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REVIEW

Ichthyology 50 years in Japan—Celebrating its history to set the stage for the next generations

Comparative phylogeography of coastal gobies in the Japanese Archipelago: future perspectives for the study of adaptive divergence and speciation

Shotaro Hirase[1]

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Abstract
Phylogeography infers the demographic history of various species by resolving genetic relationships among populations across a geographic range. Comparison of phylogeographic patterns of multiple species with similar geographic distributions, i.e., comparative phylogeography, allows us to assess the roles of regional historical events and species-specific ecological factors in shaping intraspecific genetic diversity, providing model systems for studying the processes and genetic basis of adaptive evolution and speciation. In addition, these patterns can also be compared among species from different regions to infer the impact of global-scale historical and present events, such as Pleistocene glacial cycles, on current biodiversity. In this review, I summarize and integrate recent findings of phylogeographic studies for two geographic lineages, Pacific Ocean (PO) and Sea of Japan (SJ) lineages, of five coastal gobies distributed around the Japanese Archipelago. Using mitochondrial and nuclear DNA markers, these studies revealed genetic divergences of the PO and SJ lineages in the coastal gobies. However, the two types of markers showed discordant patterns for genetic divergences between the two lineages (mitonuclear discordance), suggesting different coalescent processes between these genetic markers. Ecological features that depend on shallow coastal resources may contribute to restricted gene flow and be responsible for the existence of the two lineages that are predominantly found in the coastal gobies. All coastal gobies shared sharp contrasts in genetic diversity between the two lineages, with the SJ lineages rapidly expanding during Pleistocene interglacial periods. Such rapid population expansions can provide alternative ways to obtain recent calibration points to estimate divergence times of the two lineages. A comparison of the geographic distributions between the two lineages indicated that the centers of their secondary contact zones vary, which may appear to represent the continuous transition process of the two lineage distributions. Compared with results of phylogeographic studies from other oceans, multiple divergence times, sharply contrasting demographic histories, and two independent secondary contact zones are unique characteristics of the divergence between the PO and SJ lineages. These characteristics will allow us to test the continuous processes of genomic divergence during geographical isolation with environmental fluctuations and the consequences of hybridization of divergent lineages in independent secondary contact zones with different environmental settings.

Keywords Mitonuclear discordance · Sea of Japan · Hybridization · Speciation continuum

Introduction

Distributions of present-day species have been strongly affected by past climatic and topographical changes. As evidence, phylogeographic studies identified significant genetic divergences within species or between sister-species caused by past geographic barriers, mostly accompanied by environmental changes (Avise 2000). Comparative phylogeography, i.e., synthesis and comparisons of these phylogeographic findings from multiple species with similar distributions, is useful for assessing the relative roles of regional historical

✉ Shotaro Hirase
cashirase@g.ecc.u-tokyo.ac.jp

[1] Fisheries Laboratory, Graduate School of Agricultural and Life Sciences, The University of Tokyo, 2971-4 Bentenjima, Maisaka, Hamamatsu, Shizuoka 431-0214, Japan

events and species-specific ecological factors, such as habitat and tolerance, in shaping intraspecific genetic diversity at the regional scale. Furthermore, the phylogeographic patterns of species from different regions can be compared to infer the impact of global-scale historical and present events on current global species diversity (Bernatchez and Wilson 1998; Bowen et al. 2016).

Phylogeographic knowledge also provides a key platform for evolutionary biology because geographic isolation is the most common mechanism behind the separation of gene pools, which can result in speciation (Coyne and Orr 2004). Specifically, genome-wide analyses of geographically separated and divergent populations can help to understand the genomic processes of speciation (Ravinet et al. 2018; Yamasaki et al. 2020). Moreover, if such genetic divergences occurred in concert with hybridization in secondary contact zones, such hybrid zones will provide useful research basis to investigate the genomic consequences of hybridization between divergent populations (April et al. 2013; Montanari et al. 2014; Hirase et al. 2020a). In addition, if multiple species displayed a wide range of genetic divergences owing to geographic events occurring at different times, we could address the relationships between genetic and phenotypic divergence, and the consequence of their hybridization, by considering them a continuous process of divergence (Hendry 2009).

Marine fishes often show low genetic differentiation throughout their geographic distribution areas, while phylogeographic studies of freshwater fishes have often demonstrated substantial genetic divergences within species (Beheregaray 2008). In general, extensive dispersal promoted by ocean currents in open environments is believed to counteract genetic differentiation in marine environments (Beheregaray 2008). Nonetheless, recent advances indicate that a significant number of marine, especially coastal, fish populations possess deep genetic divergences generated by sea-level fluctuations during Pleistocene glacial–interglacial cycles in multiple regions. Indeed, such genetic divergences were also found in marine geographic areas worldwide (Soltis 2006; Patarnello et al. 2007; Gaither and Rocha 2013; Ni et al. 2014). Accumulating knowledge about these phylogeographic patterns in coastal fishes would provide useful insights into how past global-scale environmental changes and subsequent geographic isolations have generated modern-day species diversity in local and global marine environments.

This review focused on recent phylogeographic studies of the five coastal gobies distributed in the Japanese Archipelago, which have distinct Pacific Ocean (PO) and Sea of Japan (SJ) lineages (Akihito et al. 2008; Hirase et al. 2012a; Kokita and Nohara 2011; Hirase and Ikeda 2014a). Sea of Japan (SJ) is a semi-enclosed sea located between the Japanese Archipelago and the Asian continent and connected to PO and other seas through narrow and shallow (≈ 130 m depth) straits. Currently, the warm Tsushima Current flows into SJ through the southern Tsushima Straits, but paleoenvironmental studies have suggested that this sea was largely isolated in Pleistocene glacial periods when the surrounding straits were closed by sea-level declines (Tada 1994) (Fig. 1). Previous phylogeographic studies based on samples collected extensively along the Japanese Archipelago coast suggested that these isolation events arose in the PO and SJ lineages of multiple coastal gobies (Akihito et al. 2008; Hirase et al. 2012a; Hirase and Ikeda 2014a; Kokita and Nohara 2011), and three-spined stickleback, *Gasterosteus aculeatus* (Higuchi and Goto 1996). Considering the accumulated paleoenvironmental data (Oba et al. 1991; Tada 1994; Crusius et al. 1999; Gorbarenko and Southon 2000; Kitamura et al. 2001; Kitamura and Kimoto 2006) and parallel genetic divergence, PO and SJ lineages provide a significant testbed to perform comparative phylogeographic analyses. The PO and SJ lineages of *Gasterosteus aculeatus* showed reproductive isolation (Kitano et al. 2009; Ishikawa et al. 2019; the SJ lineage was described as *Gasterosteus nipponicus*; Higuchi et al. 2014), while lineage pairs of coastal gobies are not reproductively isolated and generate later-generation hybrids in secondary contact zones (Hirase and Ikeda 2015; Hirase et al. 2020a, c; Kato et al. 2021). Therefore, such lineage pairs are

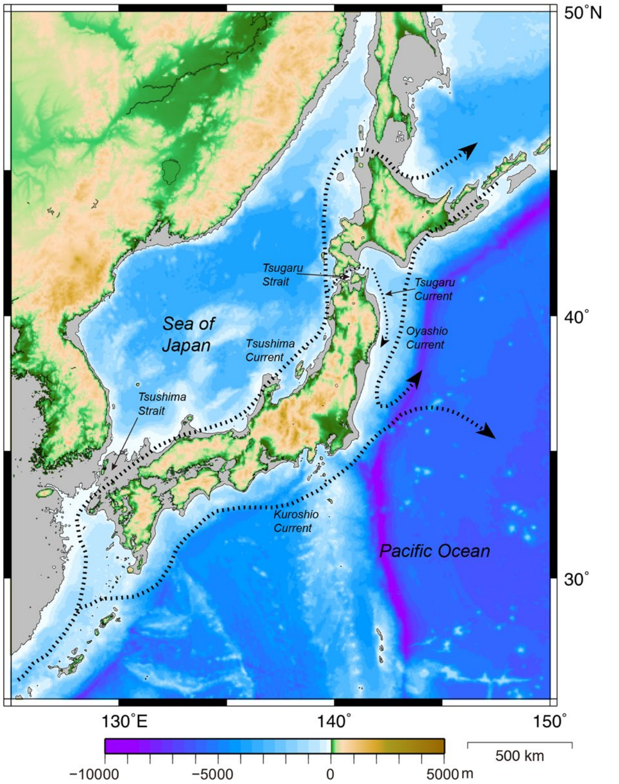


Fig. 1 Submarine topography around the Japanese Archipelago illustrated by GMT 4.0 (Wessel et al. 2013). Gray represented the land area when sea level dropped 125 m during the last glacial period

presumably in the preliminary step of speciation and would provide significant opportunities to investigate the evolutionary processes in this phase. This review summarizes and integrates previous phylogeographic findings about the PO and SJ lineages of coastal gobies, demonstrating their potential as a model system for future evolutionary biology studies.

