Population Genetic Structure and Phylogeography of Co-Distributed *Pachymeniopsis* Species (Rhodophyta) along the Coast of Korea and Japan

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Abstract: Inferring phylogeographic patterns of macroalgal species is essential for understanding the population structure and for the conservation of macroalgal species. In this study, the phylogeographic patterns of two co-distributed macroalgal species along the coast of Korea and Japan, *Pachymeniopsis lanceolata* and *Pachymeniopsis elliptica*, were analyzed. *Pachymeniopsis lanceolata* (215 specimens from 36 sites) and *P. elliptica* (138 specimens from 24 sites), using the plastid *rbc*L gene, are characterized by fifteen and six haplotypes, respectively. Mitochondrial COI-5P gene sequences revealed a low variation for both species. An analysis of molecular variance (AMOVA), pairwise F_{ST} comparisons, and haplotype networks based on the *rbc*L data suggest a weak genetic differentiation of both species. The shared haplotypes (*P. lanceolata*: LR01; *P. elliptica*: ER01) found in the entire sampling range indicate that these two *Pachymeniopsis* species can disperse over long distances along the coast of Korea and Japan. Despite the similar phylogeographic pattern, our results suggest that *P. lanceolata* has a higher genetic diversity, with a wider distribution along the Korean Peninsula than *P. elliptica*. Moreover, it is adapted to low sea surface temperatures and survived in more of the available habitats during periods of climatic change, whereas *P. elliptica* is less adaptable and more susceptible to environmental disturbance. This phylogeographic study provides a rationale for the conservation of the wild *Pachymeniopsis* population.

Keywords: genetic diversity; haplotype network; *Pachymeniopsis*; phylogeography; macroalgae; Northwest Pacific

1. Introduction

The climate change during the Late Pleistocene glaciation has impacted the current distribution of marine populations [1–3]. Temperate species have responded to fluctuations between glacial and interglacial periods with range contractions and expansions [4]. Some lineages have been able to survive in refugia and expand northward as temperatures increased [5,6]. These refugia, with long-term population survival, often display a high genetic diversity and a unique gene variation [6]. Therefore, valuable information for conserving local genetic variation can be obtained by identifying the locations of refugia and population recolonization pathways [3].

Over the past century, ocean warming driven by global climate change has led to a shift in geographic ranges toward higher latitude environments for many marine species [3]. Previous studies have shown that rising sea surface temperatures cause some marine macroalgal species to experience a geographical range contraction, and even the extinction of genetic lineages [7–9]. Several macroalgal species have exhibited northward range shifts [10–12], and climate change also leads to a decline in natural resources [13]. This highlights the necessity of conducting biogeographic surveys to document the population distribution of economically and ecologically critical macroalgal species [14].

The Northwestern Pacific (NWP) is a key marine region known for its biodiversity and, specifically, large populations of endemic algae [15]. This region is characterized by complex oceanic circulation patterns that greatly influence the composition and distribution of marine species [16,17]. The Kuroshio Current, which originates from the North Pacific Equatorial Current, is the dominant warm surface current in the NWP (Figure 1). It carries warm saline water from the East China Sea toward the southern Korean coast, impacting the climate and environment in this region [18]. The North Korea Cold Current carries cold water to the south, and mixes with the East Korea Warm Current along the eastern coast of Korea (Figure 1). These differing and complex current systems, combined with the dynamic nature of marginal seas, create distinct marine environments along the coast of Korea.
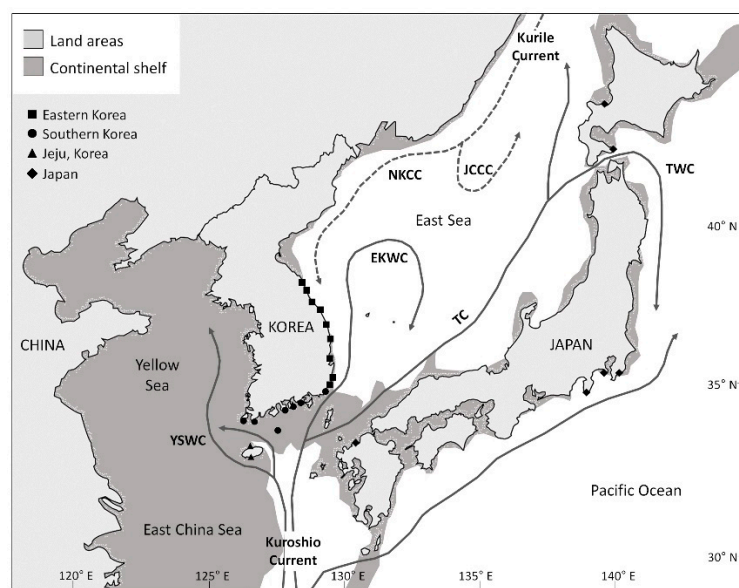

Figure 1. Map of the Korean Peninsula displaying the currents and collection sites of two *Pachymeniopsis* species. Shaded areas indicate sea regions that would have been exposed during periods of sea level (~130 m). Dotted arrow lines indicate the cold currents, and solid arrow lines show the warm currents. YSWC, Yellow Sea Warm Current; EKWC, East Korea Warm Current; TC, Tsushima Current; TWC, Tsugaru Warm Current; NKCC, North Korea Cold Current; JCCC, Japan Central Cold Current.

Molecular marker-based phylogeographic analyses offer powerful approaches for tracking population and species histories [19]. Phylogeographic studies have recently been used to understand the population structure and demographic history of marine macroalgae in the NWP including red algae, *Gelidium elegans* [20], *Chondrus ocellatus* [2], *Gloiopeltis furcata* [21–23], and *Agarophyton vermiculophyllum* [24]. Brown algae in the NWP, such as *Sargassum fusiforme* [17] and *Saccharina japonica* [3], have also been characterized. However, few studies have compared the macroalgal phylogeographic structure and genetic connectivity focused on the populations along each coast of the Korean Peninsula [20,23,24].

