博士論文 (要約)

論文題目 Phylogeographic study of the Asian horn snail Batillaria attramentaria (Mollusca, Gastropoda)

(ホソウミニナの系統地理学的研究)

氏 名 伊藤 萌

Contents

Chapter 1. General introduction

Chapter 2. Elucidation of population structure of *Batillaria attramentaria* based on mitochondrial gene sequences

- 2-1. Introduction
- 2-2. Materials and Methods
 - 2-2-1. Sample collection
 - 2-2-2. Sequencing of the gene for cytochrome c oxidase subunit I (COI)
 - 2-2-3. Identification of haplotypes
 - 2-2-4. Phylogenetic analyses of haplotypes
 - 2-2-5. Analyses of population genetic structure
 - 2-2-6. Estimation of divergence ages between local populations
- 2-3. Results
 - 2-3-1. Phylogeny of haplotypes
 - 2-3-2. Geographical distribution of haplotypes and population genetic structure
 - 2-3-3. Genetic difference among local population
 - 2-3-4. Estimation of divergence ages between local populations
- 2-4 Discussion
 - 2-4-1. Phylogeny of haplotypes
 - $2\mathchar`-2$ Geographical distribution of haplotypes and population genetic structure
 - 2-4-3. Genetic difference among local population
 - 2-4-4. Estimation of divergence ages between local populations

Chapter 3. Development of microsatellite markers for Batillaria attramentaria

- 3-1. Introduction
- 3-2. Materials and methods
 - 3-2-1. Isolation of microsatellite loci using the dual-suppression technique
 - 3-2-2. Isolation of microsatellite loci using next generation sequencing
 - 3-2-3. PCR condition for microsatellite markers obtained by the dual-suppression technique
 - 3-2-4. PCR condition for microsatellite markers obtained by the next generation sequencing technique
 - 3-2-5. Characterization of developed microsatellite loci
- 3-3. Results
 - 3-3-1. Isolation of microsatellite loci using the dual-suppression technique
 - 3-3-2. Isolation of microsatellite loci using the next generation sequencing
 - 3-3-3. Characterization of developed microsatellite loci
- 3-4. Discussion

Chapter 4. Elucidation of population structure of *Batillaria attramentaria* using 14 microsatellite markers

- 4-1. Introduction
- 4-2. Materials and methods
 - 4-2-1. Sample collection
 - 4-2-2. Genotyping of each individual
 - 4-2-3. Characterization of microsatellite loci
 - 4-2-4. Genetic differentiation among local populations

4-2-5. Inference of population structure using Bayesian clustering approach

- 4-2-6. Detecting of first generation migrants
- 4-2-7. Assessment of contemporary gene flow
- 4-3. Results
 - 4-3-1. Characterization of microsatellite loci
 - 4-3-2. Genetic differentiation among local populations
 - 4-3-3. Inference of population structure using Bayesian clustering approach
 - 4-3-4. Detection of first generation migrants
 - 4-3-5. Assessment of contemporary gene flow
- 4-4. Discussion
 - 4-4-1. Deviation from HWE and LD between loci
 - 4-4-2. Characterization of microsatellite loci
 - 4-4-3. Genetic differentiation among local populations
 - 4-4-4. Inference of population structure using Bayesian clustering approach
 - 4-4-5. Contemporary migration among local populations

Chapter 5. General discussion

Acknowledgements

References

Chapter 1 General introduction

1-1. Phylogeography and environmental fluctuations in the Quaternary

Populations of many species are not genetically homogenous and show some kinds of geographical structure for genetic characteristics. Current patterns of the geographic distribution of genetic as well as morphological intraspcific diversity have been formed by historical events such as climatic and geomorphological changes as well as biotic and abiotic selection processes (Ruzzante et al. 2011).

