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Inconsistency between morphological diversity and genetic structuring: proposal for one species of *Undaria* in Japan

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Abstract: Genetic structure analyses have yielded some examples of inconsistencies between genetic and morphological information. Here, eleven nuclear microsatellite markers and mitochondrial haplotypes were used to examine the genetic structure and gene flow among Japanese *Undaria pinnatifida* populations and the congeneric species *U. undarioides* and *U. peterseniana*. *Undaria pinnatifida* was subdivided into four "Groups" of populations based on Bayesian clustering analysis, Neighbor-net analysis and Principal coordinate analysis (PCoA). *Undaria undarioides* samples formed a unique Group. In contrast, *U. peterseniana* samples either grouped with a mixture of *U. pinnatifida* and *U. undarioides* clusters or were included within one of the *U. pinnatifida* clusters. More significantly, Groups of populations shared alleles with geographically adjacent Groups even between different morphospecies. No clear differences between the inter-and intra-specific genetic divergence were observed in either nuclear or mitochondrial markers. As a result, *U. undarioides* and *U. peterseniana* were synonymized with *U. pinnatifida*. Isolation-by-distance suggested the significance of geographical isolation for maintaining the observed divergence.

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1 Introduction

Many species, both terrestrial and marine, are genetically heterogeneous across their range; single species frequently show subdivision into several groups of populations according to geographical proximity, i.e., a population structure (Rousset 1997). The amount of gene flow between populations determines the strength of structuring among conspecific populations (Bohonak 1999), and in the case of marine species the amount of gene flow can be determined by the duration of planktonic larvae (Weersing and Toonen 2009), the long dispersal ability of adults (Collins et al. 2010; Grant 2016), and the oceanographic traits in different regions (Alberto et al. 2011; Billot et al. 2003; Kojima et al. 1997). In addition, genetic structural analyses have revealed incongruence between morphology and genetic relationships, e.g., morphologically indistinguishable cryptic species and small amounts of gene flow between morphologically distinct species (Akita et al. 2021; Harrison and Larson 2014; Petit and Excoffier 2009; Zardi et al. 2011). In a few studies, the presence of shared alleles (or haplotypes) between morphological species was reported, which, together with known morphological plasticity, resulted in taxonomic revision of well-known macroalgal groups, such as *Macrocystis* (Demes et al. 2009; Macaya and Zuccarello 2010) and *Ecklonia* (Akita et al. 2020).

Clear genetic structures have been reported in macroalgae (Akita et al. 2020; Hu et al. 2016; Zhong et al. 2020), including *Undaria* spp. (Uwai et al. 2006a, b, 2007). *Undaria* is a genus originally endemic in East Asia. Members of the genus, like other laminarian species, have a heteromorphic life cycle that includes macroscopic sporophytes up to 3 m in height and microscopic dioecious filamentous gametophytes. *Undaria pinnatifida* (Harvery) Suringar, the generitype and the most common species, is well known as a

food in its native range and is notorious as an invasive species throughout the world (e.g., Castric-Fey et al. 1999; Dellatorre et al. 2014; Hay 1990). Along the Japanese coast, three species, *U. pinnatifida*, *U. undarioides* (Yendo) Okamura, and *U. peterseniana* (Kjellman) Okamura, have been recognized and distinguished by the presence or absence of a midrib and incisions on the blade (Okamura 1915). These species have allo-or parapatric distributions; *U. pinnatifida* can be found widely in the lower intertidal zone in most of Japan, from Kyushu to Hokkaido, whereas *U. undarioides* is restricted to warmer coasts that are strongly affected by the Kuroshio warm current, where *U. pinnatifida* cannot be found; *U. peterseniana* is also widely distributed along Honshu; however, the details of its distribution are somewhat unclear due to its habitat preference for deeper water compared to the other two species (Okamura 1915; Yendo 1903).

The genetic diversity of the three *Undaria* species found along the Japanese coast was investigated using mitochondrial markers (Muraoka and Saito 2005; Shan et al. 2022; Uwai et al. 2006a, b, 2007; Voisin et al. 2005). Uwai et al. (2006b) found clear genetic structure across its native range; the group dominant in continental Asia, plus three geographical and genetic groups, i.e., northern Japan, Central Honshu and western Japan (Uwai et al. 2006b). More significantly, a low variation among the three species was reported, and all three species were shown to be polyphyletic, with a few haplotypes shared between species (i.e., between *U. pinnatifida* and *U. undarioides*, and between *U. pinnatifida* and *U. peterseniana*) (Uwai et al. 2007). Due to the low sequence divergence and the possibility of incomplete lineage sorting, it is hard to evaluate the polyphyly observed. Similarly, the potential for gene flow between "species" suggested by shared haplotypes necessitates measurement using nuclear markers.