Existence of the Pacific Ocean and Sea of Japan lineages and mitonuclear discordance

In Japanese coastal species, the PO and SJ lineages of mitochondrial DNA (mtDNA) were first reported in the late 1990s. To date, the presence of two lineages in animals has been reported clearly in two mollusk species [*Turbo* (*Batillus*) *cornutus*, Kojima et al. 1997; *Batillaria cumingi*, Kojima et al. 2004] and five coastal fishes (*Pterogobius elapoides*, Akihito et al. 2008; *Pterogobius zonoleucus*, Akihito et al. 2008; *Leucopsarion petersii*, Kokita and Nohara 2011; *Chaenogobius annularis*, Hirase et al. 2012a; *Chaenogobius gulosus*, Hirase and Ikeda 2014b), with divergences estimated to date back into the early to late Pleistocene. Among coastal fishes with two lineages, all fishes are gobiid (Fig. 2), suggesting that unique ecological features of gobiid fishes (see the next section) lead to genetic divergence. Although mtDNA is a useful genetic tool for phylogeographic studies owing to its rapid evolution and maternal transmission without intermolecular recombination (Avise 2000), this marker can represent only a minute fraction of the total historical record (Degnan 1993; Palumbi and Baker 1994), and the stochastic nature of coalescent processes in mtDNA could differ from that in the nuclear genome (Wilson and Veraguth 2010). In particular, mtDNA analyses could yield a misleading picture of population-level processes owing to hybridization and introgression (Toews

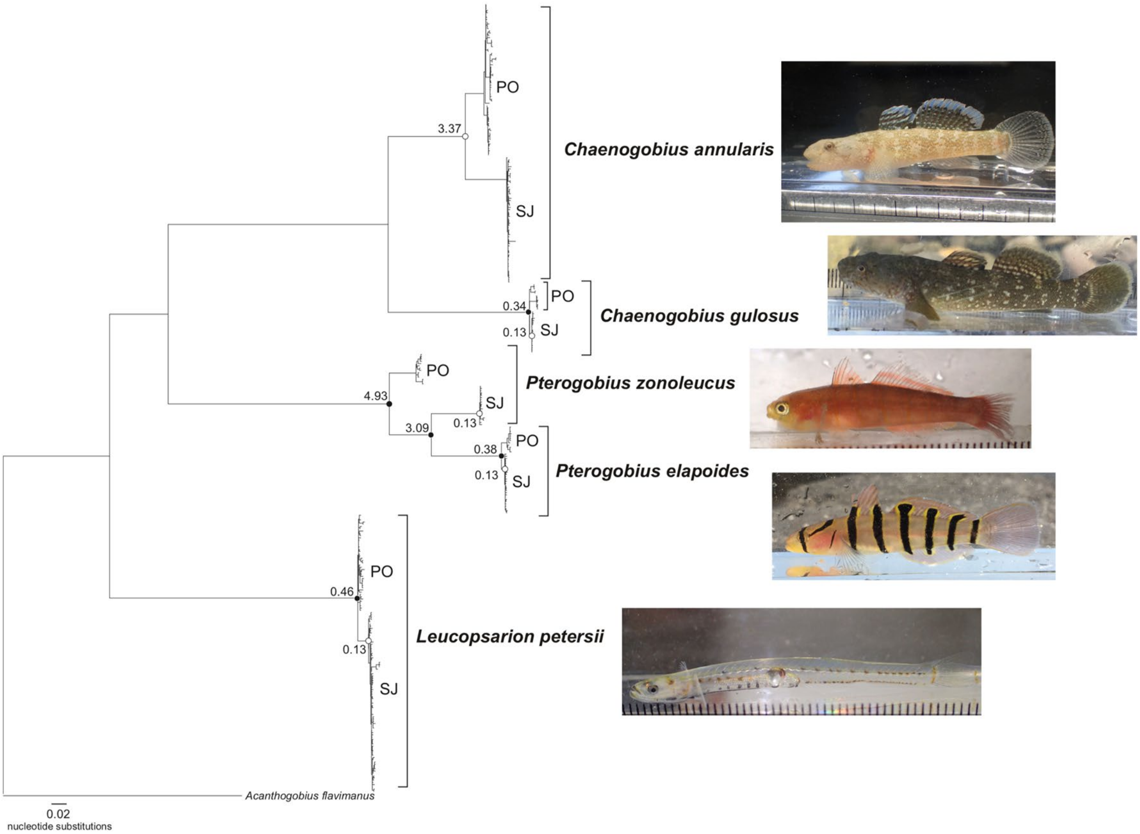


Fig. 2 Neighbor-joining tree of mitochondrial DNA sequences of the Pacific Ocean and Sea of Japan lineages for the five coastal gobies in the Japanese Archipelago. I used cytochrome *b* of mitochondrial DNA sequences of *Chaenogobius annularis* (Hirase et al. 2012a, AB684846–AB684973), *C. gulosus* (Hirase and Ikeda 2014a, AB775375–AB775405), *Leucopsarion petersii* (Kokita and Nohara 2011, AB562156–AB562280), *Pterogobius elapoides* (Akihito et al. 2008, AB440403–AB440472), and *P. zonoleucus* (Akihito et al. 2008, AB440363–AB440397). *Acanthogobius flavimanus* (AB021249) was used as an outgroup. Mitochondrial DNA sequences of the five species and an outgroup were aligned using mafft v7.402 (Katoh and Standley 2013), and a neighbor-joining trees of the aligned sequences was constructed with the Jukes-Cantor distance and complete deletion options using MEGA 7 (Tamura et al. 2011). Branch lengths were proportional to the estimated numbers of nucleotide substitutions per site. Values in nodes (closed circles) showed divergence times (million years ago: Ma) based on five calibration points (open circles). Pictures of the five coastal gobies are provided by Shuya Kato

and Brelsford 2012). Therefore, assessing congruence patterns among multi-locus nuclear DNA data will allow us to resolve reliable demography of the PO and SJ lineages.

Genetic analyses using nuclear DNA markers have been performed for four of the five coastal gobies using allozymes (*C. annularis*, Hirase et al. 2012c), sequences of several nuclear genes (*P. elapoides* and *P. zonoleucus*, Akihito et al. 2016), microsatellite DNA (*L. petersii*, Kokita et al. 2013; *C. annularis*, Hirase and Ikeda 2014a), and nuclear single nucleotide polymorphism (SNP) markers (*L. petersii*, Hirase et al. 2020a; C. *annularis*, Hirase et al. 2020c). In these studies, mtDNA and nuclear DNA markers discerned both concordance and discordance patterns for genetic divergences between the PO and SJ lineages. For example, *C. annularis* showed a concordant pattern between the genetic structures revealed by mtDNA and nuclear DNA markers and lack of gene flow between the two lineages (Hirase and Ikeda 2014a), except in two secondary contact zones (Hirase and Ikeda 2015; Kato et al. 2021). Contrastingly, *L. petersii* revealed discordant patterns in two secondary contact zones; PO mtDNA widely introgressed in the southern secondary contact zone, whereas SJ mtDNA extensively introgressed in the eastern secondary contact zone in comparison with nuclear genomic results (Hirase et al. 2020a). Extreme cases of discordance were observed in *P. zonoleucus*, with mtDNA sequences of its SJ lineage appearing closely related to *P. elapoides* but not to the PO lineage of *P. zonoleucus* (Akihito et al. 2008). In subsequent phylogenetic analyses of *P. elapoides* and *P. zonoleucus* based on three nuclear genes, two of the nuclear genes revealed monophyly for the two lineages of *P. zonoleucus*, although one nuclear gene showed similar patterns to those of mtDNA (Akihito et al. 2016). These conflicting patterns between mtDNA and nuclear DNA markers, i.e., mitonuclear discordance, have been observed in many phylogeographic studies (Toews and Brelsford 2012). These findings highlight the need for analyzing multiple nuclear DNA markers to investigate the genetic divergence of the two lineages, which will be possible by the application of high-throughput sequencing methods, such as RAD-seq (Peterson et al. 2012), MIG-seq (Suyama et al. 2015), and GRAS-Di (Hosoya et al. 2019).

