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The foliose Bangiales (Rhodophyta) in the northern part of the North Atlantic and the relationship with the North Pacific foliose Bangiales - diversity, distribution, phylogeny and phylogeography

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THE FOLIOSE BANGIALES (RHODOPHYTA) IN THE NORTHERN PART OF THE NORTH ATLANTIC AND THE RELATIONSHIP WITH THE NORTH PACIFIC FOLIOSE BANGIALES – DIVERSITY, DISTRIBUTION, PHYLOGENY AND PHYLOGEOGRAPHY

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ABSTRACT

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by

Agnes Mols–Mortensen

University of New Hampshire, December, 2014

Foliose Bangiales species have a long history of study in the North Atlantic, but regions, especially in the northern parts, need more attention. Based on both new collections and herbarium material from Iceland, the Faroe Islands, West Greenland, UK, Norway, Sweden, Denmark and the Northwest Atlantic coast (from Newfoundland to Florida) the aim was to document diversity and distribution of foliose Bangiales species in the North Atlantic and to make floristic comparisons between the geographical areas. Species Identification was based on DNA sequences using the mitochondrial *cox*1, chloroplast *rbc*L and 3' *rbc*L + 5' *rbc*L-S markers. The North Atlantic species were analysed in a larger phylogenetic context based on *rbc*L sequences, with special emphasis on the relationship between the North Atlantic and North Pacific foliose Bangiales. Using the mitochondrial *cox*2-3 and nuclear ITS1 spacers a preliminary phylogeographic study was carried out for *Wildemania amplissima* that is represented in both the North Atlantic and North Pacific.

Four foliose Bangiales genera and 26 species were documented from the North Atlantic, and including both recent collections and herbarium material, the work documented both present and historic foliose Bangiales species diversity and geographic distribution, and demonstrated the value of well-preserved historic collections. Eleven foliose Bangiales species were reported from Iceland and the Faroe Islands, and seven species were reported from West Greenland. The Northwest- and Northeast Atlantic foliose Bangiales floras were equally diverse but with some differences in species composition. *Pyropia njordii sp. nov*. was described from the Faroe Islands, with distribution records from Iceland, West Greenland, Northeast Canada and Northeast America, and *Wildemania abyssicola comb. nov*. was documented from from Iceland and northern Norway. *Pyropia thulaea* was reported for the first time from the Northwest Atlantic coast, and *Py. peggicovensis* and "*Py. novae-angliae*" were reported for the first time in the Northeast Atlantic. A close phylogenetic relationship was observed between the North Atlantic and North Pacific foliose Bangiales, especially between the West Greenland flora and the North Pacific flora. The ITS1 spacer was used in resolving phylogeogaphic patterns in *W. amplisima*, with 16 haplotypes recovered, and a much higher haplotype diversity recovered in the North Atlantic than in the North Pacific.

CHAPTER I

Introduction

Biological diversity or simply biodiversity is defined by the Convention on Biological Diversity as “the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems” (http://www.cbd.int/convention/text). Diversity can therefore be studied at the population, species and community levels. Biodiversity is important for ecosystem functioning (Duffy, 2009 and references therein), and there is consensus among researchers that at least a minimum number of species is essential for ecosystem functioning under constant conditions, and in a changing environment a larger number of species is probably essential for maintaining stability (Loreau *et al*., 2001). In order to enable change to be determined it is essential to know the biodiversity, and this can be documented by for example, long-term observations of diversity, surveys of areas that have not previously been sampled, and resurveys of previously sampled areas. Long-term observations and resurveys in particular are essential methods to monitor potential changes.

The Marine biome has a rich biodiversity and there are numerous and important interactions between climate, physical oceanographic processes, and marine biology, for example, the recycling of carbon and nitrogen (Brierley & Kingsford, 2009). The marine environment is under pressure from human activities due to, for example, heavily populated coastlines, large-scale agriculture, aquaculture, and fisheries. The North

Atlantic coastal areas are examples of a marine environment that is largely impacted by human activities. It is generally accepted that global climate change induced by contemporary human activity is a reality, and increased heating in the lower atmosphere due to increased CO_2, has already had direct physical consequences for the marine environment, with increases of 0.13 °C in the mean global sea surface temperatures per decade recorded since 1979 (Intergovernmental Panel on Climate Change [IPCC], 2007; Brierley & Kingsford, 2009). Other consequences of cumulative post-industrial CO_2 emissions include perturbed regional weather patterns, rising sea levels, acidification of oceans, altered nutrient loads and ocean circulations (Brierley & Kingsford, 2009).

Biodiversity and distribution of species are affected by these pressures, with population extinctions reported due to climate change (Thomas *et al.*, 2001; Parmesan, 2006), and shifts in range and distribution for a number of species (e.g. Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Berge *et al.*, 2005). The effect of changing CO_2 levels on different marine organisms varies (Fabricius *et al.*, 2011; Rodolfo–Metalpa *et al.*, 2011; Kroeker *et al.*, 2013; Koch *et al.*, 2013), and in general calcifying organisms seem to be the most sensitive (Kroeker *et al.*, 2010; Hofmann *et al.*, 2012a,b). Based on observations from a mesocosm experiment with two red algal species, including the calcifying *Corallina officinalis* and the non-calcifying *Chondrus crispus*, Hofmann *et al.* (2012b) concluded that with elevated surface-seawater CO_2 concentrations that could potentially be reached within the next 100 to 200 years, the structure of temperate intertidal macroalgal communities could change, and that this would have important ecological implications. A proper assessment of changes in species diversity and distribution requires solid baselines on species occurrences, abundance and biomass (Bluhm *et al.*, 2011), and to formulate conservation strategies for potentially threatened species, insights into genetic diversity within and between populations will be crucial (Provan & Maggs, 2012).

Biogeographic regions and effects of glaciation in the North Atlantic

In the Mesozoic, ca. 165 Ma the super continent Pangea was breaking up, and the North Atlantic Ocean started to form. North America separated from Africa, and Eurasia and North America moved away from each other (Valentine, 1973; Lüning, 1990). The North Atlantic Ocean stretches from the Arctic Ocean to north of Equator and four biogeographic regions are recognized (from north to south): sub-arctic, cold-temperate, warm-temperate and tropical (Lüning, 1990; Adey & Hayek, 2011). Due to the warm North Atlantic Current and the effect of the clock-wise Coriolis force on the Northern Hemisphere, the biogeographic regions on the Northeast Atlantic coast are broader compared to the Northwest Atlantic coast. Thus, the cold-temperate biogeographic region extends far north on the east side of the North Atlantic (van den Hoek, 1982a; Lüning, 1990). Such biogeographic regions are defined by seawater isotherms and the distribution of species is often limited by either the summer- or winter isotherms to certain regions (van den Hoek, 1982a,b). The cold-temperate region of the Northwest Atlantic extends from the Strait of Belle Isle south to Cape Hatteras in North Carolina, and the warm-temperate region extends southward from Cape Hatteras to Cape Kennedy in Florida (Lüning, 1990). In the Northeast Atlantic the cold-temperate region extends southward from Norway and Iceland to Northwest Brittany in France and western Ireland. The warm-temperate region extends from there southward to Cape Verde, where the tropical region begins (Lüning, 1990). The Northwest and Northeast Atlantic shores have many macroalgal species in common, but the degree of endemism differs significantly between the two coasts, with higher endemism and species diversity in the Northeast Atlantic (Lüning, 1990). Van den Hoek (1975) attributed most of the differences between the two coasts to how severely they were impacted by the last Pleistocene glaciations. Overall the macroalgal flora of the cold-temperate region in the North Atlantic was severely impacted by the last glacial period ca. 110,000 to 12,000 years ago, and during the last glacial maximum (LGM) ca. 18,000 years ago. Large areas in the north were covered by ice and in order to survive, marine benthic species migrated southward to reach more suitable conditions. The open-sea distance between Greenland, Iceland, Svalbard and the Faroe Islands and the continental coast was a migration barrier to benthic organisms, and so was the soft substratum on the Northwest Atlantic coast, extending all the way from Long Island Sound, NY to Florida (Lüning, 1990). The effects of the glacial events with regard to species extinctions were more severe on the Northwest Atlantic coast, and the long continuous stretches of soft substratum are thought to be an important factor in this regard (Ingolfsson, 1992). Putative refugia in the North Atlantic, where species were able to survive during the harsh conditions, have been identified in the Faroe Island/Southern Iceland, Southwest Ireland, English Channel ("Hurd Deep"), Northwest Iberia, Northeast U.S.A. and Maritime Canada (Maggs *et al*., 2008; Provan & Maggs, 2012; Provan, 2013). However, Ingolfsson (2009) argues, that there is no geological evidence of ice-free coastal areas in Iceland during the LGM, and that a Faroe Islands/Southern Iceland refugium is unlikely.

Connection between the North Atlantic and the North Pacific Oceans

The cold-temperate benthic floras and faunas of the North Atlantic and North Pacific are very different from each other, with many more genera represented in the North Pacific (Lüning, 1990). The explanations for these differences given by Lüning (1990) were that more taxa were able to evolve in the North Pacific because of its old age compared to the North Atlantic, and the biotas of the two oceans evolved separately until the first opening of the Bering Strait ca. 5.4 to 5.5 Mya (Gladenkov *et al.*, 2002) that interconnects the North Atlantic and the North Pacific via the Arctic Ocean. After the opening of the Bering Strait marine species could migrate between the two oceans. However, the prevailing species migration direction was from the North Pacific to the North Atlantic (Durham & MacNeil, 1967; Lüning, 1990; Lindstrom, 2001; Adey *et al.*, 2008). Species migration was possible during the interglacial periods, but during glacial periods biotas became separated and allopatric speciation occurred. Lindstrom (1987, 2001) reported several close connections between the macroalgal flora of the Northeast Pacific and the North Atlantic. Currently, the Bering Strait is open and species migration can occur again between the North Atlantic and North Pacific. The Northwest Passage is becoming a reality for shipping traffic with the ice melting in the Arctic, and this might create important vectors for marine species to migrate between the two oceans. New species will potentially be introduced into both oceans and biodiversity will change.

The macroalgae

Biodiversity in the shallow marine environment worldwide is significantly represented by macroalgal species, with over 10,000 species described and many yet undescribed (Guiry, 2012). Macroalgae are photosynthesizing organisms that occur in the rocky intertidal and shallow subtial zones of the world, and they are differentiated into red (Rhodophyta), green (Chlorophyta) and brown (Heterokontophyta). Kelp (brown algae of the order Laminariales) can form forest ecosystems that provide important habitats for a diverse assemblage of invertebrates, fish and marine top-predators such as seabirds and sea mammals (Lorentsen *et al.*, 2010). Many macroalgal species are also commercially important (Morrissey *et al.*, 2001; Blouin *et al.*, 2010).

Discriminating between species is essential when studying biodiversity, but this can be extremely difficult in the macroalgae for a number of reasons such as their simple morphologies, their complex life-histories with heteromorphic stages, phenotypic plasticity, and convergence between species. Molecular techniques have revealed a hitherto unrecognized diversity within the macroalgae, and molecular tools have become widely accepted and used in taxonomic and systematic macroalgal work.

The Bangiales

The cosmopolitan red algal order Bangiales includes high and low intertidal and subtidal species that show different responses to desiccation stress (Kim *et al*., 2009; Blouin *et al*., 2010). The Bangiales represent an ancient lineage with the filamentous *Bangia*-like fossil *Bangiomorpha pubescens* dated to ca. 1198 Ma BP (Butterfield *et al*., 1990; Butterfield, 2000), and the similarity seen in the fossil and modern material suggests that these algae had the capacity to survive through dramatic climatic changes that have taken place during that time (Broom *et al*., 2004). The Bangiales include a single family, the Bangiaceae (Engler, 1892) and now include fifteen genera, seven filamentous and eight foliose (Sutherland *et al*., 2011). Members of the Bangiales are the most economically valuable seaweed crop in the world, and the history of harvesting and trading these algae goes back thousands of years in Japan, China, Korea and Southeast Asia (Mumford & Miura, 1988; Blouin *et al*., 2010). The life-history of Bangiales species is heteromorphic where gametophytes can be either filamentous or foliose and sporophytes, known as the conchocelis phase, consist of branched filaments found in shells and other calcareous substrata (Brodie & Irvine, 2003). Both sexual and asexual reproduction is recognized in both filamentous and foliose Bangiales species (Drew, 1956; Hawkes, 1978; Kornmann, 1994; Nelson *et al*., 2005), and a complex diversity of different reproductive units is acknowledged (Nelson *et al.*, 1999). Prior to the taxonomic revision by Sutherland *et al*. (2011) five genera were recognized within the Bangiales: *Porphyra*, *Bangia*, *Dione*, *Minerva* and *Pseudobangia*, with *Porphyra* being the only foliose genus. However, based on sequence data it became clear that neither *Bangia* nor *Porphyra* were monophyletic genera (Oliveira *et al*., 1995; Müller *et al*., 1998; Nelson *et al*., 2006). Due to these findings it was clear that the Bangiales needed fundamental revision, and joining forces with several Bangiales researchers from different geographic regions, Sutherland *et al*. (2011) based their revised Bangiales taxonomy on a concatenated dataset of nuclear SSU and plastid *rbc*L sequences.

The North Pacific has been the suggested center of diversity for the Bangiales (eg. Krishnamurthy, 1972; Conway *et al*., 1975). However, explorations in the Southern Hemisphere have revealed many more taxa than previously recognized, and based on the high diversity and the findings of phylogentically basal taxa in New Zealand, Broom *et al*. (2004) suggested eastern Gondwana as the center of origin for modern Bangiales.

Even though species of Bangiales almost certainly evolved elsewhere, they are common in the North Atlantic. Many North Atlantic Bangiales species have a North Pacific link, which supports the hypothesis suggested by Lindstrom (2001) that macroalgal species dispersed through the Bering Strait into the North Atlantic via the Arctic Ocean, and due to subsequent isolation of the floras allopatric speciation occurred. Several pairs of putative sibling species of foliose Bangiales have been reported from the North Pacific and the North Atlantic (Lindstrom & Cole, 1992, 1993).

Diversity, distribution and molecular tools

Identification of Bangiales species has traditionally been difficult because of morphological similarities among the species but with the advent of molecular tools it has become clear that existing genetic diversity is not reflected in the morphology (Sutherland *et al*., 2011). Molecular tools have proved essential in identifying, differentiating between and revealing new species, and they have enabled the diversity of foliose Bangiales to be studied in many parts of the world, including the North Atlantic (eg. Brodie *et al*., 1998; Neefus *et al*., 2002; Brodie & Irvine, 2003; Klein *et al*., 2003; Brodie & Nielsen, 2005; Bray *et al*., 2006, 2007; Brodie *et al*., 2007, 2008; Kucera & Saunders, 2012). As more geographic areas are studied floristic comparisons can be made and the geographic distribution of the species can be determined more accurately. The northern parts of the North Atlantic, including Iceland and Greenland, were identified as regions that needed further attention to understand species diversity and distribution within the foliose Bangiales (Brodie & Nielsen, 2005; Brodie *et al*., 2008).

The foliose Bangiales species *Wildemania amplissima* was until recently regarded as a North Atlantic sibling species of the North Pacific *W. cuneiformis* (Lindstrom & Cole, 1992). Based on sequence similarities in the cytochrome c oxidase subunit 1 (*cox*1), ribulose-1,5-bisphosphate carboxylase-oxygenase large subunit (*rbc*L) and Universal Plastic Amplicon (UPA) markers of *W. amplissima* and *W. cuneiformis*, Kucera & Saunders (2012) proposed to synonymize *W. cuneiformis* with *W. amplissima*, the latter having priority as the older name. Other reports on genetic, anatomical and ecological similarities between these species support this proposal (Lindstrom & Cole, 1992, 1993; Lindstrom & Fredericq, 2003; Mols–Mortensen *et al*., 2012). Molecular tools have enabled species concepts within the Bangiales to be more firmly defined, and we are now in a position to study diversity within species and to better understand different species' evolutionary histories. Milstein *et al*. (2008) used group I introns to study diversity in populations of *Porphyra spiralis* var. *amplifolia* (now *Pyropia spiralis* var. *amplifolia*) along the eastern coast of South America, and Teasdale & Klein (2010) used both the *cox*2-3 spacer, ITS1 and ITS2, and group I introns to study the diversity in populations of *Porphyra umbilicalis* in the North Atlantic.

Aims

The overal aim of this thesis is to document diversity and distribution of foliose Bangiales species in the North Atlantic with focus on hitherto understudied areas mostly in the northern parts of the North Atlantic. The work used both recent collections and herbarium (historic) material for analysis. Identifications were based on DNA sequence data using the mitochondrial marker *cox*1 and the chloroplast markers *rbc*L and 3' *rbc*L + 5' *rbc*L-S. The North Atlantic species were analyzed in a larger phylogenetic context based on the *rbc*L, with special emphasis on the connection between the North Atlantic and North Pacific foliose Bangiales floras. In addition a preliminary phylogeographic study was undertaken of *Wildemania amplissima*, a species represented both in the North Atlantic and the North Pacific Oceans.

In Chapter II the diversity of foliose Bangiales species in Iceland and the Faroe Islands was studied, and the diversity and distribution of the species was compared between the two areas, as well as in a larger North Atlantic context. Phylogenetic analyses were undertaken based on *cox*1 and *rbc*L sequences, and the Icelandic and Faroese foliose Bangiales species were considered in a larger phylogenetic context, including Bangiales species from the North Atlantic and the Pacific. Chapter II was published as: Mols–Mortensen, A., Neefus, C.D., Nielsen, R., Gunnarsson, K., Egilsdóttir, S., Pedersen, P.M. and Brodie, J. (2012). New insights into the biodiversity and generic relationships of foliose Bangiales (Rhodophyta) in Iceland and the Faroe Islands. *European Journal of Phycology* **47**: 146–159.

In Chapter III the diversity and distribution of foliose Bangiales species in West Greenland was studied based on the chloroplast 3' *rbc*L + 5' *rbc*L-S and *rbc*L markers, and an identification key based on observed morphological and ecological characters was developed. The Greenland species were analyzed based on the *rbc*L marker, using a broad phylogenetic context including Bangiales species from the North Atlantic and the Pacific. The link between the North Atlantic and North Pacific foliose Bangiales flora was also analyzed. Chapter III was published as: Mols–Mortensen, A., Neefus, C.D., Pedersen, P.M. and Brodie, J. (2014). Diversity and distribution of foliose Bangiales (Rhodophyta) in West Greenland: a link between the North Atlantic and the North Pacific. *European Journal of Phycology* **49**: 1–10.

In Chapter IV the foliose Bangiales flora of the Northwest Atlantic was studied based on the chloroplast 3' *rbc*L + 5' *rbc*L-S marker. Collections from Newfoundland to Florida were studied, with special emphasis on the understudied coast south of Long Island Sound. The diversity and distribution of these species were presented in a wider North Atlantic context. Chapter IV is a manuscript submitted to Nova Hedwigia as: Mols–Mortensen, A., Neefus, C.D. and Brodie, J. Diversity and distribution of foliose Bangiales (Rhodophyta) species in the Northwest Atlantic in the context of the North Atlantic.

In Chapter V the phylogenetic relationships in the foliose Bangiales genus *Wildemania* was studied based on *rbc*L sequences. A preliminary phylogeographic study was carried out for *Wildemania amplissima* populations from the North Atlantic and North Pacific, using the mitochondrial *cox*2-3 spacer and nuclear ITS1 markers. Chapter V is a manuscript in preperation as: Mols–Mortensen, A., Neefus, C.D., Lindstrom, S.C., Woods, H., Ramírez, M.E. and Brodie, J. *Wildemania amplissima* (Bangiales, Rhodophyta) in the North Atlantic and North Pacific: a preliminary phylogeographic analysis.

CHAPTER II

NEW INSIGHTS INTO THE BIODIVERSITY AND GENERIC RELATIONSHIPS OF FOLIOSE BANGIALES (RHODOPHYTA) IN ICELAND AND THE FAROE ISLANDS

(The chapter was published in the European *Journal of Phylology* **47**, 2012)

Abstract

Foliose species of the Bangiales (*Porphyra* sensu lato) have a long history of study in the North Atlantic, but there are still regions, especially in the northern parts of the North Atlantic that need more attention. A molecular study using *rbc*L and *cox*1 sequences was undertaken to assess the diversity of foliose Bangiales species in Iceland and the Faroe Islands. Herbarium collections from the intertidal and subtidal of Iceland (summer and winter) and the Faroe Islands (all seasons) revealed a total of 13 species (11 common to both areas), which could be referred to four genera in a recent two-gene global phylogeny. *Boreophyllum birdiae*, *Porphyra dioica*, *P. linearis*, *P. purpurea*, *P. umbilicalis*, *Pyropia* "*leucosticta*" A, *Pyropia njordii* Mols–Mortensen, J. Brodie & Neefus, *sp. nov.*, *Wildemania amplissima* and *W. miniata* were common to both areas, while *Pyropia thulaea* and *Wildemania abyssicola* (Kjellman) Mols–Mortensen & J. Brodie, *comb. nov.* (=*Porphyra abyssicola* Kjellman) were reported from Iceland but not from the Faroe Islands; *Porphyra* sp. FO and *Pyropia elongata* were reported from the Faroe Islands but not from Iceland. *Boreophyllum birdiae* is reported for the first time for Iceland and *Porphyra* sp. FO is reported for the first time for the Faroe Islands. *Pyropia njordii* is described from the Faroe Islands and is also recorded for Iceland, Greenland,

New England, USA and Nova Scotia, Canada. A total of 25 foliose Bangiales species are now reported from the North Atlantic and these results demonstrate the importance of investigating as many areas as possible to reach a more complete understanding of species diversity and distribution.

Introduction

Foliose Bangiales species (*Porphyra* sensu lato) occur in the intertidal and shallow subtidal of marine environments and have been studied in detail in several areas of the world (e.g. Brodie *et al*., 2001; Brodie & Irvine, 2003; Broom *et al*., 2004; Lindstrom & Fredericq, 2003; Lindstrom, 2008). Comparing species composition from different geographical areas requires correct identification and this has been a central problem within the group. Before molecular methods were available, identifications were based primarily on reproductive, morphological and ecological characteristics, and the highly variable morphology made species identification and delimitation notoriously difficult. Now molecular markers can verify species identity and the research is global in approach (Brodie *et al*., 2008; Sutherland *et al*., 2011). The geographical distributions of species can now be determined more accurately, and introduced species can be identified with more certainty (Neefus *et al*., 2008). Recent work on foliose Bangiales floras has identified certain areas of the world that require further attention to understand species diversity and distribution. The northern North Atlantic, including Iceland and Greenland, is one of these regions (Brodie & Nielsen, 2005; Brodie *et al*., 2008).