Microsatellite (SSR) markers have been used to analyze the genetic structures of numerous species. Their polymorphic and codominant natures are suitable for detecting detailed genetic structures and gene flow between populations. In *U. pinnatifida*, several SSR markers have been developed (Daguin et al. 2005; Shan et al. 2018) and utilized in order to analyze genetic diversity among cultivated strains and gene flow between cultivated and adjacent wild populations (Shan et al. 2018). In the present study, our primary objective was to analyze the genetic structures of *Undaria* species based on SSR markers in comparison to the previously reported genetic structures based on mitochondrial markers. As a secondary goal, we sought to estimate the genetic divergence between "species" and potential isolation-by-distance. Finally, we examined whether the genetic structure and clustering reflected the morphospecies found in Japan.

2 Materials and methods

The samples used in this study were collected in Japan between 2001 and 2010. Genomic DNAs used by Uwai et al. (2006a, b, 2007) as well as those collected from 10 additional sites were included in the analyses. Species were morphologically identified in the field. Sampling and DNA extractions were performed as described in Uwai et al. (2006b). DNA sequences of the mitochondrial *cox*3 and tRNA region (tTrp-tGln) were determined as described in Uwai et al. (2006b). A maximum likelihood (ML) tree was reconstructed using PhyML v3.0 (Guindon et al. 2010; http://www.atgc-montpellier.fr/phyml/) with HKY85+G model selected by SMS v2.0 (Lefort et al. 2017) implemented in the PhyML. The statistical support for each clade was estimated by standard bootstrap analysis (1000 replicates). TCS 1.21 was used to determine the phylogenetic network between haplotypes under the 95% confidence limit (Clement et al. 2000).

Eleven SSR markers (Supplementary Table S2) were selected from those developed by Daguin et al. (2005) and Shan et al. (2018) based on stability in amplifications. Using a Type-it PCR kit (Qiagen, Germany), three or four markers were simultaneously amplified. The reactions were performed in a 12-μL volume containing 1.8 μL genomic DNA solution, 1 x reaction buffer, 10% Q-solution and 0.2 μM of each primer; however, modifications were made in order to obtain fluorescent signals of comparable intensity between markers. The combinations of SSR loci and PCR conditions for each primer set are listed in Supplementary Table S2. GeneScan analyses using the ABI 3130 genetic analyzer were carried out commercially (Fasmac, Kanagawa, Japan). For some samples, PCRs were performed separately for each locus and then combined to examine the stability of the resulting genotypes. The size of PCR fragments and genotypes of each individual were determined manually using Peak Scanner v. 1.0 (Applied BioSystems).

Indices of genetic diversity, such as the effective number of alleles (N_E), observed (H_O) and expected (H_E) heterozygosity and inbreeding coefficient (F) were analyzed using GenAlEx 6.51b2 (Peakall and Smouse 2012). Genetic divergences, such as F_{ST} and Jost's D_{EST}, of which the latter has been considered suitable for hyperpolymorphic markers such as SSR, were calculated for pairs of populations using GenAlEx. In addition, Nei's genetic distance between populations was estimated in order to conduct Principal coordinate analysis (PCoA) with GenAlEx. Relationships between populations were also analyzed by Neighbor-net analysis implemented in Splitstree v.4.17.1 (Huson and Bryant 2006) based on Nei's genetic distance.

Genetic structures along Japanese coasts were estimated by Bayesian clustering analysis using STRUCTURE v. 2.3.3 (Pritchard et al. 2000). Analyses were conducted using an admixture model with a 100,000 burn-in and 500,000 replicates of *Markov Chain Monte Carlo* (MCMC) after the burn-in, for numbers of clusters (K) = 1–15, with 10 replicates for each K. Using the delta K method (Evanno et al. 2005) and STRUCTURE HARVESTER (Earl and von Holdt 2012; http://taylor0.biology.ucla.edu/structureHarvester/), the most plausible number of K was estimated.

