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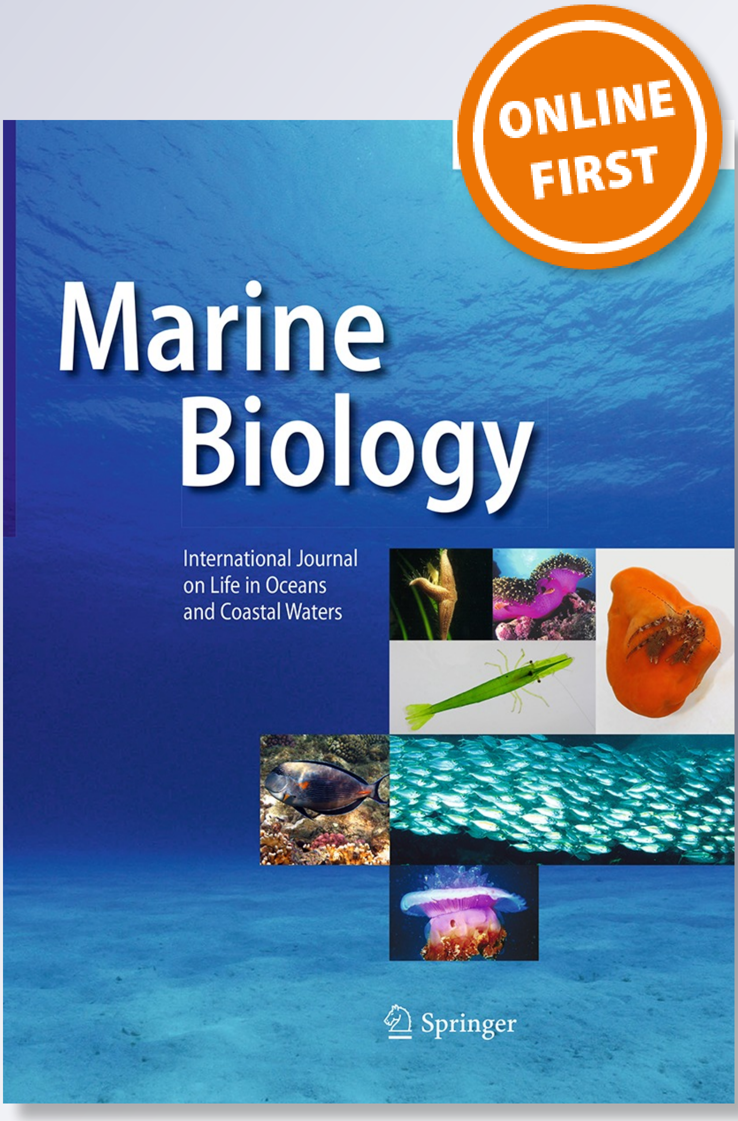

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ORIGINAL PAPER

Asymmetric genetic exchange in the brown seaweed *Sargassum fusiforme* (Phaeophyceae) driven by oceanic currents

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Abstract Geological phenomena (e.g. drastic sea level fluctuations during the Quaternary Ice Age in the Northern Hemisphere) have been demonstrated to intensively affect the biogeographic patterns and tempo-spatial compositions of genetic diversity of marine organisms. However, it is poorly understood whether contemporary factors such as oceanic surface currents have also shaped inter-regional population genetics of specific coastal marine flora, with or without limited dispersal capability. In this study, we determined mtDNA Cox1 gene sequences of the brown seaweed *Sargassum fusiforme* from nine populations along the Chinese coast and one population from the west coast of South Korea, in an effort to understand what factors are contributing to their current genetic structure and geographic distribution patterns. Genetic analyses indicated a deep genetic break between the Yellow-Bohai Sea (YBS) and the other two marginal seas, the East China Sea (ECS) and the South China Sea (SCS). In particular, the amount of genetic exchange from the SCS to each of the ECS and YBS was significantly higher than that from the opposite directions. Our analyses supports the hypothesis that biogeographic patterns of genetic variation in *S. fusiforme* are probably an interactive consequence of post-glacial colonization from two scattered refugia driven by the offshore Kuroshio Current and asymmetric gene flow among adjacent sea margins.