Studies in the northern parts of the North Atlantic show that foliose Bangiales species have a great ability to survive and spread (Brodie *et al*., 2001; Brodie & Nielsen, 2005; Brodie *et al*., 2008). Iceland is isolated but its central geographical position in the northern North Atlantic, facing the Iceland Sea to the north and Denmark Strait to the west, makes it potentially a stepping-stone (MacArthur & Wilson, 1967) between the east and west North Atlantic and also between the Northeast Pacific and the North Atlantic via the Arctic Sea (Brodie & Nielsen, 2005 and refs therein). The climate of Iceland, with warm sea temperatures in the southwest part and cooler temperatures in the northeast

(Astthorsson *et al*., 2007), can potentially support a diverse seaweed flora. The Faroese archipelago, which is more or less equidistant from Iceland, Norway and northern Great Britain, is suitable for colonization both by species that thrive in cooler areas north of the Faroe Islands, as well as species from warmer areas south of the islands (Brodie & Nielsen, 2005).

Systematic studies of the seaweed flora in Iceland began in the 19th century (Lyngbye, 1819; Kjellman, 1879; Strömfelt, 1886a, 1886b). The history of *Porphyra* research in Iceland (summarized in Table 2.1) began with Kjellman (1879), who recorded two foliose species of Bangiales, followed by Strömfelt (1886b) who listed four species, three of which he referred to the genus *Diploderma*. Of the species recorded by Jónsson (1901), *Porphyra coccinea* was transferred to *Porphyropsis* (Rosenvinge, 1909) and belongs to the Erythropeltidales; it is therefore omitted from Table 2.1. Over 60 years passed before the next contribution, in which Caram & Jónsson (1972) listed five species of *Porphyra*. The most recent checklist of the seaweeds of Iceland (Gunnarsson & Jónsson, 2002), recordes six foliose Bangiales species, which included *P. thulaea* Munda & Pedersen. *Porphyra abyssicola* Kjellman and *P. leucosticta* Thuret were both recorded from the intertidal by Munda (1979) but not included by Gunnarsson & Jónsson (2002), as specimens were not available for examination at the time. A study of Munda's material concluded that all specimens of *P. abyssicola* were misidentified (J. Brodie, personal observation). *Porphyra leucosticta* has since been recognized in the flora by K. Gunnarsson and R. Nielsen (Personal observations).

Porphyra research in the Faroe Islands (Table 2.2) began with Lyngbye (1819), but the best part of a century elapsed before further records were made by Simmons (1897) and Børgesen (1902). Foliose Bangiales were not studied again until Irvine (1982), who listed five species (Table 2.2); he did not himself record *P. linearis* but based on Børgesen's (1902) observations, concluded that the species would be there in winter and probably spring. The next studies were by Brodie *et al*. (2001) and Brodie & Nielsen (2005) who, in addition to listing seven species, concluded that there were at least three unidentified *Porphyra* species in the flora. One of these was later found to be conspecific with *Boreophyllum birdiae* (as *Porphyra birdiae*), described from Nova Scotia, Canada and also reported from Norway (Neefus *et al*., 2002; Brodie & Nielsen, 2005). The most recent findings have added *Pyropia elongata* (as *Porphyra rosengurttii:* Brodie *et al*., 2008; Neefus & Brodie, 2009). Given that *Boreophyllum birdiae* has not been reported further south than the Faroe Islands in the Northeast Atlantic (J. Brodie, personal observations), this species, along with *Wildemania amplissima* and *W. miniata* (both formerly classified in *Porphyra*), can be regarded as northern elements of the North Atlantic flora.

The aim of this paper is to identify species of Bangiales from Iceland and the Faroe Islands and determine their generic relationships using molecular sequence data. Apart from a few foliose Bangiales specimens for which molecular sequence data are available (Brodie & Nielsen, 2005; Brodie *et al*., 2008), species identifications from the Faroe Islands and Iceland have previously been based primarily on morphology. Here we base identifications primarily on *rbc*L sequences, supplemented by a more restricted *cox*1 sequence dataset. The chloroplast gene *rbc*L, which codes for the large subunit of the enzyme ribulose-1,5-bisphosphate carboxylase oxygenase, is widely used to delineate species within the red algae (Neefus *et al*., 2008). The mitochondrial gene *cox*1, which codes for the protein cytochrome c oxidase subunit 1, has proved useful for identification at the species and intra-species level in red algae, including foliose bangiophytes (Saunders, 2005; Robba *et al*., 2006). We make references to specimens from other parts of the world and we discuss the foliose Bangiales flora in Iceland and the Faroe Islands in a wider geographical context.

Until recently, foliose species in the Bangiales have been referred to a single genus, *Porphyra*. However, a molecular study by Sutherland *et al.* (2011) splits them into eight genera. Here we present our results in the context of this new classification, which includes the genera *Boreophyllum*, *Pyropia* and *Wildemania*, as well as *Porphyra sensu stricto*.

Materials and methods

Collections

Comprehensive foliose Bangiales collections were made in Iceland as part of a general macroalgal survey initiated in 1999 (southwest coast) and continued in 2005 (west and northwest coasts), 2006 (north coast) and 2007 (northeast and east coasts). In total,125 stations were sampled within the intertidal and shallow subtidal by SCUBA divers (Appendix A). Herbarium specimens used in this work have been deposited in the Natural History Museum in Reykjavík (ICEL), with duplicates in the Botanical Museum in Copenhagen (C) and the Natural History Museum, London (BM).

Porphyra collections in the Faroe Islands were made primarily from Trongisvágsfjord, Suðuroy (southeast), in the autumn (October–November), winter (December–January), spring (April–May), and summer (July) 2005-2006, and again in November 2007 and January 2008. One collection was from Hvannhagi, Suðuroy (southeast) in July 2004, one from Kvívík, Streymoy (northwest) in June 2008 and one from Saksun, Streymoy (northwest), also in June 2008. The collections from Trongisvágsfjord, Hvannhagi and Saksun were intertidal, while the collection from Kvívík was subtidal and collected by SCUBA divers. The collections used have been deposited in the Faroese Museum of Natural History in Tórshavn (NGS), with duplicates in Albion Hodgdon Herbarium (NHA) at the University of New Hampshire. Details of the specimens used in the analysis, including collections from other regions of the North Atlantic and northeast Pacific, are presented in Appendix A.

Identification

Collections from Iceland and the Faroe Islands comprised ca. 1000 foliose Bangiale*s* specimens each. The specimens were initially grouped into possible species by morphology, based on previous experience and literature (Bird & McLachlan, 1992; Brodie *et al*., 2001; Brodie & Irvine, 2003; Brodie & Nielsen, 2005). Specimens from each initial morphological grouping were then selected for DNA extraction and molecular analysis (Appendix A), yielding chloroplast *rbc*L and mitochondrial *cox*1 sequence data that could be used for identification by comparison with sequences already deposited in GenBank.

DNA extraction, PCR amplification and sequencing

The material was processed partly at the Natural History Museum, London (NHM) and partly at the University of New Hampshire, USA (UNH), using different methods as described below. At NHM, DNA was extracted from ca. 4–5 mm^2 of herbarium or silica-gel-preserved material using a modified cetyl trimethyl ammonium bromide (CTAB) microextraction protocol (Rogers *et al*., 1994). Extracted DNA was purified, after precipitation in isopropanol using a GFX PCR DNA purification kit (GE Healthcare Ltd., UK), following the manufacturer's protocols. The *rbc*L region was amplified using the forward primer KitoF1 (5'- ATGTCTCAATCCGTAGAATCA-3', From GenBank entries and the reverse primer JrSR (5'-AAGCCCCTTGTGTTAGTCTCAC-3': Broom *et al.,* 2010). The *cox*1 region was amplified using the forward primer GazF1 (5'-TCAACAATCATAAAGATATTGG 3': Saunders, 2005) and the reverse primer GazR1 (5'-ACTTCTGGATGTCCAAAAAAYCA-3': Saunders, 2005). Each PCR run contained 2.5 μL NH_4 RXN buffer, 1.5 μL $MgCl_2$, 0.5 μL Taq (all from BIOTAQ DNA Polymerase kit, Bioline Ltd., UK), 0.5 μL dNTP stock, 1 μL 10 μM forward primer, 1 μL 10 μM reverse primer, 17.5 μL H_2O and 1 μL of DNA template. The PCR reaction was run on a Techne Thermal Cycler model FT Gene 5D (Fisher Scientific, Loughborough, UK). PCR amplification profile followed Robba *et al.* (2006). The PCR products were purified and sequenced as described by Walker *et al.* (2009).

At UNH, DNA was extracted using a Puregene ™ Isolation Kit per manufacturer's instructions. The *rbc*L region and *rbc*L-*rbc*S intergenic spacer were amplified using forward primers F1 (5'- ATGTCTCAATCCGTAGAATCACG-3'), F67 (5'-TACGCTAAAATGGGTTACTG-3': Teasdale *et al.*, 2002), F461 (5'-GTCCTGCAACTGGATTGATTGT-3'), F870 (5'-TGACATGATTTTACATTTACATAGAC-3'), and RBCL5RC (5'-GTGGTATTCATGCTGGTCAAA-3' the reverse complement of RBCL in Klein *et al.*, 2003) and reverse primers R502 (5'-TATCCATACGCTCACGTTCTACAA-3'), R901 (5'-TACCAGCTCTATGTAAATGTAAAA-3'), R1312 (5'-GGCCTTCATTTCTTGCCATAAC-3'), and RBCSPC (5'-CACTATTCTATGCTCCTTATTKTTAT-3': Teasdale *et al.*, 2002). Primers F1, F461, F870, R502, R901 and R1312 were designed using DNASTAR Lasergene PrimerSelect Version 7.2.1 (1) and are published for the first time here. The *cox*1 region was amplified using the same primers as described in the previous NHM section except that a modified pair of primers was used for *Porphyra purpurea*; these were forward primer C1PPUR-F138 (5'-GCTAGCCCAACCAGGTAATCAACT-3') and reverse primer C1PPUR-R749

(5’-TCCGGGTGTCCAAAGAATCAG-3’). Again, the primers were designed using DNASTAR Lasergene PrimerSelect Version 7.2.1 (1) and are published for the first time here. PCR was performed as described in Bray *et al.* (2006). The PCR products were gel-purified by gel electrophoresis on low melting point agarose (Invitrogen, Life Technologies, UltraPure™), and the agar plugs digested with agarase (Sigma, St Louis, MO). The amplified and purified partial *rbc*L products were sequenced with an ABI 373 Automated Sequencer at the University of New Hampshire’s Hubbard Center for Genome Sciences.

Sequence alignment

The raw sequence chromatograms were assembled and proofread in SeqMan Pro v. 7.2.1 (1) [DNASTAR inc. 2006] and the sequences were aligned using Muscle (Edgar, 2004), implemented in the Seaview version 4 platform (Gouy *et al.*, 2010). Twenty-nine foliose Bangiales *rbc*L sequences, including 16 from Iceland, eight from the Faroe Islands, two from Greenland, one from Norway, one from Denmark and one from Pacific Canada, were aligned with 25 foliose and filamentous Bangiales sequences downloaded from GenBank. *Phycodrys rubens* and *P. riggii rbc*L sequences from GenBank were used as an outgroup. The alignment comprised 56 *rbc*L sequences with a length of 1333 base pairs (bp).

Eleven *cox*1 sequences of foliose Bangiales species, including three from Iceland, six from the Faroe Islands, one from North Atlantic USA and one from North Atlantic Canada, were aligned with ten foliose Bangiales sequences downloaded from GenBank and one *Corallina officinalis* sequence, also from GenBank, which was used as the outgroup. The alignment comprised 22 *cox*1 sequences with a length of 454 bp.

Floridean red algal species were used to form the outgroup in both the *cox*1 and the *rbc*L analyses. The outgroup species were considered to be distantly enough related to the Bangiales to form a clear outgroup but close enough to allow for inference from the data.

Phylogenetic analyses

Maximum Likelihood (ML) and Bayesian Inferences (BI) analyses were performed for both the *rbc*L and the *cox*1 data sets. ML analysis was carried out using PhyML (Guindon & Gascuel, 2003), implemented in the Seaview version 4 platform (Gouy *et al.*, 2010). The BI analysis was carried out using MrBayes version 3.1.1 (Ronquist & Huelsenbeck, 2003). The ML analyses for the *rbc*L and *cox*1 dataset were run using the GTR + Γ model, with 1000 bootstrap replicates. Prior to the BI analysis MrModeltest version 2.3 (Nylander, 2004) was employed to determine the preferred model. The BI analysis for the *rbc*L data was run with the GTR + Γ model for 2 000 000 generations with four chains. The software tool Tracer v1.4 (Rambaut & Drummond, 2007) was used to determine the burn-in. The first 2001 trees of 20 000 were discarded and the remaining 17999 were used to estimate the posterior probabilities (PP) from the 50 % majority rule consensus of the kept tree. The GTR + I + Γ model was implemented in the *cox*1 BI analysis, which was run for 1 000 000 generations with four chains. The parameters converged after 100 000 generations and the burn-in was set to 1001. The remaining 8999 trees were used to estimate the PP from the 50 % majority rule consensus of the kept tree. Estimates of evolutionary divergence between the sequences were conducted using the maximum composite likelihood method in MEGA 4 (Tamura *et al.*, 2007).

Results

Diversity of the foliose Bangiales in Iceland

A total of 45 *rbc*L and 12 *cox*1 sequences were successfully obtained from the Icelandic collection of foliose Bangiales species (Appendix A). Based on the sequence data, four genera (sensu Sutherland *et al*., 2011) of Bangiales were recognized: *Boreophyllum*, *Porphyra*, *Pyropia* and *Wildemania*. These were represented by 11 species (Table 2.1). *Pyropia* "*leucosticta*" A is an undescribed species that has been confused with *Py. leucosticta* (Thuret) Neefus et J. Brodie. *Pyropia thulaea* was not found among the specimens studied here (which were collected between 1999 and 2007) but Brodie *et al*. (2008) verified its presence in Iceland with molecular data, based on an earlier collection. *Boreophyllum birdiae* and *Pyropia njordii sp. nov.* (described below: this species has previously been confused with *Porphyra linearis*) are new records for Iceland. One species matched the description of *Porphyra abyssicola*. This alga has been regarded by some as a synonym of *Porphyra miniata* (Rosenvinge, 1893), now transferred to *Wildemania*. However, as our specimen was genetically distinct from *W. miniata*, we decided to refer to it as *W. abyssicola* and to make the new combination *W. abyssicola* (see below).

The gross morphology of the 11 foliose Bangiales species from Iceland is illustrated in Figs 2.1-2.11. *Boreophyllum birdiae* (Fig. 2.1), *Porphyra umbilicalis* (Fig. 2.6), *Wildemania amplissima* (Fig. 2.10) and *W. miniata* (Fig. 2.11) each showed pronounced colour variation, and *P. umbilicalis* in particular showed a pronounced variation in shape (Fig. 2.6). Only one specimen of *P. dioica* was verified with molecular data in the Icelandic collection (Fig. 2.2), and *Pyropia thulaea* is illustrated by the specimen Brodie *et al*. (2008) verified with molecular data (Fig. 2.8).

Diversity of the foliose Bangiales in the Faroe Islands

A total of eight *rbc*L and 32 *cox*1 sequences were successfully obtained from the Faroese foliose Bangiales collection (Appendix A). As in Iceland, four genera were recognized (*Boreophyllum*, *Porphyra*, *Pyropia* and *Wildemania*) and 11 species, but the composition was slightly different (Table 2.2). *Pyropia njordii* and *Porphyra* sp. FO are new records for the Faroe Islands. *Porphyra* sp. FO, which has only been reported from the Faroe Islands, was observed only once and we are therefore reluctant to describe it formally as a new species.

Molecular analyses

The *rbc*L sequence alignment had 415 variable sites and 312 parsimony-informative characters. Based on the available *rbc*L sequences from the North Atlantic including Iceland and the Faroe Islands, a total of 22 foliose Bangiales species were recognized (Fig. 2.12). The entire foliose Bangiales species diversity known from Iceland was represented in the *rbc*L tree, while the Faroese diversity was repreented by *Boreophyllum birdiae*, *Porphyra dioica, Porphyra* sp. FO*, Pyropia elongata*, *Py*. "*leucosticta*" A and *Py*. *njordii* (Fig. 2.12). Partial *rbc*L sequences were obtained from *Porphyra linearis, P. purpurea, P. umbilicalis, Wildemania amplissima* and *W. miniata* samples from the Faroe Islands (data not shown), but because they were only c. 400 bp long they were not included in the analysis.

ML analysis suggested a division of the North Atlantic foliose Bangiales flora into four major clades (Fig. 2.12). Clade I comprised the *Porphyra* species. The Pacific *Boreophyllum aestivalis* (S.C. Lindstrom et Fredericq) S.C. Lindstrom and North Atlantic

B. birdiae comprised clade II, which had full bootstrap and PP support. Clade III, *Wildemania*, had bootstrap support of 75% and 1.00 PP. *Boreophyllum* and *Wildemania* were resolved as sister clades but little support (<50% bootstrap and 0.52 PP). The *Pyropia* species formed clade IV with high bootstrap (96%) and PP (1.00) support. The filamentous species *Minerva aenigmata* W.A. Nelson and *Dione arcuata* W.A. Nelson from New Zealand and the foliose species *Fuscifolium papenfussii* (V. Krishnamurthy) S.C. Lindstrom from Alaska were basal to clades II–IV. The deeper branches, however, were not well supported.

Pyropia sp. DK was distinct genetically but it was observed only once and we are therefore reluctant to describe it as a new species. *Pyropia* "*spatulata*", *Py.* "*collinsii*", *Py.* "*novae-angliae*" and *Py.* "*stamfordensis*" are all undescribed species from northeast USA.

Intraspecific sequence variation was observed within seven species (Table 2.3 and Fig. 2.12). Some recognized species were scarcely separated or inseparable in their *rbc*L sequences. For example, the sequence difference between Pacific *Porphyra mumfordii* (n=1) and North Atlantic *Porphyra linearis* (n=3) was at most only 5 bp (0.4%), while between Pacific *Wildemania cuneiformis* (n=1) and North Atlantic *W.* amplissima (n=5) it was 0 or 1 bp (0.1%); between Pacific *W. variegata* (n=1) and *W. miniata* (n=8) there was a maximum of 5 bp difference (0.3%). Figure 2.12 shows *W. amplissima* to be paraphyletic, with *W. cuneiformis* nested within it, and *W. miniata* to be paraphyletic, with *W. variegata* nested within.

The *cox*1 sequence alignment had 189 variable sites and 142 parsimony-informative characters. Ten foliose Bangiales species were resolved in the phylogenetic analyses and presented in the ML phylogram with bootstrap values and PP from the BI analysis (Fig. 2.13). At the highest level, *Porphyra dioica, P. purpurea* and *P. umbilicalis* formed an unsupported clade, while *Boreophyllum birdiae, Pyropia elongata*, *Py.* "*leucosticta*" A, *Py.* "*leucosticta*" B, *Py. njordii, Wildemania amplissima* and *W. miniata* comprised a second, poorly supported clade (0.71 PP but bootstrap <50%).

Poprhyra linearis (n=3) and *P. umbilicalis* (n=30) were indistinguishable but together formed a clade with 99% bootstrap support and 1.00 PP (Fig. 2.13). The sequence variation within the clade was 6 bp (0.9%). Table 2.3 shows a comparison in pairwise distance in the *cox*1 and partial *rbc*L sequences. Both genes showed a large pairwise distance for both *P. linearis* and *P. umbilicalis* to *P. dioica*. The distance was, however, much less between *P. linearis* and *P. umbilicalis*. The pairwise distance in *rbc*L between *P. linearis* and *P. umbilicalis* was consistent (0.8%) while in *cox*1, the distance was between 0.2 and 0.4%.

*Cox*1 sequences from *P. dioica* AMM69 (JN847311) from the Faroe Islands and *P. dioica* JB347 (DQ191340) from the type location in England differed by only 1 bp (0.2%), as did *P. purpurea* AMM07USA08 (JN847317) from New Hampshire, USA and *P. purpurea* AF114794 from Nova Scotia, Canada. *Boreophyllum birdiae* (n=7)*,* *Wildemania amplissima* (n=4) and *W. miniata* (n=2) showed no intraspecific variation and are therefore represented in the phylogram by one sequence each. Only one *cox*1 sequence was available for *Py. njordii*.

Specimens initially identified as *Py. leucosticta* on the basis of morphology were not resolved as monophyletic (Fig. 2.13). One highly supported clade comprised specimens that we refer to here as *Pyropia* "*leucosticta*" A, namely AMMSF1240 (AM943398) and AMM06SF2269 (JN847324) from the Faroe Islands, together with JB372 (JN847325) from Iceland. The observed sequence variation within *Py.* "*leucosticta*" A (n=4) was between 1 and 7 bp (0.2 and 1.6%). In contrast, a second alga identifiable from morphology as *Py. leucosticta*, collected from the British Isles and referred to here as *Pyropia* “*leucosticta*” B (DQ442890), was resolved as sister species to *Py. elongata*. Within *Py. elongata*, AM943399 from the Faroe Islands and DQ191335 from the British Isles differed by just 1 bp (0.2%). Together, *Py. elongata* and two *Py.* “*leucosticta*” species formed a very well-supported clade (Fig. 2.13).

Taxonomic treatments

***Pyropia njordii* Mols-Mortensen, J. Brodie & Neefus *sp. nov*.**

DESCRIPTIO: *Lamina* monostromatica, e haptero exoriente sed stipite minute instructa, 4-20 cm longa, 1-12 cm lata, 27.5-47.5 cm crassa, obovata, falcata vel elongata, interdum laciniata, leviter plicata, basi leviter vel profunde cordata, a viso superficiali cellulis vegetativis 12.5-20 *μ*m longis, 7.5-12.5 *μ*m latis, in vivo brunnescens vel porphyrea vel carnea vel rosea, in sicco aliquot purpurea. Thalli monoecii; gametangii masculini 12.5-22.5 *μ*m longi, 12.5-15 *μ*m lati, spermatiis 64 in massis 8 x 8 dispositis; zygotosporangii 15-20 *μ*m longi, 12.5-20 *μ*m lati, zygotosporis 16 in massis 4 x 4 dispositis. Numero GenBankii holotypi: *rbc*L: JN847259; *cox*1: JN847326.

DESCRIPTION: Gametangial blade (Fig. 2.14) foliose, monostromatic, arising from a minute discoid holdfast and minute but distinct stipe, 4-20 cm long, 1-12 cm wide and 27.5-47.5 *μ*m in transverse section, obovate, falcate to elongate, occasionally laciniate, slightly ruffled; base slightly to deeply cordate; apex sometimes subacute; vegetative cells 12.5-20 *μ*m long, 7.5-12.5 *μ*m wide in surface view (Fig. 2.15). Colour pale–brown to red–brown and pale to dark pink when fresh, sometimes with a hint of purple when dried. Monoecious, with pale yellow male gametangial sori and dark pink to bronze–red zygotosporangial sori on separate sectors of blade; male gametangial packets in 8 tiers of 8 (64 spermatia), 12.5-15 μm x 12.5-22.5 μm in surface view (Figs 2.16, 2.19); zygotosporangial packets in 4 tiers of 4 (16 zygotospores), 12.5-20 μm x 15-20 μm insurface view (Figs 2.17, 2.20), each dividing periclinally to give 4 cells in TS, making 16 zygotospores in each packet. GenBank numbers of holotype: *rbc*L: JN847259; *cox*1: JN847326.