The genus *Pachymeniopsis* Y. Yamada *ex* S. Kawabata, a temperate species inhabiting the coastal ecosystem of the NWP, is the most taxonomically changed genus of the family Halymeniaceae [25]. This genus is based on the type species, *Pachymeniopsis lanceolata*, transferred from *Aeodes lanceolata* Okamura [26], and was once contained with the genus *Grateloupia* C. Agardh [27] with other genera [28–30]. New molecular and morphological data have provided a taxonomic revision that includes the reinstatement of the genus *Pachymeniopsis* [25,31]. Currently, five species belong to this genus (*P. elliptica*, *P. lanceolata*, *P. pseudoelliptica*, *P. volvita*, and *P. gargiuli*), all of which occur in the NWP [32].

Two species of this genus, *P. elliptica* and *P. lanceolata*, coexist in the temperate region of the NWP [33,34] and are native to Korea and Japan [35]. *Pachymeniopsis elliptica* inhabits

rocky substrates in the lower littoral to sublittoral zones and exhibits extreme morphological variation [36]. *Pachymeniopsis lanceolata* occurs in the same habitats as *P. elliptica* and has been recognized as an introduced species in North America [37], the Mediterranean Sea [38], and the Atlantic Ocean [39]. These two species have common features, such as blade-like thalli with leather texture (Figure 2), which makes it difficult to distinguish them [40]. Due to the similarity of the external morphology and habitat, the distribution of each species in the NWP may be underestimated by a morphological approach.
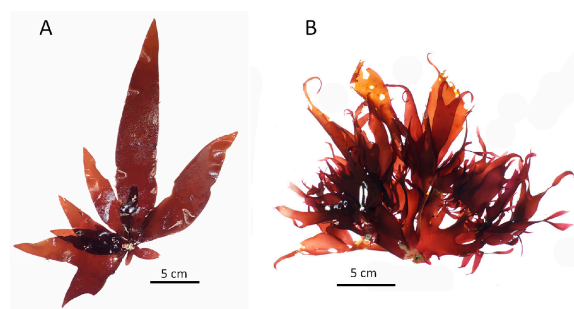
Figure 2. External morphology of two *Pachymeniopsis* species. (**A**) *P. lanceolata*, (**B**) *P. elliptica*.

In this study, two *Pachymeniopsis* species were collected, covering a latitudinal distribution range in Korea and several sites in Japan. The sequences of the plastid ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbc*L) and the 5′ end of the cytochrome *c* oxidase subunit I (COI-5P) markers were analyzed. This study aimed to investigate the distribution range of *P. lanceolata* and *P. elliptica* from Korea and Japan to compare the level of population genetic structuring in the two species according to the biogeographic region, and to determine whether each species shows a similar pattern of demographic history.

2. Materials and Methods

A total of 353 specimens were analyzed in the intertidal and subtidal zones of 39 locations in Korea and Japan: 215 specimens were from 36 populations of *P. lanceolata*, and 138 were from 24 populations of *P. elliptica* (Supplementary Tables S1 and S2). Field-collected specimens were identified according to Yang et al. [40] and pressed into an herbarium sheet for dried specimens. A 4-5 cm portion of the frond was excised from each plant and desiccated with silica gel for DNA analysis.

Genomic DNA was extracted using the LaboPass Tissue Genomic DNA Isolation Kit (Cosmogenetech, Seoul, Korea), according to the manufacturer's protocol. Targeted gene sequences of *rbc*L and COI-5P were amplified and sequenced using the primers F145-R898 and F762-R1442 for *rbc*L [41], and GHalF-COX1R1 for COI-5P [42]. All polymerase chain reaction (PCR) amplifications were conducted in an All-In-One-Cycler (Bioneer; Daejeon, Korea) using MasterMix 2x (MGmed; Seoul, Korea), under the following conditions: *rbc*L, initial denaturation at 96 °C for 4 min, 35 cycles of 1 min at 94 °C for denaturation, 1 min at 50 °C for annealing, 2 min at 72 °C for extension, and a final extension at 72 °C for 7 min; COI-5P, initial denaturation at 96 °C for 4 min, and 40 cycles of 30 s at 94 °C for denaturation, 30 s at 45 °C for annealing, 1 min at 72 °C for extension, and a final extension at 72 °C for 7 min. All PCR runs included a negative control reaction tube containing all reagents, except for template DNA. PCR products were purified using an Exo-AP PCR Clean-up Mix (MGmed) and then sequenced commercially (Macrogen; Seoul, Korea).

Sequences of the forward and reverse strands were determined for all specimens. The electropherograms were edited using the Chromas v.1.4.5 program [43] and checked manually for consistency. Consensus sequences were generated using the Geneious software (Geneious R9 ver.9.1.4, http://www.geneious.com (accessed on 18 July 2021)). The *rbc*L and COI-5P sequences from Korea and Japan were downloaded from GenBank, which had been previously analyzed [35,40,44], and were aligned with newly generated sequences

from this study. The obtained *rbc*L and COI-5P sequences were aligned using ClustalO [45] and manually edited.

In addition to evaluating the relationships among *rbc*L and COI-5P haplotypes, a minimum spanning network was generated using the program ARLEQUIN 3.5 [46]. The haplotype diversity (*h*) and nucleotide diversity (π) were calculated for each population, and at the species level using ARLEQUIN. Due to the low variation observed in COI-5P sequences, this marker was not used for downstream analyses.

Tajima's *D* [47] and Fu's F_S [48] tests were used to assess any significant excess of rare alleles, performing 10,000 bootstrap replicates in ARLEQUIN. Under the assumption of neutrality, negative values characterize the populations in expansion, while positive values associated with the loss of rare haplotypes are considered a signature of recent bottlenecks. The fixation index, F_{ST}, was used to identify the genetic differentiation between each group.