Introduction

The Asia Northwestern Pacific (ANP) is one of the marine systems most drastically influenced by historical climate change (e.g. the repeated glacial-interglacial cycles during the Quaternary ice ages in the Northern Hemisphere) (Voris 2000; Lambeck et al. 2002). In the past decade, molecular phylogeographic investigations have shown that sea level oscillations in the Pleistocene epoch played a crucial contribution to the extant population connectivity and biogeographic gradients of multiple marine organisms in the ANP (Rodriguez-Lanetty and Hoegh-Guldberg 2002; Kojima et al. 2006; Liu et al. 2008; He et al. 2010; Hu et al. 2011; Kokita and Nohara 2011). However, it is unknown to what extent contemporary factor like oceanic current also affects the tempo-spatial genetic structure in this area.

Geological evidence shows that the Kuroshio Current (KC) is a complex surface current system distributed in the ANP (Fig. 1). Originating from the North Pacific Equatorial Current, the KC is the dominant surface warm current in the ANP. It flows northeastward along the outer edge of the East China Sea (ECS) continental shelf and divides into three branches: the northwestward-running Yellow Sea Warm Current (YSWC), the northward-flowing Tsushima Current through the Tokara Strait, and the KC offshoot extending northeastward along the Japan-Pacific coast

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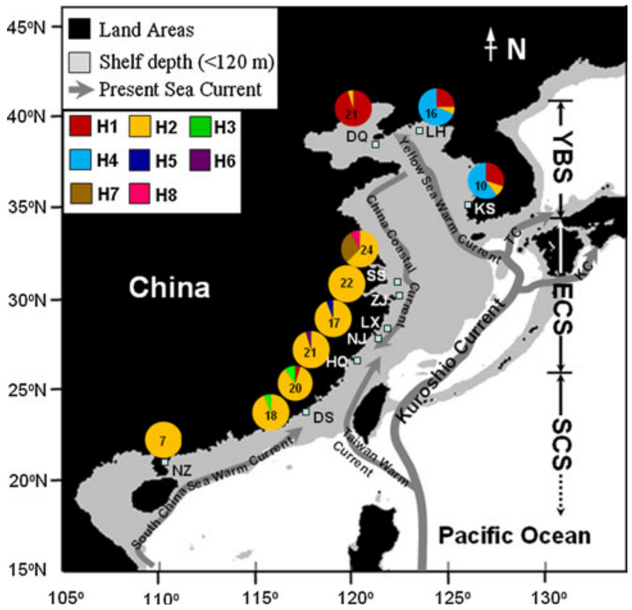


Fig. 1 Map showing the sampling locations, the established land-bridge during the LGM, and schematic oceanic currents. The yielded mtDNA Cox1 haplotypes and the proportion at each site were also depicted in different *colors*, and the numbers in each pie *chart* show population size

(Hu et al. 2000). Meanwhile, the China Coastal Current (CCC) flows southward to the Taiwan Strait and meets both the northeastward-running Taiwan Warm Current (TWC) and the South China Sea Warm Current (SCSWC) (Fig. 1). These multidirectional oceanic currents were shown to have a profound impact on marine environment and biodiversity richness in the ANP region (Tittensor et al. 2010), and hypothetically, such influences should be evident in the genetics and distribution of a given organism in this ecosystem.

Sargassum fusiforme (Harvey) Setchell is a large annual brown macroalgae endemically found in middle to lower rocky intertidal zones along the ANP coastlines. As edible seaweed, *S. fusiforme* has traditionally been utilized as food in China, Japan, and South Korea (Hwang et al. 1999). In recent years, the market demand for this seaweed has greatly increased due to its previously unknown nutritional, pharmaceutical, and industrial values (Zou et al. 2006). In the overseas market, *S. fusiforme* is one of the four most widely used edible seaweeds (along with *Porphyra*, *Laminaria* and *Undaria*) (FAO 2008), and most of them were exported to Japan from China and South Korea and consumed as a health food product. It was reported that in China, the total production of *S. fusiforme* reached 32,000 tons (FW) in 2007 (Pang et al. 2008). Nevertheless, the mariculture of this seaweed with current technology has not been viable, and the wild *S. fusiforme* populations in China have been severely devastated due to over-exploitation in the past decades (Zou et al. 2006). Meanwhile, anthropogenic activity has greatly contracted the range of *S. fusiforme* through habitat fragmentation and destruction. It is therefore essential to explore the current status of spatial genetic diversity and distribution patterns of *S. fusiforme* in China in order to take measures to protect this natural resource.