HOLOTYPE: BM001032349 (Fig. 2.14), collected at Tjaldavík, Trongisvágsfjørður, Suðuroy, Faroe Islands (61˚31'88''N, 006˚46'73''W) on 27th April 2006 by Agnes Mols–Mortensen. The specimen was epilithic in the low intertidal zone on an exposed shore. ISOTYPES: University of New Hampshire, Albion Hodgdon Herbarium (NHA), USA: NHA552091 (AMM06SF1204, AMM06SF1205); C: AMM06SF1206, AMM06SF1262; ICEL: 11437 1 (AMM06SF1207), 11438 1 (AMM06SF1233, mid-intertidal); BM: BM001032348 (AMM06SF1226, mid-intertidal); Faroese Museum of Natural History, Faroes (NGS): AMM06SF1254 (Fig. 2.14).

PARATYPE: ICEL: 11439 1 (JB422); from Stokksnes, Iceland, 20th June 2007, leg. K. Gunnarsson, S. Egilsdóttir (Fig. 2.7).

ETYMOLOGY: The specific epithet is named after Njörðr (known as Njørður and Njörður in the Faroe Islands and Iceland, respectively) who was the god associated with sea and weather in Norse mythology.

HABITAT AND SEASONALITY: *Pyropia njordii* was found in the mid- to low intertidal, growing mostly on rock but also on mussels and barnacles. It was collected from Trongisvágsfjord in the Faroe Islands in April and May. In Iceland, the species was found in June at Hrísey, Víkurbakki and Merakkaslétta on the north coast, Vattarnes and

Reyðarfjörður on the east coast, and Stokksnes on the southeast coast. In Greenland, the species is known from Hunde Ejlande, near Aasiaat on the west coast, where it was collected in September. In New England, USA, the species is reported from Hampton Beach, New Hampshire, in April and June, and from the Isles of Shoals, New Hampshire and Bar Harbor, Maine, in May (Shelly Dare Smith personal communication).

DISTRIBUTION: North Atlantic: Faroe Islands, Iceland, Greenland, New England, USA and Nova Scotia, Canada. An *rbc*L sequence in GenBank (AF168673) identified as *Porphyra linearis* (Müller *et al*., 2001) matched *Py. njordii*. The sequence was based on a culture (CCAP 1379/1) that was initiated by Chen in 1969 from collections at Sandy Cove, Halifax, Nova Scotia, Canada. The Müller *et al*. (2001) GenBank sequence was not included in our *rbc*L analysis because it was only 1026 bp long.

New combination

Wildemania abyssicola* (Kjellman) Mols-Mortensen & J. Brodie *comb. nov.

BASIONYM: *Porphyra abyssicola* Kjellman (1883), *Kongaliga Svenska Vetenskaps Akademiens Handlingar*, 20: 240.

TYPE LOCALITY: Norwegian Arctic Sea.

DISTRIBUTION: Greenland (Davis Strait): Maniitsoq; Iceland (Munda, 1979); Norway: Nordland, Finnmark, Maasö and Gjesvær; Russia: Lappland (Murman Sea), White Sea (Kjellman, 1883).

REMARKS: *Wildemania abyssicola* was described by Kjellman (1883, as *Porphyra*) as a monostromatic, carmine- to violet-coloured species, found in deep waters in the Norwegian Arctic Sea, Murman Sea, White Sea and the west coast of Greenland at Sukkertoppen (Maniitsoq). Kjellman (1883) mentioned that the species was dioecious but that specimens with both male and female reproductive structures were also observed. It was later synonymized with *P. miniata* by Rosenvinge (1893) but not everyone agreed with this transfer (Hus, 1902; Scagel, 1957; Rueness, 1977; Munda, 1979), and Brodie *et al*. (1998) noted that *P. abyssicola* was a species that needed further attention. Based on morphological and habitat similarities between the molecularly distinct species in the Icelandic material studied here and Kjellman's description of *Wildemania abyssicola*, we are confident that they are the same species and that *W. abyssicola* should not be regarded as a synonym of *W. miniata*. An *rbc*L sequence from authentic *W. abyssicola* material is critical for this to be verified but despite searches in the Uppsala (UPS), Stockholm (S) and Leiden (L) herbaria, we have not yet been able to locate Kjellman's material. Munda (1979) reported *W. abyssicola* as common in the intertidal all around Iceland, growing on *Mastocarpus stellatus*. However, her report of the species does not correspond with other findings of *W. abyssicola* in the deep subtidal zone (Kjellman, 1883; this paper).

Discussion

Our results confirm that there is considerably more diversity than previously reported in the northern parts of the North Atlantic. Brodie *et al*. (2008) reported 15 foliose Bangiales species for the North Atlantic. An additional ten species are now reported (*Porphyra* sp. FO, *Pyropia katadae*, *Py.* "*leucosticta*" B, *Py. njordii*, *Py.* "*collinsii*", *Py.* "*novae-angliae*", *Py.* "*spatulata*", *Py.* "*stamfordensis*", *Py.* sp. DK and *Wildemania abyssicola*), so that in total 25 foliose Bangiales species are known from the North Atlantic (Table 2.4). These represent four of the eight foliose Bangiales genera that are currently recognized (*Boreophyllum*, *Porphyra*, *Pyropia* and *Wildemania*). Eighteen of the species have been reported from the northwest Atlantic (Canada, USA) and 17 from the northeast Atlantic (Faroe Islands, Norway, Denmark, UK and Helgoland). The diversity is therefore similar for the two areas but the species composition is different. Several species that occur in the northwest Atlantic have not been reported from the northeast Atlantic (*Py. katadae*, *Py. yezoensis*, *Py.* "*collinsii*", *Py.* "*novae-angliae*", *Py.* "*spatulata*", and *Py.* "*stamfordensis*"), while others occur in the northeast but not the northwest (*Porphyra yezoensis* sensu Kornmann [see Brodie *et al*., 2008], *Porphyra* sp. FO, *Py. drachii*, *Py.* "*leucosticta*" B and *Py.* sp. DK). *Boreophyllum birdiae* and *Py. njordii* are new records for Iceland, *Py. njordii* and *Porphyra* sp. FO are new records for the Faroe Islands. So far, *Porphyra* sp. FO and *Pyropia* sp. DK are only reported from the Faroe Islands and Denmark, respectively.

Some recent additions to the North Atlantic foliose Bangiales flora (*Py. katadae*, *Py. suborbiculata*, *Py. yezoensis*) are introductions from other areas (Neefus *et al*., 2008) while other species may be hitherto overlooked components of the natural flora (*Py. njordii*, *Py.* "*collinsii*", *Py.* "*novae-angliae*", *Py.* "*spatulata*", *Py.* "*stamfordensis*"). Until more specimens are found of *Porphyra* sp. FO and *Py.* sp. DK (currently represented by only one collection each), it will not be possible to conclude whether these species are recent introductions or native to the northeast North Atlantic.

Intraspecific sequence variation in the *rbc*L dataset was between 1 bp (0.1%) and 5 bp (0.4%) (Table 2.5), which is comparable to the level of diversity (1-7 bp) observed in *Py. columbina* (as *P. columbina*) by Nelson & Broom (2010). *Porphyra linearis*, *Wildemania amplissima* and *W. miniata* from Iceland have similar *rbc*L sequences to North Pacific *P. mumfordii*, *W. cuneiformis* and *W. variegata*, respectively. The difference within each of these species pairs are comparable to levels of intraspecific variation elsewhere. *Wildemania amplissima* and *W. cuneiformis* have been considered to be a pair of sibling species, as have *W. miniata* and *W. variegata* (Lindstrom & Cole, 1993). However, based on *rbc*L sequence data, each pairs could be considered conspecific. Sequences from type or authentic material should be obtained from these four species to determine their status.

Although the *cox*1 marker is useful for identifying foliose Bangiales species (Robba *et al.*, 2006; Brodie *et al.*, 2008), it does not separate *Porphyra linearis* and *P. umbilicalis*. These two are known to be closely related, but their status as two separate species is well documented in the literature based on both *rbc*L and SSU data (Klein *et al.*, 2003; Brodie *et al.*, 2007; this paper). Furthermore, *Porphyra linearis* and *P. umbilicalis* are the only *Porphyra* species, for which there are data, that *cox*1 does not separate. The presence of the same mitochondrial *cox*1 in both species suggests recent hybridization between these two taxa.

It seems unlikely that our study has exhausted the diversity of the North Atlantic foliose Bangiales flora and more intense sampling, together with molecular identification of herbarium material, will almost certainly add further species, as well as reveal valuable information about species distribution.

Table 2.1. History of foliose Bangiales collections in Iceland.

Reference	Species
Kjellman (1879)	*Porphyra vulgaris* Harvey
	P. laciniata C. Agardh
Strömfelt (1886b)	*Diploderma amplissima* Kjellman
	D. miniatum (C. Agardh) Kjellman
	D. tenuissimum Strömfelt
	P. laciniata (Lightfoot) C. Agardh f. *typica*
	P. laciniata f. *umbilicalis* (Linnaeus) Kleen
Jónsson (1901)[1]	*P. umbilicalis* (Linnaeus) J. Agardh f. *typica*
	P. umbilicalis f. *laciniata* [no authority given]
	P. umbilicalis f. *linearis* [no authority given]
	P. miniata (C. Agardh) C. Agardh f. *typica*
	P. miniata f. *amplissima* (Kjellman) Rosenvinge
Caram & Jónsson (1972)	*P. helenae* A. D. Zinova
	P. linearis Greville
	P. miniata (C. Agardh) C. Agardh
	P. purpurea (Roth) C. Agardh
	P. umbilicalis (Linnaeus) J. Agardh
Gunnarsson & Jónsson (2002)[2]	*Porphyra amplissima* (Kjellman) Setchell & Hus ex Hus
	P. dioica J. Brodie & L. Irvine
	P. linearis Greville
	P. miniata (C. Agardh) C. Agardh
	P. purpurea (Roth) C. Agardh
	P. umbilicalis (Linnaeus) Kützing
This paper	*Boreophyllum birdiae* (Neefus et A. C. Mathieson) Neefus
	Porphyra dioica J. Brodie & L. Irvine
	P. linearis Greville
	P. purpurea (Roth) C. Agardh
	P. umbilicalis Kützing
	Pyropia '*leucosticta*' A
	Pyropia njordii Mols-Mortensen, J. Brodie & Neefus *sp. nov.*
	Pyropia thulaea (Munda et P. M. Pedersen) Neefus
	Wildemania abyssicola (Kjellman) Mols-Mortensen & J. Brodie *comb. nov.*
	W. amplissima (Kjellman) Foslie
	W. miniata (C. Agardh) Foslie

[1] *Porphyra coccinea* J. Agardh was included by Jónsson (1901) but later transferred to *Porphyropsis coccinea* (J. Agardh ex Areschoug) Rosenvinge.

[2] *Porphyra thulaea* Munda & Pedersen was included by Gunnarsson & Jónsson (2002) as a synonym of *Porphyra amplissima* (cf. Brodie *et al.*, 1998).

Table 2.2. History of foliose Bangiales collections in the Faroe Islands

Reference	Species
Lyngbye (1819)	*Porphyra umbilicalis* (as *Ulva umbilicalis* Linnaeus) for the Faroes [Lyngbye only mentiones 'varietas as saxa maritime probe Qvalböe Færoæ, copiose']
	P. purpurea f. *elongata* (as *U. purpurea* f. *elongata* Lyngbye).
Simmons (1897)[1]	*Porphyra laciniata* (Lightfoot) C. Agardh f. *linearis* Greville
	P. laciniata f. *umbilicalis* (Linnaeus) Kleen
	P. laciniata f. *vulgaris* Harvey
	P. leucosticta Thuret
	P. miniata (Lyngbye) C. Agardh
Børgesen (1902)[1]	*P. leucosticta* Thuret *in* le Jolis
	P. miniata (C. Agardh) C. Agardh f. *typica* Rosenvinge
	P. miniata f. *amplissima* (Kjellman) Rosenvinge
	P. miniata f. *abyssicola* (Kjellman) Rosenvinge
	P. umbilicalis (Linnaeus) J. Agardh f. *laciniata* (C. Agardh) Le Jolis
	P. umbilicalis f. *linearis* (Greville) Le Jolis
	P. umbilicalis f. *umbilicalis* (Linnaeus) Kleen
Irvine (1982)	*Porphyra leucosticta* Thuret
	P. linearis Greville
	P. miniata (C. Agardh) C. Agardh
	P. purpurea (Roth) C. Agardh
	P. umbilicalis (Linnaeus) J. Agardh
Brodie *et al.* (2001) and Brodie & Nielsen (2005)	*P. amplissima* (Kjellman) Setchell & Hus
	P. dioica J. Brodie & L.M. Irvine
	P. leucosticta Thuret in Le Jolis
	P. linearis Greville
	P. miniata (C. Agardh) C. Agardh
	P. purpurea (Roth) C. Agardh
	P. umbilicalis (Linnaeus) Kützing
	Three unidentified species
This paper	*Boreophyllum birdiae* (Neefus & A.C. Mathieson) Neefus
	Porphyra dioica J. Brodie & L.M. Irvine
	P. linearis Greville
	P. purpurea (Roth) C. Agardh
	P. umbilicalis Kützing
	Porphyra sp. FO[2]
	Pyropia elongata (Kylin) Neefus & J. Brodie
	Py. '*leucosticta*'A
	Py. njordii Mols–Mortensen, J. Brodie & Neefus, *sp. nov.*
	Wildemania amplissima (Kjellman) Foslie
	W. miniata (C. Agardh) Foslie

[1] *Porphyra coccinea* J. Agardh was included by Simmons (1897) and Børgesen (1902) but later transferred to *Porphyropsis coccinea* (J. Agardh *ex* Areschoug) Rosenvinge

[2] FO = Faroe Islands

Table 2.3. Pairwise distances between *P. linearis*, *P. umbilicalis* and *P. dioica*, based on *cox*1 (537 bp) and *rbc*L (367 bp at the 3' end) sequences. Key: *cox*1/*rbc*L.

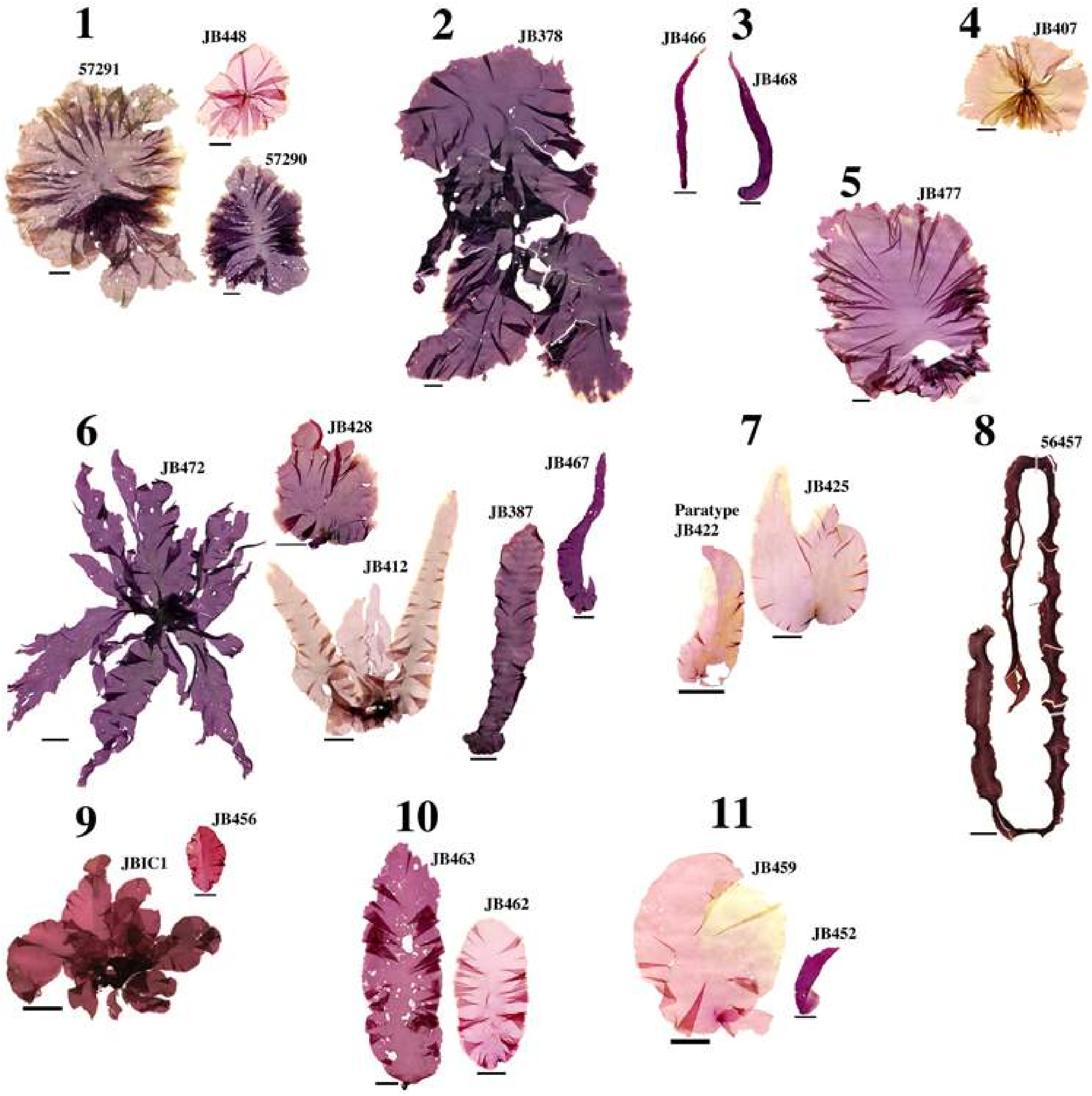
	1	2	3	4	5
P. linearis AMM71					
P. linearis AMM73	0.000/0.000				
P. linearis AMM83	0.000/0.000	0.000/0.000			
P. umbilicalis 57249	0.002/0.008	0.002/0.008	0.002/0.008		
P. umbilicalis JB435	0.004/0.008	0.004/0.008	0.004/0.008	0.002/0.000	
P. dioica AMM69	0.087/0.036	0.087/0.036	0.087/0.036	0.087/0.039	0.089/0.039

Table 2.4. The 25 foliose Bangiales species recorded from the Northwest Atlantic (from Maine to Long Island; *Pyropia njordii* has also been observed in Nova Scotia, Canada), Northeast Atlantic, Iceland and the Faroe Islands. + = present – = absent.

Species	**Northwest Atlantic**	**Northeast Atlantic**	**Iceland**	**Faroes**
Boreophyllum birdiae (Neefus et Mathieson) Neefus	+	+	+	+
Porphyra dioica J. Brodie et L. Irvine	-	+	+	+
Porphyra drachii J. Feldmann	-	+	-	-
Porphyra linearis Greville	+	+	+	+
Porphyra purpurea (Roth) C. Agardh	+	+	+	+
Porphyra umbilicalis Kützing	+	+	+	+
Porphyra ‘yezoensis’ sensu Kornmann	-	+	-	-
Porphyra sp. FO	-	+	-	+
Pyropia elongata (Kylin) Neefus et J. Brodie	+	+	-	+
Pyropia katadae (A. Miura) M.S. Hwang, H.G. Choi, N. Kikuchi et M. Miyata	+	-	-	-
Pyropia ‘*leucosticta*’A	+	+	+	+
Pyropia ‘*leucosticta*’B	-	+	-	-
Pyropia njordii sp. nov. A. Mols-Mortensen, J. Brodie et Neefus	+	+	+	+
Pyropia olivii (Orfanidis, Neefus et Bray) J. Brodie et Neefus	+	+	-	-
Pyropia suborbiculata (J. Coll et J. Cox) J.E. Broom, H.G. Choi, M.S. Hwang et W.A. Nelson	+	+	-	-
Pyropia thulaea (I.M. Munda et P.M. Pedersen) Neefus	-	-	+	-
Pyropia yezoensis (Ueda) M.S. Hwang et H.G. Choi f. *yezoensis*	+	-	-	-
Pyropia yezoensis (Ueda) M.S. Hwang et H.G. Choi f. *narawensis* A. Miura	+	-	-	-
Pyropia sp. ‘*collinsii*’	+	-	-	-
Pyropia sp. ‘*novae-angliae*’	+	-	-	-
Pyropia sp. ‘*spatulata*’	+	-	-	-
Pyropia sp. ‘*stamfordensis*’	+	-	-	-
Pyropia sp. DK	-	+	-	-
Wildemania abyssicola (Kjellman) A. Mols-Mortensen et J. Brodie	-	-	+	-
Wildemania amplissima (Kjellman) Foslie	+	+	+	+
Wildemania miniata (C. Agardh) Foslie	+	+	+	+
Totals	**18**	**17**	**11**	**11**

Table 2.5. Intraspecific sequence variation in the *rbc*L gene.

Species	Number of specimens	Variation (bp)	Variation (%)
Boreophyllum birdiae	11	1 – 5	0.1 – 0.4
Porphyra dioica	3	1 – 4	0.1 – 0.3
Pyropia elongata	3	4	0.3
Py. “*leucosticta*” *A*	3	1	0.1
Py. njordii	9	1 – 5	0.1 – 0.2
Wildemania amplissima	5	1	0.1
W. miniata	8	2 – 3	0.2



Figures 2.1 - 2.11. Gross morphology of the Bangiales flora in Iceland. 1. *Boreophyllum birdiae* (57291, JB448, 57290); 2. *Porphyra dioica* (JB378); 3. *Porphyra linearis* (JB466, JB468); 4. *Porphyra purpurea* (JB407); 5. *Pyropia 'leucosticta'* A (JB477); 6. *Porphyra umbilicalis* (JB472, JB428, JB412, JB387, JB467); 7. *Pyropia njordii* sp. nov. (paratype JB422, JB425); 8. *Pyropia thulaea* (56457); 9. *Wildemania abyssicola* (JBIC1, JB456); 10. *Wildemania amplissima* (JB463, JB462); 11. *Wildemania miniata* (JB459, JB452). Scale bars represent: Figs 2.1-2.11, 2 cm.

