



Serrão et al. (1999) also used ITS sequences, but included several geographically separated specimens of each of 16 species and 6 genera of the family. Their study revealed that *Fucus* was a monophyletic and derived genus in the family, consisting of two distinct lineages: (1) *F. serratus* sister to *F. gardneri*, *F. distichus*, and *F. evanescens*, and (2) *F. vesiculosus*, *F. spiralis*, *F. ceranoides*, and *F. virsoides*. Because ITS sequences are used widely in phylogenetic studies of plants and algae at the species level, the inability of ITS sequences to resolve relationships within the two *Fucus* lineages was attributed to hybridization and/or incomplete lineage sorting or homogenization, both of which are typical of recent and rapid radiation (Serrão et al., 1999).

Over the past five years, studies in *Fucus* have shifted from a predominantly phylogenetic perspective to population genetics. The availability of microsatellite loci for the principal species (Coyer et al., 2002c; Engel et al., 2003; Wallace et al., 2004) has considerably advanced our understanding of population structure.

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**Table 1**  
Location and number of samples for *Fucus* specimens used in the study

Species	Location	Latitude, longitude	Number of mtDNA sequences examined	
			Spacer	23S
<i>F. distichus</i>	Appledore Island, Maine (USA)	42° 58'N, 70° 37'W	4 (exposed); 5 (sheltered)*	
<i>F. distichus</i>	Garðskagi (Iceland)	64° 04'N, 22° 42'		

### 3.3. Lineage 1

The tree based on the variable spacer region revealed two highly supported major clusters (A and B) within Lineage 1 (Fig. 4). Cluster A (posterior probability = 1.0; MP bootstrap = 96%) consisted of *F. distichus* (including various subspecies and formae), *F. evanescens*, and *F. gardneri*, which we synonymized under *F. distichus*. The cluster was a polytomy with three highly supported branches. No correlation was evident between groups and habitat or groups and geographic regions.

Cluster B was a monophyletic grouping (posterior probability = 1.0; MP bootstrap = 97%) of *F. serratus* collected from throughout its biogeographic range (Spain to

distributional ranges) and an adequate phylogenetic signal (e.g., mtDNA gene trees with high support values) (Barracough and Nee, 2001; Funk and Omland, 2003); conditions that were met in our study. Potential explanations for discordance between trees based on genes and morphology include philosophical differences among taxonomists (e.g., “splitters” vs. “lumpers”) and real biological differences related to interspecific hybridization (Funk and Omland, 2003).

Although ITS and mtDNA sequence data were unable to satisfactorily distinguish morphologically based *Fucus* species within Lineage 2, microsatellite allele frequencies have revealed clear separation among *F. spiralis*, *F. vesiculosus*, and *F. ceranoides* (Billard et al., 2005a), as well as among *F. vesiculosus* and the newly described *F. radicans* (Bergström et al., 2005). In Lineage 1A, however, neither microsatellite allele frequencies (Coyer et al., unpub. data), nor mtDNA could distinguish *F. distichus*,

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(Fig. 5) despite distinct differences in their habitat (salinity)

in species-level paraphyly/polyphyly (Funk and Omland, 2003). Hybridization between *Fucus* species is widespread, having been observed in the field for decades, (Burrows and Lodge, 1953; Gard, 1910; Lein, 1984a; Sauvageau, 1909; Scott and Hardy, 1994; Stomps, 1911) and verified by recent molecular work on *F. evanescens* × *F. serratus* (Lineages 1A and 1B) (Coyer et al., 2002b, 2006) and *F. spiralis* × *F. vesiculosus* (Lineage 2) (Billard et al., 2005b; Engel et al., 2005; Wallace et al., 2004). While the divergent mating systems within the genus may contribute to the maintenance of the parental types, backcrossing and the maintenance of introgressed genotypes can blur species distinctions (Billard et al., 2005b; Engel et al., 2005).

#### 4.2. Species designations within *Fucus*

Which species concept is most useful for *Fucus*? Most species concepts acknowledge the importance of isolating barriers, suffer from ambiguities, require subjective evaluations, and are unable to encompass sexual, asexual, and mixed modes of reproduction (Brookfield, 2002; Coyne and Orr, 2004; Kitcher, 1984). The most common “solution” is to choose a concept based on characteristics of the taxon under study. As Coyne and Orr (2004) point out, one can consider speciation as the conversion of “genotypic cluster” species into “biological” species as a continuous process that produces ever increasing barriers to gene flow. Species status, therefore involves a sliding scale: “bad” species, or taxa having substantial gene flow despite morphological distinctness on one end and “good” species, or taxa characterized by substantial, but not necessarily complete reproductive isolation at the other (Coyne and Orr, 2004). Species designations of intermediate taxa require variable degrees of subjective judgments. Although reproductive isolation is a crucial focus for speciation, complete reproductive isolation is not a necessary criterion for species designation (e.g., the modified biological species concept (BSC) of Coyne and Orr, 2004).