Molecular population genetic approaches have been used frequently to identify genetic drift (genetic diversity in populations losses and maintains small for several generations), gene flow, founder event (reduced genetic diversity as a result of limited contribution to the gene pool), population bottleneck (rapid fluctuation of population size over time), and demographic patterns (historical extinction or survival, and geographic expansion or contraction). Specifically, genetic investigations of population structure and spatial differentiation can provide important insights into interactive dynamic processes between marine organisms and environmental factors (Deng and Hazel 2010; Mach et al. 2011; Tulchinsky et al. 2012). Recent surveys revealed that low-to-moderate genetic variability existed among regional populations of a few *Sargassum* species (Cheang et al. 2008; Cheang et al. 2010; Hu et al. 2011), and this specific biogeographic architecture could correlate with vicariance events (Cheang et al. 2010), drastic climatic oscillations (e.g. ice age during the late Pleistocene) (Hu et al. 2011), and even contemporary oceanic circulations (Thiel and Haye 2006; Hu et al. 2011). These studies show that population genetics can be an insightful platform for better understanding demographic history and evolutionary process of seaweed species.

In this study, we used partial mitochondrial cytochrome c oxidase subunit-I (mtDNA Cox1) gene sequences with the goal to explore the distribution pattern of intraspecific genetic variation in *S. fusiforme* along the China coastline. Our main objectives are as follows: (1) to evaluate the population structure and genetic connectivity of *S. fusiforme* along the Chinese Northwest Pacific; (2) to examine whether tempo-spatial genetic patterns (direction and amount) exhibited by *S. fusiforme* at a regional scale are driven by present-day oceanic circulations.

Materials and methods

Sampling and sequence collection

One hundred and seventy-six specimens of *S. fusiforme* were sampled from ten localities (39°03′N–20°51′N) (Fig. 1; Table 1). To facilitate subsequent genetic analysis, these ten populations were partitioned into three groups according to their natural geographic boundaries (marginal seas): Yellow-Bohai Sea (YBS) (KS + LH + DQ), SCS (DS + NZ) and ECS (the rest). More details on population grouping can be found in Fig. 1. At each locality, multiple individuals (7–24)

Table 1 Population diversity measurements for *Sargassum fusiforme*

Sampling location	Coordinates	N	h	S	H_d	π	AR	C_T^r	Tajima's D	Fu's F_S	θ ($\times 10^{-3}$)
Sinan, South Korea (KS)	34°51′N, 125°59′E	10	3	2	0.6000	0.0170	0.600	0.103	1.3372^{ns}	0.4770^{ns}	0.334
Haiyang Island, Dalian (LH)	39°03′N, 123°07′E	16	3	2	0.4917	0.1073	0.492	0.282	1.0855^{ns}	0.6676^{ns}	0.294
Daqing Island, Yantai (DQ)	38°16′N, 120°51′E	21	2	1	0.1000	0.0125	0.100	0.301	-1.1644^{ns}	-0.8793^{ns}	0.179
Shengsi Island, Zhoushan (SS)	30°38′N, 122°28′E	24	3	3	0.5671	0.1483	0.567	0.120	1.1415^{ns}	1.7494^{ns}	0.586
Zhujiajian, Zhoushan (ZJ)	29°54′N, 122°26′E	22	1	0	0.0000	0.0000	0.000	0.011	0.0000^{ns}	n/a	0.230
Luxi Island, Wenzhou (LX)	27°59′N, 121°10′E	17	2	1	0.1333	0.0167	0.133	0.002	-1.1595^{ns}	-0.6490^{ns}	0.577
Nanji Island, Wenzhou (NJ)	27°30′N, 121°05′E	21	2	1	0.1000	0.0125	0.100	0.037	-1.1644^{ns}	-0.8793^{ns}	0.540
Huangqi Island, Fuzhou (HQ)	26°19′N, 119°48′E	20	3	2	0.3072	0.0400	0.307	0.038	-1.0963^{ns}	-1.0961^{*}	0.591
Dongshan Island, Zhangzhou (DS)	23°41′N, 117°29′E	18	2	1	0.1333	0.0167	0.133	0.002	-1.1595^{ns}	-0.6490^{ns}	0.354
Naozhou Island, Guangdong (NZ)	20°51′N, 110°34′E	7	1	0	0.0000	0.0000	0.000	−0.016	0.0000^{ns}	n/a	
Yellow-Bohai Sea (YBS)	34°51′N, 39°03′N	47	3	2	0.5517	0.0017	1.618	0.388	2.0958^{ns}	1.9555^{ns}	0.326
East China Sea (ECS)	27°30′N, 30°38′N	104	5	5	0.2593	0.0008	1.942	0.254	-1.5234^{*}	-4.0152^{*}	2.112
South China Sea (SCS)	20°51′N, 26°19′N	25	3	2	0.1111	0.0002	1.027	0.036	-1.1647^{ns}	-0.7943^{*}	0.344
Total	39°03′N, 26°19′N	176	8	8	0.5550	0.0016	n/a	n/a	-1.0289^{ns}	-2.5710^{*}	