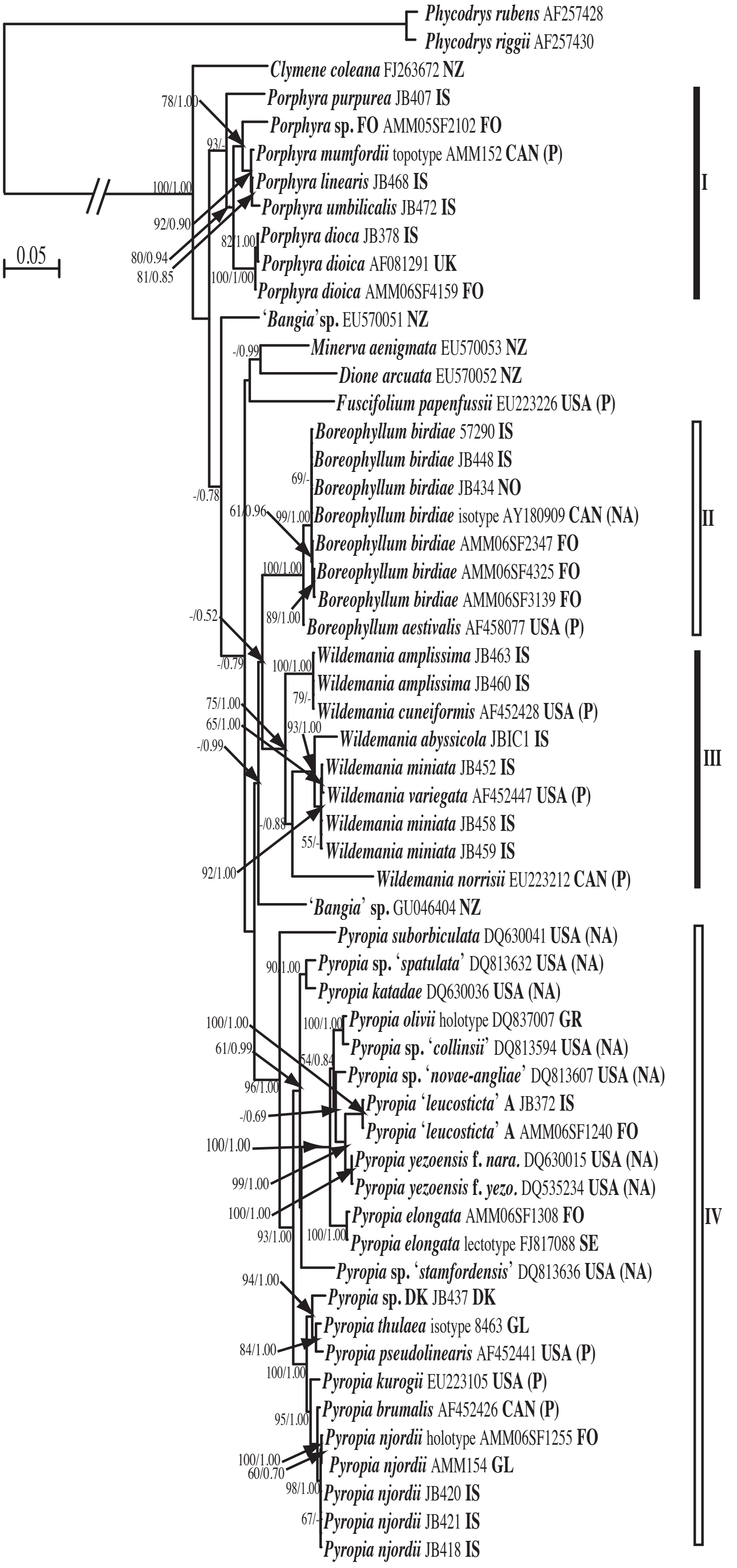


Figure 2.12. Maximum Likelihood (ML) phylogram based on rbcL sequences. ML Bootstrap values (>50%) and Bayesian Inference (BI) posterior probabilities (>0.50) indicated on the branches (ML/BI). Abbreviations: CAN = Canada, DK = Denmark, FO = Faroe Islands, GL = Greenland, GR = Greece, IS = Iceland, NA = (North Atlantic), NO = Norway, P = Pacific, SE = Sweden.

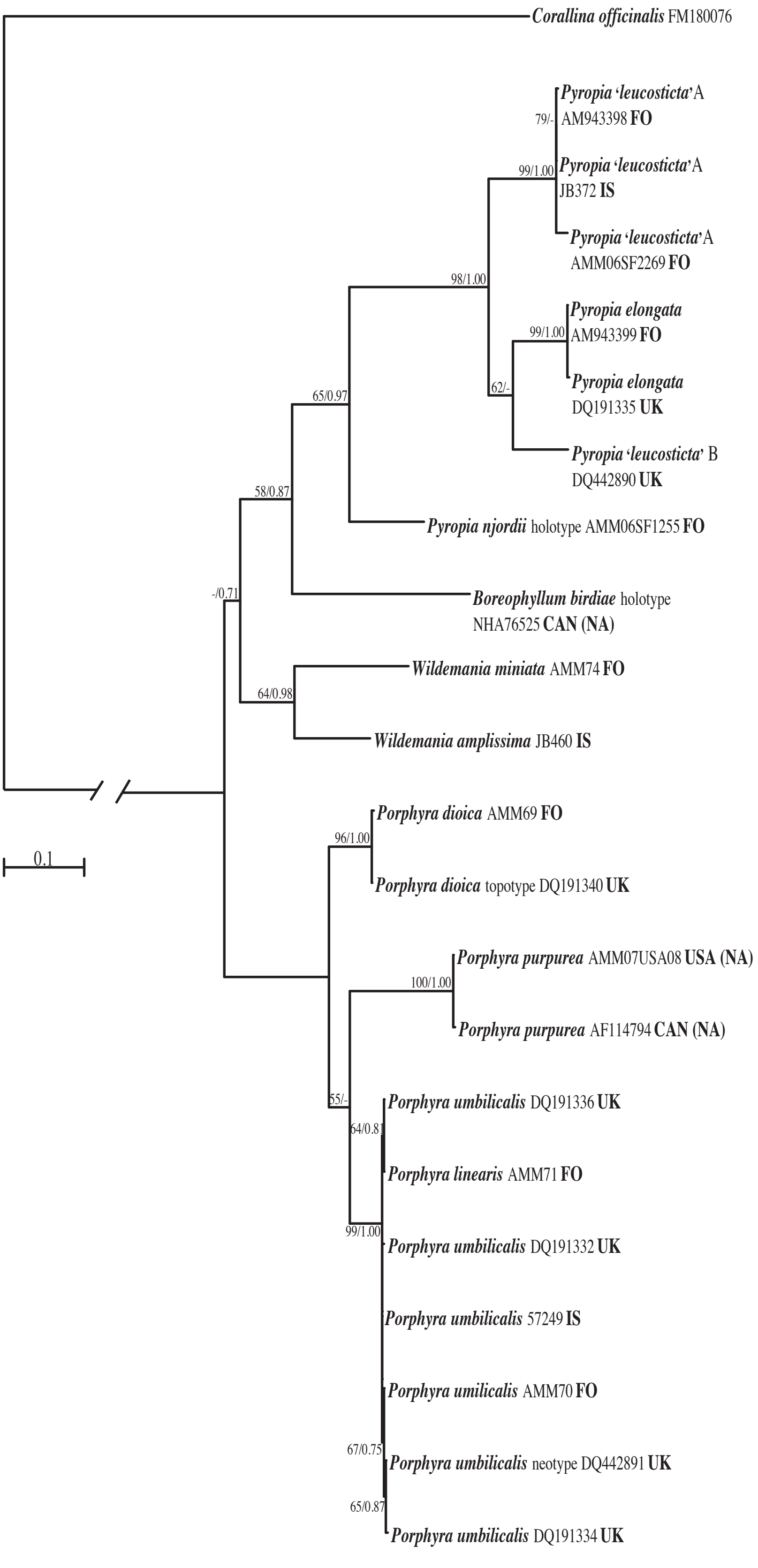
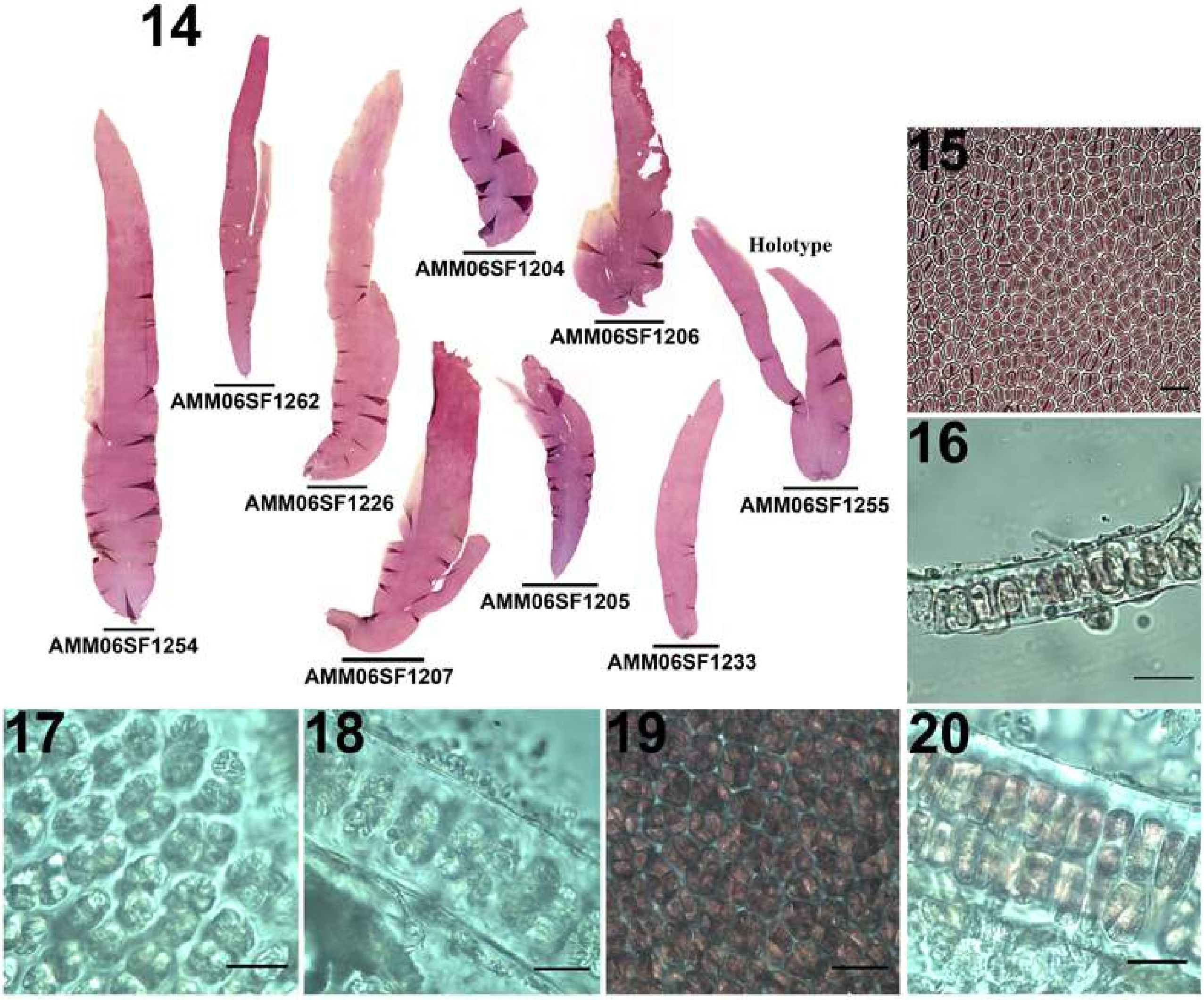


Figure 2.13. Maximum Likelihood (ML) phylogram based on *cox*1 sequences. ML Bootstrap values (>50%) and Bayesian Inference (BI) Posterior probabilities (>0.50) indicated on the branches (ML/BI). Abbreviations: CAN = Canada, FO = Faroe Islands, IS = Iceland, NA = (North Atlantic).



Figures 2.14-2.20. *Pyropia njordii* sp. nov. 14. Isotypes (AMM06SF1254, AMM06SF1262, AMM06SF1226, AMM06SF1207, AMM06SF1204, AMM06SF1205, AMM06SF1206 and AMM06SF1233. Holotype (AMM06SF1255).
15. Vegetative cells in surface view.16. Male gametangia in surface view. 17. Zygotosporangia in surface view. 18. Vegetative cells in transverse section. 19. Male gametangia in transverse section. 20. Zygotosporangia on transverse section. Scale bars represent Fig. 14, 2 cm; Figs 15 & 18, 25 *μ*m; Figs 16, 17, 19 & 20, 15 *μ*m.

CHAPTER III

DIVERSITY AND DISTRIBUTION OF FOLIOSE BANGIALES (RHODOPHYTA) IN WEST GREENLAND: A LINK BETWEEN THE NORTH ATLANTIC AND THE NORTH PACIFIC

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Abstract

Greenland is a continental island in the northern part of the North Atlantic where the foliose Bangiales flora is poorly known. It is an important area for the study of algal biogeography because of the region’s glacial history, in which Greenland has been alternately exposed to or isolated from the North Pacific via the Bering Strait. A molecular study using 3′ *rbc*L + 5′ *rbc*L–S sequences was undertaken to assess the diversity of foliose Bangiales on the west coast of Greenland and *rbc*L sequences were used to study the Greenland flora in a larger phylogenetic and floristic context. New and historic collections document seven species in four genera from the west coast of Greenland. All species had a close link to North Pacific species, being either conspecific with them or North Atlantic–North Pacific vicariant counterparts.

Introduction

The Bangiales include seven filamentous and eight foliose genera of red algae that until recently were classified as *Bangia* and *Porphyra,* respectively (Sutherland *et al*., 2011). Members of the foliose Bangiales include the most economically valuable seaweed crop in the world, and the history of harvesting and trading these algae goes back thousands of years in Japan, China, Korea and Southeast Asia (Mumford & Miura, 1988). The geographical distribution of foliose Bangiales species is worldwide, ranging from tropical waters to polar seas (Sutherland *et al*., 2011). The gametangial thalli of foliose Bangiales can be monostromatic or distromatic, and they are found in the intertidal and/or the subtidal zones. The sporophyte, known as the conchocelis phase, consists of branched filaments found in shells and other calcareous substrata (Brodie & Irvine, 2003).

Recent studies in the northern parts of the North Atlantic, including the Faroe Islands and Iceland, have reported a diverse foliose Bangiales flora (e.g. Klein *et al*., 2003; Brodie & Nielsen, 2005; Brodie *et al*., 2007, 2008; Kucera & Saunders, 2012; Mols-Mortensen *et al*., 2012). However, until now the foliose Bangiales flora of Greenland has remained poorly known. Greenland (Fig. 3.1) is a northern North Atlantic continental island that is separated from the North American continent by Baffin Bay and David Strait. It stretches from 59°N to 82°N, and its east coast is influenced by the cold East Greenland Current, which originates in the Polar Sea, while the west coast is influenced by both the East Greenland Current and the warmer and more saline Irminger Current, which branches off the North Atlantic Current. The East Greenland Current runs along the entire east coast of Greenland, rounds Cape Farewell, and continues north along the west coast. The Irminger Current meets the East Greenland Current at Cape Farewell, and runs north along the west coast (Merkel *et al*., 2012). The climate of coastal and subtidal West Greenland is subarctic (Dunbar, 1954; Wilce, 1990).

Due to biotic interchange through the Bering Strait during interglacial periods, followed by glacial periods when biotas became separated again, the northern areas of the North Atlantic, including boreal (cool temperate) and subarctic thermogeographical regions (Adey & Steneck, 2001; Adey & Hayek, 2011), are important areas to study biodiversity. Lindstrom (1987, 2001) reported several close links between macroalgal species (from the Chlorophyta, Phaeophyceae and the Rhodophyta) in the Northeast Pacific and the North Atlantic. The geographically separated species were thought of as vicariant counterparts that had evolved in the two oceans due to separation during glacial periods, after the first opening of the Bering Strait in the Late Miocene, c. 5.4 to 5.5 Mya (Gladenkov *et al.*, 2002). Several pairs of putative sibling species of foliose Bangiales have also been reported from the Northeast Pacific and the North Atlantic (Lindstrom & Cole, 1992, 1993).

Kjellman (1883) reported *Porphyra abyssicola* (now *Wildemania abyssicola*) from Maniitsoq on the west coast of Greenland, and Rosenvinge (1893) reported *Porphyra miniata* f. *typica* (now *Wildemania miniata*), f. *amplissima* (now *W. amplissima*), f. *tenuissima*, and f. *abyssicola* (now *W. abyssicola*), and *Porphyra umbilicalis* from the west coast; Jónsson (1904) and Christensen (1971) reported *P. miniata* from the east coast of Greenland. '*Conchocelis rosea*' was also reported both from the west and east coast (Rosenvinge, 1910; Lund, 1959; Wilce, 1964), but in 1949 the monotypic genus *Conchocelis* was linked to the *Porphyra* life history, and it is now known to be the sporophyte (conchocelis–phase) in Bangiales life histories (Drew, 1949). Munda & Pedersen (1978) described *Porphyra thulaea* (now *Pyropia thulaea*), based on a specimen collected by T. Christensen in 1958 in Nuuk, Greenland, and sequence data were later obtained for the species (Brodie *et al.*, 2008; Pedersen, 2011; Mols-Mortensen *et al.*, 2012). In May and June 2010, I collected foliose Bangiales on the west coast of Greenland from Qaqortoq (60°N) to Ilulissat (69°N). The preliminary results from this effort were published by Pedersen (2011), who reported the occurrence of *Boreophyllum birdiae*, *Porphyra purpurea*, *P. umbilicalis*, *Pyropia thulaea*, *Wildemania miniata*, and '*Porphyra njordii*' (now *Pyropia njordii*). The species were all verified by DNA sequence data.

The aim of the present study was to report on the diversity of foliose Bangiales flora from the west coast of Greenland, based on new and historic collections. Morphological, ecological, and molecular characteristics were examined and a dichotomous key to species developed. Finally, the flora was analysed in the broader context of the phylogeny of the group and compared with other floras.

Materials and methods

Collections, identification and molecular methods

Collections were made from the west coast of Greenland (Fig. 3.1) from the intertidal and shallow subtidal at low tide, in Isungua (August 2006), Ilulissat (May and August 2010), Hunde Ejlande and Kumikume (September 2009), Sisimiut (May and June 2010), Maniitsoq (June 2010), Nuuk (March, June and July 2010), Kangilinnguit (July 2008), Arsuk (June 2010), Qaqortoq (July 2005 and June 2010), Nanortalik (October 2007), and Anorliúitsup qeqertaa and Ikigaat (September 2011). A few of the collections from the Qaqortoq area in July 2005 were made by SCUBA divers. Samples were preserved in silica gel and voucher specimens were dried onto herbarium sheets. Herbarium voucher specimens produced in this work were deposited in the Albion Hodgdon Herbarium (NHA), University of New Hampshire, USA, with duplicates in the Botanical Museum, Copenhagen (C), the Natural History Museum, London (BM), and the Faroese Museum of Natural History, Tórshavn (NGS). Herbarium abbreviations follow Thiers (2012).

Historic collections from Greenland collected by P.M. Pedersen, T. Christensen and L.K. Rosenvinge were made available by the Botanical Museum, Copenhagen. The specimens from which we were able to produce a DNA sequence were from the Qaqortoq area (July and August 1970 and August 1888), Sulugssugut (July 1957), Eqalugialik (July 1957), Nuuk (August 1958), Sisimiut (August 1886), Arsuk (June 1888) and Agsanguit (July 1888).

In total, the collections from Greenland comprised c. 100 specimens, including historical specimens. A segment of the plastid-encoded *rbc*L gene at its 3′ end and part of the contiguous *rbc*L–*rbc*S spacer was selected as a species identification marker. This region, referred to here as 3′ *rbc*L + 5′ *rbc*L–S, started from base 1192 in the *rbc*L gene (the base numbering is based on the sequence of *P. umbilicalis*, published on GenBank with reference number AB118584) and extended 22 bp into the spacer (298 bp in total; 297 bp in *Pyropia thulaea* due to a deletion in the spacer). Sequences were generated for 85 specimens (Appendix B). Mols–Mortensen *et al*. (2012) found that the suggested standard barcoding marker *cox*1 (Saunders, 2005; Robba *et al.*, 2006) was not able to distinguish between two closely related Bangiales species (*Porphyra umbilicalis* and *P. linearis*) and therefore we decided to use the 3′ *rbc*L + 5′ *rbc*L–S marker, which we have found to have excellent species-resolving power within the Bangiales (A. Mols–Mortensen & C. Neefus, personal observations). Species identity was verified using the BLAST function on the National Center for Biotechnology Information database and, to ensure correct usage of names, we compared our sequences with sequences deposited in GenBank and, when available, with those from type specimens. A longer region of *rbc*L, extending from base 218 to base 1398, was generated for one or two specimens of each species identified in the collection. However, *Wildemania amplissima*, for which there was only one specimen in the collection, was only represented by a 3′ *rbc*L + 5′ *rbc*L–S sequence.

The collection sites were located between 59°N to 69°N, excluding 62°N to 63°N, where no collections were made. It was assumed that if a species was present south of 62°N and north of 63°N, it would also be present at 62°N and 63°N. For most specimens collected, notes were made on where they grew on the coast (the high, mid- or low intertidal, and/or the subtidal), and on which substratum (rock, wood, barnacles or other algae), and the lengths, widths and thicknesses of the blades were measured for three to five specimens of each species.

DNA extraction, PCR amplification, purification, and sequencing were carried out as described in Bray *et al*. (2006) and Mols-Mortensen *et al*. (2012). The primer pairs used to amplify the 3′ *rbc*L + 5′ *rbc*L–S and *rbc*L regions are listed in Appendix C. All primers were used both to amplify and sequence. The following amplification profile was used for all the primer pairs, with the lid temperature at 105°C: 2.5 min at 95°C; 29 cycles of 45 s at 50°C, 1 min at 72°C and 30 s at 95°C; 45 s at 50°C; 5 min at 72°C; ending with a hold at 4°C. The sequences are deposited in GenBank and listed in Appendix B.

Phylogenetic analyses

The raw sequence chromatograms were assembled and proofread in Geneious® 6.1.2 (Biomatters Ltd., Auckland, New Zealand) and aligned using the Muscle algorithm (Edgar, 2004) implemented in Geneious® 6.1.2. The 3′ *rbc*L + 5′ *rbc*L–S alignment comprised 85 sequences with a length of 298 bp. Eighty–one sequences were from the

Greenland collections, one from the Faroe Islands (from the *Pyropia njordii* holotype), one from the UK (from the *Porphyra umbilicalis* neotype) and two *Wildemania amplissima* sequences were from Iceland (GenBank accession numbers JN847272 and JN847273); the Icelandic specimens were included to enable intraspecific variation analysis in *W. amplissima*.

The *rbc*L sequence alignment comprised 78 sequences (Appendix B) with a length of 1181 bp (the *Bangia* sp. AF043371 sequence was 1101 bp long). Eight sequences were produced from Greenland material, including GenBank accession numbers JN847258 and JN847268. A sequence from the *Porphyra umbilicalis* type specimen was also produced and included in the alignment. To place the Greenland foliose Bangiales flora in a wider phylogenetic context (see Sutherland *et al.*, 2011), 67 foliose and filamentous Bangiales sequences were downloaded from GenBank (Appendix B). *Erythrocladia* sp. (EF660273) and *Smithora naiadum* (HQ687545) were also downloaded from GenBank to form the outgroup; the overall groupings remained the same when we used florideophyte outgroups (*Phycodrys rubens* and *P. riggii*). The 3′ *rbc*L+ 5′ *rbc*L–S and *rbc*L alignments are available in TreeBase (http://treebase.org) as submission ID 14598 and 14577, respectively.