1-2. Phylogeography of marine species around Japan

The Japanese waters are divided into six climate regimes between the sub-boreal (the Sea of Okhotsk and the Pacific east of Hokkaido Island) and tropical (the Ryukyu and Izu-Ogasawara (Bonin) Islands) zones where various and unique ecosystems are associated with each type of environments (Fujikura et al. 2010). In addition, fluctuations in the marine environments surrounding Japan were noticeable during the Quaternary. The Japan Sea (East Sea) is a semi-enclosed sea in the northwestern Pacific, which is connected with adjacent marginal seas and the Pacific Ocean only by shallow and narrow straits with sill depths of < 130 m. A large variation of the divergence time has been indicated to be related with species-specific characteristics in the life history and distributional ranges, genetic differentiation associated with the historical events has been reported between the Pacific Ocean side and the Japan Sea (East Sea) side of the Japanese Islands for many coastal marine organisms (e.g. Kojima et al. 1997, 2004; Akihito et al. 2008, Kokita & Nohara 2011; Hirase et al. 2012).

1-3. Batillaria attramentaria

Intertidal snails of the genus *Batillaria* belonging to the family Batillariidae are a dominant group of benthic animals in coastal areas around Japan. They play an important role in maintaining healthy environments of coastal areas (Kamimura & Tsuchiya 2006). Among them, the Asian horn snail *Batillaria attramentaria* (G. B. Sowerby II, 1855) is a species with the highest cold-resistance and distributed from Sakhalin, throughout the Japanese waters to the China Seas (Hasegawa 2000). For this species, the scientific name *B. cumingi* (Crosse, 1862) has been frequently used especially in papers by Japanese researchers. However, Ozawa et al. (2009) stated that B. cumingi is a junior synonym of B. attramentaria on the basis of the geographical distribution, taxonomic references, and molecular phylogenetic analysis. In this thesis, I use the latter according to their recommendation. In the previous study based on partial nucleotide sequences of mitochondrial cytochrome c oxidase subunit I (COI) gene, individuals of *B. attramentaria* were divided into two phylogenetically distinct groups, which are distributed along two warm currents (Kojima et al. 2004). They are referred to the Tsushima group and the Kuroshio group after the names of the currents. Individuals in the Tsushima group inhabit coasts along the Tsushima Current and its branches, while the individuals belonging to the Kuroshio group mainly inhabit coasts along the Kuroshio Current.

1-4. Human-mediated transport of B. attramentaria

Since the early days of the last century, the human-mediated transport of B. attramentaria has been reported. It had been introduced to the Pacific coast of the North America with the importation of seedlings of the Pacific (Japanese) oyster Crassostrea gigas from Japan (Bonnot 1935). The seedlings had been transported for the purpose of aquaculture and introduced to the bays and estuaries of the Pacific coast of the USA from the 1900s to the 1970s, until sufficient natural resources were established and domestic aquaculture operations started to supply adequate amounts of seeds (Carlton 1992). Indeed, Miura et al. (2006) reported that nucleotide sequences of mitochondrial DNA obtained from all individuals of this species collected in the USA are identical to those of individuals of Miyagi Prefecture In recent years, great efforts to eradicate *B. attramentaria* have been made in San Francisco Bay by volunteers under the initiative of environmental protection organization, the Bay Institute (see the site http://www.bay.org/). Accidental release of marine organisms transported with commercial marine products such as the short-necked clam Ruditapes philippinarum has been reported within Japan (Okoshi 2004; Koike et al. 2006).

1-5. Aim of this study

As mentioned above, it is thought that the geographical distribution of B. *attramentaria* has been determined by historical major environmental changes associated with the glacial-interglacial cycle and been altered by the human activities. The aim of this study is to reveal the detailed population genetic structure of B. *attramentaria* and gene flow among its local populations. Such information is important to conserve not only local populations of this species but also coastal ecosystems in Japan. It is also helpful to understand the effects of the past environmental fluctuations on populations of coastal species and to foresee those in the future.