Based on STRUCTURE analysis that assigns each individual, as well as PCoA and Neighbor-net analysis based on interpopulation genetic distances, five "Groups" of populations were recognized along Japanese coasts (Supplementary Table S1). The allele frequency per Group and genetic divergence (Jost's D_{EST}) between Groups were calculated using GenAlEx. Gene flow based on the private allele method (Slatkin 1995) was estimated using Genepop on the web (Raymond and Rousset 1995; Rousset 2008; https://genepop.curtin.edu.au/).

Isolation-by-distance (IBD) was analyzed using Genepop on the web. IBD was only analyzed for the populations along the Pacific coast; the populations along the coasts of the Sea of Japan and the Seto Inland Sea were excluded to simplify the estimation of geographical distances and to remove negative effects on gene flow other than geographical distance as a result of the complexity of the coastlines. Following Rousset (1997) and de Meeûs et al. (2007), the linearized genetic distance $D_{EST}/(1-D_{EST})$ and geographical distance without logarithmic transformation were used. The approximate geographical distances between populations were computed along the coast using Google Maps. The Pearson's correlation coefficients (R) between genetic and geographical distances, and their statistical significance were analyzed based on Mantel tests implemented in the R package Vegan 2.6–2 (Oksanen et al. 2022). The strength of correlation was assessed based on conventional interpretation (e.g., Mukaka 2012) of the correlation coefficient.

3 Results

3.1 Genetic diversity and structure among Japanese *Undaria* samples

Forty-two mitochondrial haplotypes were detected based on a 908-bp mitochondrial DNA sequence in alignment among Japanese *Undaria* samples used in this study. Although only a few clades in the ML tree were well supported (>80%, Supplementary Figure S1), clades and clusters of mitochondrial haplotypes observed in the ML tree and network (Supplementary Figure S2) showed limited geographical distributions. Based on the mitochondrial haplotypes, no *Undaria* species displayed monophyly (Supplementary Figures S1 and S2).

The diversity metrics, i.e., N_E, H_O, H_E and F, for each population are given in Supplementary Table S1. Based on nuclear SSR, STRUCTURE analysis and subsequent evaluation of K-values indicated that samples were grouped in five genetic clusters (K = 5, Figure 2 and Supplementary Figure S3). The five clusters roughly corresponded to each individual's geographical origin (Figures 1 and 2): (1) *U. undarioides* (pop. 1–8); (2) *U. pinnatifida* along the Northern Japan (pop. 9–16), and Sea of Japan coasts (pop. 34–36); (3) *U. pinnatifida* in south-central Pacific Honshu (pop. 17–25); (4) *U. pinnatifida* on the coast of Kii Peninsula (pop. 26–28); and (5) *U. pinnatifida* along the East China Sea (western) coast of Kyushu (pop. 37–41) and *U. peterseniana* from the East China Sea and the Sea of Japan coasts (pop. 43, 45, 46). *Undaria pinnatifida* populations in the Seto Inland Sea (pop. 29–31) and *U. peterseniana* populations at Shimoda, Central Honshu (pop. 44) exhibited admixture of the genetic clusters. Some populations (e.g., pop. 2, 8, 16, 17, 28 and 45) also exhibited an admixture, as some individuals exhibited high assignment probabilities to two genetic clusters.