Intra- and interspecific variation was calculated in the 3′ *rbc*L + 5′ *rbc*L–S dataset using the Tamura–Nei genetic distance model and neighbour-joining tree building method, implemented in Geneious® 6.1.2. jModelTest 0.1.1 was used to identify the appropriate model of sequence evolution for the *rbc*L dataset (Posada, 2008). Based on a corrected Akaike Information Criterion (AICc) (Hurvich & Tsai, 1989) GTR+I+Γ; was the preferred model for the *rbc*L dataset and was implemented in the phylogenetic analyses. Maximum likelihood (ML) searches were carried out using PhyML (Guindon & Gascuel, 2003; Guindon *et al.*, 2010) implemented in Geneious® 6.1.2, with 1000 bootstrap replicates. Bayesian inference (BI) analysis was also carried out for the *rbc*L dataset, using MrBayes 3.2.1 (Huelsenbeck & Ronquist, 2001), also implemented in Geneious® 6.1.2. The BI analysis was started from random trees and consisted of three heated and one cold chain with temperature set at 0.2, of 1,100,000 generations. The software tool Tracer v1.5 (Rambaut & Drummond, 2007) was used to assess whether the stationary phase had been reached, and based on this a burn-in after 150,000 runs was found appropriate.

Results

Diversity, phylogeny and distribution of the foliose Bangiales in West Greenland

Six partial *rbc*L sequences and 81 3′ *rbc*L + 5′ *rbc*L–S sequences were successfully obtained from the Greenland collection of foliose Bangiales (Appendix B). Based on the sequence data, seven species of foliose Bangiales were recognized in the flora: *Boreophyllum birdiae*, *Porphyra purpurea*, *P. umbilicalis*, *Pyropia njordii*, *P. thulaea*, *Wildemania amplissima* and *W. miniata*. Tamura–Nei distance analysis of the 298 bp 3′ *rbc*L + 5′ *rbc*L–S identification sequence showed intraspecific variation, measured in patristic distance, of 0.000 and 0.006 and interspecific variation of 0.024 and 0.110 (Table 3.1). *Pyropia njordii*, *P. thulaea*, *W. amplissima* (including two samples from Iceland) and *W. miniata* showed no intraspecific variation in the identification marker, while *B. birdiae* showed intraspecific variation of 0.000–0.004, *Porphyra purpurea* 0.000–0.005 and *P. umbilicalis* 0.000–0.006.

The ML phylogram included 76 Bangiales sequences, with bootstrap values ≥ 70% and posterior probabilities (PP) ≥ 0.8 (Fig. 3.2). PhyML analysis suggested a division of the foliose and filamentous Bangiales sequences into three major groups (Groups I–III), with the filamentous '*Bangia*' 2 from New Zealand on its own branch.

Group I was supported by a boostrap of 87.1% and 0.96 PP; *Porphyra* formed a well-supported clade within it, with *Clymene coleana* as the sister taxon. However, *Porphyra corallicola* did not group with the other *Porphyra* species but with the filamentous '*Bangia*' 1 from New Zealand. Of the two *Porphyra* species found in the Greenland material, *P. purpurea* was represented by specimens from both the North Atlantic and the North Pacific while *P. umbilicalis* was sister to the North Pacific *P. mumfordii*. Group II comprised '*Bangia*' 3, *Dione* and *Minerva*, which are all filamentous, and *Boreophyllum*, *Fuscifolium, Lysithea*, *Miuraea* and *Wildemania*, which are foliose. There was no bootstrap or PP support for Group II but *Wildemania* and *Boreophyllum* were well-supported clades within the group. *Wildemania miniata*, *W. amplissima* and *B. birdiae* were the three species in Group II found in the material from Greenland. The North Atlantic *Wildemania miniata* and North Pacific *W. variegata* could not be distinguished from each other based on the *rbc*L gene. The intraspecific variation in *W. miniata* was 0.006 and the interspecific variation between *W. miniata* and *W. variegata* was 0.002–0.008, measured in patristic distances (data not shown). *Wildemania amplissima* was present in both the North Atlantic and the North Pacific, while the sister taxon to North Atlantic *B. birdiae* was the North Pacific *B. aestivalis*. Group III was supported by a bootstrap of 93.7% and 0.99 PP and comprised the foliose genus *Pyropia*; *Py. njordii* and *Py. thulaea* were the two *Pyropia* species found in the material collected from Greenland. The North Pacific *Py. kurogii* and *Py. brumalis* formed a well-supported clade with North Atlantic *Py. njordii*, while the North Atlantic *Py. peggicovensis* and North Pacific *Py. pseudolinearis* formed a well-supported clade with North Atlantic *Py. thulaea*.

Pyropia njordii and *Py. thulaea* had the longest latitudinal distribution in Greenland, stretching over 11° of latitude (Table 3.2 and Fig. 3.1). *Pyropia njordii* occurred between Ikigaat (59°N) and Isungua (69°N), and *Py. thulaea* between Qaqortoq (60°N) and Ilulissat (69°N), *Py. njordii* being the only foliose Bangiales species found south of 60°N. *Boreophyllum birdiae* and *W. miniata* were both distributed from Qaqortoq (60°N) to Sisimiut (66°N), and the northernmost distribution of *Porphyra umbilicalis* was also Sisimiut but it had a much more restricted southward distribution, reaching only Nuuk (64°N). *Porphyra purpurea* was distributed between Qaqortoq and Sulugssugut (64°N) and showed less northward distribution compared to *B. birdiae*, *P. umbilicalis* and *W. miniata*. *Wildemania amplissima* was reported only from Uppernaviarsuk in the Qaqortoq area (60°N).

All species collected from the west coast of Greenland, except for *W. amplissima*, were growing on rock (Fig. 3.3), and this was the overall most important substratum for foliose Bangiales growth. The single *W. amplissima* specimen occurred on a wooden piling. *Pyropia thulaea* was found only on rock but *Py. njordii*, *Porphyra purpurea* and *P. umbilicalis* also grew on barnacles. In addition to rock and barnacles, *B. birdiae* and *W. miniata* also grew on other algae.

Two of the seven foliose Bangiales species, *W. amplissima* and *W. miniata*, were found in the subtidal zone (Fig. 3.4). *Wildemania miniata* was found from the mid intertidal zone to a depth of 5–10 m, while the single specimen of *W. amplissima* was collected in the shallow subtidal. *Boreophyllum birdiae* and *Pyropia njordii* were found throughout the intertidal zone, although mostly in the mid intertidal. *Porphyra purpurea* and *Pyropia thulaea* were found in the mid and low intertidal zone, with *Porphyra purpurea* mostly occurring in the mid intertidal and *Pyropia thulaea* in the low intertidal. *Porphyra umbilicalis* was mostly found in the high intertidal but extended down into the mid intertidal zone.

Key to the species of foliose Bangiales of West Greenland

1. Blade distromatic…………………………………………………………………….........2

1. Blade monostromatic…………………………………………………………………....3

2. Sori intermixed around the blade margin; colour pink, blade c. 55 μm thick; latitudinal distribution 60°N…………………..……………………………………*Wildemania amplissima*

2. Sori on separate halves of the blade; colour pale to intense pink; blade c. 45 μm thick; latitudinal distribution 60°N to 66°N………………………………………*Wildemania miniata*

3. Dioecious, male or female sori around the margin ……………………………….........4

3. Monoecious, male and female sori on separate halves of the blade…………………....5

4. Blade radially symmetrical, c. 65–87.5 μm thick; colour dark to pale brown, greenish brown and pale pink with a grayish tone, attached to rock and barnacles, mostly in the high intertidal zone; latitudinal distribution 64°N to 66°N……………....*Porphyra umbilicalis*

4. Blade linear to lanceolate, c. 34–64 μm thick; colour pink, purple and brown, attached to rock in the low and mid intertidal zones; latitudinal distribution 60°N to 69°……………………………………………………………………………..*Pyropia thulaea*

5. Blade ovate, typically < 12 cm long, < 4 cm wide and c. 22.5–35 μm thick, attached to rock and barnacles throughout the intertidal zone but mostly in the mid intertidal; latitudinal distribution 59°N to 69°……..………………………………………...*Pyropia njordii*

5. Blade round to broad-lanceolate with cordate base, ca. 30 – 100 μm thick; colour light brown, grayish purple, pale purple or pale pink……..6

6. Blade up to 18 cm long, 18 cm broad, and ca. 30-37.5 μm thick; colour pale brown and grayish purple; mainly on rock, sometimes epizooic on barnacles within the mid to low intertidal zones; latitudinal distribution 60°N to 61°N……………….*Porphyra purpurea*

6. Blade up to 12.5 cm long, 14.5 cm broad, and ca. 67.5-100 μm thick; colour light pink, light purple or pale brown; mainly on rock and barnacles but also epiphytic on other algae; throughout the intertidal zone; latitudinal distribution 60°N to 66°N……………......…………………………………………………..*Boreophyllum birdiae*

Discussion

The present work represents the first comprehensive study of foliose Bangiales in Greenland. From the west coast we have confirmed the presence of four foliose Bangiales genera and seven species. The preliminary diversity reports based on our work, presented by Pedersen (2011), are confirmed, and in addition we report *W. amplissima* from the southwest coast of Greenland. Four of the eight foliose Bangiales genera described in Sutherland *et al*. (2011) are reported from Greenland, and the same four genera have also been reported from other areas in the North Atlantic (Mols-Mortensen *et al*., 2012). However, species diversity of foliose Bangiales in Greenland is less than that reported from other northerly areas in the North Atlantic (Table 3.3), e.g. Iceland and the Faroe Islands (Mols-Mortensen *et al*., 2012). Only seven of the 25 species Mols-Mortensen *et al*. (2012) recorded from the North Atlantic are reported from Greenland, while 11 species are reported from both Iceland and the Faroe Islands. Six of the foliose Bangiales species in Greenland (*B. birdiae*, *Porphyra purpurea*, *P. umbilicalis*, *Pyropia njordii*, *W. amplissima* and *W. miniata*) occur both in Iceland and the

Faroe Islands, while three that occur in Iceland and the Faroe Islands (*Porphyra dioica*, *P. linearis* and *Pyropia* ‘*leucosticta*’) have not been found in Greenland.

Porphyra dioica appears to be endemic to the northeast Atlantic, being confined to European coasts, the Faroe Islands and Iceland (Brodie & Irvine, 2003; Brodie *et al*., 2008; Mols-Mortensen *et al*., 2012). The species has been sought extensively in the Northwest Atlantic but it has not been found (C.D. Neefus, personal observations; Kucera & Saunders, 2012).

Porphyra linearis is a common winter annual in the North Atlantic (Brodie & Irvine, 2003), and its northernmost confirmed report is from Iceland (Mols-Mortensen *et al*., 2012). The foliose phase of *P. linearis* is recorded from the British Isles between October and May (Brodie & Irvine, 2003), and it has been found in the Faroe Islands from October to April, and in New Hampshire, USA from November to May (A. Mols-Mortensen, personal observations). Even though collections were made in Nuuk in late March and in Nanortalik in early October, *P. linearis* was not observed.

Foliose Bangiales species with spermatangial sori arranged in pale patches or streaks, as in *Pyropia* ‘*leucosticta*’, have not been found in Greenland, and this type of sorus seems to be rare in cold-water areas of the North Atlantic. The northernmost reports of *Py. ‘leucosticta’* are from Newfoundland (Kucera & Saunders, 2012) and Iceland (Mols-Mortensen *et al*., 2012), where it is confined to the west and southwest coasts, which have warmer sea temperatures (Astthorsson *et al*., 2007). The northernmost record of *Py. elongata*, which also has this type of sorus arrangement, is in the Faroe Islands (Brodie *et al*., 2008; Mols-Mortensen *et al*., 2012), but at the northern limit no reproductive specimens of the species have been observed (A. Mols-Mortensen, personal observations).

Pyropia njordii is widely distributed and a common species on the west coast of Greenland. Using DNA sequence analysis it has been possible to verify this species in historic collections (Appendix B). It was collected by Rosenvinge (in 1888) in Arsuk, Asanguit and Qaqortoq, and identified as *Porphyra umbilicalis* f. *laciniata*. Current work confirms that *Pyropia njordii* was included in Rosenvinge's concept of *P. umbilicalis* f. *laciniata*. *Pyropia thulaea* is a cold-water species that has so far been reported only from western Greenland and eastern Iceland (Munda & Pedersen, 1978; Brodie *et al*., 2008; Pedersen, 2011; Sutherland *et al*., 2011; Mols-Mortensen *et al*., 2012). It is widespread on the west coast of Greenland (see Table 3.2), but in Iceland it is confined to the east coast (Munda & Pedersen, 1978), where the cold East Icelandic Current influences the climate. *Pyropia thulaea* seems to be rare in Iceland, and it was not observed by Mols-Mortensen *et al*. (2012).

Rosenvinge (1893) reported *Wildemania amplissima* (as *Porphyra miniata* var. *amplissima*) from Qaqortoq in southwest Greenland, but the taxon has not been reported again until now. *Wildemania amplissima* seems to be rare in Greenland and confined to the Qaqortoq area (60°N) in the southwest, where both Rosenvinge's (1893) and our observations were made, 117 years apart. *Wildemania abyssicola*, which Kjellman (1883) reported (as *P. abyssicola*) from the deep waters at Maniitsoq and Rosenvinge (1893) reported (as *P. miniata* var. *abyssicola*) from several locations in the subtidal zone in West Greenland, was not found in our study. It is possible however, that we overlooked the species due to limited subtidal sampling. *Wildemania abyssicola* was originally described by Kjellman (1883) from deep waters in the Norwegian Arctic Sea, Murman Sea, White Sea, as well as the west coast of Greenland at Sukkertoppen (Maniitsoq). Mols-Mortensen *et al*. (2012) reported *W. abyssicola* in Iceland from 17 m depth, but it is also found in the shallow subtidal (J. Brodie & K. Gunnarsson, unpublished observations).

Our observations support the hypothesis of dispersal of macroalgal species through the Bering Strait followed by vicariant speciation due to subsequent isolation, as proposed by Lindstrom (2001). All of the foliose Bangiales species found in Greenland have a North Pacific–North Atlantic link, either as closely related sibling species or conspecific populations. *Boreophyllum birdiae* and *B. aestivalis*, *Porphyra umbilicalis* and *P. mumfordii*, *Pyropia njordii* and *Py. brumalis*, and *Pyropia thulaea* and *Py. pseudolinearis* are each North Atlantic and North Pacific vicariant counterparts. *Porphyra purpurea* and *W. amplissima* have populations in both the North Atlantic and North Pacific (Bray *et al*., 2007; Kucera & Saunders, 2012). *Wildemania miniata* and *W. variegata* have been regarded as North Atlantic and North Pacific vicariant counterparts (Lindstrom & Cole, 1992), but observations from current work and Mols-Mortensen *et al*. (2012) show that the two species are very closely related and should possibly be regarded as the same species, with populations in the two oceans.

Table 3.1. Pairwise distances for the 3’ *rbc*L + 5’ *rbc*L-S marker. The distances (for *N* specimens) are calculated based on Tamura-Nei model and presented as patristic distances (sum of branch lengths).

	B. birdiae (*N* = 16)	*P. purpurea* (*N* = 6)	*P. umbilicalis* (*N* = 9)	*Py. njordii* (*N* = 33)	*Py. thulaea* (*N* = 9)	*W. amplissima* (*N* = 3)[1]	*W. miniata* (*N* = 6)
B. birdiae	**0.000-0.004**						
P. purpurea	0.086-0.090	**0.000-0.005**					
P. umbilicalis	0.075-0.085	0.062-0.068	**0.000-0.006**				
Py. njordii	0.086-0.090	0.104	0.094-0.099	**0.000**			
Py. thulaea	0.083-0.087	0.101	0.091-0.096	0.024	**0.000**		
W. amplissima	0.070-0.074	0.088	0.077-0.083	0.053	0.050	**0.000**	
W. miniata	0.092-0.096	0.110	0.099-0.105	0.075	0.072	0.042	**0.000**

[1] One sequence is based on Greenland material and two on Icelandic material.

Table 3.2. The latitudinal distribution of foliose Bangiales species on the west coast of Greenland. ND = no data (no samples from this latitude); + = species present; – = species not recorded.

	59° N	60° N	61° N	62° N	63° N	64° N	65° N	66° N	67° N	68° N	69° N
Boreophyllum birdiae	–	+	+	ND	ND	+	–	+	–	–	–
Porphyra purpurea	–	+	+	ND	ND	–	–	–	–	–	–
Porphyra umbilicalis	–	–	–	ND	ND	+	–	+	–	–	–
Pyropia njordii	+	+	–	ND	ND	+	+	+	+	+	+
Pyropia thulaea	–	+	–	ND	ND	+	–	–	+	–	+
Wildemania amplissima	–	+	–	ND	ND	–	–	–	–	–	–
Wildemania miniata	–	+	–	ND	ND	+	–	+	–	–	–

Table 3.3. Folise Bangiales species recorded from the North Atlantic, Iceland, Faroe Islands and Greenland. + = present; – = absent.

Species	North Atlantic	Iceland	Faroe Islands	Greenland
Boreophyllum birdiae (Neefus et Mathieson) Neefus	+	+	+	+
Porphyra corallicola H. Kucera & G.W. Saunders	+	-	-	-
Porphyra dioica J. Brodie et L. Irvine	+	+	+	-
Porphyra drachii J. Feldmann	+	-	-	-
Porphyra linearis Greville	+	+	+	-
Porphyra purpurea (Roth) C. Agardh	+	+	+	+
Porphyra umbilicalis Kützing	+	+	+	+
Porphyra 'yezoensis' sensu Kornmann	+	-	-	-
Porphyra sp. FO	+	-	+	-
Pyropia elongata (Kylin) Neefus et J. Brodie	+	-	+	-
Pyropia katadae (A. Miura) M.S. Hwang, H.G. Choi, N. Kikuchi et M. Miyata	+	-	-	-
Pyropia '*leucosticta*'A	+	+	+	-
Pyropia '*leucosticta*'B	+	-	-	-
Pyropia njordii Mols-Mortensen, J. Brodie et Neefus	+	+	+	+
Pyropia olivii (Orfanidis, Neefus et Bray) J. Brodie et Neefus	+	-	-	-
Pyropia peggicovensis H.Kucera et G.W.Saunders	+	-	-	-
Pyropia suborbiculata (J. Coll et J. Cox) J.E. Broom, H.G. Choi, M.S. Hwang et W.A. Nelson	+	-	-	-
Pyropia thulaea (I.M. Munda et P.M. Pedersen) Neefus	+	+	-	+
Pyropia yezoensis (Ueda) M.S. Hwang et H.G. Choi f. *yezoensis*	+	-	-	-
Pyropia yezoensis (Ueda) M.S. Hwang et H.G. Choi f. *narawensis* A. Miura	+	-	-	-
Pyropia sp. '*collinsii*'	+	-	-	-
Pyropia sp. '*novae-angliae*'	+	-	-	-
Pyropia sp. '*spatulata*'	+	-	-	-
Pyropia sp. '*stamfordensis*'	+	-	-	-
Wildemania abyssicola (Kjellman) A. Mols-Mortensen et J. Brodie	+	+	-	-
Wildemania amplissima (Kjellman) Foslie	+	+	+	+
Wildemania miniata (C. Agardh) Foslie	+	+	+	+
Total	**26**	**11**	**11**	**7**

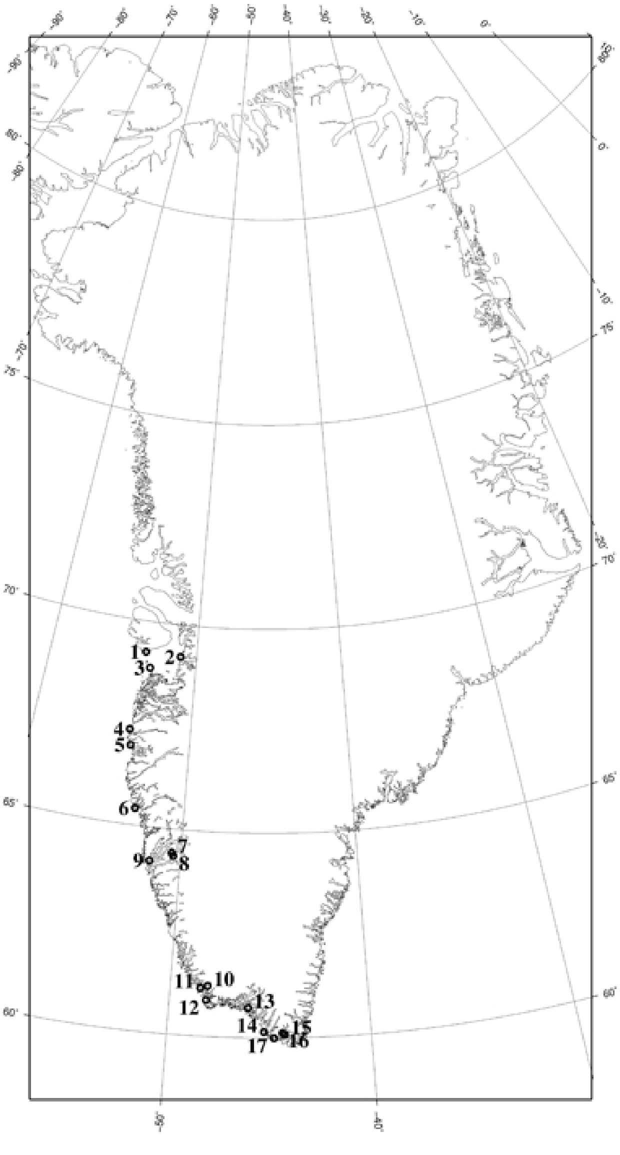

Figure 3.1. Map of collecting locations on the west coast of Greenland. 1. Isungua, 2. Ilulissat, 3. Hunde Ejlande, 4. Kumikume, 5. Sisimiut, 6. Maniitsoq, 7. Sulugssugut, 8. Eqalugialik, 9. Nuuk, 10. Kangilinnguit, 11. Arsuk, 12. Asanguit, 13. Qaqortoq, 14. Nanortalik, 15. Anorliuitsup qeqertaa, 16. Umigssat qeqertai, 17. Ikigaat.

Figure 3.2. Maximum likelihood (ML) phylogram based on rbcL sequences, placing foliose Bangiales species from Greenland in a wider phylogenetic context. ML bootstrap values (>70%) and Bayesian Inference (BI) posterior probabilities (>0.80) are indicated on the branches (ML/BI). Abbreviations: CA = Canada, DK = Denmark, FO = Faroe Islands, GL = Greenland, GR = Greece, IE = Ireland, IS = Iceland, JP = Japan, MX = Mexico, NA = North Atlantic, NO = Norway, NP = North Pacific, NZ = New Zealand, SE = Sweden.