Chapter 2

Elucidation of population structure of *Batillaria attramentaria* based on mitochondrial gene sequences (5年以内に出版予定)

Chapter 3

Development of microsatellite markers for *Batillaria attramentaria* (本章の内容は Molecular Ecology Resources, Volume 13, Issue 4, p 760–762, July 2013 に掲載, 契約内容によりインターネット公表に対する許諾が得られていない)

Chapter 4

Elucidation of population structure of *Batillaria attramentaria* using 14 microsatellite markers

(5年以内に出版予定)

Chapter 5. General discussion

5-5. Conclusion

By using two distinct genetic markers which are different in the hereditary mode and the resolution, the detailed phylogeographic structure, histories of local populations, and connectivity among local populations were revealed for B. *attramentaria* covering a large proportion of its distributional range. As expected in the general introduction (Chapter 1), the present genetic structure of this species has been formed by both historical major environmental changes and contemporary human activities. In addition, in spite of its low dispersal ability, the unexpected long-distance dispersion was also clarified. This study will greatly contribute to understand the influences of environmental changes and human activities on coastal species around Japan.

References

Adachi N, Wada K (1999) Distribution in relation to life history in the direct-developing gastropod *Batillaria cumingi* (Batillariidae) on two shores of contrasting substrata. J Moll Stud 65, 275–287.

Akihito, Fumihito A, Ikeda Y, Aizawa M, Makino T, Umehara Y, Kai Y, Nishimoto Y, Hasegawa M, Nakabo T, Gojobori T (2008) Evolution of Pacific Ocean and the Sea of Japan populations of the gobiid species, *Pterogobius elapoides* and *Pterogobius zonoleucus*, based on molecular and morphological analyses. Gene 427, 7–18.

An HS, Han SJ (2006) Isolation and characterization of microsatellite DNA markers in the Pacific abalone, *Haliotis discus hannai*. Mol Ecol Notes 6, 11–13.

Avise JC (2000) Phylogeography, the history and formation of species. Harvard University Press, Cambridge, MA

Avise JC, Walker DE, Johns GC (1998) Speciation durations and Pleistocene effects on vertebrate phylogeography. Proc R Soc Lond B 265, 1707–1712.

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Statist Soc B 57, 289–300.

Blacket MJ, Robin C, Good RT, Lee SF, Miller AD (2012) Universal primers for fluorescent labelling of PCR fragments—an efficient and cost-effective approach to genotyping by fluorescence. Mol Ecol Resour 12, 456–463.

Bonnot P (1935) A recent introduction of exotic species of molluscs into California waters from Japan. Nautilus 49, 1–2.

Brookfield JF (1996) A simple new method for estimating null allele frequency from heterozygote deficiency. Mol Ecol 5, 453–455.

Byers JE (1999) The distribution of an introduced mollusc and its role in the long-term demise of a native confamilial species. Biol Invas 1, 339–352.

Byers JE (2000) Competition between two estuarine snails: implications for invasions of exotic species. Ecology 81, 1225–1239.

Carlton JT (1992) Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. J Shellfish Res 11, 489–505.

Castelloe J, Templeton AR (1994) Root probabilities for intraspecific gene trees under neutral coalescent theory. Mol Phylogenet Evol 3, 102–113.

Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. Mol Ecol 9, 1657–1659.

Crandall KA, Bininda-Emonds ORP, Mace GM, Wayne RK (2000) Considering evolutionary processes in conservation biology. Trends Ecol Evol 15, 290–295.

Dupont L, Viard F (2003) Isolation and characterization of highly polymorphic microsatellite markers from the marine invasive species *Crepidula fornicate* (Gastropoda: Calyptraeidae). Mol Ecol Notes 3, 498–500.

Earl DA, von Holdt BM (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4, 359–361.

Emiliani C (1955) Pleistocene temperatures. J Geol 63, 538-578.

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14, 2611–2620.

Excoffier L, Laval G, Schneider S (2005) Arlequin ver 3.0: an integrated software package for population genetic data analysis. Evol Bioinf Online 1, 47-50.

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164, 1567–1587.

Figuerola J, Green AJ (2002) Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshw Biol 47, 483–494.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol Mar Biol Biotechnol 3, 294-299.