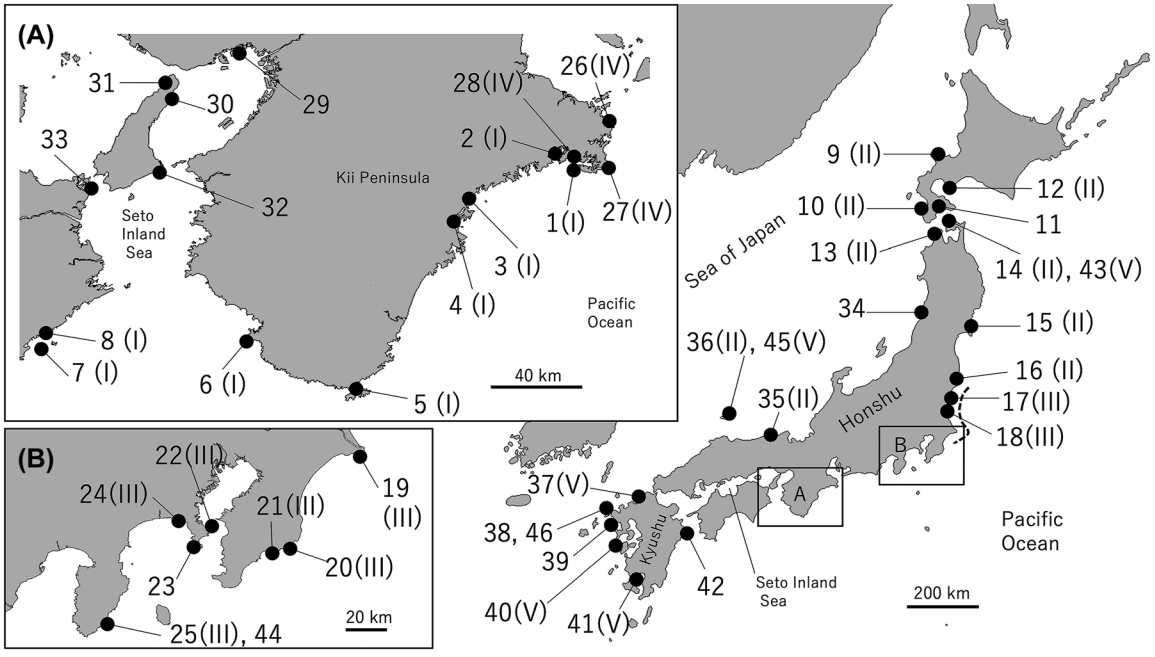

Figure 1: Sampling sites. Arabic numerals represent population numbers shown in Supplementary Table S1. Genetic clusters (i.e., Groups) estimated based on the SSR genetic diversity are shown as Roman numerals in parentheses. Some populations (29–33, 42 and 44) were genetically similar to one of the Groups, but were not considered as a member due to genetic admixture and/or geographical isolation from other members. Populations with less than three individuals (the populations 11, 23, 34, 38, 39, 46) were excluded from such groupings. Approximate location of a genetic break along the Pacific coast of Honshu is shown by a broken line.

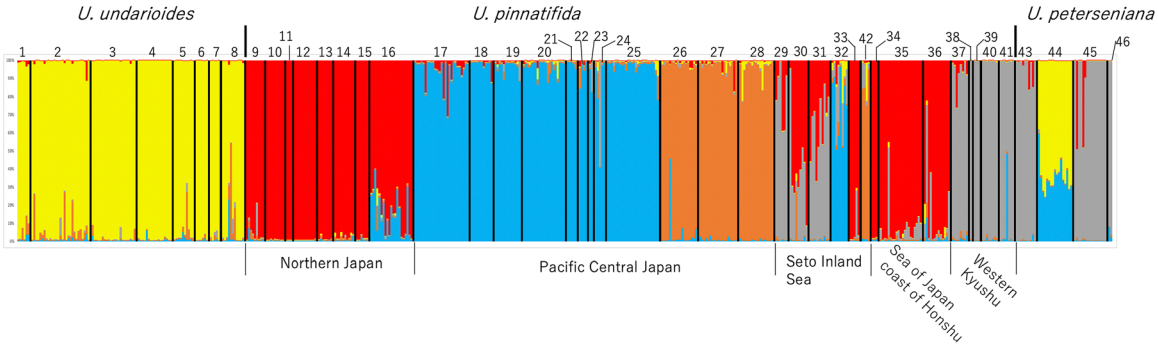

Figure 2: Genetic structure among Japanese *Undaria* populations (K = 5) based on 11 SSR loci. Colors represent each of the five genetic clusters, and the bar plot displays the estimated probabilities of assignment for each individual. Populations are arranged north (left) to south (right) by species. The population numbers shown in Supplementary Table S1 and the populations' approximate geographical origins are also displayed above and below the plot, respectively.

3.2 Genetic divergence between populations

The results of the PCoA (Figure 3) and the Neighbor-net analysis (Supplementary Figure S4) revealed that populations of *U. pinnatifida* showed a wider divergence than the other two species. *Undaria pinnatifida* and *U. peterseniana* were divided into several groups approximately congruent with their geographical origins. Although the *U. undarioides* populations were grouped together in the PCoA, as well as in the Neighbor-net analysis, they were genetically close to some of the *U. pinnatifida* populations (Figure 3).