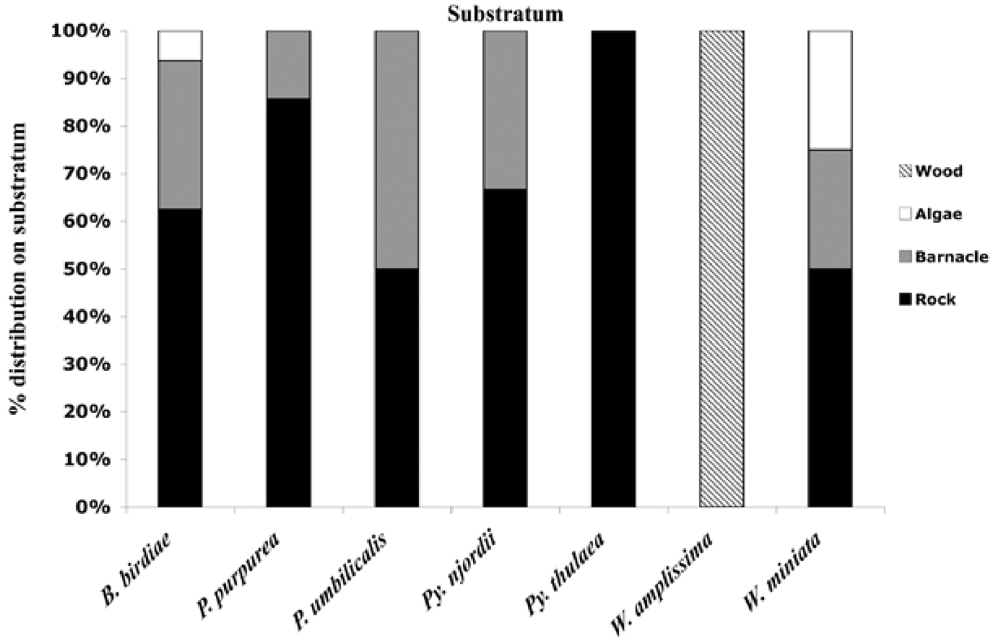

Figure 3.3. Distribution of the species on different substrata based on 75 specimens; *Boreophyllum birdiae* (*N* = 16), *Porphyra purpurea* (*N* = 7), *Porphyra umbilicalis* (*N* = 6), *Pyropia njordii* (*N* = 30), *Pyropia thulaea* (*N* = 7), *Wildemania amplissima* (*N* = 1), *Wildemania miniata* (*N* = 8).

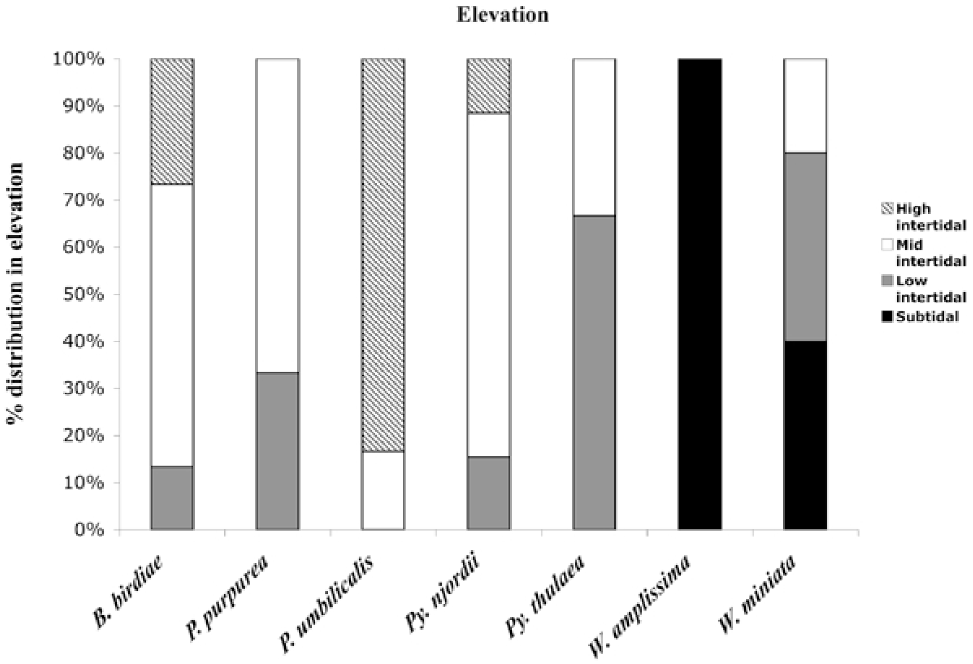

Figure 3.4. Distribution of the species in relation to elevation based on 62 specimens; *Boreophyllum birdiae* (*N* = 15), *Porphyra umbilicalis* (*N* = 6), *Pyropia njordii* (*N* = 26), *Pyropia thulaea* (*N* = 6), *Wildemania amplissima* (*N* = 1) and *Wildemania miniata* (*N* = 5).

CHAPTER IV

DIVERSITY AND DISTRIBUTION OF FOLIOSE BANGIALES (RHODOPHYTA) SPECIES IN THE NORTHWEST ATLANTIC IN THE CONTEXT OF THE NORTH ATLANTIC

(Manuscript submitted to Nova Hedwigia on the 7th of May 2014)

Abstract

Studies of species diversity and distribution are essential to gain baseline information and to document potential changes in the flora. Molecular tools such as DNA sequencing have enabled individual species in the Bangiales that could not be identified based on morphological data alone to be delimited, and this has made floristic comparisons between geographic areas possible. A study of the diversity and distribution of foliose Bangiales species on the Northwest Atlantic coast was undertaken from Labrador, Canada to Florida, USA, with special focus on the understudied coast south of New York, USA. The plastid 3’ *rbc*L + 5’ *rbc*L-S marker was used for species identification, and the study was based on both new collections and herbarium material. Foliose Bangiales material from other areas of the North Atlantic was also included to provide new insights into a broader geographic distribution of the species. Four foliose Bangiales genera were revealed from the Northwest Atlantic: *Boreophyllum*, *Porphyra*, *Pyropia* and *Wildemania*, and a total of fifteen species: *Boreophyllum birdiae*, *Porphyra linearis*, *P. purpurea*, *P. umbilicalis*, *Pyropia elongata*, *Py. njordii*, *Py. peggicovensis*, *Py. suborbiculata*, *Py. thulaea*, *Py. yezoensis* (f. *yezoensis* and f. *narawensis*), “*Py. collinsii*”,

“*Py. leucosticta*”, “*Py. novae-angliae*”, *Wildemania amplissima* and *W. miniata*. New distributions were verified for eight of the species on the Northwest Atlantic coast, and *Pyropia thulaea* was reported from this coast for the first time. A clear difference in the diversity of foliose Bangiales species was observed south of New Jersey, with only three species found south of New Jersey and fifteen species found from New Jersey and northward. The species that were documented south of New Jersey had broad distributions and were also documented further north. Two of these species *Pyropia suborbiculata* and *Py. elongata* exended south of Cape Hatteras, North Carolina, where the warm-temperate biogeographic region begins. Based on current work, nineteen foliose Bangiales species were recognized in the North Atlantic. *Pyropia yezoensis* (f. *yezoensis* and f. *narawensis*) was reported only from the Northwest Atlantic and *Porphyra dioica* and *Wildemania abyssicola* together with the two unidentified species (*Porphyra* sp. and *Pyropia* sp.) were only reported from the Northeast Atlantic. “*Pyropia novae-angliae*” was reported in the Northeast Atlantic for the first time.

Introduction

The Bangiales is a cosmopolitan red algal order that includes species that are common components of rocky intertidal shores and the shallow subtidal zone. The order also contains several species that are grown commercially and are the most economically valuable seaweed crop in the world (Blouin *et al.*, 2010). Fifteen genera are included in the Bangiales, seven filamentous and eight foliose (Sutherland *et al.*, 2011), and in the North Atlantic four of the foliose genera have been discovered to date (Mols–Mortensen *et al.*, 2012). Foliose Bangiales species diversity has been studied in many areas of the North Atlantic (e.g. Neefus *et al.*, 2002; Brodie & Irvine 2003; Klein *et al.*, 2003; Brodie & Nielsen, 2005; Bray *et al.*, 2006, 2007; Brodie *et al.*, 1998, 2007, 2008; Neefus *et al.*, 2008; Kucera & Saunders, 2012; Mols-Mortensen *et al.*, 2012, 2014), and all recent studies have been based on molecular identification, which has enabled floras to be compared between areas (e.g. Brodie *et al.*, 2008; Sutherland *et al.*, 2011; Mols-Mortensen *et al.*, 2012, 2014).

The North Atlantic Ocean stretches from the Arctic Ocean to the Equator encompassing four biogeographic regions from north to south: subarctic, cold-temperate, warm-temperate and tropical (Lüning, 1990; Adey & Hayek, 2011). The same biogeographic regions are recognized on both sides of the North Atlantic except for the subarctic region that is not defined in the Northeast Atlantic. Due to the clock-wise Coriolis force on the Northern Hemisphere the latitudinal intervals between the isotherms on the western sides of both the North Atlantic and the North Pacific are compressed.

Especially the cold temperate biogeographic region extends farther north on the Northeast Atlantic coast compared to the Northwest Atlantic coast due to the Coriolis force on the warm North Atlantic Current (van den Hoek, 1982; Lüning, 1990).

The macroalgal flora of what is today the cold temperate region in the North Atlantic was severely impacted by the last glacial period. During the last glacial maximum (LGM), which ended ca. 18,000 years ago (Provan & Maggs, 2012) large areas in the north were covered by ice and the distribution of surviving marine benthic species shifted to the south where conditions were more suitable. The open-sea distance between Greenland, Svalbard, Iceland, Faroe Islands, and the continental coasts was a dispersal barrier to marine benthic organisms, and so was the soft-substratum south of Long Island, New York on the Northwest Atlantic coast (Lüning, 1990). The ice-shield covered the Northwest Atlantic coast as far south as Long Island during the LGM, and the lack of rocky substratum and a steep temperature gradient south of the ice-shield is thought to have been a limiting factor for survival of many arctic and cold-temperate species (van den Hoek & Breeman, 1990). It has been suggested that the rocky shore flora and fauna of the Northwest Atlantic became extinct during the LGM but not that of the Northeast Atlantic, and the hypothesis that the rocky shore biota of Iceland and the Northwest Atlantic is largely a result of post-glacial colonization from the Northeast Atlantic is supported by Ingolfsson (1992). He found that the rocky shore fauna of Iceland and Atlantic Canada was largely a result of post-glacial colonization from the Northeast Atlantic.

Recent studies of foliose Bangiales in the North Atlantic have been based on both new collections and well-preserved historic material (e.g. Brodie *et al.*, 2007;

Neefus & Brodie, 2009; Mols–Mortensen *et al.*, 2014). The most important historic collections on the Northwest Atlantic coast were made by Frank Shipley Collins in the late 19th and early 20th century, and through a comparison of these collections to more recent collections, Mathieson *et al.* (2008) documented non-native species introductions into the northern Northwest Atlantic flora over the last 100 years, and their range expansion.

Critical examination of foliose Bangiales species diversity has been undertaken in both the Northwest, Northeast and on North Atlantic Islands and comparisons have been made between the areas (e.g. Klein *et al.*, 2003; West *et al.*, 2005; Bray *et al.*, 2006, 2007; Neefus *et al.*, 2008; Brodie *et al.*, 2007, 2008; Kucera & Saunders, 2012; Mols–Mortensen *et al.*, 2012, 2014). A total of 26 foliose Bangiales species have been documented in the North Atlantic (Mols–Mortensen *et al.*, 2014), with twenty species documented from the Northwest Atlantic, eleven species documented from Iceland and the Faroe Islands, and seven species from Greenland (Kucera & Saunders, 2012; Mols–Mortensen *et al.*, 2012, 2014). Most of the foliose Bangiales work in the Northwest Atlantic has been carried out in Atlantic Canada and New England and less so south of Long Island, New York.

Many areas of the world, including the North Atlantic, are under environmental pressure from human activities, and biodiversity and species distributions are affected (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Berge *et al.*, 2005; Parmesan, 2006). Species diversity and distribution studies provide essential baseline information that enables documentation of potential changes. The morphological variability within Bangiales species and often lack of consistent differences between species has made identification and delimitation notoriously difficult. Molecular tools are now enabling floras to be compared between geographic areas and information on species distribution range to be reliably documented. Using identification based on molecular sequence data, the aim of this work was to study the diversity and distribution of foliose Bangiales species in the Northwest Atlantic between Newfoundland and Florida with special focus on the understudied coast south of Long Island. Both new collections and herbarium specimens from the Northwest Atlantic were studied, and to give new insights into the broader geographic distribution of the foliose Bangiales in the North Atlantic, material from other North Atlantic areas was also included in this work.

Materials and Methods

Collections

New collections were made between 21st of May and 4th of June, 2011 on the east coast of the USA from Connecticut to Florida (Table 4.1), and the results from these collections will be treated separately. Twenty-nine intertidal sites were visited during low tide, and the criteria used to locate the sites were accessibility and availability of hard substrata. The rest of the collections from the Northwest Atlantic coast studied in this work were from north of Connecticut, and collected primarily between August 2007 and June 2012 from the intertidal and the shallow subtidal (Appendix D). Other intertidal and subtidal collections from the North Atlantic also included in this work were collected between July 2004 and April 2011 (see Appendix D). The herbarium vouchers prepared from the new material collected as a part of this work were deposited in the Albion Hodgdon

Herbarium (NHA), University of New Hampshire, USA, with duplicates deposited in the Faroese Museum of Natural History (NGS), Tórshavn, Faroe Islands. Historical and more recent herbarium material of foliose Bangiales species were made available from the Norwegian University of Science and Technology (TRH), Tromsø, Botanical Museum, Copenhagen (C), Denmark, New York Botanical Garden (NY), USA and the National Research Council of Canada (NRCC), Nova Scotia Herbarium abbreviations follow Thiers (continuously updated, 14.07.2014). The studied material comprised a total of ca. 370 new and historic foliose Bangiales specimens (Appendix D).

Molecular identification

All specimens were identified using the 3' *rbc*L + 5' *rbc*L-S marker, which is a 298 bp segment from the 3' end of the plastid-encoded *rbc*L gene and extending into the *rbc*L-*rbc*S spacer, following the method described in Mols-Mortensen *et al.*, (2014). The 3' *rbc*L + 5' *rbc*L-S marker was used as an identification barcode instead of the standard barcode *cox*1 (Saunders, 2005; Robba *et al.*, 2006) because Mols–Mortensen *et al.* (2012) found that *cox*1 was not able to distinguish between two closely related Bangiales species (*Porphyra umbilicalis* and *P. linearis*). Species identity was verified using the BLAST function on the National Center for Biotechnology Information database, and when available we compared our sequences with sequences from type specimens deposited in GenBank, to ensure correct usage of names. The geographic distribution of the species reported in this work was found combining our data with distribution data in the published literature.

The DNA extraction, PCR amplification, purification, and sequencing were carried out as described in Bray *et al.*, (2006) and Mols-Mortensen *et al*. (2012, 2014). The sequences were deposited in GenBank and accession numbers listed in Appendix D.

The raw sequence chromatograms were assembled and proofread in Geneious® 6.1.2 (Biomatters Ltd., Auckland, New Zealand) and aligned using the Muscle algorithm (Edgar, 2004) implemented in Geneious® 6.1.2. A distance analysis based on 75 3' *rbc*L + 5' *rbc*L-S sequences was calculated using the Tamura-Nei genetic distance model and neighbor joining tree building method, implemented in Geneious® 6.1.2. The distance matrix data are presented in Appendix E.

Results

Species diversity and distribution in the Northwest Atlantic

Foliose Bangiales specimens were collected at 14 of the 29 sites between Connecticut and Florida on the collecting trip in May-June 2011. Specimens were found in Connecticut, New Jersey, Delaware, North Carolina and South Carolina, but not in Maryland, Virginia, Georgia and Florida (see Table 4.1). Based on this collection, *Pyropia* was the only genus collected on the Northwest Atlantic coast between Connecticut and Florida, and three species were recognized: "*Pyropia collinsii*", *Py. yezoensis* (f. *yezoensis* and f. *narawensis*) and *Py. suborbiculata*. All three species were found in Connecticut and New Jersey, and only *Py. suborbiculata* was collected south of New Jersey (see Table 4.1). All the specimens collected between New Jersey and South Carolina grew on man made structures (see Table 4.1).

Including the rest of the foliose Bangiales material from the Northwest Atlantic coast that was studied in our work four foliose Bangiales genera were revealed: *Boreophyllum*, *Porphyra*, *Pyropia* and *Wildemania*, and fifteen species identified: *Boreophyllum birdiae*, *Porphyra linearis*, *P. purpurea*, *P. umbilicalis*, *Pyropia elongata*, *Py. njordii*, *Py. peggicovensis*, *Py. suborbiculata*, *Py. thulaea*, *Py. yezoensis* (f. *yezoensis* and f. *narawensis*), "*Py. collinsii*", "*Py. leucosticta*", "*Py. novae-angliae*", *Wildemania amplissima* and *W. miniata*.

The geographic distributions on the Northwest Atlantic coast between Labrador, Canada and Florida, USA, found by our work and by already published records with DNA based identifications, were presented in Table 4.2. New distribution records verified by DNA sequences were reported for *Pyropia peggicovensis*, *Py. suborbiculata*, *Py. thulaea*, *Py. yezoensis* (f. *yezoensis* and f. *narawensis*), "*Py. collinsii*", "*Py. novae-angliae*", *Wildemania amplissima* and *W. miniata* (see Table 4.2), and this was the first report of *Py. thulaea* from the Northwest Atlantic coast.

The southernmost record of *Porphyra umbilicalis* was from Long Island, New York (Teasdale & Klein, 2010; see Table 4.2), and *Pyropia yezoensis* (f. *yezoensis* and f. *narawensis*) and *Wildemania amplissima* were found to have their southern distribution range in New Jersey. South of New Jersey only *Pyropia elongata*, *Py. suborbiculata* and "*Py. collinsii*" were found (see Table 4.2). The three species that were found south of New Jersey were also found further north with northern distribution limits in Rhode Island, Massachusetts and New Hampshire, respectively.

North Atlantic distribution of the foliose Bangiales species

The herbarium material from TRH, Norway and C, Denmark together with a few other collections from Norway, the Faroe Islands, Iceland, Greenland, Denmark, Sweden, UK and Spain, revealed four foliose Bangiales genera and eighteen species in the Northeast Atlantic, including Iceland and the Faroe Islands (Table 4.3). Based on our work a total of nineteen foliose Bangiales species were recognized in the North Atlantic, with *Pyropia yezoensis* (f. *yezoensis* and f. *narawensis*) reported only from the Northwest Atlantic and *Porphyra dioica* and *Wildemania abyssicola* together with the two unidentified *Porphyra* sp. and *Pyropia* sp. reported only from the Northeast Atlantic. “*Pyropia novae-angliae*” was reported in the Northeast Atlantic for the first time.

Listed below are the foliose Bangiales species that were recognized by our work, including distribution records available in the published literature. Only distribution records with identifications based on DNA sequences were used apart for one *P. linearis* record, and in total we reported new distribution records for twelve of the North Atlantic foliose Bangiales species.

Boreophyllum birdiae (Neefus & A.C. Mathieson) Neefus in Sutherland *et al*., 2011: 1140
Type location: (Holotype) Herring Cove, Nova Scotia, Canada.
Distribution verified by DNA sequence: Newfoundland, New Brunswick and Nova Scotia, Canada, Maine and New Hampshire, USA, Greenland, Iceland, the Faroe Islands, and Norway (Brodie & Nielsen, 2005; Kucera & Saunders, 2012; Mols-Mortensen *et al*., 2012, 2014; Neefus *et al*., 2002; Pedersen, 2011; Sutherland *et al*., 2011).

Current paper: no further distribution records were added. Sequence from isotype material was used as identification reference (GenBank accession: AY180909).

Porphyra dioica J. Brodie & L.M. Irvine, 1997: 286

Type location: (Holotype) Sidmouth, Devon, England

Distribution verified by DNA sequence: Iceland, the Faroe Islands and UK (Brodie & Irvine, 1997; Mols–Mortensen *et al*., 2012).

Current paper: a new distribution record was verified from Norway. Sequences from *P. dioica* type material were not available but another specimen from Sidmouth, UK was used as identification reference (GenBank accession: HQ687546).

Porphyra linearis Grev., 1830: 170

Type Location: (Lectotype) Sidmouth, Devon, England.

Distribution verified by DNA sequence: UK, Iceland and the Faroe Islands, Massachusetts, New Hampshire and Maine, USA, Nova Scotia, Canada (A. Mols–Mortensen pers. obs.; Brodie *et al*., 1998; Klein *et al*., 2003; Kucera & Saunders, 2012; Mathieson & Hehre, 1986 [identification not based on sequence data]; Mols–Mortensen *et al*., 2012; C. Neefus pers. obs.).

Current paper: A new distribution record was verified from Denmark. We were not able to obtain a sequence from *P. linearis* type material, but the distribution records matched *P. linearis* topotype material, which was used as identification reference (GenBank accession: KP171739).

Porphyra purpurea (Roth) C. Agardh, 1824: 191

Type location: (Neotype) Nord-Ost Watt Helgoland, Germany.

Distribution verified by DNA sequence: Iceland, the Faroe Islands, UK, Denmark, Greenland, Germany, Ireland and France, Labrador, Newfoundland, Quebec, New Brunswick and Nova Scotia, Canada, Maine, New Hampshire, Connecticut, Washington and Oregon, USA (Bray *et al*., 2006, 2007; Kucera & Saunders, 2012; Mols–Mortensen *et al*., 2012, 2014).

Current paper: no further distribution records were added. Sequence from neotype material was used as identification reference (GenBank accession: DQ418732).

Porphyra umbilicalis Kütz., 1843: 383

Type location: (Neotype) Easdale, Scotland.

Distribution verified by DNA sequence: Iceland, the Faroe Islands, Denmark, Greenland, Norway, UK, Ireland, Germany and Portugal, New Brunswick, Newfoundland and Labrador, Canada, Maine, New Hampshire, Rhode Island and New York, USA (Brodie *et al*., 2008; Klein *et al*., 2003; Kucera & Saunders, 2012; Mols–Mortensen *et al*., 2012, 2014; Teasdale & Klein, 2010; Teasdale *et al*., 2009).

Current paper: a new distribution record was verified from Spain (Atlantic coast). Sequence from neotype material (published in this paper) was used as identification reference (GenBank accession: KF478700).

Porphyra sp.

The taxon is unidentified and perhaps undescribed, and originally reported by Mols–Mortensen *et al*. (2012). A large number of described foliose Bangiales have not yet been sequenced, and until molecular information is available from reliably identified specimens of these taxa, it is impossible to determine if a specimen with a previously unreported sequence is in fact undescribed.