3. Results

A 1199 portion of *rbc*L was analyzed from 215 specimens of *P. lanceolata*, and 15 haplotypes with 14 polymorphic sites were detected (Table 1). The same portion of *rbc*L sequenced for 138 individuals of *P. elliptica* revealed six haplotypes with six polymorphic sites (Table 1). The 153 specimens of *P. lanceolata* were also sequenced for the COI-5P marker (704 bp alignment), and seven haplotypes that differed by four polymorphic sites were detected (Supplementary Figure S1). The sequencing of 70 specimens of *P. elliptica* (same bp as *P. lanceolata*) revealed seven haplotypes with two polymorphic sites (Supplementary Figure S1).

Table 1. Diversity measures and neutrality tests for populations of two *Pachymeniopsis* species based on *rbc*L sequences. Number of specimens (N), number of haplotype (Nh), haplotype diversity (*h*), and nucleotide diversity (π). Significant *p*-values indicated by * $p < 0.01$.

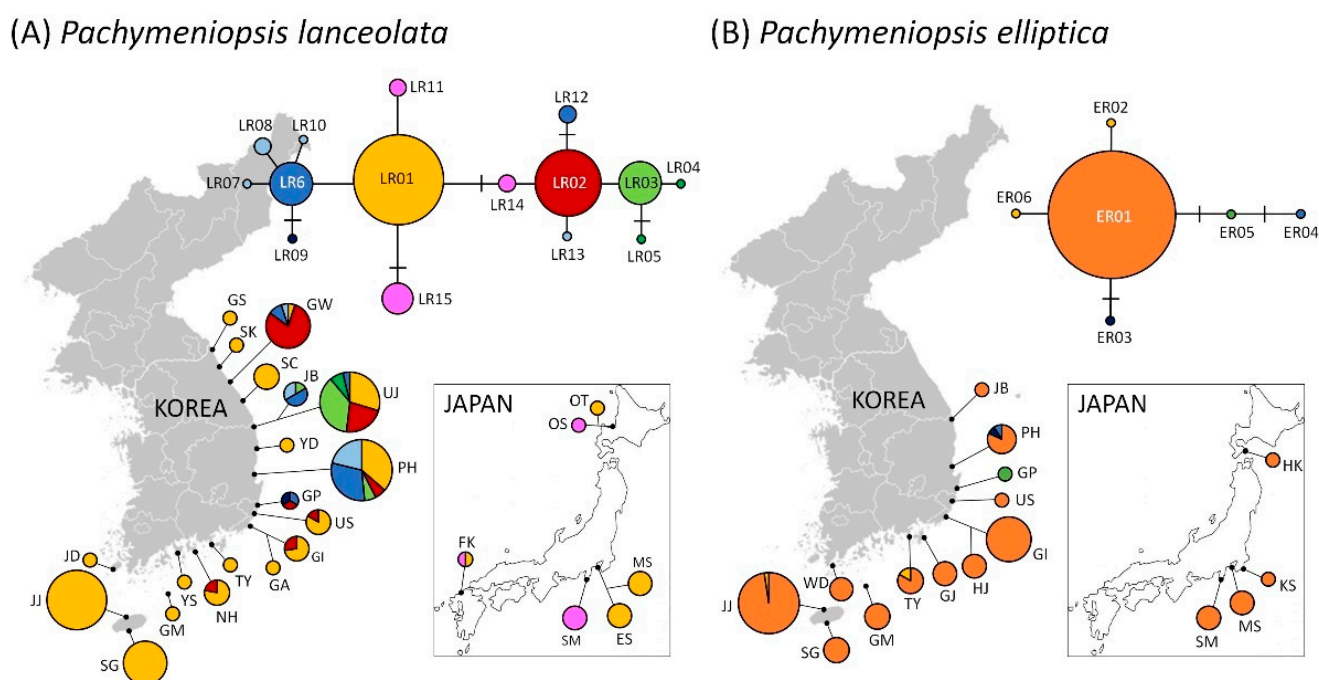| Region	*Pachymeniopsis lanceolata*						*Pachymeniopsis elliptica*					
	N	Nh	*h*	π	Tajima's *D*	Fu's *Fs*	N	Nh	*h*	π	Tajima's *D*	Fu's *Fs*
Total	215	15	0.624	0.00143	−0.6827	−3.9598 *	138	6	0.071	0.00012	—	—
Korea	191	10	0.609	0.00143	−0.4063	−1.9044	128	6	0.076	0.00013	—	—
Eastern Korea	127	12	0.752	0.00179	−0.0801	−1.4365	38	4	0.153	0.00034	—	—
Southern Korea	17	2	0.308	0.00077	—	—	37	2	0.054	0.00005	—	—
Jeju	47	1	—	—	—	—	53	2	0.037	0.00003	—	—
Japan	24	4	0.634	0.00103	0.4288	0.7110	10	1	—	—	—	—

The *h* for *rbc*L was 0.624 in *P. lanceolata* and 0.071 in *P. elliptica*, while the π was 0.00143 and 0.00012, respectively (Table 1). For the COI-5P marker, the *h* was 0.4553 in *P. lanceolata* and 0.5704 in *P. elliptica*, whereas the π was 0.00017 and 0.00095, respectively.

For *P. lanceolata*, 9 of the 15 *rbc*L haplotypes were private (haplotypes found at a single location); most of these (5 haplotypes) were unique (haplotypes found only in a single individual), while for *P. elliptica*, 5 of the 6 *rbc*L haplotypes were private, and all of them were unique.