Population size (N), number of haplotypes (h), number of segregating sites (S), haplotype diversity (H_d), nucleotide diversity (π), allelic richness (*AR*), contribution of each population to the total allelic richness (C_T^r), and effective population size (θ). * $P < 0.05$; *ns* not significant, *n/a* not available

were collected over 10 m of intervals along a parallel transect line. For each individual, 3–4 cm length of apical thallus was excised. Genomic DNA was isolated either following the modified CTAB-SDS (cetyltrimethylammonium bromide-sodium dodecyl sulfate) method developed by Hu et al. (2004) or using the Plant Genomic DNA Extraction Kit (Tiangen Biotech. Co. Ltd., Beijing). The mtDNA Cox1 region was amplified using the primers BRCOX1F (5′-GTGCTCCAGATATGGCGTTCC-3′) and BRCOX1R (5′-AATCATCGTAGCCGCAGTAA-3′) described by Kogame et al. (2005). PCR products were cleaned with a TIANgel Midi Purification Kit (Tiangen Biotech. Co. Ltd., Beijing) and commercially sequenced on an ABI Prism 3700 (Applied Biosystems, Foster City, USA) automatic sequencer with both forward and reverse primers. All mtDNA Cox1 sequences have been deposited in GenBank under accession numbers JX999783-JX999790.

Molecular diversity and population genetic dynamics

Sequences were aligned and manually edited using DNASTAR (DNASTAR Inc., Madison, USA). Genetic diversity measurements including number of haplotypes, haplotype and gene diversity, and number of segregating sites were calculated with ARLEQUIN 3.1 (Excoffier et al. 2005). Because unequal numbers of specimens sampled for each population in this study, allelic richness (AR) and the contribution of each population to total diversity (C_T^r) were measured after rarefaction using CONTRIB 1.02 (Petit et al. 1998). Other genetic parameters such as neutrality tests (Tajima's D and Fu's F_S) (Tajima 1989) and raggedness index (RI) (Harpending 1994) were also calculated using ARLEQUIN.

A hierarchical molecular variance analysis (AMOVA) and the conventional population F_{ST} comparisons were conducted in ARLEQUIN to assess the population configuration and the geographical pattern of population subdivision within *S. fusiforme*, and the significance of covariance components associated with the different possible levels of genetic structure was tested using 10,000 permutations. To examine the potential isolation by distance (IBD) (Slatkin 1993), pairwise values of genetic differentiation were plotted against geographical distance (one-dimensional stepping-stone model) among sampling localities. The strength and significance of IBD analysis was evaluated with reduced major axis (RMA) regression and Mantel tests using IBDWS (http://ibdws.sdsu.edu/~ibdws/) (Jensen et al. 2005).