Ecological features leading to genetic divergence

Low-dispersal species are often composed of genetically and geographically highly structured populations that reflect past geographical events (Pelc et al. 2009). The five coastal gobies in this study deposit sticky eggs on rocks or shells along coasts or rivers, and their parent fish defend the eggs until the larvae hatch (Dotsu and Tsutsumi 1959; Tsutsumi and Dotsu 1961; Sasaki and Hattori 1969; Matsui 1986). Therefore, dispersal presumably only occurs during the pelagic larval stages and limited dispersal of their larvae and adults should be associated with the genetic divergence between PO and SJ lineages. Indeed, a population genetic study of *Chaenogobius annularis* across a small geographic scale revealed genetic differentiation within 10 km, suggesting a remarkable low dispersal for this species owing to site fidelity of adults, larval retention, and presumably short (a few days or 1 week) pelagic larvae duration which may characterize tidepool fishes (Hirase et al. 2012b). As *C. gulosus* is a tidepool fish as well as *C. annularis*, one would expect its dispersal to be limited by similar ecological characteristics. *Leucopsarion petersii* has an anadromous life history, with adults ascending to the lower reaches of rivers for reproduction in spring and dying after reproduction. Then, newly-hatched larvae descend to the sea where they grow in coastal waters until the following spring (Matsui 1986). Therefore, larval retention in coastal areas near natal rivers is expected to prevent dispersal. Additionally, as *Pterogobius elapoides* and *P. zonoleucus* have free-floating life history throughout their lifetime (Suzuki et al. 2004), site fidelity of adults and larval retention in these coastal gobies may also contribute to limited dispersal.

In contrast to the five gobiid fishes, genetic divergences within the yellowfin goby *Acanthogobius flavimanus* have not been found neither by mtDNA nor nuclear DNA markers (Hirase et al. 2017, 2020b) despite *A. flavimanus* being distributed in both coastal areas of PO and SJ as the five gobiid fishes. A similar discordance phylogeographic pattern was also reported in gobiid fishes distributed along coastal areas in California, by showing a considerably shallower phylogeographic structure in *Clevelandia ios* compared to that of *Eucyclogobius newberryi*, which suggested that the high dispersal ability of *C. ios* owing to its open habitat, high abundance, and long pelagic larvae duration contributed to the structure (Dawson et al. 2002). Among these factors, Hirase et al. (2017) inferred that longer pelagic larvae duration of *A. flavimanus* contributed to its shallow phylogeographic structure. The deeper breeding site of *A. flavimanus* compared to those of the other five gobies may also promote the dispersal of their pelagic larvae. Additionally, Hirase et al. (2017) proposed another possible scenario by focusing on *A. flavimanus* breeding sites, i.e., the extinction of its SJ lineage and subsequent SJ colonization by its PO lineage. Juvenile of *A. flavimanus* settles mainly in shallow estuarine waters such as tidal flats and boulder areas, while adults are observed to inhabit and reproduce in deeper bay waters (Dotsu and Mito 1955; Katayama et al. 2000; Sakai et al. 2000; Kanou et al. 2005). In contrast, the five gobies that showed genetic divergences reproduce in shallow coastal areas or rivers (Dotsu and Tsutsumi 1959; Tsutsumi and Dotu 1961; Sasaki and Hattori 1969). If we assume environments in deep bay waters to be more severe than those in shallow coastal areas during Pleistocene glacial periods, when the SJ was isolated (Oba et al. 1991; Tada 1994; Gorbarenko and Southon 2000), the absence of genetic differentiation between the PO and SJ populations in *A. flavimanus* can be explained by the extinction of the ancestral SJ lineage owing to the disappearance of spawning sites. Conversely, the presence of SJ lineages in the five coastal gobies may suggest their survival during past severe environments during the glacial periods. Local extinctions were suggested as important in eliminating genetic divergence resulting from past geographic barriers (Cunningham and Collins 1998). Although it is generally difficult to determine the involvement of local extinctions (Provan and Bennett 2008), further accumulation of phylogeographic studies on other coastal gobies with various ecological characteristics will help us address this issue.

Contrasting demography between the Pacific Ocean and Sea of Japan lineages and its application to calibration of mitochondrial DNA evolutionary rates

Previous phylogeographic studies found sharp contrasts in genetic diversity and branching patterns of phylogenetic trees between the PO and SJ mtDNA lineages for coastal gobies (Akihito et al. 2008; Kokita and Nohara 2011; Hirase et al. 2012a). Notably, the PO mtDNA lineage showed a deep branching pattern, whereas the SJ mtDNA lineage had a shallow branching pattern with a "star-like" phylogeny (Table 1; Fig. 3). In general, the deep branching pattern indicates a comparatively long evolutionary history, while the shallow star-like branching pattern suggests a rapid increase in the survival probability of mtDNA lineages owing to rapid population expansion (Avise et al. 1984; Di Rienzo and Wilson 1991; Grant and Bowen 1998). Low nucleotide diversity and negative Tajima's *D* value in the SJ mtDNA lineages of the five coastal gobies also suggested their rapid population expansion (Table 1). Sea of Japan (SJ) was expected to represent a severe environment during the glacial periods for marine warm-water species, such as coastal gobies, but a much less severe one during the interglacial interludes owing to the inflow of the warm Tsushima Current (Kitamura et al. 2001; Kitamura and Kimoto 2006). Hence, following severe bottlenecks during glacial periods, populations of the SJ lineages are believed to have rapidly expanded during the Pleistocene interglacial periods (Akihito et al. 2008; Kokita and Nohara 2011; Hirase et al. 2012a, 2016).

Estimating when rapid population expansion occurs is an important issue (Provan and Bennett 2008). Rapid population expansion after the end of the last glacial period (LGM), called as postglacial expansion, is a common phenomenon in several warm-dwelling terrestrial species (Hewitt 2004). However, previous estimates suggested that populations of SJ lineages expanded before LGM (pre-LGM) because the mtDNA evolutionary rate would be too fast assuming it expanded after LGM (Kokita and Nohara 2011; Hirase et al. 2012a, 2016). Actually, pre-LGM population expansion has been suggested in several marine realms, including the northeastern Pacific (Marko et al. 2010), northeastern Atlantic (Hoarau et al. 2007; Derycke et al. 2008), northeast European seas (Laakkonen et al. 2013), and East China Sea (Ni et al. 2014).

Divergence and expansion time estimation in phylogeography is important and has mainly be conducted using mtDNA. Its maternal transmission, extensive intraspecific variation, and general absence of intermolecular recombination have facilitated evolutionary rate estimations (Galtier et al. 2009), with data accumulation of these rates providing a standard for evaluating newly calculated ones. mtDNA evolutionary rate estimation is of also a challenging task, with being calculated by calibrating nucleotide divergences with calibration points, such as divergence time or lineage expansion time, based on fossil or paleobiogeographic data (Tringali et al. 1999; Watanabe et al. 2003). In phylogeographic studies focusing on closely related lineages, recent calibration points are preferred because of the time dependency of molecular clocks (Ho et al. 2015). However, a general lack of recent calibration points for marine species often prevents using this estimation procedure for their

Table 1 Summary of mitochondrial DNA genetic diversity of the Pacific Ocean (PO) and Sea of Japan (SJ) lineages of five coastal gobies. These estimates were calculated in this review