Consistent with the STRUCTURE analysis (Figure 2), which assigns each individual regardless of the populations sampled, five clusters of populations were identified in the PCoA and the Neighbor-net analyses (Groups I–V; see also Supplementary Table S1). Groups were clustered more by geographical proximity than by species status. Some populations showing admixture in the STRUCTURE analysis (e.g., pop. 29, 30, 31, and 44) and geographically isolated populations (e.g., pop. 32, 33, and 42) were not included in any "Group". Pairwise comparisons of Groups showed statistically significant D_{EST} values, with the largest value being that between Groups I and II, two distant Groups (Table 1). The least differentiation was observed between Groups III and IV, followed by Groups I and IV; both of these pairs are geographically close. The largest estimated number of migrants was between Groups II and III, and the second largest was between Groups I and IV.

Table 1: Gene flow and genetic differentiation among geographic groups (I–V).

	Group I (n = 106)	Group II (n = 113)	Group III (n = 114)	Group IV (n = 54)	Group V (n = 55)
Group I	–	0.249	0.710	0.887	0.159
Group II	0.850	–	1.115	0.537	0.731
Group III	0.626	0.691	–	0.835	0.867
Group IV	0.449	0.619	0.407	–	0.369
Group V	0.655	0.702	0.556	0.561	–

Numbers of migrants after correction for mean sample size and Jost's D_{EST} are shown above and below diagonal, respectively. All D_{EST} values were significant ($p \leq 0.001$).

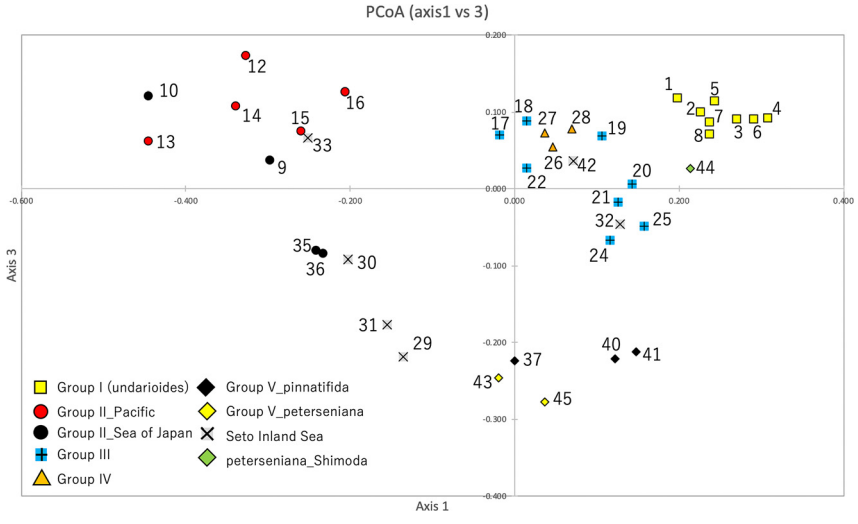

Figure 3: Result of Principal coordinate analysis (PCoA) based on Nei's genetic distance. Numbers are population numbers listed in Supplementary Table S1. Symbols indicate species names or geographical origins of populations. Populations in Seto Inland Sea (29–33 and 42) and population 44 were not included into any of the Groups due to genetic admixture and/or geographical isolation from other populations. Populations of small sample size (n < 4) were excluded from this analysis.

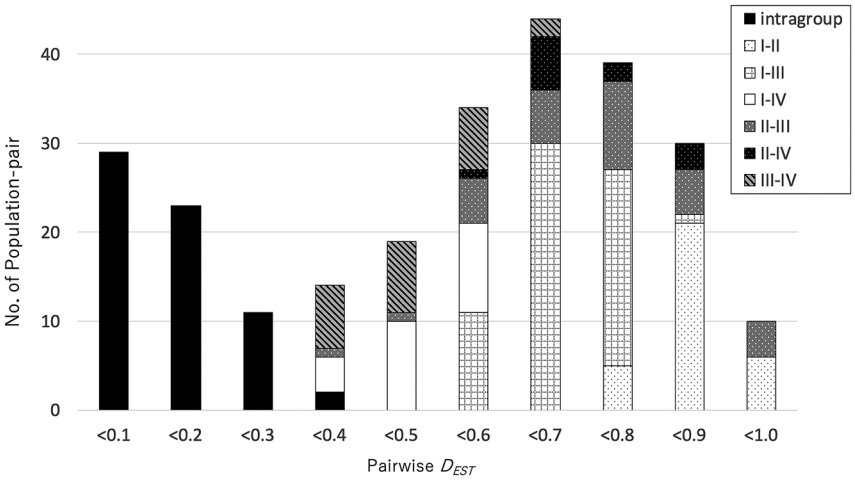

Figure 4: Distributions of genetic distances (D_{EST}) among populations belonging to the same Group and those belonging to different Groups. The genetic differences between *Undaria undarioides* (Group I) and Pacific populations of *U. pinnatifida* (Groups II–IV) were comparable to those among Pacific *U. pinnatifida* populations (Groups II–IV).