Furota T, Suzuki K (1999) Sediment conditions and macro-zoobenthos distribution in the winter of 1986-87 on the Yatsu tidal flat of innermost Tokyo Bay. Jap J Benthol 54, 36–43. (in Japanese with English abstract)

Furota T, Sonobe T, Arita S (2002) Contrasting population status between the planktonic and direct development batillariid snails *Batillaria multiformis* (Lischke) and *B. cumingi* (Crosse) on an isolated tidal flat in Tokyo Bay. Venus 61, 15–23.

Fujikura K, Lindsay D, Kitazato H, Nishida S, Shirayama Y (2010) Marine Biodiversity in Japanese Waters. PLoS One 5, e11836.

Geist J, Kuehn R (2005) Genetic diversity and differentiation of central European freshwater pearl mussel (*Margaritifera margaritifera* L.) populations: implications for conservation and management. Mol Ecol 14, 425–439.

Green AJ, Figuerola J (2005) Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. Divers Distrib 11, 149–156.

Green AJ, Sánchez MI (2006) Passive internal dispersal of insect larvae by migratory birds. Biol Lett 2, 55–57.

Guerra-Varela J, Colson I, Backeljau T, Breugelmans K, Hughes RN, Rolán-Alvarez E (2009) The evolutionary mechanism maintaining shell shape and molecular differentiation between two ecotypes of the dogwhelk *Nucella lapillus*. Evol Ecol 23, 261–280.

Guichoux E, Lagache S, Wagner S, Chaumeil P, Leger P, Lepais O, Lepoittevin C, Malausa T, Revardel E, Salin F, Petit RJ (2011) Current trends in microsatellite genotyping. Mol Ecol Resour 11, 591–611.

Guo SW, Thompson EA (1992) Performing the exact test of Hardy-Weinberg proportion for multiple alleles. Biometrics 48, 361–372.

Hara M, Sekino M (2005) Genetic difference between Ezo-awabi *Haliotis discus hannai* and Kuro-awabi *H. discus discus* populations: Microsatellite-based population analysis in Japanese abalone. Fisheries Sci 71, 754–766.

Hardy OJ, Vekemans X (2002) SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Mol Ecol Notes 2, 618–620.

Hasegawa K (2000) Batillariidae. In: Okutani T (ed) Marine mollusks in Japan. Tokai University Press, Tokyo, 130–133.

Hasegawa M, Kishino H, Yano T (1985) Dating of the Human-Ape Splitting by a Molecular Clock of Mitochondrial DNA. J Mol Evol 22, 160–174.

Hedgecock D (1986) Is gene flow from pelagic larval dispersal important in the adaptation and evolution of marine invertebrates? Bull Mar Sci 39, 550–564.

Hedgecock D (1994) Temporal and spatial genetic structure of marine animal populations in the California current. Calif Coop Ocean Fish Investig Rep 35, 73–81.

Hewitt G (2000) The genetic legacy of the Quaternary ice ages. Nature 405, 907–913.

Hey J (2010) Isolation with migration models for more than two populations. Mol Biol Evol 27, 905–920.

Highsmith RC (1985) Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. Mar Ecol Prog Ser 25, 169–179.

Hirase S, Ikeda M, Kijima A (2012) Phylogeography of the intertidal goby *Chaenogobius annularis* associated with paleoenvironmental changes around the Japanese Archipelago. Mar Ecol Prog Ser 450, 167–179.

Holleley CE, Geerts PG (2009) Multiplex Manager 1.0: a crossplatform computer program that plans and optimizes multiplex PCR. Biotechniques 46, 511–517.

Inoue K (2007) Batillariid and potamidid gastropods from the Middle Miocene Kukinaga Group, Tanegashima Island, southwest Japan, and their paleobiogeographic implications. Paleontol Res 11, 277–292.

Irizuki T, Taru H, Taguchi K, Matsushima Y (2009) Paleobiogeographical implications of inner bay Ostracoda during the Late Pleistocene Shimosueyoshi transgression, central Japan, with significance of its migration and disappearance in eastern Asia. Palaeogeogr Palaeoclimatol Palaeoecol 271, 316–328.