Species	Nucleotide divergence	Nucleotide diversity			Tajima's *D*		mtDNA regions	References
		PO	SJ	PO/SJ ratio	PO	SJ		
Chaenogobius annularis	7.44%	1.09%	0.55%	2.0	1.57*	2.23**	cyt *b* + ND2	Hirase et al. (2012a)
Chaenogobius gulosus	1.08%	1.01%	0.30%	3.3	0.63	1.89**	cyt *b*	Hirase and Ikeda (2014a)
Leucopsarion petersii	1.94%	0.77%	0.45%	1.7	1.88*	2.43**	cyt *b*	Kokita and Nohara (2011)
Pterogobius zonoleucus	–	0.93%	0.48%	2.0	0.73	1.85**	cyt *b* + ND2	Akihito et al. (2008)
Pterogobius elapoides	1.68%	0.93%	0.26%	3.6	0.53	2.19**	cyt *b* + ND2	Akihito et al. (2008)

$^{*}P < 0.05$; $^{**}P < 0.01$

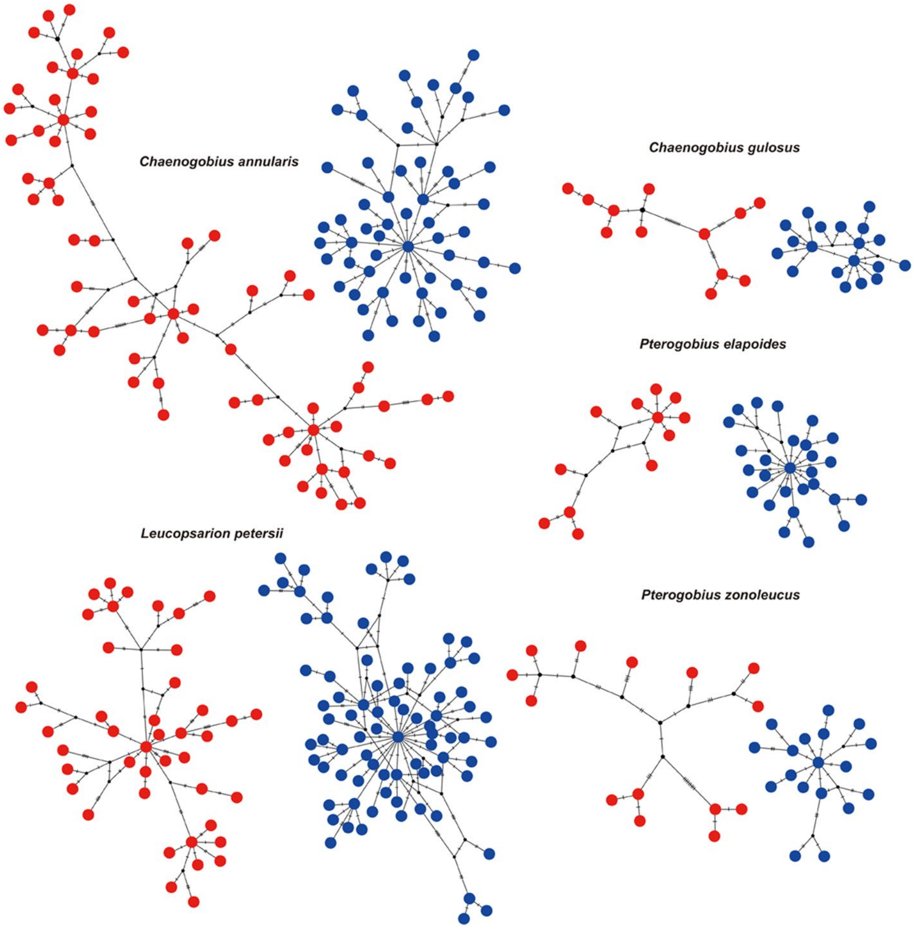


Fig. 3 TCS networks of mitochondrial DNA sequences of the Pacific Ocean (red) and Sea of Japan (blue) lineages for five coastal gobies drown by PopArt (Leigh and Bryant 2015). I used cytochrome b of mitochondrial DNA sequences that used for the neighbor joining tree in Fig. 2. Dashes and small black circles represented mutational steps and branching points, respectively

evolutionary rates (Marko 2004; Lessios 2008). Therefore, several studies have used "universal" evolutionary rates that have been estimated for other related species. However, these universal rates may not be applicable to all species because evolutionary rates often vary among lineages (Zhang and Ryder 1995).

Based on the above problem, the evolutionary rate of *Chaenogobius annularis* was tried to be calibrated based on paleoenvironmental events (Hirase et al. 2016). In this previous study, based on the assumption that the SJ lineage of *C. annularis* expanded during any interglacial periods, the evolutionary rates were calculated using any interglacial periods as the calibration point and average pairwise sequence divergences within the SJ lineage (i.e., average pairwise sequence divergences were divided by the times of any interglacial periods), and reasonable rates were selected by comparing with previously reported mtDNA evolutionary rates of fishes. Consequently, Hirase et al. (2016) inferred that the SJ lineage of *C. annularis* expanded during the last interglacial period, 130 thousand years ago (ka). Such rapid population expansions during interglacial periods have provided alternative ways to obtain recent calibration points in other studies (Akihito et al. 2008; Crandall et al. 2012; Sakuma et al. 2019). I applied the above strategy to the other four gobies, and obtained their evolutionary rates of mitochondrial cytochrome *b* (cyt *b*), as shown in Table 2. Assuming rapid population expansion in the last interglacial period, the evolutionary rates of *Leucopsarion petersii* (4.2%/million years:Myr) and *Pterogobius zonoleucus* (3.1%/Myr) were faster than previously reported cyt *b* evolutionary rates of gobiid fishes [those of the *Gymnogobius* genus (2.2–2.7%/Myr, Harada et al. 2002; Sota et al. 2005)], whereas the rates of *C. annularis* (2.3%/Myr), *C. gulosus* (2.3%/Myr), and *P. elapoides* (2.5%/Myr) were similar to those. It is difficult to determine whether the faster rates were caused by artifacts (i.e., incorrect calibration) or differences in evolutionary rate. However, given that rapid population expansion during the last interglacial periods has been estimated for marine species in other areas (Provan et al. 2005; Hoarau et al. 2007; Ni et al. 2014), simultaneous rapid population expansion of SJ lineages and differences in the evolutionary rate may be a reasonable inference. Such pre-LGM expansions mean that the five coastal gobies survived despite the presumed severe environments in SJ during LGM (Oba et al. 1991). In contrast, SJ lineages of deep-sea fishes expanded after LGM (Sakuma et al. 2014), which suggests

Table 2 Pairwise evolutionary rates of mitochondrial cytochrome *b* of five coastal gobies. The evolutionary rates of four of five coastal gobies were recalculated in this review

Species	Mean pairwise distance within Sea of Japan lineage	Presumed TMRCA of Sea of Japan lineage			
		130 ka	243 ka	337 ka	References
Chaenogobius annularis	0.296%*	2.3%/Myr*	1.2%/Myr*	0.9%/Myr*	Hirase et al. (2016)
Chaenogobius gulosus	0.304%	2.3%/Myr	1.3%/Myr	0.9%/Myr	Hirase and Ikeda (2014a)
Leucopsarion petersii	0.548%	4.2%/Myr	2.3%/Myr	1.6%/Myr	Kokita and Nohara (2011)
Pterogobius zonoleucus	0.401%	3.1%/Myr	1.7%/Myr	1.2%/Myr	Akihito et al. (2008)
Pterogobius elapoides	0.328%	2.5%/Myr	1.3%/Myr	1.0%/Myr	Akihito et al. (2008)

*These estimates were retrieved from Hirase et al. (2016); TMRCA: time of the most recent common ancestor; ka: thousand years ago; Myr: million years

that environmental changes during LGM may be severe for deep-sea fishes if the evolutionary rates of these species were correctly calibrated. On the other hand, we could not eliminate the possibility that postglacial expansions of the SJ lineages of coastal gobies, which lead to too fast mtDNA evolutionary rates, when considering the acceleration of evolutionary rates in a recent period (< 1 million years ago: Ma) suggested by Ho et al. (2005). Therefore, the timing of expansion of the SJ lineages should also be examined carefully using the other strategies, such as Pairwise Sequentially Markovian Coalescent model based on nuclear SNP loci and their mutation rates (Li and Durbin 2011).