A sliding scale is the best description of speciation in *Fucus*. On one end lies *F. serratus* (Lineage 1B), a “good” species as both mtDNA and ecological data suggest that substantial barriers to gene flow exist between it and all

members of Lineage 2. Furthermore, mtDNA and microsatellite allele frequencies have resolved *F. serratus* from *F. distichus* (Lineage 1A), suggesting that the hybridization reported between these species (Coyer et al., 2002b, 2006) is not a significant source of gene flow and therefore, the species are characterized by substantial but not complete reproductive isolation (modified BSC of Coyne and Orr, 2004).

At the other end, lies the hermaphroditic members of Lineage 1A (*F. distichus*), characterized by widespread paraphyly/polyphyly (mtDNA), lack of species distinction with microsatellite allele frequencies (Coyer et al., unpub. data), and widespread selfing (Coleman and Brawley, 2005b; Coyer et al., unpub. data; Engel et al., 2005). Such evidence of substantial gene flow among Lineage 1A members has resulted in our designating all members as *F. distichus*.

In between the two extremes of *F. serratus* and *F. distichus*, lies Lineage 2. Although extensive paraphyly/polyphyly was revealed with mtDNA and hybridization among members is common, microsatellite analysis was able to differentiate several members of the Lineage (Billard et al., 2005b,c; Engel et al., 2005; Wallace et al., 2004). Consequently, effective isolation barriers are beginning to form in Lineage 2.

The glacial-relict *F. virsoides* (Lineage 2) is restricted to the upper Adriatic Sea and thousands of kilometers from the nearest population of any other *Fucus* species. Although mtDNA was unable to significantly resolve *F. virsoides* from other members of Lineage 2 and no hybridization studies have been conducted between *F. virsoides* and any *Fucus*