Kamimura S, Tsuchiya M (2006) Effects of opportunistic feeding by the intertidal gastropods *Batillaria zonalis* and *B. flectosiphonata* on material flux on a tidal flat. Mar Ecol Prog Ser 318, 203–211.

Kawai K, Hughes RN, Takenaka O (2001) Isolation and characterization of microsatellite loci in the marine gastropod *Nucella lapillus*. Mol Ecol Notes 1, 270–272.

Kawase M (2013) Molluscan fossil from Atsumi group of Aichi Prefecture—Molluscan fossil of Shuji Ukai collection. Bull Segigakuen 7, 44–54. (in Japanese)

Kirst M, Cordeiro CM, Rezende GDSP, Grattapaglia D (2005) Power of microsatellite markers for fingerprinting and parentage analysis in *Eucalyptus grandis* breeding populations. J Hered 96, 161–166.

Kitamura A, Takano O, Takata H, Omote H (2001) Late Pliocene–early Pleistocene paleoceanographic evolution of the Sea of Japan. Palaeogeogr Palaeoclimatol Palaeoecol 172, 81–98.

Kojima S, Segawa R, Hayashi I (1997) Genetic differentiation among populations of the Japanese turban shell *Turbo (Batillus) cornutus* corresponding to warm currents. Mar Ecol Prog Ser 150, 149–155.

Kojima S, Ota N, Mori K, Kurozumi T, Furota T (2001) Molecular phylogeny of Japanese gastropods in the genus *Batillaria*. J Moll Stud 67, 381–388.

Kojima S, Kamimura S, Kimura T, Hayashi I, Iijima A, Furota T (2003) Phylogenetic relationships between the tideland snails *Batillaria flectosiphonata* in the Ryukyu Islands and *B. multiformis* in the Japanese Islands. Zool Sci 20, 1423–1433.

Kojima S, Hayashi I, Kim D, Iijima A, Furota T (2004) Phylogeography of an intertidal direct-developing gastropod *Batillaria cumingi* around the Japanese Islands. Mar Ecol Prog Ser 276, 161–172.

Koike F, Clout MN, Kawamichi M, Poorter MD, Iwatsuki K, eds (2006) Assessment and control of biological invasion risks. Kyoto, Japan: Shoukadoh Book Sellers, Kyoto, Japan and the World Conservation Union (IUCN), Gland, Switzerland.

Kokita T, Nohara K (2011) Phylogeography and historical demography of the anadromous fish *Leucopsarion petersii* in relation to geological history and oceanography around the Japanese Archipelago. Mol Ecol 20, 143–164.

Lee KE, Bahk JJ, Choi J (2008) Alkenone temperature estimates for the East Sea during the last 190,000 years. Org Geochem 39, 741–753.

van Leeuwen CHA, van der Velde G, van Lith B, Klaassen M (2012) Experimental quantification of long distance dispersal potential of aquatic snails in the gut of migratory birds. PLoS ONE 7, e32292.

Li CC, Weeks DE, Chakravarti A (1993) Similarity of DNA fingerprints due to chance and relatedness. Hum Hered 43, 45–52.

Li G, Hubert S, Bucklin K, Ribes V, Hedgecock D (2003) Characterization of 79 microsatellite DNA markers in the Pacific oyster *Crassostrea gigas*. Mol Ecol Notes 3, 228–232.

Li YC, Korol AB, Fahima T, Beiles A, Nevo E (2002) Microsatellites: genomic distribution, putative functions, and mutational mechanisms: a review. Mol Ecol 11, 2453–2465.

Lian CL, Hogetsu T (2002) Development of microsatellite markers in black locust (*Robinia pseudoacacia*) using dual-suppression-PCR technique. Mol Ecol Notes 2, 211–213.