The SJ lineages of five coastal gobies show a star-like phylogeny lacking large genetic divergences, and the southern populations of *C. annularis* and *L. petersii* SJ lineages around Tsushima Strait have the highest genetic diversity (Kokita and Nohara 2011; Hirase et al. 2012a; Hirase and Ikeda 2014b). In general, such genetic signatures are believed to reflect the rapid postglacial expansion from southern refugia (Provan and Bennett 2008). Accordingly, SJ lineages likely rapidly expanded from southern refugia during Pleistocene interglacial periods (Kokita and Nohara 2011; Hirase and Ikeda 2014b). The star-like phylogeny, lacking large genetic divergences within SJ lineages, was key evidence for the southern refugia hypothesis. However, this finding was indicated by analyses of partial genes of the mitochondrial genome, and several signatures of genetic divergence within the lineage may have been missed owing to the lack of informative nucleotide sites. As it is expected that the mitochondrial genome as a whole (mitogenome) would provide greater resolution of possible genetic differentiation within the SJ lineage (Jacobsen et al. 2012), Hirase et al. (2016) investigated genetic differentiation within *C. annularis* SJ lineage using parallel mitogenome sequencing. They discovered that the northern sub-lineage is clearly distinct from southern sub-lineages, and likely experienced rapid population expansion (Fig. 4; Hirase et al. 2016); this finding was a result that the mitogenome data successfully rooted the SJ lineage by alleviating the “random rooting effect”, which hindered phylogenetic analysis based on specific gene sequences (Fig. 4). Consequently, Hirase et al. (2016) proposed the presence of glacial refugia in northern SJ coastlines, and that the entire SJ lineage did not expand from the southern refugia alone. Identification of cryptic refugia offers important insights for predicting biological responses to future global climate change (Provan and Bennett 2008). It will be a future work to clarify whether the northern sub-lineage is shared by other coastal gobies that possess PO and SJ lineages. Although the importance of using multiple nuclear DNA markers has been highlighted, further mitogenomic phylogeographic investigations will provide additional important information about the biological responses to past environmental changes in the SJ and other seas.

Although mtDNA markers have shown lower genetic diversity in SJ than in PO mtDNA lineages in coastal gobies commonly, it should be noted that nuclear genetic markers do not necessarily show such contrasts. For example, whereas *C. annularis* showed lower genetic diversity of the SJ lineage also in microsatellite DNA loci (Hirase and Ikeda 2014b), *L. petersii* did not show such trends in neither microsatellite DNA (Kokita et al. 2013) nor SNP loci (Hirase et al. 2020a). Kokita et al. (2013) explained that similar levels of microsatellite DNA diversity between the PO and SJ lineages were caused because sufficient time has passed for microsatellite DNA, which is characterized by high mutation rates, to lose the molecular footprint of old demographic events and restore the genetic diversity. However, given that Hirase et al. (2020a) found similar levels of genetic diversity also in SNP loci, whose mutation rate is not high, between the two lineages, it is reasonable to assume that the diversity of the mitogenome, which has a small effective population size, decreased more severely in the SJ lineages (Ballard and Whitlock 2004). The difference in genetic diversity between PO and SJ lineages using nuclear DNA markers for other

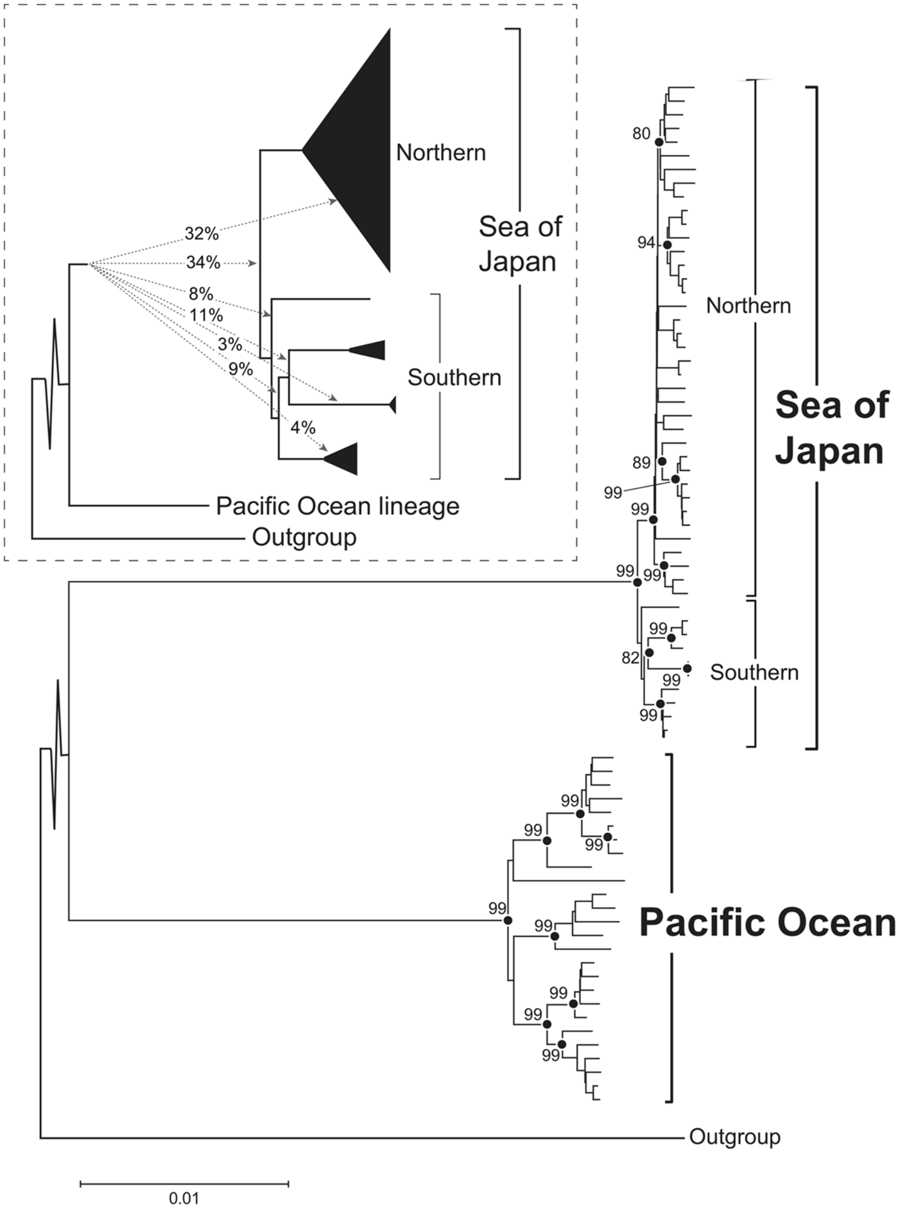


Fig. 4 Phylogenetic tree of 75 *Chaenogobius annularis* mitogenomes [reproduced with from Hirase et al. (2016)]. Branch lengths were proportional to the estimated numbers of nucleotide substitutions per site. Closed circles and numbers indicated highly (> 80%) supported geographical clades and their bootstrap values, respectively. In the upper-left side, proportions of branches of the Sea of Japan lineage to which the outgroup branch was connected among the bootstrap trees of a single mitochondrial gene (*ND1*) were indicated. The outgroup branch was connected to diverse ingroup branches, thus failing to root the tree reliably, i.e., random rooting effect. Collectively, the use of mitogenome sequence solved the random rooting problem in the Sea of Japan lineage

species should be more investigated to infer the demographic history of each lineage.

Re-estimation of divergence times between the Pacific Ocean and Sea of Japan lineages

Accumulation of paleoenvironmental data is important for estimating the historical processes of population divergence. In this regard, SJ has been a target field for several paleoenvironmental studies (Oba et al. 1991; Tada 1994; Crusius et al. 1999; Gorbarenko and Southon 2000; Kitamura et al. 2001; Kitamura and Kimoto 2006). The Tsushima Strait in the southwest of SJ was closed from 10.5 to 3.5 Ma (Tada 1994), and after 3.5 Ma, the Tsushima Current flowed into SJ during the interglacial periods. Kitamura et al. (2001) proposed that the Tsushima Strait was closed again from 2.5 to 1.71 Ma, and suggested that 1.7 Ma was an important turning point for SJ because its southern straits widely opened (Kitamura et al. 2001; Kitamura and Kimoto 2006). Finally, during each interglacial period after 1.7 Ma, SJ was connected to other seas, accompanied by inflow from the Tsushima Current (Kitamura et al. 2001; Kitamura and Kimoto 2006). Thus, we can expect several timings of geographical isolation for SJ lineages, and multiple events might have led to various divergence times between the SJ and PO lineages among the five coastal gobies.

