assessed the phylogeographical pattern of marine species in the north-west pacific marginal seas and revealed the association between divergence and historical environmental changes.

2. Materials and methods

2.1. Sample collection

The study region was selected because several marginal seas were once separated during glaciations. A total of 621 samples of the two marine species of crustacean were collected in this study. Samples of 208 individuals of *O. oratoria* were obtained from 15 localities representing the geographical range of this species across the China Sea, and 413 samples of *E. japonica* from 19 locations along the northwest Pacific Ocean were also integrated from GenBank to corroborate the results (Fig. 1, Appendix 1). The materials were sampled and preserved in 95% ethanol for later analysis. We chose to focus on the mt cytochrome oxidase c subunit I (mt COI) gene and the cytochrome b (mt Cytb) gene

because these were more informative sites and because of their ability to estimate the mutation rate. The main limitation was that these sites represented only one evolutionary history. However, a lower effective sample size of mtDNA relative to that of nuclear DNA was needed due to their faster rate at the population level. We thus considered the use of mt sequences as the best strategy for accurate estimation.

2.2. DNA extraction, amplification and sequencing

The genomic DNA from tissue muscle was extracted using the standard phenol–chloroform method. PCR amplification was executed using the primers described by Folmer et al. (1994). Each 30- μ l amplification reaction consisted of thermophilic buffer (50 mM KCl and 10 mM Tris–HCl pH 8.3), 2.0 mM MgCl₂, 10 pmol of each primer, 0.2 mM dNTPs, and 1 unit *Taq* DNA polymerase. Polymerase chain reaction (PCR) was performed on a GeneAmp® PCR System 9700 (ABI) or Mastercycler® gradient (Eppendorf) thermocycler with a temperature profile of 30 cycles at 94 °C for 40 s, 50 °C for 40 s, and 72 °C for 60 s. The PCR products were purified using a PCR purification kit and cycle-sequenced on an ABI Prism 3730 automated sequencer.

2.3. Sequence alignment, genetic diversity and phylogenetic analysis

The sequences were aligned with the Clustal W algorithm in Mega 5.0 (Tamura et al., 2011). The nt diversity (π) and haplotype diversity (h) were estimated using Arlequin version 3.1 (Excoffier et al., 2005). The divergences within- and between-populations were determined using Mega 5.0 (Tamura et al., 2011). Haplotype neighbour-joining trees (NJ) were constructed using the Kimura 2-parameter model in

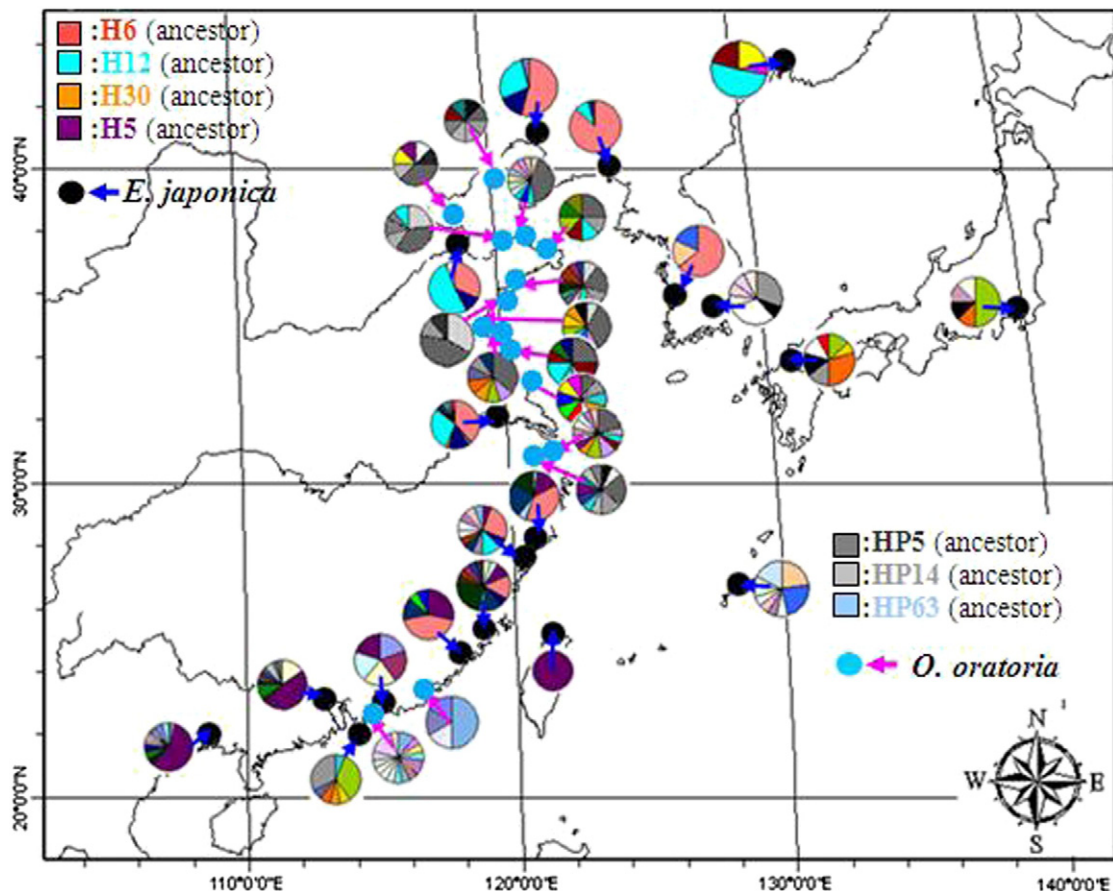


Fig. 1. Map showing the sampling locations for the two marine species in this study. ●: locations for *E. japonica*; ●: locations for *O. oratoria*. Colours in circles represented different haplotypes and their proportions. The four ancestral haplotypes of *E. japonica* were H5 (purple), H6 (red), H12 (cyan), and H30 (orange). The three ancestral haplotypes of *O. oratoria* were HP5 (grey), HP14 (light grey), and HP63 (light blue).

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