Distribution verified by DNA sequence: the taxon has until now only been reported from the Faroe Islands (Mols–Mortensen *et al*., 2012).

Current paper: no further distribution records were added.

Pyropia elongata (Kylin) Neefus & J. Brodie in Sutherland *et al*., 2011: 1143

Type location: (Lectotype) Koster, Bohuslän, Sweden

Distribution verified by DNA sequence: The Faroe Islands, Sweden, UK and Mediterranean Spain, Connecticut, Rhode Island, North Carolina and Texas, USA (Brodie *et al*., 2007; as *Porphyra rosengurttii;* Brodie *et al*., 2008; as *Porphyra rosengurttii;* Mols–Mortensen *et al*., 2012; Neefus & Brodie, 2009; Sutherland *et al*., 2011).

Current paper: no further distribution records were added. Sequence from lectotype material was used as identification reference (GenBank accession: FJ817088).

Pyropia njordii Mols–Mortensen, J. Brodie & Neefus in Mols–Mortensen *et al*., 2012: 154

Type location: (Holotype) Tjaldavík, Trongisvágsfjørður, Faroe Islands.

Distribution verified by DNA sequence: Iceland, the Faroe Islands and Greenland, Nova Scotia and Quebec, Canada, Maine and New Hampshire, USA (Kucera & Saunders, 2012; Mols–Mortensen *et al.*, 2012).

Current paper: new distributional records were verified from Norway, Denmark and New Brunswick, Canada. Sequence from holotype material was used as identification reference (GenBank accession: JN847259).

Pyropia peggicovensis H. Kucera & G.W. Saunders, 2012: 880

Type location: (Holotype) Peggy's Cove, Nova Scotia, Canada.

Distribution verified by DNA sequence: Nova Scotia, Canada (Kucera & Saunders, 2012).

Current paper: new distributional records were verified from Prince Edward Island, Canada, Sweden and Denmark. Sequence from holotype material was used as identification reference (GenBank accession: JN028991).

Pyropia suborbiculata (Kjellm.) J.E. Sutherland, H.G. Choi, M.S. Hwang & W.A. Nelson in Sutherland *et al.*, 2011: 1145

Type location: (Lectotype) Goto–retto, Nagasaki Prefecture, Japan.

Distribution verified by DNA sequence: Massachusetts, Connecticut, North Carolina, USA, New Zealand, Australia, Mexico, China, Japan, Korea, Portugal, Spain and Brazil (Broom *et al.*, 2002; Klein *et al.*, 2003; Milstein *et al.*, 2011; Neefus *et al.*, 2008; Sutherland *et al.*, 2011; Teasdale *et al.*, 2009; Vergés *et al.*, 2013).

Current paper: new distributional records were verified from New Jersey, Delaware and South Carolina, USA. No sequence data were available from type material and a sequence published by Sutherland *et al.*, 2011 was used as identification reference (GenBank accession: HQ728201).

Pyropia thulaea (Munda & P.M. Pedersen) Neefus in Sutherland *et al.*, 2011: 1145
Type location: (Holotype) Godthåb (Nuuk) West Greenland.
Distribution verified by DNA sequence: Greenland and Iceland (Mols–Mortensen *et al.*, 2014; Munda & Pedersen, 1978; Sutherland *et al.*, 2011).
Current paper: new distributional records were verified from Newfoundland and New Brunswick, Canada. Sequence from isotype material was used as identification reference (GenBank accession: JN847268).

Pyropia yezoensis (Ueda) M.S. Hwang & H.G. Choi in Sutherland *et al.*, 2011: 1145
Type location: (Holotype) Hokkaido, Japan
Distribution verified by DNA sequence: Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut and New York, USA, Japan, Korea, China. *Pyropia yezoensis* f. *yezoensis* was distributed on the Northwest Atlantic coast from Maine to Long Island Sound, and *P. yezoensis* f. *narawensis* was reported only south of Cape Cod (He *et al.*, 2013; Klein *et al.*, 2003; Kucera & Saunders, 2012; Li *et al.*, 2012; Neefus *et al.*, 2008; Park *et al.*, 2007; Sutherland *et al.*, 2011).
Current paper: a new distribution record for both forms was verified from New Jersey, USA. No sequence data were available from type material; *rbc*L and ITS sequences

cited in Neefus *et al.*, (2008) were used as identification reference (GenBank accessions: AB118590, AB118574 and AB019191).

"*Pyropia collinsii*"

The taxon is unidentified and possibly undescribed, and originally reported by Bray (2006; GenBank accession: DQ813598).

Distribution verified by DNA sequence: Massachusetts, Connecticut, Rhode Island, New York and Virginia, USA (Kucera & Saunders, 2012; Mols–Mortensen *et al.*, 2012; published on GenBank).

Current paper: new distributional records were verified from New Hampshire and New Jersey, USA and Denmark.

"*Pyropia leucosticta*"

The taxon is unidentified and possibly undescribed, and has been entangled in the *Porphyra leucosticta* (now *Pyropia leucosticta*) complex. Based on *rbc*L sequences Neefus (2007) revealed at least eight distinct entities in the complex, and concluded that the species that fits the North Atlantic morphological and ecological concept of the species was molecularly distinct from an isotype specimen of *P. leucosticta*. The epithet *epiphytica* was proposed for the taxon but the formal description has not yet been published.

Distribution verified by DNA sequence: Iceland and the Faroe Islands, UK, Newfoundland, New Brunswick, Nova Scotia, Canada, Maine, Rhode Island, New Hampshire and New York, USA (Brodie *et al.*, 2007; Holmes & Brodie, 2005; Klein *et al.*, 2003; Kucera & Saunders, 2012; Mols–Mortensen *et al*., 2012; Robba *et al*., 2006; Teasdale *et al*., 2009).

Current paper: a new distribution record was verified from Denmark.

“*Pyropia novae–angliae*”

The taxon is unidentified and possibly undescribed, and originally reported by Bray (2006; GenBank accession: DQ813608).

Distribution verified by DNA sequence: Maine, USA (Mols–Mortensen *et al*., 2012; published on GenBank).

Current paper: new distributional records were verified from New Hampshire, USA and Denmark.

Pyropia sp.

The taxon is unidentified and possibly undescribed and is identified for the first time in current paper.

Distribution verified by DNA sequence: the Faroe Islands (GenBank accession: KP171958).

Wildemania abyssicola (Kjellm.) Mols–Mortensen & J. Brodie in Mols–Mortensen *et al*., 2012: 156

Type location: Norwegian Arctic Sea

Distribution verified by DNA sequence: Iceland (Mols–Mortensen *et al*., 2012).

Current paper: verified the species in Norway. No sequence data were available from type material and a sequence published by Mols–Mortensen *et al*. (2012) was used as identification reference (GenBank accession: JN847269).

Wildemania amplissima (Kjellm.) Foslie, 1891: 49

Type location: (Lectotype) Maasö, Norway

Distribution verified by DNA sequence: Iceland and the Faroe Islands, Norway and South West Greenland, Labrador, Newfoundland, Quebec, New Brunswick and Nova Scotia, Canada, Maine and New Hampshire, USA, from Alaska to California on the Northeast Pacific coast, Japan (A. Mols–Mortensen personal observations; Klein *et al*., 2003; Kucera & Saunders, 2012; Lindstrom & Fredericq, 2003; Mols-Mortensen *et al*., 2012, 2014; Sutherland *et al*., 2011).

Current paper: new distributional records verified from New Jersey, USA and Denmark. No sequence data were available from type material and a sequence published by Kucera & Saunders (2012) was used as identification reference (GenBank accession: JN029015).

Wildemania miniata (C.Agardh) Foslie, 1891: 49

Type location: (Lectotype) Greenland

Distribution verified by DNA sequence: Iceland and Faroe Islands, Greenland, Labrador, Newfoundland, Quebec and New Brunswick, Canada, Nova Scotia, Canada, Maine, USA (Klein *et al*., 2003; Kucera & Saunders, 2012; Mols–Mortensen *et al*., 2012, 2014; Pedersen, 2011)

Current paper: no further distribution records were added. No sequence data were available from type material and a sequence published by Kucera & Saunders (2012) was used as identification reference (GenBank accession: JN029016).

Discussion

Using newly collected material as well as historic herbarium specimens of foliose Bangiales our study revealed new distribution information for twelve of the North Atlantic species. The restricted availability of stable substratum together with warm temperatures from New Jersey and southwards are probably important factors determining species diversity. South of Cape Hatteras, North Carolina, where the warm-temperate biogeographic region on the Northwest Atlantic coast begins (Lüning, 1990) only *Pyropia elongata* and *Py. suborbiculata* were reported. *Pyropia suborbiculata* is now documented from southern Massachusetts (Neefus *et al*., 2008) to Myrtle Beach, South Carolina (this paper) on the Northwest Atlantic coast. Humm (1979) suggested that *Py. suborbiculata* (as *Porphyra carolinensis*) was introduced to North Carolina after 1960, and Neefus *et al*. (2008) reported that the earliest specimens confirmed from the east coast of the USA dated back to 1964. Vergés *et al*. (2013) reported *Py. suborbiculata*, based on sequence identification, from the Iberian Peninsula (Northeast Atlantic and Mediterranean coast) in 2010. The species was reported from the Canary Islands (as *Porphyra carolinensis*) in the Northeast Atlantic by Haroun *et al*. (2002), although their report was not verified by DNA sequences. *Pyropia suborbiculata* was originally described as *Porphyra suborbiculata* by Kjellman (1897) from the North Pacific, and given its cosmopolitan distribution and identical haplotypes in the western Atlantic and western Pacific, the species is thought to have extensive dispersal ability (Broom *et al*., 2002).

Pyropia yezoensis, the only species in this study recorded only from the Northwest Atlantic, was most likely introduced to this region from Japan (West *et al*., 2005; Mathieson *et al*., 2008; Neefus *et al*., 2008). The two forms of *Pyropia yezoensis* (f. *yezoensis* and f. *narawensis*) are both present on the Northwest Atlantic coast, and Neefus *et al*., (2008) reported that *Py. yezoensis* f. *narawensis* occurred only south of Cape Cod and *Py. yezoensis* f. *yezoensis* occurred from Maine to Long Island. Based on our results both forms were found in New Jersey (NJ) with the southernmost distribution record for f. *narawensis* in Surf City, NJ and f. *yezoensis* reaching further south to Cape May, NJ, and as was reported by Neefus *et al*. (2008) we did not find both forms co-occurring at any of the visited sites. Based on our data it cannot be determined whether *Pyropia yezoensis* is a new introduction in New Jersey or if earlier workers overlooked the species in the flora, but overall we can conclude that both *Py. suborbiculata* and *Py. yezoensis* are introduced into the North Atlantic. *Pyropia yezoensis* has not been verified from the Northeast Atlantic coast and Brodie *et al*., (1998) found that a species identified as *Porphyra yezoensis* from Helgoland (Kornmann, 1986) did not have matching RUBISCO spacer sequence with Japanese material.

Prior to this work, where *Pyropia thulaea* was reported for the first time on the Northwest Atlantic coast, the species was only known from West Greenland and East

Iceland (Munda & Pedersen, 1978; Brodie *et al*., 2008; Mols–Mortensen *et al*., 2012, 2014). One of the Northwest Atlantic *Py. thulaea* records based on herbarium material was collected in Newfoundland in 1901 (see Appendix D), and therefore *Py. thulaea* is not a new introduction to the Northwest Atlantic coast but has gone unrecognized in the flora until now. Mols–Mortensen *et al*. (2014) concluded that the cold-water species *Py. thulaea* was widespread on the West Greenland coast, the eastern most distribution record was from East Iceland and *Py. pseudolinearis* was its North Pacific vicariant counterpart.

Pyropia peggicovensis was recently described from Nova Scotia, Canada in the Northwest Atlantic (Kucera & Saunders, 2012), and based on herbarium material we reported the species from Prince Edward Island, Canada and the earliest herbarium record of the species on the Northwest Atlantic coast to date is a collection from Nova Scotia in 1970 (see Appendix D). Mols–Mortensen *et al*. (2012) reported the unidentified species *Pyropia* sp. DK from Denmark based on a collection from 1994 (see Appendix D). Due to matching *rbc*L sequences we can now identify this species as *Py. peggicovensis*, and herbarium collections confirm that *Py. peggicovensis* was already collected in Denmark in 1928 and in Sweden in 1978 (see Appendix D). *Pyropia peggicovensis* is therefore not a recent introduction into the North Atlantic, and both morphological and sequence data demonstrate that the species has been mixed up in the *Porphyra linearis* complex (Mortensen *et al*., 2009; Kucera & Saunders, 2012).

The two unidentified and possibly undescribed taxa, "*Pyropia collinsii*" and "*Pyropia novae-angliae*" were originally identified from the Northwest Atlantic by Bray (2006). Prior to our study "*Pyropia collinsii*" was reported from Massachusetts and south to Chesapeake Bay, Virginia on the Northwest Atlantic coast (Kucera & Saunders, 2012; Mols–Mortensen *et al.*, 2012; GenBank). The current study extends the distribution on the Northwest Atlantic coast to include New Hampshire. Based on herbarium material the oldest record to date of "*Pyropia collinsii*" in the Northwest Atlantic was collected at Bridgeport, Connecticut in 1887. Kucera & Saunders (2012) reported that an unidentified taxon from the UK published by Robba *et al*. (2006) matched "*Pyropia collinsii*", and concluded that the species was distributed both in the Northwest and Northeast Atlantic. Current work also reported "*Pyropia collinsii*" from Denmark. Prior to our work "*Pyropia novae-angliae*" was only reported from Maine in the Northwest Atlantic and current study extended the distribution on the Northwest Atlantic coast to include New Hampshire. We also confirmed the species in Denmark in the Northeast Atlantic, with the oldest specimen collected in Korsør, Denmark in 1936. Based on our results "*Pyropia collinsii*" and "*Pyropia novae-angliae*" were also not recent introductions into the North Atlantic foliose Bangiales flora. Compared to prior work in the Northwest Atlantic current work did not find *Pyropia katadae*, *Py. olivii* (currently regarded as a taxonomic synonym of *Py. koreana*), "*Py. spatulata*" and "*Py. stamfordensis*" (Bray, 2006; Brodie *et al.*, 2007; Neefus *et al.*, 2008; Mols–Mortensen *et al.*, 2012).

Due to the antiquity of the Bangiales it is a challenge to interpret the evolution and distribution of the extant taxa (Sutherland *et al.*, 2011), and the pattern is further complicated as a result of human-mediated transport of some species e.g. the introduction of *Pyropia yezoensis* to the Northwest Atlantic (Neefus *et al.*, 2008). Brodie *et al*. (1998) suggested that "*Pyropia leucosticta*" (as *Porphyra leucosticta*) was introduced into the North Atlantic, and recently published *rbc*L phylogenies suggested that all the North Atlantic *Pyropia* species had a close North Pacific link (Mols–Mortensen *et al*., 2012, 2014). *Pyropia* is probably not native to the North Atlantic.

The 3’ *rbc*L + 5’ *rbc*L-S marker was a useful tool to differentiate between the North Atlantic foliose Bangiales species as was also found in Mols–Mortensen *et al*. (2014). The largest intraspecific variation observed in this work was 0.006 (see Appendix E) measured in “*Pyropia collinsii*”, “*Py. leucosticta*” and *Wildemania amplissima*, and this was also the level of intraspecific variation observed for the 3’ *rbc*L + 5’ *rbc*L-S marker in Mols–Mortensen *et al*. (2014). The very limited interspecific variation between *Py. peggicovensis* and *Py. thulaea* (0.004) caused the overlap between the intra- and interspecific variations (see Appendix E), and the only difference between the two species was that *Py. thulaea* had a single deletion in the spacer. Based on an *rbc*L gene phylogeny *Py. peggicovensis* and *Py. thulaea* together with the North Pacific species *Py. pseudolinearis* were resolved in a well-supported clade, but as separate species (Mols–Mortensen *et al*., 2014). Comparing the *rbc*L sequences of the *Py. peggicovensis* holotype (JN028991) and *Py. thulaea* isotype (JN847268) available on GenBank, they are clearly distinct species (19 bp differences in the 1111 bp long *rbc*L sequence), and with the consistent deletion observed by our work in the *rbc*L-*rbc*S spacer, the 3’ *rbc*L + 5’ *rbc*L-S can be used to differentiate between them. The overlap between the intra- and interspecific variation in the 3’ *rbc*L + 5’ *rbc*L-S demonstrates that when using DNA sequences to differentiate between species one should not expect a consistent variation that can be used to draw the limit between what we call the same species.

The findings of this work demonstrate the value of working through both historic and new collections, and how well preserved historic collections can contribute to our understanding of species diversity and their geographic distribution. The work also demonstrates the need for formal descriptions of taxa within the foliose Bangiales in the North Atlantic and more importantly, sequence data from reliably identified specimens of all previously described taxa.

Table 4.1. Sites visited between Connecticut and Florida during May and June, 2011. N/A = not applicable.

Sites	**Coordinates**	**Species found**	**Substratum**
Avery Point, Groton, CT	41°19’56.87”N; 72°02’58.27”W	“*Pyropia collinsii*”, *Pyropia yezoensis* f. *narawensis*	On algae (natural rocky substratum)
Light House Point, New Haven, CT	41°14’53.07”N; 72°54’13.45”W	*Pyropia yezoensis* f. *yezoensis*	On barnacle (natural rocky substratum)
Lighthouse, Belmar, NJ	40°11’19.06”N; 74°00’24.11”W	*Pyropia yezoensis* f. *narawensis*, *Pyropia suborbiculata*	On mussel and on rock (man-made structures)
Jetty, Lavalette, NJ	39°58.297N; 74° 02.942W	*Pyropia yezoensis* f. *narawensis*	On rock (man-made structures)
Lighthouse, Barneget, NJ	39°46’03.77”N; 74°06’30.20”W	*Pyropia yezoensis* f. *narawensis*	On rock and on barnacle (man-made structures)
Surf City, NJ	39°39’43.12”N; 74°09’52.49”W	*Pyropia yezoensis* f. *narawensis*	On rock (man-made structures)
Atlantic City, NJ	39°21’51.81”N; 74°24’30.70”W	*Pyropia yezoensis* f. *yezoensis*	On rock (man-made structures)
Longport, NJ	39°18’31.05”N; 74°31’14.93”W	*Pyropia yezoensis* f. *yezoensis*	On barnacles and mussel (man-made structures)
Ocean City, NJ	39°15.309N; 74°37.842W	“*Pyropia collinsii*”	On concrete (man-made structures)
Lighthouse jetty, Cape May, NJ	38°55.936N; 74°57.782W	*Pyropia yezoensis* f. *yezoensis*	On barnacle and on mussel (man-made structures)
Rehobath Bay jetty, DE	38°36.503N; 75°03.843W	*Pyropia suborbiculata*	On rock (man-made structures)
Ocean City, MD	38°19’27.12”N; 75°05’05.51”W	No foliose Bangiales	N/A
Chrisfield Marina, MD	37°58’36.42”N; 75°51’15.15”W	No foliose Bangiales	N/A
Fishermans Island, Cape Charles, VA	37°05’33.47”N; 75°58’36.02”W	No foliose Bangiales	N/A
Buckroe Beach jetty, Hampton, VA	37°03’48.48”N; 76°16’54.08”W	No foliose Bangiales	N/A
Virginia Beach jetty, VA	36°’49’48.06”N; 75°58’12.31”W	No foliose Bangiales	N/A
Nags Head, NC	35°’57’26.34”N; 75°37’26.29”W	No foliose Bangiales	N/A
Rodanthe, NC	35°’35’37.23”N; 75°28’04.36”W	No foliose Bangiales	N/A
Cape Hatteras, NC	35°’14’14.66”N; 75°31’34.68”W	No foliose Bangiales	N/A
Pea Island, Oregon Inlet, NC		No foliose Bangiales	N/A
Pivers Island, Beaufort, NC	34°43’03.62”N; 76°40’19.96”W	No foliose Bangiales	N/A
Radio Island Jetty, Beaufort, NC	34°42’58.22”N; 76°40’50.21”W	No foliose Bangiales	N/A

Surf City, NC	34°25’29.21”N; 77°32’43.29”W	*Pyropia suborbiculata*	Pier on the beach, specimens on barnacle sitting on the piling (man-made structures)
Wrightsville Beach, Wilmington, NC	34°12’937”N; 77°45’415”W	*Pyropia suborbiculata*	On pier pilings (man-made structures)
Myrtle Beach, SC	33°41’769”N; 78°52’623”W	*Pyropia suborbiculata*	On wooden piling and on barnacles on the wooden piling (man-made structures)
Savannah, Tybee Beach jetty, GA	32°01’24.27”N; 80°50’43.51”W	No foliose Bangiales	N/A
St. Simmons Island, GA	31°09’37.50”N; 81°22’55.97”W	No foliose Bangiales	N/A
Jacksonville Beach pier, FL	30°17’35.24”N; 81°23’23.27”W	No foliose Bangiales	N/A
Marineland, FL	29°43’31.78”N; 81°14’06.50”W	No foliose Bangiales	N/A

Table 4.2. Distribution of the foliose Bangiales species on the Northwest Atlantic coast. * indicates a new distribution record. LA= Labrador, NF=Newfoundland, QE=Quebec, PEI=Prince Edward Island, NB=New Brunswick, NS=Nova Scotia, ME=Maine, NH=New Hampshire, MA=Massachusetts, RI=Rhode Island, CT=Connecticut, NY=New York, NJ=New Jersey, DE=Delaware, MD=Maryland, VA=Virginia, NC=North Carolina, SC=South Carolina, GE=Georgia, FL=Florida.

	LA	NF	QE	PEI	NB	NS	ME	NH	MA	RI	CT	NY	NJ	DE	MD	VA	NC	SC	GE	FL
Boreophyllum birdiae	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Porphyra linearis	-	-	-	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-
Porphyra purpurea	+	+	+	-	+	+	-	+	+	-	+	-	-	-	-	-	-	-	-	-
Porphyra umbilicalis	+	+	-	-	+	-	+	+	-	+	-	+	-	-	-	-	-	-	-	-
Pyropia elongata	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	+	-	-	-
Pyropia njordii	-	-	+	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Pyropia peggicovensis	-	-	-	+*	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pyropia suborbiculata	-	-	-	-	-	-	-	-	+	-	+	-	+*	+*	-	-	+	+*	-	-
Pyropia thulaea	-	+*	-	-	+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pyropia yezoensis f. *yezoensis*	-	-	-	-	-	-	+	+	+	-	+	+	+*	-	-	-	-	-	-	-
Pyropia yezoensis f. *narawensis*	-	-	-	-	-	-	-	-	+	+	+	-	+*	-	-	-	-	-	-	-
"*Pyropia collisii*"	-	-	-	-	-	-	-	+*	+	+	+	+	+*	-	-	+	-	-	-	-
"*Pyropia leucosticta*"	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
"*Pyropia novae-angliae*"	-	-	-	-	-	-	+	+*	-	-	-	-	-	-	-	-	-	-	-	-
Wildemania amplissima	+	+	+	-	+	+	+	+	-	-	-	-	+*	-	-	-	-	-	-	-
Wildemania miniata	+	+	+	-	+	+	+	+*	-	-	-	-	-	-	-	-	-	-	-	-

Table 4.3. Northeast Atlantic (including Iceland and the Faroe Islands) foliose Bangiales species diversity and new distribution records based on DNA sequence identification.