Comparison of the allele frequencies between the Groups (Supplementary Figure S5) showed that common alleles (i.e., those of the highest frequency) at each locus were different between the Groups, with some exceptions (e.g., allele 260 at 4G2 and allele 202 at 4H6). Usually, common alleles of one Group were also observed more rarely in another Group; for example, the major allele of Group I in 2A2 (allele 207) was also observed as one of minor alleles in Groups III and IV. A similar phenomenon was observed between Groups I and IV at loci 2B2, 4488 and 4E9; between Groups II and V (especially *U. peterseniana* in Group V) at 2A2, 4E9 and 4H6; and between Groups II and III at 4G2 and 4488.

D_{EST} values between Pacific populations showed two peaks, one peak composed of values within a single Group and the other peak composed of values between populations belonging to different Groups (Figure 4; see also Supplementary Figure S6). Although the *U. undarioides* populations formed their own Group, pairwise D_{EST} values between Group I (*U. undarioides*) and Groups III, VI, and the Pacific populations in Group II (*U. pinnatifida*) and those between Groups III, VI, and the Pacific populations in Group II were similar.

Isolation-by-distance analysis (IBD) of Groups I, III and IV, from southern to central Honshu, resulted in a stronger correlation (R = 0.8141, p = 0.0001; Figure 5, solid line) than IBD using all Pacific Coast populations (Groups I–IV, R = 0.6457, p = 0.0001; Figure 5, dotted line) or *U. pinnatifida* populations only (i.e., Groups II–IV, R = 0.4814, p = 0.0012; data not shown). High IBD was also observed over smaller geographical ranges (<350 km) in Group III (R = 0.7705, p = 0.0004; data not shown). However, the correlation was not significant among the populations of Group I (R = 0.1717, p = 0.1514; data not shown), even though Group I had a comparable number of populations and geographical range.

4 Discussion

Analyses of genetic divergence and its geographical structure among Japanese *Undaria* samples clearly suggested the

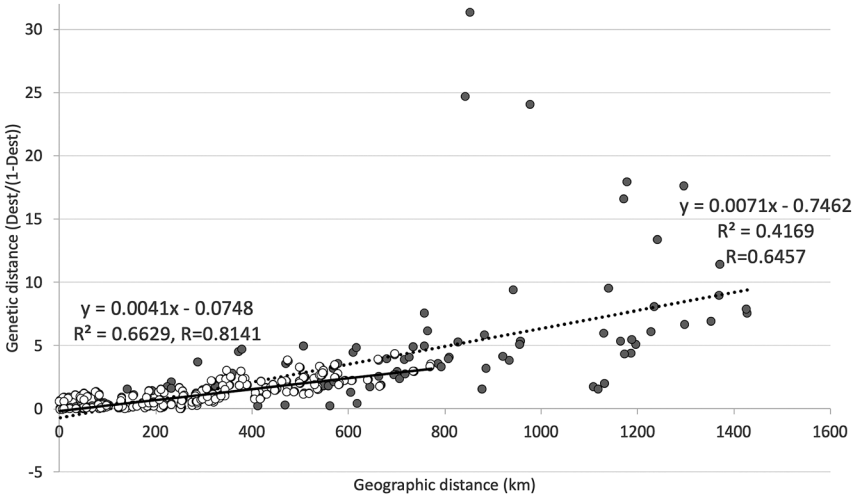

Figure 5: Isolation-by-distance (IBD) among *Undaria* populations along the Pacific coast of Japan. Dotted line: regression for all Pacific populations (open and filled circles, 23 populations); solid line: regression for Groups I, III and IV (open circles, 19 populations). R, correlation coefficient. R^2, coefficient of determination.

subdivision of *U. pinnatifida* into four genetically and geographically distinct clusters (i.e., "Groups"), in addition to a cluster consisting only of *U. undarioides*. However, the genetic divergence between the Groups did not show a clear gap between the morphologically defined inter- and intra-species, as suggested by the presence of shared alleles among the Groups irrespective of morphospecies. The results of IBD, with moderate to strong correlations between genetic and geographical distances, suggested that genetic divergence among *Undaria* populations is largely dependent on geographical distances and entirely independent of morphological characteristics. Collectively, these results do not support the existence of species boundaries in *Undaria*, despite the traditionally accepted morphological definitions (Okamura 1915; Yendo 1903).