Within *P. lanceolata*, two dominant haplotypes (LR01 and LR02) occurred in 58.5% and 16% of the specimens, respectively (Figure 3). The most dominant *rbc*L haplotype (LR1) was widespread and shared among geographically distant locations, including 13 locations distributed along the southern to eastern coast of Korea, and four locations in Japan (Figure 3). LR02 was found along the southern and eastern coasts of Korea. Of the 15 haplotypes, most (10 haplotypes; LR03-LR10 and LR12-LR13) are endemic to the eastern coast of Korea, and three haplotypes (LR11, LR14, and LR15) are endemic to Japan (Figure 3). The *rbc*L genetic diversity was generally higher in the eastern coast of Korea than in Jeju Island (Table 1).

Figure 3. Geographic distribution of haplotypes and haplotype networks of *Pachymeniopsis lanceolata* (**A**) and *P. elliptica* (**B**) based on the plastid *rbc*L gene. On the map, each circle represents a location, and the proportions of the pie chart indicate the frequency of specimens for each haplotype. The pie chart color corresponds to the one used in the haplotype networks. In the network, each connecting line represents single mutational steps. The vertical bars represent the number of mutational steps between two haplotypes when >1.

Within *P. elliptica*, almost all haplotypes were singletons (haplotypes represented by a single sequence in the sample). One dominant haplotype (ER01) was present in 96.4% of the specimens and was shared among all distant locations (Figure 3). Three haplotypes (ER03-ER05) were endemic to the eastern coast of Korea (Figure 3). The *rbc*L genetic diversity was higher on the eastern coast of Korea than on the southern coast and Jeju, with the highest haplotype diversity (the highest percentage of unique haplotypes) found within the eastern coast populations (Table 1).

The genetic structure of the populations of the two *Pachymeniopsis* species analyzed by an AMOVA showed little to no genetic structuring (*P. lanceolata*: 15.25%; *P. elliptica*: −7.54%) among regions, but a high variation (*P. lanceolata*: 52.02%; *P. elliptica*: 72.69%) within populations (Table 2). Differences among localities within each group (Φ_{SC}) explained a small portion of the total genetic variance (*P. lanceolata*: 32.74%; *P. elliptica*: 34.85%). This indicated that the populations were not genetically differentiated among regions, and the genetic variation primarily occurred at the population level. Table 2 shows that genetic subdivision was highly significant among populations within groups (Φ_{SC} = 0.386/0.324; $p < 0.01$) and within populations (Φ_{ST} = 0.479/0.273; $p < 0.01$).

Neutrality tests detected a recent population expansion for the populations of *P. lanceolata* with a negative Tajima's *D* index, although this was not significant (*D* = −0.68, p = 0.286), with a negative and significant Fu's *Fs* index (*Fs* = −3.96, $p < 0.01$) (Table 1). In a *P. elliptica* population of constant size, Tajima's *D* is expected to be zero under neutrality (Table 1). Pairwise F_{ST} values based on *rbc*L data revealed low genetic differentiation among regions in two *Pachymeniopsis* species (Table 3).

Table 2. Analysis of molecular variance (AMOVA) among populations based on *rbc*L data.

Source of Variation	d.f. [1]	Percentage of Variation	Φ Statistic	*p*-Value
P. lanceolata				
Among groups	3	15.25	$F_{CT} = 0.1525$	0.01369
Among populations within groups	32	32.74	$F_{SC} = 0.3861$	<0.00001
Within populations	176	52.02	$F_{ST} = 0.4798$	<0.00001
P. elliptica				
Among groups	3	−7.54	$F_{CT} = -0.0756$	0.41349
Among populations within groups	20	34.85	$F_{SC} = 0.3244$	0.00293
Within populations	108	72.69	$F_{ST} = 0.2733$	0.00684

[1] degree of freedom.

Table 3. Pairwise F_{ST} values for *P. lanceolata* (lower left) and *P. elliptica* (upper right). Significant *p*-values indicated by * *p* < 0.05.

	Eastern Korea	Southern Korea	Jeju	Japan
Eastern Korea	-	0.0232	0.0356 *	−0.0304
Southern Korea	0.0834 *	-	0.0015	−0.0489
Jeju	0.2604 *	0.2597 *	-	0.3541 *
Japan	0.1670 *	0.0940 *	0.3541 *	−0.0508

4. Discussion

Although the present study indicated generally similar phylogeographical patterns between *P. lanceolata* and *P. elliptica* based on a low genetic diversity and distribution, the two species displayed certain important differences in terms of genetic diversity, distribution, and genetic structures. *P. lanceolata* exhibited a higher genetic diversity (for both *h* and π) than *P. elliptica* and a wider distribution range along the Korean Peninsula despite sharing habitats. Our results were discussed based on the results of the *rbc*L gene, which presented an interesting population structure for two *Pachymeniopsis* species, although it is known to a conserved gene [49].

Historically, the identification of these two *Pachymeniopsis* species has been difficult because of their similar morphological variations [40]. Therefore, previous records of species distribution need to be verified using molecular approaches. The present study provides the evidence of distributional differences between the two species, with a wide northward distribution of *P. lanceolata* at Goseong (GS), Sokcho (SK), Gangwon (GW), and Samcheok (SC), along the east coast of Korea, whereas *P. elliptica* was not found in these regions (Figure 3). Additional sampling in the northern range of *Pachymeniopsis* would allow for a more complete evaluation of its distribution. The results of this study were similar to those of the same species in the NWP and introduced regions (*h* = 0.506, π = 0.00242) [35]. In the same study, five ribotypes were detected in *P. lanceolata* from Korea, Japan, China, the United States, and France [35], whereas the data in our study revealed 15 ribotypes in Korea and Japan. The 10 newly detected haplotypes were found along the eastern coast of Korea and Shimoda, Japan. Reconstructed haplotype networks are needed to better understand the population structure related to the range of distribution. Our study represents the first attempt to analyze the haplotype structure of *P. elliptica* in its native range. The results show that *P. elliptica* has a shallow genetic structure, with a low genetic diversity.

