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 *rbcL* 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*<sub>ST</sub> comparisons, and haplotype networks based on the *rbcL* 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.

![Map of the Korean Peninsula displaying the currents and collection sites of two Pachymeniopsis species.](image)

**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], *Gloioptis 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](image-url)

**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 (*rbcL*) 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 *rbcL* and *COI-5P* were amplified and sequenced using the primers F145-R898 and F762-R1442 for *rbcL* [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: *rbcL*, 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](http://www.geneious.com) (accessed on 18 July 2021)). The *rbcL* 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 rbcl and COI-5P sequences were aligned using ClustalO [45] and manually edited.

In addition to evaluating the relationships among rbcl and COI-5P haplotypes, a minimum spanning network was generated using the program ARLEQUIN 3.5 [46]. The haplotype diversity (\(h\)) and nucleotide diversity (\(\pi\)) 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 rbcl was analyzed from 215 specimens of \(P.\) lanceolata, and 15 haplotypes with 14 polymorphic sites were detected (Table 1). The same portion of rbcl 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).

| Region       | \(P.\) lanceolata | \(P.\) elliptica |
|--------------|-------------------|------------------|
|              | \(N\)  | \(Nh\) | \(h\) | \(\pi\) | Tajima’s \(D\) | Fu’s \(F_S\) | \(N\)  | \(Nh\) | \(h\) | \(\pi\) | Tajima’s \(D\) | Fu’s \(F_S\) |
| 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 rbcl was 0.624 in \(P.\) lanceolata and 0.071 in \(P.\) elliptica, while the \(\pi\) 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 \(\pi\) was 0.00017 and 0.00095, respectively.

For \(P.\) lanceolata, 9 of the 15 rbcl 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 rbcl 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 rbcl 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 rbcl genetic diversity was generally higher in the eastern coast of Korea than in Jeju Island (Table 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 *rbcL* genetic diversity was generally higher in 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 (ΦSC) 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 (ΦST = 0.479/0.273; p < 0.01) and within populations (ΦST = 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 FST values based on *rbcL* data revealed low genetic differentiation among regions in two *Pachymeniopsis* species (Table 3).
Table 2. Analysis of molecular variance (AMOVA) among populations based on rbcL data.

| Source of Variation | d.f. | Percentage of Variation | Φ Statistic | p-Value |
|---------------------|------|-------------------------|-------------|---------|
| *P. lanceolata*     |      |                         |             |         |
| Among groups        | 3    | 15.25                   | F_CT = 0.1525 | 0.01369 |
| Among populations  | 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  | 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 FST 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 rbcL 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 de-
scribed 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 Quater-
nary, 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 $D = -0.6827; F_s = -3.9599$, 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 popu-
lations 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 *rbcL* haplotypes of *Pachymeniopsis lanceolata*. Table S2: Distribution of *rbcL* 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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