As expected, my reanalysis based on a uniform phylogenetic method suggested variation of genetic distance between PO and SJ lineages among species, which could be attributed to multiple vicariance events (Fig. 2; Table 1), and allow us to statistically distinguish between "single-event" and "multiple-event" biogeographic hypotheses (Edwards and Beerli 2000). However, owing to potential differences in mtDNA evolutionary rates among species (Gissi et al. 2000), it is difficult to conclude whether a wide range of genetic distances reflects multiple vicariant events. In this regard, pairs of closely related species that possess similar ecological features may facilitate ensuring the robustness of differences in divergence time (Hills and Moriz 1994). Hirase and Ikeda (2014a) focused on closely related *Chaenogobius gulosus* and *C. annularis* as suitable models to compare levels of genetic divergence, and tested the hypothesis of multiple vicariance events. Both species have the same geographic distribution (Akihito et al. 2002), and mainly inhabit tide pools and possess similar ecological features (Sasaki and Hattori 1969). On the basis of the molecular clock and a hierarchical approximate Bayesian computation (ABC) model, they showed more recent divergence time in the two lineages of *C. gulosus* than those of *C. annularis*, suggesting multiple isolation events for SJ in the Pleistocene.

Accumulated paleoenvironmental data for SJ could provide suitable calibration points for estimating evolutionary rates and divergence times, as the time of the most recent common ancestor (TMRCA) of the SJ lineages possibly correspond to interglacial periods when warm water flows into SJ and the rapid expansion of the SJ lineages occurred (Akihito et al. 2008; Hirase et al. 2016). As mentioned in the previous section, Hirase et al. (2016) assumed rapid population expansion of the SJ lineage of *C. annularis* (i.e., the SJ northern sublineage suggested by the mitogenomic sequences) in the last interglacial period (130 ka), and estimated that the two lineages diverged 3.37 Ma. Here, I re-estimated divergence times between the two lineages for the other four gobies using Reltime of MEGA 7, by relaxing the assumption of a strict molecular clock in a phylogeny (Tamura et al. 2018). In this analysis, I assumed that the TMRCA of the SJ lineage for each of the four coastal gobies (*Pterogobius elapoides*, *P. zonoleucus*, *Leucopsarion petersii*, and *C. gulosus*) was 130 ka, implying simultaneous rapid population expansion of the SJ lineages in last interglacial periods, and that divergence between the SJ and PO lineages of *C. annularis* occurred 3.37 Ma (Hirase et al. 2016) (Fig. 2). [In *C. annularis*, the northern sub-lineage of the SJ lineage showed a rapid population expansion (Hirase et al. 2016) and was not used as a calibration point here because this sublineage was not shown in the cyt *b* tree (Fig. 2). Instead, the divergence time between the PO and SJ lineages (i.e., 3.37 Ma), which was estimated by the northern sublineage calibration point, was used as an older calibration point.] The two lineages of the four gobies were estimated to diverge from 340−460 ka (Fig. 2), suggesting that they diverged in a similar period. Contrastingly, the divergence time between the SJ lineage of *P. zonoleucus* and *P. elapoides* (3.09 Ma) was close to that between the two lineages of *C. annularis* (Fig. 2). The unexpected monophyletic relationship of mtDNA between the SJ lineage of *P. zonoleucus* and *P. elapoides* was inferred to be caused by introgression of mtDNA from *P. elapoides* to the SJ lineage of *P. zonoleucus* upon ancient hybridization (Akihito et al. 2016). Given that the opening of the Tsushima Strait 3.5 Ma was estimated to cause divergence between the two lineages of *C. annularis* (Hirase et al. 2016), this same geographic event may also be associated with ancient hybridization between *P. elapoides* and the SJ lineage of *P. zonoleucus*. In addition, this event has been reported to account for the divergence between the continental and Japanese Archipelago populations of a related group, the *Gymnogobius castaneus* and *Gymnogobius taranetzi* species complex (Sota et al. 2005). Therefore, this re-estimation of divergence times between the two lineages may suggest two geographic isolation event waves in the SJ.

Although mtDNA is a good molecular tool to estimate divergence time, we should note that it may not always share the same topology and branch lengths as other genomic regions (Toews and Brelsford 2012). Moreover, the timing of gene divergence predates the population divergence event, leading to overestimation of population divergence times (Edwards and Beerli 2000; Carstens and Knowles 2007). In this regard, multi-locus coalescent approach allows for much more accurate estimation of the divergence history (McCormack et al. 2011) and should be applied to divergence time estimation of the SJ and PO lineages for coastal marine species. For example, Akihito et al. (2016) estimated divergence times of the two lineages of *P. elapoides* and *P. zonoleucus* based on three nuclear genes (*P. elapoides*, 810 ka; *P. zonoleucus*, 560 ka). In addition, Ravinet et al. (2018) used coalescent analyses and ABC based on genome-wide SNP markers and estimated that *Gasterosteus aculeatus* and *G. nipponicus* diverged approximately 0.68–1 Ma. In the future, comparison of divergence times between the two lineages based on mtDNA and multi-locus coalescent analyses will be important to increase dating precision of genetic divergences.

Secondary contact zones between the Pacific Ocean and Sea of Japan lineages

There are two potential secondary contact zones between the PO and SJ lineages of coastal gobies, i.e., the western and eastern coastal areas of the Japanese Archipelago, where these seas are connected. Both secondary contact zones were identified in *Leucopsarion petersii* and *Chaenogobius annularis* based on mtDNA and nuclear DNA markers.

The western and eastern secondary contact zones were the Seto Inland Sea and the Joban-Kashimanada or the Sanriku coast, respectively (Kokita and Nohara 2011; Hirase and Ikeda 2015; Hirase et al. 2020a; Kato et al. 2021) (Fig. 5). These two secondary contact zones have been suggested to be formed at different periods in both species (Hirase et al. 2020a; Kato et al. 2021). As the Seto Inland Sea was terrestrial during LGM (Fig. 1), it is probable that the secondary contact zones in this inland sea formed as a consequence of subsequent postglacial colonization (Kokita and Nohara 2011; Hirase et al. 2020c; Kato et al. 2021). In contrast, assuming that the SJ lineage expanded and formed geographic distribution into the PO side under the influence of the Tsugaru Current, which is part of the Tsushima Current, during the last interglacial period as discussed above, the secondary contact zones in Joban-Kashimanada or Sanriku Coast were inferred to establish before LGM (Fig. 1) (Hirase and Ikeda 2015; Hirase et al. 2020a).

Hybridization between the PO and SJ lineages occurred in the two secondary contact zones in both *L. petersii* and *C. annularis*; however, mtDNA and nuclear DNA markers demonstrated different genetic structures in these zones. For *C. annularis*, an admixture of both DNA markers was observed in the center of the secondary contact zone and showed their concordance pattern (Fig. 5). Contrastingly, in the secondary contact zones of *L. petersii*, the dominant mtDNA is inconsistent with the results of nuclear genomic clustering, suggesting that mating preference and/or local adaptive pressure may cause asymmetric introgression of mtDNA in both secondary contact zones (Fig. 5) (Hirase et al. 2020a). This mitonuclear discordance in the secondary contact zone has been commonly observed across a wide range of organisms (Toews and Brelsford 2012), and the