Understanding the population genetic structure of a species in relation to its distribution can help in the identification of glacial refugia [2]. Widely distributed *Pachymeniopsis* species showed only weak genetic structuring across sampling localities, shown by the AMOVA results in this study. Most of the genetic variation (*P. lanceolata*: 52.02%; *P. elliptica*: 72.69%) was attributed to the differentiation within populations, showing that there

was no population structure between the coasts in either species. The shared haplotypes (*P. lanceolata*: LR01; *P. elliptica*: ER01) found in the entire sampling range indicated that two *Pachymeniopsis* species can disperse over long distances along the coast of Korea and Japan.

The complex oceanic circulation in the NWP, which includes the Kuroshio Current and the East Korea Warm Current, may have contributed to the shared haplotypes in this region (Figure 1). Genetic connectivity observed from Korea to northern Japan is most likely influenced by the Tsushima Warm Current that supplies a large quantity of heat and transports marine organisms to the East Sea [50]. The occurrence of LR01/ER01 in central Japan and the presence of similar haplotypes along the Korean Peninsula and northern Japan can be explained by the movement of the Tsugaru Warm Current that flows through the Tsugaru Strait between Honshu and Hokkaido, Japan (Figure 1). Low F_{ST} values between populations also support the gene flow along all coasts of Korea and Japan (Table 3).

The spatial population structure and the location of refugia can provide essential information for the conservation and management of species and the associated genetic diversity [17,24,51,52]. The phylogeographic patterns of the two *Pachymeniopsis* species found in the present study are not consistent with those observed for other macroalgae described in the NWP [20,22,23,52]. In marine organisms, including macroalgae, a reduction in genetic diversity from lower to higher latitudes has been commonly observed, matching the theoretical expectations from recolonization events among de-glaciated areas at the end of the Last Glacial Maximum [23,51]. The phylogeography of two *Pachymeniopsis* species in this study displays a relatively high genetic diversity in the higher latitudes with some endemic haplotypes, and a low genetic diversity in lower latitudes in Korea. These results suggest that the two *Pachymeniopsis* species survived in the eastern coast glacial refugia during the Late Pleistocene, and subsequently migrated southward. Historically, sea levels in the NWP dropped by 120-140 m during the glacial maxima in the late Quaternary, leading to the isolation of the East Sea [53]. This disjunction significantly impacted the distribution range and genetic diversity of marine species [2,16,54]. The existence of numerous haplotypes along the eastern coast of Korea suggests more isolation during the Pleistocene and defines this specific area as the central origin of the distribution of the *Pachymeniopsis* species. By contrast, the populations in Jeju and the southern coast of Korea are characterized by only a few common haplotypes. This pattern may reflect a more recent founder event than that on the eastern coast [19].

All results obtained to date suggest that *P. lanceolata* has a much longer demographic history, with a higher nucleotide diversity in the Korean Peninsula than *P. elliptica*. Indeed, high haplotype diversity and low nucleotide diversity patterns suggest that *P. lanceolata* in the NWP may have experienced a rapid population growth over a short period. Sudden population expansion does not allow sufficient time for this species to have nucleotide mutations [55,56]. Similarly, the more complex star-like haplotype network for *P. lanceolata*, which displays several common haplotypes, is indicative of a growing population [57]. This suggestion of population expansion is also in agreement with the neutrality test of *P. lanceolata* (Tajima's *D* = −0.6827; *Fs* = −3.9599, Table 1). During this population expansion, the haplotype that originated from the eastern coast of Korea (LR01) migrated southward, causing newly derived haplotypes to appear along the eastern coast of Korea as well as in Japan. In particular, haplotypes that occurred only along the eastern coast of Korea (LR03-LR10, LR12, and LR13) probably adapted to lower seawater temperatures in that location and migrated southward.

The very low genetic diversity and neutrality of *P. elliptica* suggests that the populations are in genetic equilibrium [58]. Despite the low levels of diversity recovered (six haplotypes), all *P. elliptica* populations are characterized by the occurrence of one high-frequency haplotype (ER01), which occurred in 96.4% of samples. Population-endemic haplotypes were at very low frequencies. This distribution pattern of haplotype frequencies in *P. elliptica* is characteristic for many marine organisms, including invertebrates [59,60], and particularly for seaweeds [51,61]. An explanation for this phenomenon is probably

related to the enormous population size of many marine species, which may result in the retention of numerous haplotypes during population expansion [60,61]. The existence of an abundant haplotype throughout the distribution range of *P. elliptica* indicated a high degree of genetic homogeneity among populations. No genetically or geographically distinct populations within this species were revealed from the haplotype network (Figure 3), pairwise F_{ST}, or AMOVA results. This phenomenon is also observed in agricultural cultivation and often indicates conservation concerns [62]. The genetic similarity between populations of *P. elliptica* could reflect a recent reduction in diversity by gene flow, or, alternatively, a historical lack of diversity [58].