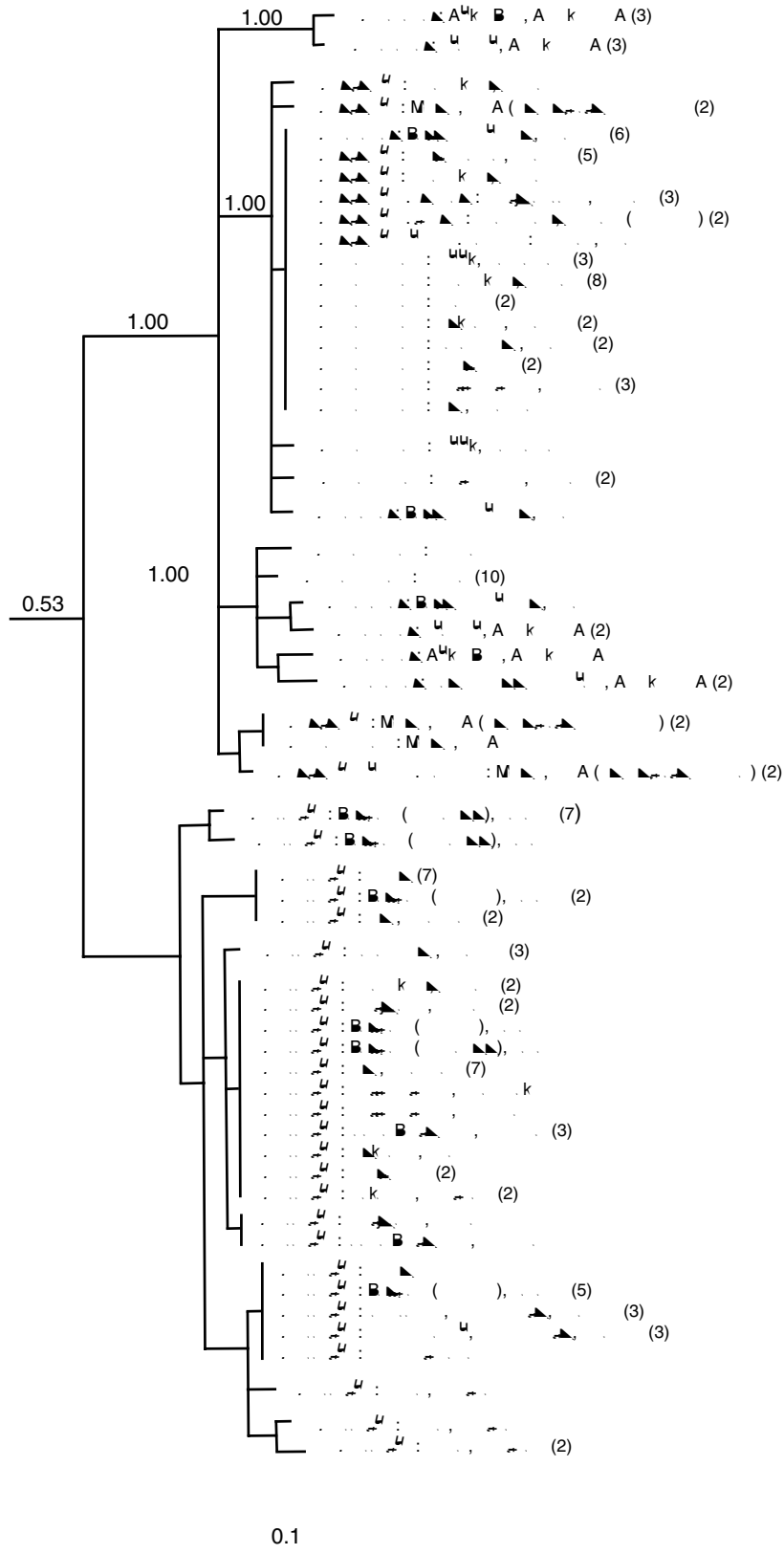


Fig. 4. Detailed Bayesian phylogenetic tree of Lineage 1 (A and B) from Fig. 3. See Fig. 3 for legend. Parenthetical values indicate the number of individuals with identical sequences.

glacial-interglacial episodes, the last being the last glacial maximum (LGM) (18,000–20,000 years BP). Thus, a series of regional extinctions, refugial populations, and recolon-

ization undoubtedly have shaped extant distributions as evidenced by: (1) the glacial relict species *F. virsoides*, which currently is confined to the northern Adriatic Sea in the



ditic, thereby greatly increasing the chances of successful dispersal because only one individual is necessary to successfully colonize new habitats (Baker, 1955; P n(s 0 v g,l8(s 0 v

Two scenarios are hypothesized for the North Pacific to North Atlantic dispersal. First, we speculate that an ancestral hermaphroditic (see Engel et al., 2005; for discussion of monoecy and hermaphroditism in *Fucus*) *F. distichus* ancestor and *F. spiralis* ancestor (precursors to Lineages 1A and 2, respectively) both evolved in the North Pacific from a hermaphroditic *Fucus* ancestor, then dispersed through the Arctic Ocean and radiated within the North Atlantic (Fig. 6). The alternative scenario postulates that only the *F. distichus* ancestor existed in the North Pacific, which dispersed into the North Atlantic and radiated into Lineages 1 and 2. Implicit in the latter scenario is a second trans-Arctic dispersal or introduction, namely *F. spiralis* from the North Atlantic to the North Pacific.

From a dispersal standpoint, it is important to realize that: (1) both *F. distichus* and *F. spiralis* are hermaphro-

and *Silvetia*) and the Gigartinales (intertidal red algae). On the other hand, the mid-to-low intertidal *F. distichus* was afforded a refuge in depth during the LGM and their persistent existence is revealed by extant high levels of haplotype and nucleotide diversity. This scenario assumes that colonization of the North Atlantic by the *F. spiralis* ancestor and *F. distichus* ancestor occurred before the LGM.

The hypothesis that *F. spiralis* evolved in the North Atlantic and dispersed naturally into the North Pacific seems unlikely. If dispersal occurred before the LGM, then the high intertidal species most likely would have been forced into southern refugia along the western North American coast during the LGM, with subsequent recolonization of the northern areas after the ice receded. In this case, a greater divergence in mtDNA sequences would be expected between extant Pacific and Atlantic populations than what is observed. If on the other hand, dispersal occurred after the LGM, one would expect the species to be distributed throughout the North Pacific, not in the restricted pattern currently observed: absent from the Arctic and Japan (Lüning, 1990), rare along the Aleutians (pers. comm., K.A. Miller), absent or rare in southeastern Alaska (pers. comm., S. Lindstrom), and common in the British Columbia—Washington State area (Norris and Conway, 1974). The extant distribution further argues against any current connectivity between the North Pacific and North Atlantic through the Bering Strait.

Regardless of whether a single (scenario 1) or double (scenario 2) trans-Arctic event involving an ancestral *F. distichus* and/or *F. spiralis* is postulated, the divergence of the two lineages is strikingly similar (Fig. 6). Each contains hermaphroditic and dioecious species in which the hermaphroditic species (*F. spiralis*, *F. distichus*) have both Pacific and Atlantic distributions. Furthermore, with respect to habitat, each lineage has reciprocally specialist species (*F. spiralis*=high intertidal; *F. serratus*=low intertidal/subtidal) and generalist species (*F. vesiculosus*=high to low intertidal, with constant submergence in the Baltic, and marine to brackish salinities; *F. distichus*=high intertidal pools to low intertidal).

In conclusion, *Fucus* offers many challenges to biologists interested in phylogeny, phylogeography, and speciation. As conventional neutral loci are complemented with loci known to be experiencing selection, the number and complexity of *Fucus* entities is expected to increase, thereby revealing a more accurate picture of the rapidly evolving genus.

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