Spatial genetic dynamics of *S. fusiforme* were further surveyed at both population and group levels using LAMARC 2.2 (Kuhner 2006), which examines the effective population size (θ) and directional migration rates between pairwise comparisons under a search strategy of Bayesian Metropolis–Hastings Markov chain Monte Carlo. Most populations comprise about 20 individuals (Table 1), which means that LAMARC is more suitable for Cox1 data in this study, because it is a coalescent-based program and can perform best when sample sizes are low (Felsenstein 2006). The F_{84} model (Felsenstein 1984) of nucleotide substitution was selected by jModeltest 0.1 (Posada 2008). In LAMARC, the transition/transversion ratio (ti/tv) was set to 3.0, inferred from MEGA 5.0 (Tamura et al. 2011) and set to determine empirical base frequencies as well. For both analyses at population and group level, each started with three 500-sample initial chains and then one 50,000-sample final chain with a sampling interval of 250 steps and a burn-in of 5,000 steps. This final chain was divided into three sub-chains with different heating temperatures (1.0, 1.2 and 1.8) to search the parameter space more thoroughly (Russell et al. 2008). For the other settings, default values were implemented. All analyses were repeated three times with a different random seed to check the consistency of results, and finally, the mean values were reported. TRACER 1.4 (Drummond et al. 2005) was used to assess whether the program had run for sufficiently long, as indicated by effective sample size no less than 200, and trend lines with stable likelihood values (Teske et al. 2008).

Results

MtDNA Cox1 segment with 581 base pairs was obtained for 176 specimens of *S. fusiforme* from ten geographic populations. In total, eight polymorphic sites were found, yielding eight haplotypes, five of which (62.5 %) occurred as singletons (found only in a single population); the remaining three haplotypes were shared by more than one population (Table S1). Of the eight haplotypes, the most abundant (H2) was shared by 117 specimens from all ten populations (Table S1 and Fig. 2). Intra-population diversity measurements showed haplotype diversity (H_d) ranging from 0.6000 in Sinan, South Korea to 0.000 in both Zhujiajian, Zhoushan and Naozhou Island, Guangdong (Table 1). Nucleotide diversity (π) and allelic richness (AR) exhibited the same variation trend as H_d; however, the geographic population from Daqing Island, Yantai, made the highest contribution to the total AR (Table 1). In addition, LAMARC statistics indicated the samples from Huangqi Island, Fuzhou, had the maximum effective population size (θ), whereas that from Daqing Island harbored the minimum. Of the three systems, the YBS showed the highest indices of genetic diversity except the θ parameter (Table 1).

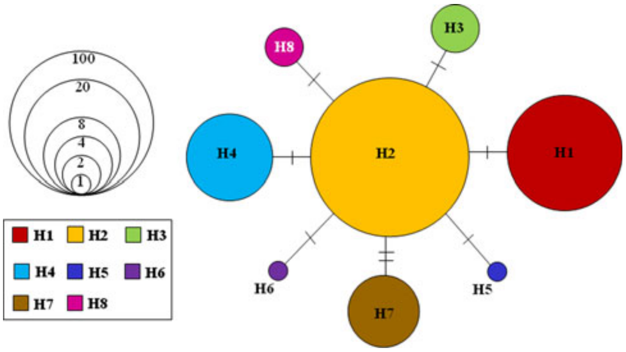


Fig. 2 The median-joining network of mtDNA Cox1 with the size of the circle corresponding to the proportion of each haplotype

Asymmetric genetic differentiations were observed in *S. fusiforme* (pairwise F_{st} tests in Table 2). Compared to other populations from ECS and SCS, the populations (DQ) from YBS exceptionally showed the highest and most statistically significant genetic divergence, with F_{st} estimates ranging from 0.6442 to 0.9487, whereas other populations (LH and KS) also from YBS exhibited moderate genetic differentiation (F_{st} varying from 0.2500 to 0.5833). The AMOVA analysis detected significant population subdivision using natural geographic boundaries (Φct $= 0.2711$, $P < 0.05$), and significant genetic differentiation was also revealed both, within populations (Φst $= 0.5644$, $P < 0.001$) and among populations within regions (Φsc $= 0.4023$, $P < 0.001$), respectively (Table 3). IBD analysis showed a positive correlation ($r = 0.4175$) between the geographic distance and corresponding genetic distance, indicating that migration and drift were in equilibrium in *S. fusiforme* (Fig. S1), but this finding was statistically non-significant ($P = 0.9580$).