These results show that the demographic signals exhibited by *P. lanceolata* and *P. elliptica* do differ to some degree, which is likely a reflection of species-specific adaptation strategies to the environment in the NWP. The low level of genetic diversity in *P. elliptica* can be explained by its lower environmental tolerance [63]. *P. lanceolata*, adapted to low sea surface temperature, survived in a greater portion of the available habitat during periods of climatic change; however, *P. elliptica* was less adaptable and more susceptible to environmental disturbance. Hence, *P. lanceolata* could be reported as an introduced species to different regions by its higher tolerance to different environmental conditions. Recent studies have revealed a significant increase in sea surface temperatures in Korean waters [64]. In particular, the East Sea showed a trend approximately 1.43 °C higher than the other coasts of Korea [64]. This suggests that climate change will play a role in the distribution of the *P. lanceolata* population in the future, particularly for the haplotypes adapted to low seawater temperature on the eastern coast of Korea. Ultimately, this phylogeographic study provides a rationale for the conservation of *Pachymeniopsis* populations in the wild. To prevent the loss of local genetic diversity, the eastern coast of Korea should be considered a special conservation priority.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d13080336/s1, Table S1: Distribution of *rbc*L haplotypes of *Pachymeniopsis lanceolata*. Table S2: Distribution of *rbc*L haplotypes of *Pachymeniopsis elliptica*. Figure S1: Geographic distribution of haplotypes and haplotype networks of *Pachymeniopsis lanceolata* (A) and *P. elliptica* (B) based on the mitochondrial COI-5P gene.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Coyer, J.A.; Hoarau, G.; Stam, W.T.; Olsen, J.L. Geographically specific heteroplasmy of mitochondrial DNA in the seaweed, *Fucus serratus* (Heterokontophyta: Phaeophyceae). *Mol. Ecol.* **2003**, *13*, 1323–1326. [CrossRef] [PubMed]
2. Hu, Z.-M.; Li, J.-J.; Sun, Z.-M.; Oak, J.-H.; Zhang, J.; Fresia, P.; Grant, S.; Duan, D.-L. Phylogeographic structure and deep lineage diversification of the red alga *Chondrus ocellatus* Holmes in the Northwest Pacific. *Mol. Ecol.* **2015**, *24*, 5020–5033. [CrossRef]
3. Zhang, J.; Yao, J.; Hu, Z.-M.; Jueterbock, A.; Yotsukura, N.; Krupnova, T.N.; Nagasato, C.; Duan, D. Phylogeographic diversification and postglacial range dynamics shed light on the conservation of the kelp *Saccharina japonica*. *Evol. Appl.* **2018**, *12*, 791–803. [CrossRef] [PubMed]
4. Provan, J.; Bennett, K.D. Phylogeographic insights into cryptic glacial refugia. *Trends Ecol. Evol.* **2008**, *23*, 564–571. [CrossRef]