Librado P, Rozas J (2009) DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25, 1451–1452

Lisiecki LE, Raymo ME (2005) A Pliocene-Pleistocene stack of 57 globally distributed benthic δ^{18} O records. Paleoceanography 20, PA1003.

Liu Z, Berge S, Saito Y, Lericolais G, Marsset T (2000) Quaternary seismic stratigraphy and paleoenvironments on the continental shelf of the East China Sea. J Asian Earth Sci 18, 441–452.

Liu JX, Gao TX, Yokogawa K, Zhang YP (2006) Differential population structuring and demographic history of two closely related fish species, Japanese sea bass (*Lateolabrax japonicus*) and spotted sea bass (*Lateolabrax maculatus*) in Northwestern Pacific. Mol Phylogenet Evol 39, 799–811.

Lynch M (1988) Estimation of relatedness by DNA fingerprinting. Mol Biol Evol 5, 584–599.

Lynch M, Ritland K (1999) Estimation of pairwise relatedness with molecular markers. Genetics 152, 1753–1766.

Mae Y, Kanno M, Kijima A (2013) Detection of a highly divergent population structure and identification of a cryptic species in the East Asian dogwhelk *Nucella heyseana*. Mar Ecol Prog Ser 484, 131–141.

Maggs CA, Castilho R, Foltz D, Henzler C, Jolly MT, Kelly J, Olsen J, Perez KE, Stam W, Väinölä R, Viard F, Wares J (2008) Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. Ecology 89, S108–S122.

Magoulas A, Castilho R, Caetano S, Marcato S and Patarnello T (2006) Mitochondrial DNA reveals a mosaic pattern of phylogeographical structure in Atlantic and Mediterranean populations of anchovy (*Engraulis encrasicolus*). Mol Phylogenet Evol 39, 734–746.

Martel A, Chia FS (1991) Drifting and dispersal of small bivalves and gastropods with direct development. J Exp Mar Biol Ecol 150, 131–147.

McInerney CE, Allcock AL, Johnson MP, Prodöhl PA (2009) Characterization of polymorphic microsatellites for the periwinkle gastropod, *Littorina littorea* (Linnaeus, 1758) and their cross-amplification in four congeners. Conserv Genet 10, 1417–1420.

Meglécz E, Costedoat C, Dubut V, Gilles A, Malausa T, Pech N, Martin JF (2010) QDD: a user-friendly program to select microsatellite markers and design primers from large sequencing projects. Bioinformatics 26, 403–404.

Miura O, Kuris AM, Torchin ME, Hechinger RF, Chiba S (2006) Parasites alter host phenotype and may create a new ecological niche for snail hosts. Proc Nat Acad Sci USA 273, 1323–1328.

Miura O, Torchin ME, Bermingham E, Jacobs DK, Hechinger RF (2012) Flying shells: historical dispersal of marine snails across Central America. Proc R Soc B 279, 1061–1067.

Moritz C (1994) Defining 'Evolutionarily Significant Units' for conservation, Trends Ecol Evol 9, 373–375.

Murphy JM, Balguerias E, Key LN, Boyle PR (2002) Microsatellite DNA markers discriminate between two *Octopus vulgaris* (Cephalopoda: Octopoda) fisheries along the northwest African coast. Bull Mar Sci 71, 545–543.

Nakano T, Sasaki T, Kase T (2010) Color polymorphism and historical biogeography in the Japanese patellogastropod limpet *Cellana nigrolineata* (Reeve) (Patellogastropoda: Nacellidae). Zool Sci 27, 811–820.

Niimura Y, Irino T, Oba T (2006) Paleoenvironmental change off Kashima, central

Japan, during the last 144000 years based on the planktonic foraminiferal assemblage. Fossils 79, 4–17. (in Japanese with English abstract)

Oba T, Kato M, Kitazato H, Koizumi I, Omura A, Sakai T, Takayama T (1991) Palaeoenvironmental changes in the Japan Sea during the last 85,000 years. Paleoceanography 6, 499–518.