Inconsistency between genetic and morphological divergence has been reported in brown algal groups, such as the Laminariales and Fucales. Such incongruence could be attributed to morphological plasticity within a single species (Akita et al. 2020; Demes et al. 2009; Macaya and Zuccarello 2010), insufficient resolution of molecular markers (Stieger et al. 2003; Yotsukura et al. 1999), or permeable boundaries between species or, even, genera and families (Akita et al. 2021; Liptik and Druehl 2000). Our finding of shared alleles among morphospecies suggested that the inconsistency observed in this study was caused by gene flows between "species", which resulted in genetically close relationships among geographically adjacent populations regardless of the morphospecies. The sequence divergence of the mitochondrial haplotypes was similar; in addition, although the clades were supported only weakly to moderately, the DNA sequences of the mitochondrial haplotypes also did not support monophyly of each morphospecies.

Morphological variations and difficulties of species delimitation have been reported previously in *Undaria* (Okamura 1915; Uwai et al. 2006a, 2007). Okamura (1915) distinguished three species, but he also pointed out that "not-pinnately-lobed but ovate or roundish fronds" of *U. pinnatifida* were "not rare", and that the depth of incisions varied even within a single locality. He further noted that the degree of development of the midribs and sporophylls/sori, which has been used as a diagnostic characteristic, varied continuously among species. Plants with intermediate morphologies were also reported by Uwai et al. (2007). These observations regarding the continuous variations of morphological characteristics also renders species boundaries ambiguous. Based on the continuous genetic and morphological variations, we consider that the three *Undaria* species are conspecific, and therefore, we propose to synonymize *U. undarioides* (Yendo) Okamura and *U. peterseniana* (Kjellman) Okamura with *U. pinnatifida* (Harvery) Suringar. Hereinafter, "*pinnatifida*", "*undarioides*" and "*peterseniana*" are used to show the morphological features of samples.

The result of IBD also suggested conspecificity of *"undarioides"* and *"pinnatifida"* and a significant role of geographical isolation on their divergence; when a regression line passes through a zero origin, the amount of gene flow is explained readily by geographical distance and the samples are considered to be conspecific (Site and Marshall 2003). As reported in other members of the Laminariales (Farrell and Fletcher 2006; Forrest et al. 2000; Fukuhara et al. 2002), *Undaria* has limited dispersal ability and this limits admixture between different Groups and maintains the observed genetic structure. Strong-to-moderate correlations in IBD along the Pacific Coast indicate that the populations in this region have persisted steadily over a long period (Hutchison and Templeton 1999; Koizumi et al. 2006). The Pacific Coast of Japan was considered to function as a refugium (or refugia) during the last glacial maximum (Hu et al. 2017), which is congruent with the suggested stable condition of *Undaria* populations along the Pacific coast.

Whether, in addition to geographical isolation, there exists an isolation mechanism that prevents gene flow between the Groups remains unclear. Population structures have been documented in various marine organisms (e.g., Laikre et al. 2005) and multiple factors—including salinity (Hayakawa et al. 2012), large rivers (Zhong et al. 2020), sea currents (Alberto et al. 2011; Engelen et al. 2001; Zhong et al. 2020), mating systems (Engel et al. 2005) and phenology (Homma et al. 2020)—have been considered as potential isolation mechanisms that maintain genetic structures in seaweed species. The geographical distributions of *U. "pinnatifida"/"undarioides"* were explained by their thermal requirements (Morita et al. 2003a, b), which also at least partially accounts for the restricted gene flow between Groups I and IV despite their geographical proximity. On the other hand, the isolation mechanism between Group II and Group III on the Northern Pacific coast is unclear; but it is noteworthy that boundaries of genetic groups within a single species have been reported in this region (*Sargassum horneri*, Hu et al. 2011; Uwai et al. 2009; *Sargassum fusiforme*, Hu et al. 2017; *Agarophyton vermiculophyllum*, Zhong et al. 2020; *Sargassum thunbergii*, Song et al. 2021) and that this region has been considered a genetic breakpoint (Zhong et al. 2020). In addition, the boundary between Groups II and III roughly corresponds to a boundary in marine ecoregions (Spalding et al. 2007). Provinces in marine ecoregions are characterized by distinct biota, possibly resulting from differences in abiotic factors (Spalding et al. 2007).