5.   Hewitt, G.M. Post-glacial re-colonization of European biota. *Biol. J. Linn. Soc.* **1999**, *68*, 87–112. [CrossRef]
6.   Hewitt, G. The genetic legacy of the Quaternary ice ages. *Nature* **2000**, *405*, 907–913. [CrossRef]
7.   Provan, J.; Maggs, C.A. Unique genetic variation at a species' rear edge is under threat from global climate change. *Proc. R. Soc. B* **2012**, *279*, 39–47. [CrossRef]
8.   Neiva, J.; Assis, J.; Coelho, N.C.; Fernandes, F.; Pearson, G.A.; Serrão, E.A. Genes left behind: Climate change threatens cryptic genetic diversity in the canopy-forming seaweed *Bifurcaria bifurcata*. *PLoS ONE* **2015**, *10*, e0131530. [CrossRef]
9.   Assis, J.; Araújo, M.B.; Serrão, E.A. Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. *Glob. Chang. Biol.* **2018**, *24*, e55–e66. [CrossRef] [PubMed]
10. Müller, R.; Laepple, T.; Bartsch, I.; Wiencke, C. Impacts of oceanic waring on the distribution of seaweeds in polar and cold-temperate waters. *Bot. Mar.* **2009**, *52*, 617–638. [CrossRef]
11. Jueterbock, A.; Tyberghein, L.; Verbruggen, H.; Coyer, J.A.; Olsen, J.L.; Hoarau, G. Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecol. Evol.* **2013**, *3*, 1356–1373. [CrossRef] [PubMed]
12. Neiva, J.; Assis, J.; Fernandes, F.; Pearson, G.A.; Serrão, E.A. Species distribution models and mitochondrial DNA phylogeography suggest an extensive biogeographical shift in the high-intertidal seaweed *Pelvetia canaliculata*. *J. Biogeogr.* **2014**, *41*, 1137–1148. [CrossRef]
13. Smale, D.A.; Wernberg, T. Extreme climatic event drives range contraction of a habitat-forming species. *Proc. R. Soc. B* **2013**, *280*, 20122829. [CrossRef] [PubMed]
14. Koch, M.; Bowes, G.; Ross, C.; Zhang, X.-H. Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Glob. Chang. Biol.* **2013**, *19*, 103–132. [CrossRef]
15. Kerswell, A.P. Global biodiversity patterns of benthic marine algae. *Ecology* **2006**, *87*, 2479–2488. [CrossRef]
16. Ni, G.; Li, Q.; Kong, L.; Yu, H. Comparative phylogeography in marginal seas of the northwestern Pacific. *Mol. Ecol.* **2014**, *23*, 534–548. [CrossRef]
17. Hu, Z.-M.; Li, J.-J.; Sun, Z.-M.; Gao, X.; Yao, J.-T.; Choi, H.-G.; Endo, H.; Duan, D.-L. Hidden diversity and phylogeographic history provide conservation insights for the edible seaweed *Sargassum fusiforme* in the Northwest Pacific. *Evol. Appl.* **2017**, *10*, 366–378. [CrossRef] [PubMed]
18. Barkely, R.A. The Kuroshio Current. *Science* **1970**, *6*, 54–60.
19. Avise, J.C. What is the field of biogeography, and where is it going? *Taxon* **2004**, *53*, 893–898. [CrossRef]
20. Kim, K.M.; Hoarau, G.G.; Boo, S.M. Genetic structure and distribution of *Gelidium elegans* (Gelidiales, Rhodophyta) in Korea based on mitochondrial *cox*1 sequence data. *Aquat. Bot.* **2012**, *98*, 27–33. [CrossRef]
21. Hanyuda, T.; Yamamura, K.; Boo, G.H.; Miller, K.A.; Vinogradova, K.L.; Kawai, H. Identification of true *Gloiopeltis furcata* (Gigartinales, Rhodophyta) and preliminary analysis of its biogeography. *Phycol. Res.* **2019**, *68*, 161–168. [CrossRef]
22. Yang, M.Y.; Yang, E.C.; Kim, M.S. Genetic diversity hotspot of the amphi-Pacific macroalga *Gloiopeltis furcata sensu lato* (Gigartinales, Florideophyceae). *J. Appl. Phycol.* **2020**, *32*, 2515–2522. [CrossRef]
23. Yang, M.Y.; Fujita, D.; Kim, M.S. Phylogeography of *Gloiopeltis furcata sensu lato* (Gigartinales, Rhodophyta) provides the evidence of glacial refugia in Korea and Japan. *Algae* **2021**, *36*, 13–24. [CrossRef]
24. Zhong, K.-L.; Song, X.-H.; Choi, H.-G.; Satochi, S.; Weinberger, F.; Draisma, S.G.A.; Duan, D.-L.; Hu, Z.-M. MtDNA-based phylogeography of the red alga *Agarophyton vermiculophyllum* (Gigartinales, Rhodophyta) in the native northwest Pacific. *Front. Mar. Sci.* **2020**, *7*, 366. [CrossRef]
25. Gargiulo, G.M.; Marobito, M.; Manghisi, A. A re-assessment of reproductive anatomy and postfertilization development in the systematics of *Grateloupia* (Halymeniales, Rhodophyta). *Cryptogam Algol.* **2013**, *34*, 3–35. [CrossRef]
26. Okamura, K. *Icons of Japanese Algae*; Kazamashobo: Tokyo, Japan, 1934; Volume 7, No 5; pp. 39–48, pls 321–325.
27. Kawaguchi, S. Taxonomic notes on the Halymeniaceae (Gigartinales, Rhodophyta) from Japan. III. Synonymization of *Pachymeniopsis* Yamada in Kawabata with *Grateloupia* C. Agarch. *Phycol. Res.* **1997**, *45*, 9–21. [CrossRef]
28. Wang, H.W.; Kawaguchi, S.; Horiguchi, T.; Masuda, M. A morphological and molecular assessment of the genus *Prionitis* J. Agardh (Halymeniaceae, Rhodophyta). *Phycol. Res.* **2001**, *49*, 251–261. [CrossRef]
29. Wilkes, R.J.; Morabito, M.; Gargiulo, G.M. Taxonomic considerations of a foliose *Grateloupia* species from the Strait of Messina. *J. Appl. Phycol.* **2006**, *18*, 663–669. [CrossRef]
30. De Clerck, O.; Gavio, B.; Fredericq, S.; Bárbara, I.; Coppejans, E. Systematics of *Grateloupia filicina* (Halymeniaceae, Rhodophyta), based on *rbc*L sequence analyses and morphological evidence, including the reinstatement of *G. minima* and the description of *G. capensis* sp. nov. *J. Phycol.* **2005**, *41*, 391–410. [CrossRef]
31. Calderon, M.S.; Boo, G.H.; Boo, S.M. *Neorubra decipiens* gen. & comb. nov. and *Phyllymenia lancifolia* comb. nov. (Halymeniales, Rhodophyta) from South America. *Phycologia* **2014**, *53*, 409–422.
32. Guiry, M.D.; Guiry, G.M. AlgaeBase. World-Wide Electronic Publication, National University of Ireland, Galway. Available online: http://www.algaebase.org (accessed on 2 March 2021).
33. Yoshida, T. *Marine Algae of Japan*; Uchida Rokakuho Publishing Co., Ltd.: Tokyo, Japan, 1998; pp. 1–1222.
34. Lee, Y. *Marine algae of Jeju*; Academy Publication: Seoul, Korea, 2008; pp. 1–477.
35. Kim, S.Y.; Manghisi, A.; Morabito, M.; Yang, E.C.; Yoon, H.S.; Miller, K.A.; Boo, S.M. Genetic diversity and haplotype distribution of *Pachymeniopsis gargiuli* sp. nov. and *P. lanceolata* (Halymeniales, Rhodophyta) in Korea, with notes on their non-native distributions. *J. Phycol.* **2014**, *50*, 885–896. [CrossRef] [PubMed]

36. Lee, H.B.; Lee, I.K. A taxonomic study on the genus Pachymeniopsis (Halymeniaceae Rhodophyta) in Korea. *Korean J. Phycol.* **1993**, *8*, 55–65.

37. Miller, K.A.; Hughey, J.R.; Gabrielson, P.W. First report of the Japanese species *Grateloupia lanceolata* (Halymeniaceae, Rhodophyta) from California, USA. *Phycol. Res.* **2009**, *57*, 238–241. [CrossRef]

38. Verlaque, M.; Mrannock, P.M.; Komatsu, T.; Villalard-Bohnsack, M.; Marston, M. The genus *Grateloupia* C. Agarch (Halymeniaceae, Rhodophyta) in the Thau Lagoon (France, Mediterranean): A case study of marine plurispecific introductions. *Phycologia* **2005**, *44*, 477–496. [CrossRef]

39. Burel, T.; Le Duff, M.; Ar Gall, E. Updated check-list of the seaweeds of the French coasts, Channel and Atlantic Ocean. *An aod. Les Cahiers Naturalistes de l'Observatoire Marin Brest*. 2019, pp. 1–38, 1 Figure, 2 Tables. Available online: https://www-iuem.univ-brest.fr/observatoire/l-observatoire/ressources/cahiers-naturalistes/AnAod_2019_VII_1_pp_1_38.pdf (accessed on 18 July 2021).