Estimates of spatial genetic dynamics such as θ and migration among geographic regions (YBS, ECS, and SCS) were converged with multiple runs. A unimodal posterior distribution with narrow peak was recovered for each of the three groups, but the θ mode of ECS was approximately 7 times the value of YBS and SCS, respectively (Table 1 and Fig. S2). Under the LAMARC model, the examination of mtDNA Cox1 indicated significant amount of genetic migration in both directions among adjoining areas (Fig. 3). The posterior distribution of the migration parameters was very close in each direction between YBS and SCS (513.63 vs. 557.35); however, the migration from SCS to each of YBS (746.04) and ECS (887.50) was nearly 1.5 times greater than that from the opposite direction, respectively (Fig. 3). In general, the genetic migration from south to north was notably larger than that from north to south.

Table 2 Pairwise F_{ST} estimates (*below* diagonal) and matrix of geographical distance (km) (*above* diagonal) among *Sargassum fusiforme* populations

	KS	LH	DQ	SS	ZJ	LX	NJ	HQ	DS	NZ
YBS										
KS	–	597	607	577	671	916	951	1,151	1,532	2,319
LH	-0.0753^{ns}	–	243	1,440	1,534	1,779	1,814	2,014	2,395	3,182
DQ	0.6593**	0.6834**	–	1,197	1,291	1,536	1,571	1,771	2,152	2,939
ECS										
SS	0.3860**	0.4391**	0.6442**	–	94	339	374	574	955	1,742
ZJ	0.5792**	0.5833**	0.9487**	0.3412**	–	245	280	480	861	1,648
LX	0.4677**	0.4992**	0.8875**	0.2847**	0.0232^{ns}	–	35	235	616	1,403
NJ	0.5209**	0.5415**	0.9000**	0.3189**	0.0025^{ns}	0.0025^{ns}	–	200	581	1,368
HQ	0.4118**	0.4607**	0.7971**	0.2848**	0.0506^{ns}	0.0226^{ns}	0.0339^{ns}	–	381	1,168
SCS										
DS	0.4677**	0.4992**	0.8875**	0.2847**	0.0233^{ns}	-0.0000^{ns}	0.0025^{ns}	-0.0413^{ns}	–	787
NZ	0.2500^{ns}	0.3372^{ns}	0.9073*	0.1129^{ns}	0.0000^{ns}	-0.1932^{ns}	-0.1962^{ns}	-0.1636^{ns}	-0.1932^{ns}	–

The geographical origin of each population was also indicated.* $P < 0.05$; ** $P < 0.001$; *ns* not significant

Table 3 Results of hierarchical AMOVA analysis with genetic variation accounted for different levels

Source of variation	df	SSD	Variance	% Variation	Fixation indices
Among regions	2	15.367	0.1240	27.11	Φct = 0.2711*
Among populations within regions	7	16.283	0.1341	29.32	Φsc = 0.4023**
Within populations	150	29.881	0.1992	43.56	Φst = 0.5644**
Total	159	61.531	0.4573		

Significance was tested against a null distribution of 10,000 random permutations. * $P < 0.05$; ** $P < 0.001$