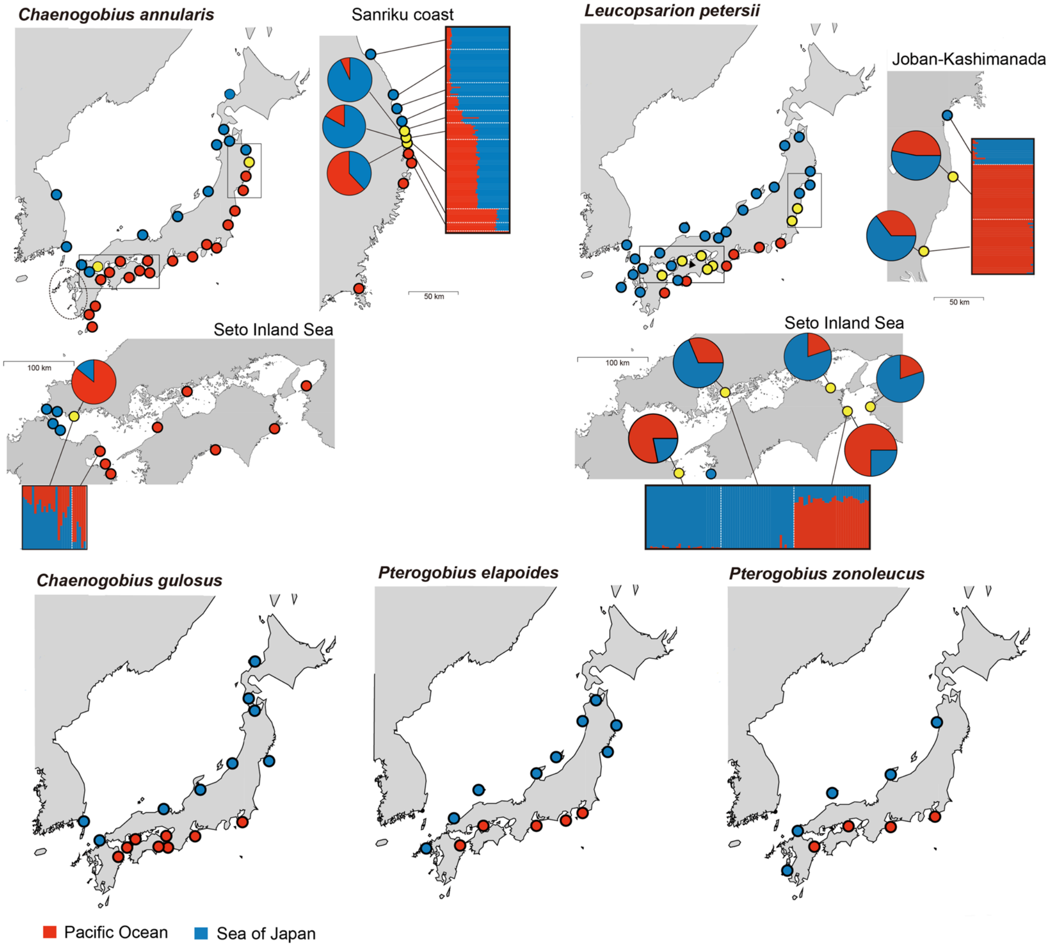


Fig. 5 Geographical distribution of the Pacific Ocean (red) and Sea of Japan (blue) lineages for five coastal gobies. Yellow denotes populations where the two mitochondrial lineages co-exist. Pie graphs showed ratios of both mitochondrial lineages, and bar plots show the individual genotype membership in populations where nuclear admixture between the two lineages has been detected. Bar plots of *Chaenogobius annularis* in the Sanriku Coast and *Leucopsarion petersii* were based on SNP markers (Hirase et al. 2020a, b), and that of *C. annularis* in Seto Inland Sea was based on microsatellite DNA markers (Kato et al. 2021). Dashed line in the map of *C. annularis* shows the region where the third lineage, the East China Sea lineage, is distributed (Kato et al. 2021)

secondary contact zone between the PO and SJ lineages are no exception to this phenomenon.

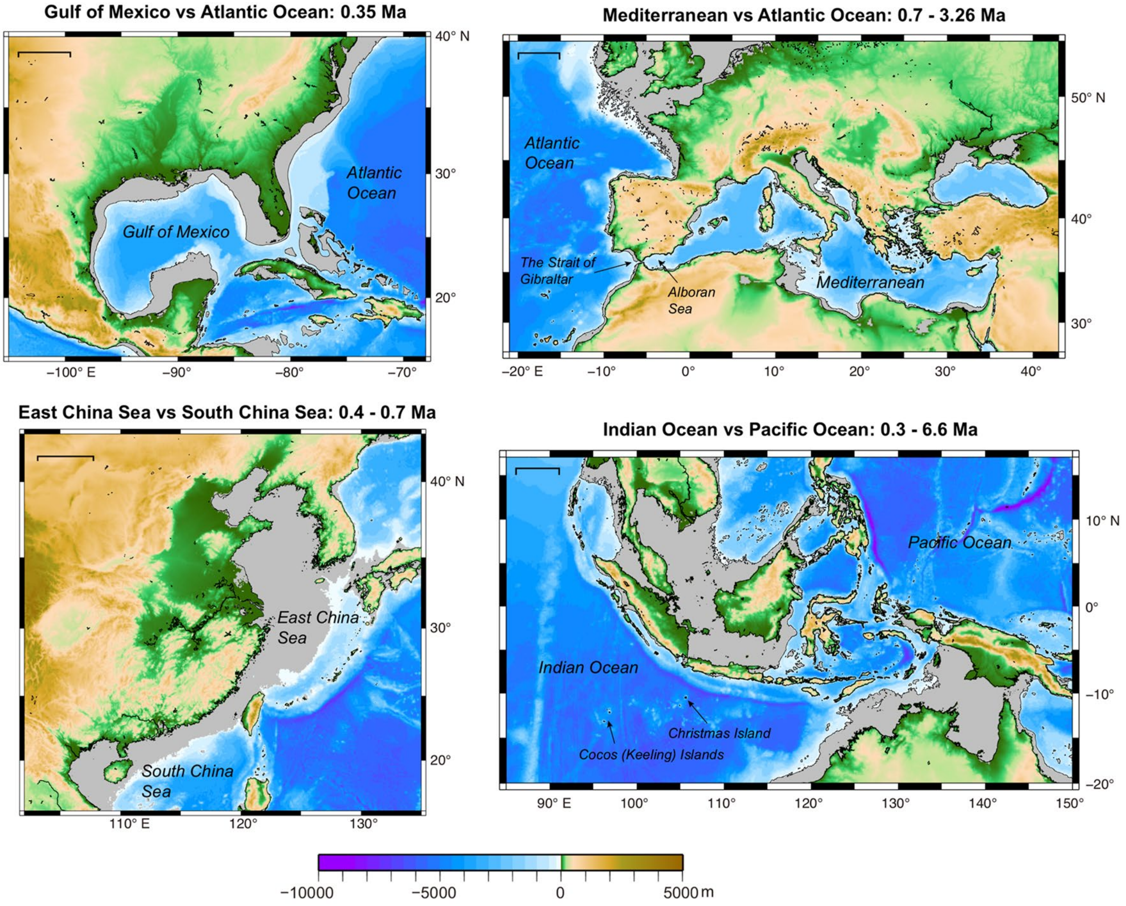
A comparison of the geographic locations of secondary contact zones may represent the continuous transition process of formation of the PO and SJ lineage distributions (Fig. 5). For *L. petersii*, the eastern secondary contact zone appears around the southern Joban-Kashimanada coast, whereas that of *C. annularis* is located on the Sanriku coast north of Joban-Kashimanada (Hirase and Ikeda 2015). Moreover, although secondary contact zones between lineages have not reported for the other three coastal gobies, *C. gulosus*, *Pterogobius elapoides*, considering the geographic distributions of the two lineages (Fig. 5), their secondary contact zones are expected to be formed in coastal areas around Joban-Kashimanada as those of *L. petersii*. Therefore, this means that only the SJ lineage of *C. annularis* has not expanded its distribution southward. Hirase and Ikeda (2015) hypothesized that the cold environments of the Sanriku coast, located in the cold Oyashio Current (Fig. 1), have restricted dispersion and lowered the abundance of the *C. annularis* population. Indeed, the cold Oyashio Current restricts the distribution of *P. zonoleucus*, which is believed to be less cold-tolerant (Akihito et al. 2008). Therefore, the southern expansion of the SJ lineages of *L. petersii* and the other two gobies (*C. gulosus and P. elapoides*) suggests that their dispersal abilities and/or cold tolerance are stronger than those of *C. annularis,* and they have colonized through the cold area. Enhanced expansion of the SJ lineage of *L. petersii* compared to that of *C. annularis* was also observed in western secondary contact zones in the Seto Inland Sea (Kokita and Nohara 2011; Hirase et al. 2020a; Kato et al. 2021), where the SJ lineage of *L. petersii* has been shown to be extend further eastward than that of *C. annularis* (Fig. 5). Given that the geographic isolation of SJ occurred due to the closing of the Tsugaru and Tsushima Straits (Fig. 1), both of western and eastern secondary contact zones of the two species in the PO side suggest unidirectional expansion of the SJ lineages and contraction of the PO lineages. This may indicate selective advantage of the SJ lineages and/or the contribution of ocean currents in these zones, including the dominant southward currents (Tsugaru Currents; Fig. 1) around the Sanriku coast and eastward currents around the Seto Inland Sea, which could promote expansion of the SJ lineages (Ishizu et al. 2017; Kurogi and Hasumi 2019). Intensive sampling is needed to determine the population genetic structures around these secondary contact zones.