The presence of an intrinsic isolation mechanism that prevents hybridization between morphologically defined *Undaria* "species" has been suggested previously. For

example, Saito (1972) reported that 55% of "*peterseniana*" (female) X "*pinnatifida*" (male) crossings and 80% of "*pinnatifida*" (female) X "*peterseniana*" (male) crossings failed, compared with success rates of 100% and 60–65% for intraspecies crossings and "*pinnatifida*" X "*undarioides*" crossings, respectively. The F_1 hybrids of "*pinnatifida*" X "*peterseniana*" were reported not to mature. This result suggests the presence of an intrinsic isolation mechanism (or mechanisms) between these morphological "species"; however, Shinmura (1985) reported a higher growth rate for sporophytes of "*pinnatifida*" (female) X "*peterseniana*" (male) than for sporophytes of intraspecific crosses of "*pinnatifida*". The differences between these studies could be due to differences in the geographical origins of the strains used. Saito (1972) used strains from the central Pacific coast of Honshu, while Shinmura (1985) used strains from western Kyushu. It is intriguing that "*pinnatifida*" and "*undarioides*" tend to form sporophytes despite their genetic distinctness compared with "*peterseniana*", which did not show genetic uniqueness. Crossing between strains representing different genetic Groups will be required to confirm the presence/absence of intrinsic isolation mechanisms among Groups.

Based on the nuclear SSR and the mitochondrial markers (Uwai et al. 2006a, b, and this study), the distribution of different lineages (clusters) of *Undaria* in the Seto Inland Sea has been confirmed. The samples from populations 32 and 42 belong to two distinct clusters found in Pacific Central Honshu. In contrast, population 33 could not be distinguished from Northern Japanese samples (Group II). Anthropogenic domestic introduction due to intensive *Undaria* mariculture is likely in this region, as the materials for mariculture were developed from gametophytes of Northern Japanese origin (Uwai et al. 2006a, b). The genetic admixture in populations 29–31 observed in STRUCTURE could be attributed to these human introductions. Gene flow has been reported between native (wild) and introduced (domestic) populations in animals (Nussberger et al. 2018) and land plants (Ellstrand et al. 1999, 2013); marine species, however, remain understudied. Additional research is required in order to assess the genetic diversity and structure, as well as the genetic impact of mariculture in this region.

Despite the synonymization of three species into one, the present results strongly suggest the importance of conserving local populations of *U. pinnatifida*. Generally, information on population structure is used to develop conservation plans for each species, taking into account genetic variations as well as the practical unit of reproduction (gene pool) of the species (Laikre et al. 2005; Shaklee and Bentzen 1998). Populations that show genetic differentiation could show different responses to an environmental fluctuation (Coleman et al. 2020; Song et al. 2021). The Groups observed in this study also could be genetic resources—for example, to produce new strains of mariculture material. Notably, the current data are based on samples collected in the early 2000 s and thus provide a snapshot of genetic structures at that time. Future detection of the effects of global warming and other environmental fluctuations could thus be aided by the current findings.

In conclusion, multiple genetic groups with limited geographical distribution were identified within *U. pinnatifida* based on nuclear SSR markers. Alleles were shared between geographically adjacent populations regardless of morphospecies, and populations were clustered geographically. Based on these results, *U. undarioides* and *U. peterseniana* were considered synonymous with *U. pinnatifida*. Geographical isolation plays an important role in maintaining the observed genetic structures, particularly in the central Pacific region of Japan.

Taxonomic change proposed

Undaria pinnatifida (Harvey) Suringar (Suringar 1873).

Heterotypic synonyms

Undaria peterseniana (Kjellman) Okamura (Okamura 1915).
Undaria undarioides (Yendo) Okamura (Okamura 1915).

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Author contributions: SU, ST, and YS conceived, designed, performed experiments and data analyses, and wrote the manuscript. NE and TS performed experiments for Northern Pacific Honshu and the Kii peninsula, respectively. TM and AK collected most of the samples along the Kii peninsula.
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Data availability: The sequence data of the mitochondrial haplotypes are deposited in Genbank. The full dataset of the SSR genotypes is available from SU on request.

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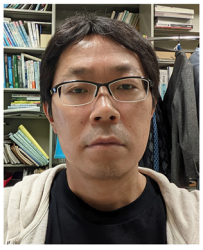
Bionotes



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