Discussion

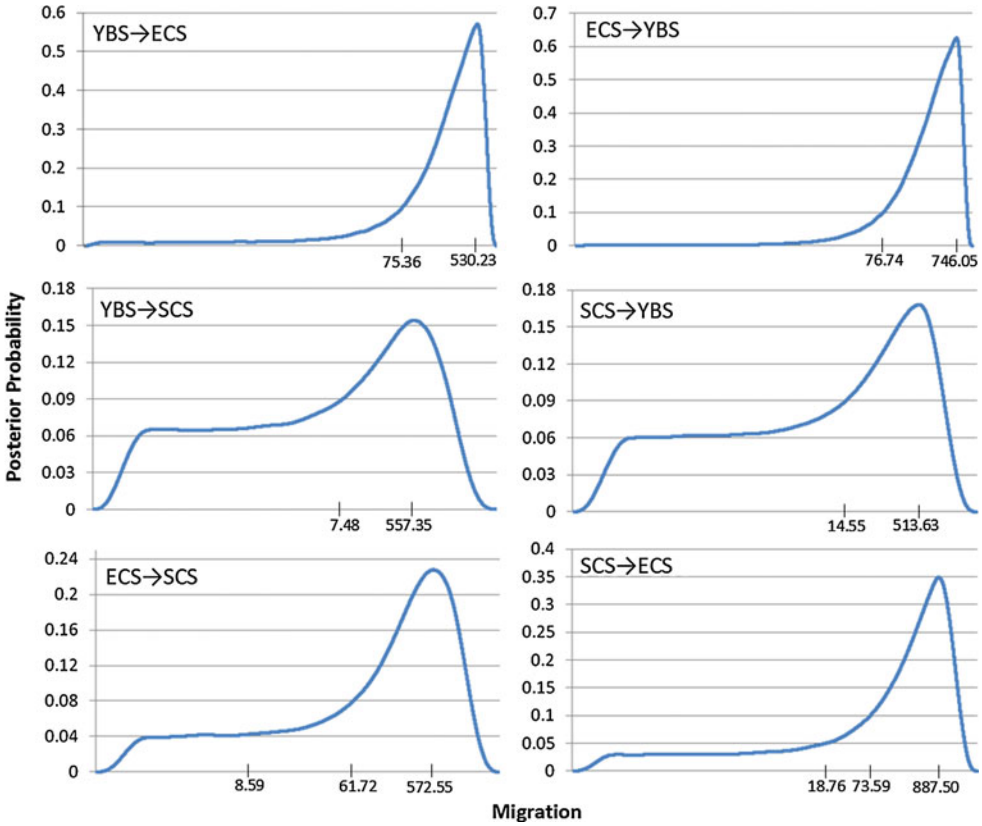
In this paper, although geographically the mtDNA Cox1 haplotype network showed no genealogical structure (Fig. 2), both F_{st} and AMOVA statistics (Tables 2 and 3) indicated *S. fusiforme* populations in the YBS were significantly divergent from other marginal seas (ECS and SCS) in which the samples exhibited high genetic connectivity. The coexistence of genetic heterogeneity and homogeneity may stem from the interactive influence of oceanic currents in the ANP.

Population genetic differentiation of marine macroalgae: homogeneity versus heterogeneity

Tempo-spatial genetic architecture in the sea can be affected by various biotic and abiotic factors (Thiel and Haye 2006). However, with an absence of obvious physical barriers to gene flow among separate ocean basins, marine organisms with high dispersal potential are generally expected to show genetic homogeneity (Vermeij 1987; Palumbi 1994). Such a scenario might imply that other species without or with weak dispersal capability in their life cycles will exhibit high levels of genetic variation over a geographical scale. This profile has been discovered in some marine algae. For instance, a geological border in the southern Kattegat leads to geographic genetic variation in *Cladophora rupestris* between the North Sea and the Baltic Sea (Johansson et al. 2003); *Gelidium canariense* in the Canary Islands exhibits a IBD signature (Bouza et al. 2006); and even the planktonic diatom *Pseudo-nitzchia pungens,* which despite its cosmopolitan distribution, shows strong IBD and limited gene flow between marine regions (Casteleyn et al. 2010). In distinct contrast, recent genetic surveys on brown macroalgae exemplified significant genetic consistency over long stretches of sea margins in the ANP [*S. hemiphyllum* (Cheang et al. 2010); *S. horneri* (Hu et al. 2011), *Ishige okamurae* (Lee et al. 2012)]. Such genetic heterogeneity at a different marine-basin scale was likely due to long-term glacial persistence after the Pleistocene ice age (Hewitt 2004).