Future perspectives: advantages of the Japanese Archipelago for evolutionary studies

Genetic divergences of coastal fishes caused by the decline in Pleistocene glacial sea levels have also been detected in other geographic regions, such as between the Gulf of Mexico (GM) and Atlantic Ocean (AO) (Soltis et al. 2006), Mediterranean Sea (MS) and AO (Patarnello et al. 2007), South China Sea (SCS) and East China Sea (ECS) (Ni et al. 2014), and Indian Ocean (IO) and PO (Gaither and Rocha 2013) (Fig. 6). I compare the genetic divergences with those between PO and SJ lineages, focusing on their divergence times, population demography, and hybridization, and discuss the advantages of SJ and PO lineages for evolutionary study.

The divergence times between GM and AO and between SCS and ECS were estimated to be in the middle Pleistocene (*Centropristis striata*, and the *Brevoortia tyrannus* and *Brevoortia patronus* pair: 0.35 Ma, Bowen and Avise 1990; *Coilia mystus* and *Chelon haematocheilus*: 0.4–0.7 Ma, Ni et al. 2014) (Fig. 6). Therefore, the genetic divergences detected in those regions were younger than those between the PO and SJ lineages (0.34–3.37 Ma; Fig. 2). Contrastingly, divergence times between the MS and AO lineages (0.7–3.26 Ma, Patarnello et al. 2007) and between the IO and PO lineages (0.3–6.6 Ma, Gaither and Rocha 2013) show a wide time range, including old divergence (Fig. 6). Therefore, the level of genetic divergence between these lineages is similar to that between the PO and SJ lineages. However, the nature of population demography and secondary contact zones of these pairs (MS and AO, and IO and PO) differs from that of the PO and SJ lineages. In the former two pairs, rapid population expansion was estimated for both lineages (Patarnello et al. 2007; Gaither and Rocha 2013). In addition, each of their hybrid zones was located in one contact region; hybridization between MS and AO lineages occurred in the Alboran Sea east of the Strait of Gibraltar that connects AO to MS (Lemaire et al. 2005), while that between IO and PO lineages was in the Christmas and Cocos (Keeling) Islands, where the IO and PO regional biotas meet (Hobbs et al. 2008) (Fig. 6). Thus, multiple divergence times, characterized by sharp contrasts of demographic histories, and two independent hybrid zones are unique characteristics of the divergence between the PO and SJ lineages.

The unique characteristics of the PO and SJ lineages can provide two major advantages for evolutionary studies. First, the PO and SJ lineages were under different environmental scenarios, as suggested by their demographic histories. Paleoenvironmental studies have demonstrated that SJ was nearly isolated from surrounding seas after the closing of the Tsushima Straits because of sea level falling during glacial



Gulf of Mexico vs Atlantic Ocean: 0.35 Ma

Mediterranean vs Atlantic Ocean: 0.7 - 3.26 Ma

East China Sea vs South China Sea: 0.4 - 0.7 Ma

Indian Ocean vs Pacific Ocean: 0.3 - 6.6 Ma

Fig. 6 Four geographic regions where genetic divergences of coastal fishes have been caused by sea-level fall during glaciation: Gulf of Mexico versus the Atlantic Ocean (Soltis et al. 2006), the Mediterranean Sea versus the Atlantic Ocean (Patarnello et al. 2007), the South China Sea versus the East China Sea (Ni et al. 2014), and the Indian Ocean and the Pacific Ocean (Gaither and Rocha 2013). Range of divergence times in each geographic region are also shown. Submarine topography around each geographic region is illustrated by GMT 4.0 (Wessel et al. 2013). Gray represented the land area when sea level dropped 125 m during the Last Glacial Maximum. Scale bar corresponds to 500 km

periods, which resulted in salinity and temperature decrease owing to freshwater inputs from rivers and the loss of the warm Tsushima Current, respectively (Oba et al. 1991; Tada 1994; Gorbarenko and Southon 2000). Therefore, the PO and SJ lineages of Japanese coastal species were subjected to vastly differing selection regimes, offering a useful model system for studies of adaptive divergence (Kokita et al. 2013; Hirase et al. 2020a). Indeed, for *Leucopsarion petersii*, it was suggested that past and present low seawater temperatures in SJ promoted the evolution of fast growth and large body sizes in SJ populations (Kokita et al. 2013). Additionally, divergence in female mate choice patterns owing to body size changes was detected in *L. petersii*, with the SJ lineage females preferring larger and same-lineage males, while the PO lineage females showed no preference (Kokita et al. 2017). However, ecological and phenotypic differences between the two lineages have not yet been evaluated for most of the coastal gobies having both lineages. Further studies on these perspectives will allow us to test the continuous process of genomic divergence during geographical isolation and their evolutionary consequences in the speciation continuum (Hendry 2009) owing to their wide spectrum of genetic divergences.

Second, there are two independent hybrid zones between the PO and SJ lineages (Hirase and Ikeda 2015; Hirase et al. 2020a; Kato et al. 2021). In general, the genomic features in independent hybrid zones vary (Nolte et al. 2009; Aboim et al. 2010), suggesting that the evolutionary outcomes of hybridization are influenced by various exogenous factors due to local environments. Genomic and phenotypic features in such multiple independent hybrid zones will provide key information about the evolutionary consequences of hybridization (Morgan-Richards and Wallis 2003; Mandeville et al. 2017). As the environments vary spatially with oceanographic conditions, hybridization impact may play a substantial role in shaping biodiversity in marine environments. However, genomic studies for hybridization on species inhabiting marine ecosystems are rare. In this regard, the two potential hybrid zones between the PO and SJ lineages, i.e., western and eastern coastal areas of the Japanese Archipelago, constitute unique systems to study the genomic features of independent hybrid zones. For example, Hirase et al. (2020a) performed integrated analyses of genotypic and phenotypic data for two independent hybrid populations of both lineages of *L. petersii*, revealing that these populations have different genotypic and phenotypic features. Moreover, phenotypic features were not explained by their nuclear genomic ancestry, suggesting that adaptive introgression of genes regulates the respective phenotypes, and they concluded that hybridization could lead to variable genomic and phenotypic consequences under different environmental conditions in marine ecosystems (Hirase et al. 2020a).

Two independent hybrid zones have also been found in *Chaenogobius annularis* (Hirase and Ikeda 2015; Kato et al. 2021). Hirase et al. (2020c) analyzed the genomic status of one hybrid zone formed on the Sanriku coast by comprehensive genome sequencing, including RNA-sequencing, RAD-sequencing, whole genome sequencing, whole mitogenome sequencing, amplicon-sequencing, and small RNA-sequencing. Although all hybrids in this population have the genomes of both groups at a ratio of approximately 50%, they also showed excess ancestry of either group in several genomic regions, suggesting mosaic features of hybrid genomes. In addition, they showed accumulation of nonsynonymous substitutions in the PO lineage mitogenomes, including two convergent substitutions as well as signals of mitochondrial lineage-specific selection on mitochondria-related nuclear genes. These substitutions were likely caused by mismatch combinations between mitogenomes and nuclear mitochondria-related genes, i.e., mitonuclear incompatibility (Hill 2019). These results suggest that novel genomic combinations formed by hybridization promoted novel mitogenome mutations. Moreover, Hirase et al. (2020c) suggested that the novel substitutions in the PO lineage mitogenomes may not only resolve the mitonuclear incompatibility with SJ-lineage nuclear genes but also aid in the local adaptation to the Sanriku coast, which is characterized by cold seawater temperature due to the Oyashio Current (Fig. 1). Whether environmental effects play a direct and general role in driving mitonuclear incompatibility in natural hybrid populations remains unclear and requires further investigation (Arnqvist et al. 2010; Zhang et al. 2017; Hill 2019), and two independent hybrid zones with different environmental settings could provide a unique system for pursuing this question.

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