40. Yang, M.Y.; Han, E.G.; Kim, M.S. Molecular identification of *Grateloupia elliptica* and *G. lanceolata* (Rhodophyta) inferred from plastid *rbc*L and mitochondrial COI genes sequence data. *Genes Genom.* **2013**, *35*, 239–246. [CrossRef]

41. Kim, M.S.; Kim, S.Y.; Nelson, W. *Symphyocladia lithophila* sp. nov. (Rhodomelaceae, Ceramiales), a new Korean red algal species based on morphology and *rbc*L sequences. *Bot. Mar.* **2010**, *53*, 233–241. [CrossRef]

42. Saunders, G.W. A DNA barcode examination of the red algal family Dumontiaceae in Canadian waters reveals substantial cryptic species diversity. 1. The foliose *Dilsea-Neodilsea* complex and *Weeksia*. *Botany* **2008**, *86*, 773–789. [CrossRef]

43. McCarthy, C. *Chromas Version 1.45*; School of Health Science, Griffith University: Southport, Australia, 1998.

44. Yang, M.Y.; Kim, M.S. Taxonomy of *Grateloupia* (Halymeniales, Rhodophyta) by DNA barcode marker analysis and a description of *Pachymeiopsis volvita* sp. nov. *J. Appl. Phycol.* **2015**, *27*, 1373–1384. [CrossRef]

45. Sievers, F.; Wilm, A.; Dineen, D.; Gibson, T.J.; Karplus, K.; Li, W.; Lopez, R.; McWilliam, H.; Remmert, M.; Söding, J.; et al. Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. *Mol. Syst. Biol.* **2011**, *7*, 539. [CrossRef] [PubMed]

46. Excoffier, L.; Lischer, H.E.L. Arlequin suite ver. 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Res.* **2010**, *10*, 564–567. [CrossRef]

47. Tajima, F. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* **1989**, *123*, 585–595. [CrossRef] [PubMed]

48. Fu, Y.X. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics* **1997**, *147*, 915–925. [CrossRef] [PubMed]

49. Freshwater, D.W.; Tudor, K.; O'Shaughnessy, K.; Wysor, B. DNA barcoding in the red algal order Gelidiales: Comparison of COI with *rbc*L and verification of the "barcoding gap". *Cryptogam Algol.* **2010**, *31*, 435–449.

50. Kitamura, A.; Takano, O.; Takata, H.; Omete, H. Late Pliocene-early Pleistocene paleoceanographic evolution of the Sea of Japan. *Palaeogeogr Palaeoclim. Palaeoecol.* **2001**, *172*, 81–98. [CrossRef]

51. Hu, Z.-M.; Uwai, S.; Yu, S.-H.; Komatsu, T.; Ajisaka, T.; Duan, D.-L. Phylogeographic heterogeneity of the brown macroalga *Sargassum horneri* (Fucaceae) in the northwestern Pacific in relation to late Pleistocene glaciation and tectonic configurations. *Mol. Ecol.* **2011**, *20*, 3894–3909. [CrossRef]

52. Hu, Z.-M.; Kantachumpoo, A.; Liu, R.-Y.; Sun, Z.-M.; Yao, J.-T.; Komatsu, T.; Uwai, S.; Duan, D.-L. A late Pleistocene marine glacial refugium in the south-west of Hainan Island, China: Phylogeographical insights from the brown *alga Sargassum polycystum*. *J. Biogeogra* **2018**, *45*, 355–366. [CrossRef]

53. Wang, P. Response of western Pacific marginal seas to glacial cycles: Paleoceanographic and sedimentological features. *Mar. Geol.* **1999**, *156*, 5–39. [CrossRef]

54. Cheang, C.C.; Chu, K.H.; Ang, P.O., Jr. Phylogeography of the marine macroalga *Sargassum hemiphyllum* (Phaeophyceae, Heterokontophyta) in northwestern Pacific. *Mol. Ecol.* **2010**, *19*, 2933–2948. [CrossRef]

55. Grant, W.S.; Bowen, B.W. Shallow population histories in deep evolutionary lineages of marine fishes: Insights from sardines and anchovies and lessons for conservation. *J. Hered* **1998**, *89*, 415–426. [CrossRef]

56. Avise, J.C. *Phylogeography, the History and Formation of Species*; Harvard University Press: Cambridge, UK, 2000; pp. 1–447.

57. Posada, D.; Crandall, K.A. Intraspecific gene genealogies: Trees grafting into networks. *Trends Ecol. Evol.* **2001**, *16*, 37–45. [CrossRef]

58. Matocq, M.; Villablanca, F. Low genetic diversity in an endangered species: Recent or historic pattern? *Biol. Conserv.* **2001**, *98*, 61–68. [CrossRef]

59. Benzie, J.A.H. Population genetic structure in penaeid prawns. *Aquat. Res.* **2000**, *31*, 95–119. [CrossRef]

60. Stamatis, C.; Triantafyllidis, A.; Moutou, K.A.; Mamuris, Z. Mitochondrial DNA variation in Northeast Atlantic and Mediterranean populations of Norway lobster, *Nephrops norvegicus*. *Mol. Ecol.* **2004**, *13*, 1377–1390. [CrossRef] [PubMed]

61. Hoarau, G.; Coyer, J.A.; Veldsink, J.H.; Stam, W.T.; Olsen, J.L. Glacial refugia and recolonization pathways in the brown seaweed *Fucus serratus*. *Mol. Ecol.* **2007**, *16*, 3606–3616. [CrossRef]

62. Roderick, G.K. Geographic structure of insect populations: Gene flow, phylogeography, and their uses. *Annu. Rev. Entomol.* **1996**, *41*, 325–352. [CrossRef] [PubMed]

63. Wood, L.E.; Grave, S.D.; Daniels, S.R. Phylogeographic patterning among two codistributed shrimp species (Crustacea: Decapoda: Palaemonidae) reveals high levels of connectivity across biogeographic regions along the South African coast. *PLoS ONE* **2017**, *12*, e0173356. [CrossRef]

64. Han, I.S.; Lee, J.-S. Change the annual amplitude of sea surface temperature due to climate change in a recent decade around the Korean Peninsula. Korean Soc. *Mar. Environ. Saf.* **2020**, *26*, 233–241.