We found herein *S. fusiforme* exhibiting a similar biogeographic pattern as the North Atlantic brown seaweed *Ascophyllum nodosum*, probably because of the existence of a few scattered cryptic refugia in the North (Olsen et al. 2010). Empirically, we can tentatively assume that *S. fusiforme* survived in two separated glacial refugia, southwestern Taiwan and Ryukyu Island, when taking into

Fig. 3 Posterior probability densities for migration rates among three marginal seas (YBS, ECS, and SCS), and the result for each pair was converged from three independent replications



account the following two references: (1) Cheang et al. (2009) revealed two geographically isolated lineages in *S. fusiforme* sharing a common ancestor along the ANP coastlines, with southwestern Japan as the boundary; (2) the present-day southernmost distribution in Leizhou Peninsula (adjoining to population NZ in Fig. 1) (Tseng 1984), the glaciation-induced temperatures drop and fluctuations of historic coastline during the last glacial maximum (Fig. 1). This hypothesis has also been derived from other organisms, such as land plant *Castanopsis carlesii* (Cheng et al. 2005) and marine crab *Scylla paramamosain* (He et al. 2010), as well as seaweeds *S. horneri* (Hu et al. 2011) and *I. okamurae* (Lee et al. 2012; Hu and Duan 2013). In this hypothetical scenario, the sea level drop during the last glacial maximum led to the narrowing of the ECS to the Okinawa Trough, and the continental shelf of both YBS and SCS was also greatly reduced (Wang 1990). As a consequence, the populations of *S. fusiforme* in the three marginal seas would have been eradicated, and only a few populations in southwestern Taiwan and Ryukyu Islands could have survived in the ANP. Since the climate changed into the present interglacial period, the Yellow Sea Warm Current, the northwestern extension of the Kuroshio Current (Fig. 1), brings large amounts of warm and saline waters into the YBS and generates variable biodiversity with higher heterogeneity (Barkley 1970; Tittensor et al. 2010). Concerning the genetic connectivity among populations between the ECS and SCS marginal seas, we hypothesize coastal surface currents might play a fundamental role contributing to this kind of connectivity (see discussion below).

Asymmetric genetic exchange in *S. fusiforme* driven by oceanic currents

Sargassum species usually have small gas-filled bladders, which keep the fronds afloat in the sub-littoral zone of the ANP. From winter to spring, the mature *Sargassum* can be detached from the benthic substratum due to grazer activity, or the action of combined wave and current, consequently forming floating mats that can drift for 1–5 months (Yoshida 1963; Komatsu et al. 2008). *S. fusiforme* is one of the moving algal masses around Southern Japan (Ohno 1984) and serves as a moving ecosystem containing other shielded planktons (Komatsu et al. 2008), which can be exported to surrounding areas or regions via the sea surface driven by sea currents. A similar dynamic pattern has also been observed in *S. horneri* in the ANP, which, when detached from the coast in the ECS in spring, could be transported to the edge of the waters influenced by the Kuroshio Current (Komatsu et al. 2008).

Because the Kuroshio Current mainly remains offshore, other coast currents along the SCS and ECS margins, namely the South China Sea Warm Current, China Coastal

Current, and Taiwan Warm Current, probably played a more predominant role in shaping the genetic homogeneity among populations of *S. fusiforme* in this basin. This hypothesis can also be reflected by the geographic distribution of the most extensively shared haplotype (H2) in the ECS and SCS (Fig. 1). Indeed, oceanographic literature shows the South China Sea Warm Current, which flows northward from the SCS, merges with the Taiwan Warm Current in the Taiwan Strait, and brings vast amounts of warm water; it then mixes with the cold water from the China Coastal Current which flows southward (with the northeastern monsoon) from the YBS and ECS (Hu et al. 2000). The influence of combined northward running currents (South China Sea Warm Current and Taiwan Warm Current) on population genetic connectivity of *S. fusiforme* is presumably stronger than the solely southward flowing CCC. This proposition can also explain why the genetic migration from the SCS to each of the YBS and ECS was nearly two times that in the opposite direction (Fig. 3).

In conclusion, molecular data from this paper revealed significant population genetic heterogeneity in the YBS toward other sea margins and that asymmetric genetic exchange occurred between *S. fusiforme* populations from the ECS and SCS areas. Such geographically contrasting genetic architecture may have been shaped by the dominant offshore Kuroshio Current and other coastal surface currents in the ANP.

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