Okoshi K (2004) Alien species introduced with imported clams: the clam-eating moon snail *Euspira fortunei* and other unintentionally introduced species. Jap J Benthol 59, 74–82. (in Japanese with English abstract)

Okumura K, Suenaga Y, Kinoshita T, Kawana H, Hayashi Y, Taguchi K (2009) List of the fossil mollusca from the upper Pleistocene Yokosuka formation of Kanagawa Prefecture, Central Japan. Bull Kanagawa Prefect Mus (Nat Sci) 37, 11–19. (in Japanese with English title)

Oliver A. Ryder OA (1986) Species conservatiaon and systematics: the dilemma of subspecies. Trends Ecol Evol 1, 9–10.

Ohshima K (1990) The history of straits around Japanese Islands in the Late-Quaternary. Quat Res Tokyo 29, 193–208 (in Japanese with English abstract).

Ozawa T, Köhler F, Reid DG, Glaubrecht M (2009) Tethyan relicts on continental coastlines of the northwestern Pacific Ocean and Australasia: molecular phylogeny and fossil record of batillariid gastropods (Caenogastropoda, Cerithioidea). Zool Scr 38, 503–525.

Paetkau D, Slade R, Burden M, Estoup A (2004) Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Mol Ecol 13, 55–65.

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6, 288–295.

Peakall R, Smouse PE (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research – an update. Bioinformatics 28, 2537–2539.

Pearson RG (2006) Climate change and the migration capacity of species. Trends Ecol Evol 21, 111–113.

Picard CJ, Wells JD (2012) A test for carrion fly full siblings: a tool for detecting postmortem relocation of a corpse. J Forensic Sci 57, 535–538.

Piry S, Alapetite A, Cornuet J-M, Paetkau D, Baudouin L, Estoup A (2004) GeneClass2: A software for genetic assignment and first-generation migrant detection. Jour Hered 95, 536–539.

Pons O, Petit RJ (1995) Estimation, variance and optimal sampling of gene

diversity. 1. Haploid locus. Theor Appl Genet 90, 462-470.

Pons O, Petit RJ (1996) Measuring and testing genetic differentiation with ordered versus unordered alleles. Genetics 144, 1237–1245.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155, 945–959.

Queller DC, Goodnight KF (1989) Estimating relatedness using molecular markers. Evolution 43, 258–275.

Rambaut A, Drummond A (2007) TRACER, Version 1.5: MCMC Trace Analysis Package. Available from http://tree.bio.ed.ac.uk/software/tracer/ (accessed March 15, 2012).

Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. Proc Nat Acad Sci USA 94, 9197–9201.

Raymond M, Rousset F (1995) GENEPOP Version 1.2: population genetics software for exact tests and ecumenicism. J Hered 86, 248–249.

Ritland K (1996) Estimators for pairwise relatedness and inbreeding coefficients. Genet Res 67, 175–186.

Rousset F (2008) Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. Mol Ecol Resour 8, 103–106.

Ruzzante DE, Wald SJ, Macchi PJ, Alonso M, Barriga JP (2011) Phylogeography and phenotypic diversification in the Patagonian fish *Percichthys trucha*: the roles of Quaternary glacial cycles and natural selection. Biol J Linn Soc 103, 514–529.

Sato S (1996) Genetic variability and population structure of *Phacosoma japonicum* (Bivalvia: Veneridae). Venus 55, 51–63.

Selkoe KA, Toonen RJ (2006) Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. Ecol Lett 9, 615–629.

Senjyu T, Matsui S, Han IS (2008) Hydrographic conditions in the Tsushima Strait revisited. J Oceanogr 64, 171–183.

Shimayama T, Himeno H, Sasuga J, Yokobori S, Ueda T, Watanabe K (1990) The genetic code of a squid mitochondrial gene. Nucleic Acids Symp Ser, 73-74.

Slatkin M, Hudson RR (1991) Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing population. Genetics 129, 555–562.

Slatkin M (2008) Linkage disequilibrium — understanding the evolutionary past and mapping the medical future. Nature Rev Genet 9, 477–485.

Smith C, Benzie AH, Wilson KJ (2003) Isolation and characterization of eight microsatellite loci from silver-lipped pearl oyster *Pinctada maxima*. Mol Ecol Notes 3, 125–127.

Sokolv EP, Sokolova IM, Pörtner H-O (2002) Polymorphic microsatellite DNA markers from the marine gastropod *Littorina saxatilis*. Mol Ecol Notes 2, 27–29.

Sunnucks P (2000) Efficient genetic markers for population biology. Trends Ecol Evol 15, 199–203.

Tada R (1994) Paleoceanographic evolution of the Japan Sea. Palaeogeogr Palaeoclimatol Palaeoecol 108, 487–508.

Tada R (1997) Paleoenvironmental Changes in and around the Japan Sea since the last glacial period. Quatern Res 36, 287–300. (in Japanese with English abstract)

Tada R, Irino T, Koizumi I (1999) Land-ocean linkages over orbital and millennial timescales recorded in late Quaternary sediments of the Japan Sea. Paleoceanography 14, 236–247.

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol 28, 2731–2739.

Tanaka N, Lim BK (2011) Genetic structure and diversity of the eelgrass *Zostera marina* L. (Zosteraceae) in Sagami Bay, Japan. Bull Natl Mus Nat Sci Ser B 37, 23–30.

Thomsen MS, Wernberg T, Tuya F, Silliman BR (2010) Ecological performance and possible origin of a ubiquitous but under-studied gastropod. Est Coast Shelf Sci 87, 501–509.

Thomsen MS, de Bettignies T, Wernberg T, Holmer M, Debeuf B (2012) Harmful algae are not harmful to everyone. Harmful Algae 16, 74–80.

Tie AD, Boulding EG, Naish K-A (2000) Polymorphic microsatellite DNA markers for the marine gastropod *Littorina subrotundata*. Mol Ecol 9, 108–110.

Ueda S, Chikuchi Y, Kondo K, Yamamuro M (2005) Macrobenthic fauna and its historical changes in brackish Lake Obuchi, Aomori Prefecture. Japan. Jpn J Limnol 66, 197–206. (in Japanese with English abstract)

Uye SI (2008) Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian marginal seas. Plankton Benthos Res 3, 125–131.

van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) Micro-checker: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4, 535–538.

van Oppen MJH, Bongaerts P, Underwood JN, Peplow LM, Cooper TF (2011) The role of deep reefs in shallow reef recovery: an assessment of vertical connectivity in a brooding coral from west and east Australia. Mol Ecol 20, 1647–1660.

Wang J (2002) An estimator for pairwise relatedness using molecular markers. Genetics 160, 1203–1215.

Wang J (2007) Triadic IBD coefficients and applications to estimating pairwise relatedness. Genet Res 89, 135–153.

Wang J (2011) COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. Mol Ecol Resour 11, 141–145.

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38, 1358–1370.

Wilke T, Davis GM (2000) Infraspecific mitochondrial sequence diversity in *Hydrobia ulvae* and *Hydrobia ventrosa* (Hydrobiidae: Rissooidea: Gastropoda): Do their different life histories affect biogeographic patterns and gene flow? Biol J Linn Soc 70, 89–105.

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. Genetics 168, 1177–1191.

Wonham MJ, O'Connor M, Harley CDG (2005) Positive effects of a dominant invader on introduced and native mudflat species. Mar Ecol Prog Ser 289, 109–116.

Yamamoto G (1954) Ecological study of bottom communities in brackish water lakes III. Bottom communities of Obuchi-numa and Takahoko-numa, with special reference to the series of communities. Jpn J Ecol 4, 60–63. (in Japanese with English abstract)

Yokoyama Y, Kido Y, Tada R, Minami I, Finkel RC, Matsuzaki H (2007) Japan Sea oxygen isotope stratigraphy and global sea-level changes for the last 50,000 years recorded in sediment cores from the Oki Ridge. Palaeogeogr Palaeoclimatol Palaeoecol 247, 5–17.