	NEA	**New distribution records**
Boreophyllum birdiae	+	-
Porphyra dioica	+	Norway
Porphyra linearis	+	Denmark
Porphyra purpurea	+	-
Porphyra umbilicalis	+	Spain (Atlantic side)
Porphyra sp.	+	-
Pyropia elongata	+	-
Pyropia njordii	+	Norway, Denmark
Pyropia peggicovensis	+	Denmark, Sweden
Pyropia suborbiculata	+	-
Pyropia thulaea	+	-
Pyropia yezoensis f. *yezoensis*	-	-
Pyropia yezoensis f. *narawensis*	-	-
"*Pyropia collisii*"	+	Denmark
"*Pyropia leucosticta*"	+	Denmark
"*Pyropia novae-angliae*"	+	Denmark
Pyropia sp.	+	Faroe Islands
Wildemania abyssicola	+	Norway
Wildemania amplissima	+	Denmark
Wildemania miniata	+	-

CHAPTER V

WILDEMANIA AMPLISSIMA (BANGIALES, RHODOPHYTA) IN THE NORTH ATLANTIC AND NORTH PACIFIC: A PRELIMINARY PHYLOGEOGRAPHIC ANALYSIS

(Manuscript in preparation)

Abstract

Wildemania is a foliose genus in the Bangiales that includes at least ten species, of which only seven have been described. *Wildemania amplissima* is the type species of the genus and is distributed both in the North Atlantic and the North Pacific. Preliminary observations have revealed an unidentified *Wildemania* species from Chile with a very simililar *rbc*L sequence to *W. amplissima*. A phylogenetic study of *Wildemania* species based on the chloroplast *rbc*L gene was undertaken as well as a phylogeographic study of North Atlantic and North Pacific *W. amplissima* populations based on the mitochondrial *cox*2-3 spacer and nuclear ITS1 spacer. The phylogenetic analysis revealed three highly supported clades within *Wildemania* and *W. amplissima* was resolved in a clade together with three unidentified taxa including the unidentified species from Chile. The *cox*2-3 spacer was not found useful in resolving phylogeographic patterns in *W. amplissima*, but ITS1 recovered a total of sixteen haplotypes; thirteen from the North Atlantic and three from the North Pacific. Seven missing haplotypes were between the most closely related North Atlantic and North Pacific haplotypes, and together with the low haplotype diversity in the North Pacific populations they were interpreted as "stable rear edge" populations, defined as

populations that have persisted at suitable growing sites through changing climatic conditions while the species expanded its range. Due to insufficient sampling only preliminary biogeopgraphic conclusions could be made.

Introduction

Severe climatic oscillations during the Quaternary (2.6 million years ago to the present) have been a major factor in shaping the distribution of extant species worldwide (Hewitt, 2000; Provan & Bennett, 2008). Phylogeographic studies have provided insights into the history of many species through changing climatic conditions, and have been particularly informative in reconstructing the glacial and postglacial history of marine organisms (Maggs *et al.*, 2008). The phylogeographic approach has also proved useful to test potential effects of modern climatic changes on the genetic variation in extant species, and providing data that can be crucial from a conservation point of view (Hampe & Petit, 2005; Provan & Maggs, 2012; Provan, 2013).

An important seaway connection and migrational route for marine organisms was formed between the North Pacific and North Atlantic via the Arctic Ocean when the Bering land bridge submerged. Despite the significance of this event, determining the age of the Bering Strait has proved difficult. Gladenkov *et al*. (2002) dated this event to the end of the Miocene at 5.32 Ma, based on the migration of the bivalve mollusk *Astarte* from the Arctic Ocean to the North Pacific when the Bering Strait first flooded. The fossil record indicates that the migration of marine species through the Bering Strait occurred primarily from the North Pacific into the North Atlantic in the late Pliocene, ca. 3.5 million years ago (Briggs, 1970; Vermeij, 1991). The apparent relationship between the boreal floras and faunas of the North Atlantic and the North Pacific has been attributed to the migrations of Pacific species through the Bering Strait into the North Atlantic in the late Pliocene at 3.5 Ma, and this date is also regarded as the calibration point of when the floras and faunas were separated (e.g. Briggs, 1970; van Oppen *et al*., 1995; Lindstrom, 2001; Teasdale & Klein, 2010). The migration of marine organisms between the North Pacific and North Atlantic through the Bering Strait via the Arctic Ocean is known as the

Great Biotic Interchange. Evidence from fossil mollusk records show that migration from the North Pacific to the North Atlantic was at least eight times greater than migration from the North Atlantic to the North Pacific (Durham & MacNeil, 1967) and the same prevailing migration direction has also been found within the macroalgae (Lüning, 1990; Lindstrom, 2001; Adey *et al*., 2008). Following the glacial and interglacial shifts through the Pleistocene (2.5 Ma –10,000 years ago) allopatric speciation occurred as the Bering land bridge repeatedly submerged and emerged and the Arctic Ocean repeatedly froze. Many macroalgal species found today in the boreal North Pacific and North Atlantic are closely related sibling species that have evolved by allopatric speciation, but there are also conspecific populations found in both oceans (e.g. Lindstrom, 1987, 2001; Lindstrom & Cole, 1992, 1993; van Oppen *et al*., 1995; Bray *et al*., 2007; Kucera & Saunders, 2012; Mols–Mortensen *et al*., 2014).

Wildemania is a genus within the red algal order Bangiales that includes monostromatic and distromatic foliose species (Sutherland *et al*., 2011; Mols–Mortensen *et al*., 2012). *Wildemania* includes at least ten species, of which only seven have been described (Sutherland *et al*., 2011; Kucera & Saunders, 2012; Mols-Mortensen *et al*., 2012): *W. abyssicola* (Kjellman) Mols-Mortensen & J. Brodie, *W. amplissima* and *W. miniata* (C.Agardh) Foslie are reported from the North Atlantic, and *W. amplissima, W. norrisii* (V.Krishnamurthy) S.C. Lindstrom, *W. occidentalis* (Setchell & Hus) S.C. Lindstrom, *W. schizophylla* (Hollenberg) S.C. Lindstrom and *W. variegata* (Kjellman) De Toni are reported from the North Pacific (Sutherland *et al*., 2011; Kucera & Saunders, 2012), and there are unidentified *Wildemania* taxa reported from Korea, the Falkland Islands, Antarctica (Sutherland *et al*., 2011) and from Chile (J. Brodie, A. Mols-Mortensen, M. E. Ramírez & H. Woods pers. obs). Preliminary observations on the unidentified *Wildemania* species from Chile have revealed a taxon with very similar *rbc*L sequences to *W. amplissima* (J. Brodie, A. Mols-Mortensen, M. E. Ramirez & H. Woods pers. obs.). The taxon was collected from the Atlantic side of the Strait of Magellan, which makes a seaway connection between the South Atlantic and South Pacific.

Wildemania amplissima is the type species of *Wildemania*, and was until recently regarded as the North Atlantic sibling species of the North Pacific *W. cuneiformis* (Setchell & Hus) S.C. Lindstrom (Lindstrom & Cole, 1992). Based on sequence similarities in the cytochrom c oxidase subunit 1 (*cox*1), ribulose-1,5-bisphosphate carboxylase–oxygenase large subunit (*rbc*L) and (Universal Plastid Amplicon (UPA) markers of *W. amplissima* and *W. cuneiformis*, Kucera & Saunders (2012) proposed to synonymize *W. cuneiformis* with *W. amplissima*, the latter having priority as the older name. Other reports on genetic, anatomical and ecological similarities between these species support this proposal (Lindstrom & Cole, 1992, 1993; Lindstrom & Fredericq, 2003; Mols–Mortensen *et al.*, 2012), and here *W. amplissima* and *W. cuneiformis* are considered conspecific entities. *Wildemania amplissima* is a low intertidal to shallow subtidal spring and summer annual with a cold temperate distribution, and is reported from Norway (Sutherland *et al.*, 2011), Svalbard (Frederiksen & Kile, 2012), Iceland and the Faroe Islands (Mols-Mortensen *et al.*, 2012), Ireland (Guiry, 2012), Northern Kattegat and Britain where the southern distribution limit is the Isle of Man (Brodie & Irvine, 2003), Southwest Greenland (Mols-Mortensen *et al.*, 2014), and from Labrador to New Jersey on the North American coast (Hehre & Mathieson, 1993; Kucera & Saunders, 2012; current work). The reported distribution in the North Pacific is from Alaska to California on the North American coast (Stiller & Waaland, 1993; Hansen, 1997; Lindstrom & Fredericq, 2003), and in Japan (Yoshida *et al.*, 1990; Yoshida, 1998). As reported for the other Bangiales species, *W. amplissima* has a heteromorphic life–history with a foliose gametophyte and a filamentous, uniseriate and branched shell–boring sporophyte, known as the conchocelis phase (Brodie & Irvine, 2003).

The Bangiales represent an ancient lineage (Butterfield, 2000), and they include the most highly valued seaweed aquaculture crop, *Porphyra* sensu lato in the world (Mumford & Miura, 1988; Blouin *et al*., 2010). The potential of *W. amplissima* as an aquaculture crop is currently being explored (L. Green pers. com.). Little is known about the biogeographic history of *W. amplissima* and how the populations from the different geographic areas relate to each other. Using a phylogeographic approach insights can be gained into the history of the species.

The aim of this paper was to study the phylogenetic relationships in *Wildemania* including the unidentified taxon from Chile using *rbc*L sequences. Another aim was to carry out a preliminary phylogeographic study of *W. amplissima*, including samples from as many parts of the geographic range of the species as could be obtained, to examine the haplotype diversity, their interrelatedness and potential geographic origin of the species. The phylogeographic study was based on nuclear internal transcribed spacer 1 (ITS1) and mitochondrial cytochrome c oxidase subunit 2 and 3 spacer (*cox*2–3) sequences, and the genetic variation between *W. amplissima* populations from the North Atlantic and North Pacific was compared. The ITS1 spacer has been found informative on the intraspecific level within the red algal genera *Mastocarpus* (Lindstrom *et al*., 2011) and *Phycodrys* (van Oppen *et al*., 1995), and the *cox*2–3 spacer has been found informative on the intraspecific level in several red algal species (Zuccarello *et al*., 1999). The two spacers were therefore considered to be potentially variable at the population level in *W. amplissima*.

Materials and Methods

Collections and identification

The samples used in the phylogenetic study of *Wildemania* were all downloaded from GenBank except for *W. abyssicola* JN847269, *W. miniata* JN847276 and KF478759, *W. amplissima* JN847273 and JN029013, and the samples of the unidentified "*W.* sp. Chile" JBCH2011.01, JBCH2011.04 and JBCH2011.13 were freshly collected from the Atlantic side of the Strait of Magellan in Chile, with samples for DNA analysis preserved in silica-gel and herbarium voucher specimens prepared (Appendix F). The herbarium vouchers of the *Wildemania* material from Chile were deposited at the Natural History Museum, London (BM).

Wildemania amplissima samples used in the phylogeographic study were obtained from Norway, Faroe Islands and Iceland in the Northeast Atlantic, Quebec, New Brunswick and New Hampshire in the Northwest Atlantic and Alaska, British Columbia and Washington in the Northeast Pacific (Fig. 5.1 & Appendix F). With the exception of the samples from New Brunswick, Quebec and British Columbia in Canada, which were provided by Dr. G. W. Saunders as DNA extracts, specimens were either freshly collected or obtained from silica-gel dried samples or herbarium samples. The herbarium vouchers prepared from the *W. amplissima* samples were deposited in the Albion Hodgdon Herbarium (NHA), University of New Hampshire, U.S.A., and in the Beaty Biodiversity Museum herbarium (UBC) for specimens collected in Alaska and Washington. The identity of the 73 *W. amplissima* specimens used in the phylogeographic study was verified by a 298 bp long plastid marker 3' *rbc*L + 5' *rbc*L-S that was found useful for identification within the Bangiales (Mols-Mortensen *et al.*, 2014).

DNA extraction, PCR amplification and sequencing

The DNA extraction, PCR amplification, purification and sequencing were carried out as described in Bray *et al.* (2006) and as the method described for the University of New Hampshire (UNH) in Mols-Mortensen *et al.* (2012). Specimens JBCH2011.01, JBCH2011.04 and JBCH2011.13 followed the protocol described for the Natural History Museum (NHM) in Mols-Mortensen *et al.* (2012). The primer pairs used to amplify and sequence the *rbc*L gene, the 3' *rbc*L + 5' *rbc*L–S, ITS1 and *cox*2–3 were listed in Table 5.1. The profiles used to amplify the *rbc*L, 3' *rbc*L + 5' *rbc*L–S, ITS1 and *cox*2–3 were as follows: ***rbc*L and 3' *rbc*L + 5' *rbc*L–S**: 95°C for 2.5 min; 29 cycles of 95°C for 30 s, 50°C for 45 s, 72°C for 1 min; and 72°C for 5 min. **ITS1**: 94°C for 5 min; 30 cycles of 94°C for 1 min, 60°C for 1 min, 72°C for 2 min; and 72°C for 5 min. ***cox*2–3**: 94°C for 4 min; 5 cycles of 93°C for 1 min, 45°C for 1 min, 72°C for 1 min; 30 cycles of 93°C for 30 s, 55°C for 30 s, 72°C for 30 s; and 1 cycle of 72°C for 5 min. The WACOX23–F and WACOX23–R primers were designed using DNASTAR Lasergene PrimerSelect Version 7.2.1 (1) and are published here for the first time.

Sequence alignment

The raw sequence chromatograms for each marker were assembled and proofread in Geneious 6.1.2® (Biomatters Ltd., Auckland, New Zealand), and the datasets were aligned using the Muscle algorithm (Edgar, 2004) implemented in Geneious 6.1.2®. The *rbc*L alignment comprised 24 sequences with a length of 1,170 bp, and the filamentous '*Bangia*' 2 HQ687506 and foliose *Porphyra umbilicalis* JN847251 formed the outgroup. The *cox*2–3 alignment comprised 66 sequences with a length of 327 bp, and the ITS1 alignment comprised 73 sequences with a length of 423 bp.

Data analysis

Interspecific and intraspecific genetic variations in the *rbc*L dataset, and intraspecific genetic variations in the *cox*2–3 and ITS1 datasets were calculated using the Tamura-Nei genetic distance model and Neighbor Joining tree building method, implemented in Geneious 6.1.2®. Maximum Likelihood (ML) and Neighbor Joining (NJ) analyses were performed on the *rbc*L dataset to infer interspecific phylogenetic relationships in *Wildemania*. Prior to the analysis JModelTest 0.1.1 with Likelihood settings Maximum Likelihood optimized was used to identify the appropriate model of sequence evolution for the *rbc*L dataset (Posada, 2008), and based on the Akaike Information Criterion (AIC) [Hurvich & Tsai, 1989] GTR+I+Γ was the preferred model for the *rbc*L dataset. The ML searches were conducted using PhyML (Guindon & Gascuel, 2003), implemented in the Seaview version 4 platform (Gouy *et al.*, 2010) with 1,000 bootstrap replicates, and the NJ analysis was conducted using the Geneious Tree Builder implemented in Geneious 6.1.2® with 1,000 bootstrap replicates.

Haplotype (*h*) (Nei, 1987) and nucleotide (π) diversities were estimated for the *cox*2–3 and ITS1 datasets using ARLEQUIN version 3.5.1.2 (Excoffier *et al.*, 2005). The data files analyzed in ARLEQUIN were prepared using the software DnaSP version 5.10.1 (Rozas *et al.*, 2010), and the frequency of the different haplotypes was also found using DnaSP. Intraspecific relationships among the *cox*2–3 haplotypes and ITS1 haplotypes were inferred using Median–Joining (MJ) network algorithm (Bandelt *et al.*, 1999) implemented in the software NETWORK version 4.6.1.1 (Fluxus Technology Ltd., Suffolk, England) and Statistical Parsimony (SP; Templeton *et al.*, 1992) implemented in the software TCS version 1.21 (Clement *et al.*, 2000). The MJ network method requires the absence of recombination in the dataset and we used the RDP v.4.22 software

(Martin *et al.*, 2010) to analyze the ITS1 dataset for potential recombination events. The outgroup weight was calculated in the TCS software where each haplotype in the SP network was assigned a 'outgroup probability' (Castelloe & Templeton, 1994) to find the most likely root haplotype. The likelihood is calculated as a function of the position of the haplotypes in the network, their frequency, and number of connections with other haplotypes (Castelloe & Templeton, 1994; Teasdale & Klein, 2010). Due to low sample numbers (1 or 2 individuals) the samples from Norway, Iceland, Quebec and British Columbia were excluded from the haplotype and nucleotide diversity measurements, and these populations were also marked with small dots in Figure 5.3.

Using 3.5 Ma as the calibration date for the trans–Arctic biotic interchange and the net nucleotide divergence *d* (Nei & Li, 1979) between the North Atlantic and North Pacific populations, the mutation rate μ for ITS1 can be estimated using the formula $\mu = (1/2)d/(3.5 * 10^6 \text{ years})$, following the method in Teasdale & Klein (2010). The estimated mutation rate and the net nucleotide divergence between the Northeast Atlantic and the Northwest Atlantic can then be used to estimate the first split between Northeast – and Northwest Atlantic haplotypes.

Results

<u>*rbc*L</u>

The ML and NJ analyses of the *Wildemania rbc*L dataset, including the three unidentified specimens from Chile ("*W*. sp. Chile") and the type species of *W. amplissima*, revealed three highly supported clades (Fig. 5.2). Clade I included *W. occidentalis*, *W. abyssicola*, *W. variegata*, *W. miniata* and a previously unidentified specimen that was resolved within *W. variegata*. *Wildemania occidentalis* and *W. abyssicola* were resolved in a sister group to *W. variegata* and *W. miniata*, and "*W. variegata*" AF452447 from Alaska was resolved within *W. miniata* and the genetic variation between *W. miniata* and "*W*. *variegata*" AF452447 was within the intraspecific variation measured in the two *W. miniata* samples (Table 5.2). Clade II included *W. norrisii* and two taxa under the name of "*W. schizophylla*" from Alaska and California, respectively, and was resolved as a sister clade to clade III, but without bootstrap support. The genetic variation between "*W. schizophylla*" AF452443 from Alaska and *W. norrisii* EU223212 from British Columbia was less than the variation between the two "*W. schizophylla*" taxa (Table 5.3), and "*W. schizophylla*" GU319871 from California was resolved as a sister taxon to "*W. schizophylla*" AF452443 and *W. norrisii*. Clade III included *W. amplissima* and three unidentified taxa from Chile ("*W*. sp. Chile"), Falkland Islands ("*W*. sp. Falkland") and Antarctica ("*W*. sp. Antarctica"), respectively, with *W. amplissima* resolved as sister species to the three unidentified taxa of which "*W*. sp. Antarctica" was resolved on its own branch. The intraspecific variation in *W. amplissima* was very small, and based on the measured genetic variation "*W*. sp. Chile" and "*W*. sp. Falkland" should possibly be regarded as the same species (Table 5.4). The overall genetic variation within the *Wildemania rbc*L dataset was between 0.000 and 0.093, and between 0 and 135 in patristic distances and base pair differences, respectively (data not shown).

cox2–3 and ITS1

The *cox*2–3 spacer was successfully sequenced for 46 North Atlantic and 20 North Pacific *W. amplissima* specimens and a total of three haplotypes were recovered in the dataset, one haplotype in the North Atlantic and two in the North Pacific (data not shown). Two substitutions were consistent differences between the North Atlantic and North Pacific haplotypes, but the difference between the two North Pacific haplotypes was based on a single specimen from Alaska that had one transition substitution from G to A. The intraspecific variation based on Tamura–Nei model between the North Atlantic and North Pacific *W. amplissima* populations was between 0.007 and 0.010, and 2 to 3 measured in patristic distances and base pair differences, respectively (data not shown). Due to very limited sequence variation in the *cox*2–3 spacer of the studied *W. amplissima* individuals the marker was not found useful in resolving phylogeographic patterns.

The ITS1 spacer was successfully sequenced for 52 North Atlantic and 21 North Pacific *W. amplissima* specimens (including the 66 specimens that *cox*2–3 sequences were obtained from), and sixteen haplotypes were recovered: thirteen from the North Atlantic, including seven from the Northeast Atlantic and nine from the Northwest Atlantic, and three from the North Pacific (Figs 5.3, 5.4 & Table 5.5). No haplotypes were shared between the North Atlantic and the North Pacific, but three haplotypes (H1, H5 and H6) were shared between the Northeast – and Northwest Atlantic. Haplotype 1 (H1) was the most common haplotype in the North Atlantic, recovered in 28 (53.8%) of the 52 North Atlantic individuals, and present in all the collected North Atlantic areas except in the single collected individual from Quebec (Figs 5.3, 5.4 & Table 5.5, 5.6). Haplotypes 3 (H3) and 5 (H5) were recovered in 5 (9.6%) individuals and haplotype 6 (H6) was recovered in 4 (7.7%) individuals from the North Atlantic (Table 5.6). Four unique haplotypes (H2, H3, H4 and H7) were recovered in the Northeast Atlantic (including Iceland), and six unique haplotypes (H8, H9, H10, H11, H12 and H13) were recovered in the Northwest Atlantic collections (Figs 5.3, 5.4 & Tables 5.5, 5.6). All unique haplotypes recovered in the North Atlantic were singletons (only recovered once), except H3 that was recovered five times in the collection from the Faroe Islands, and H10 that was recovered twice in the collection from the Bay of Fundy (Figs 5.3, 5.4 & Table 5.5, 5.6). Haplotype 1 was the most abundant haplotype in the Northwest Atlantic collections, recovered in 22 (62.9%) of the 35 individuals followed by H5 and H6, which were recovered in only 3 (8.6%) of the 35 individuals each. Haplotype 1 was also the most abundant haplotype in the Northeast Atlantic collections, recovered in 6 (35.3%) of the 17 individuals followed by H3 that was recovered in 5 (29.4%) of the 17 individuals, and H3 was recovered only in the collection from the Faroe Islands (Figs 5.3, 5.4 & Tables 5.5, 5.6). Haplotypes 15 (H15) and 16 (H16) were the most common haplotypes recovered in the North Pacific collections, with H15 recovered in 11 (52.4%) of the 21 individuals and H16 recovered in 9 (42.9%) individuals (Figs 5.3, 5.4 & Tables 5.5, 5.6). Haplotype 16 was a unique haplotype recovered only in the collection from Washington, and it was the only haplotype recovered in this area (Figs 5.3, 5.4 & Tables 5.5, 5.6). The collections from Alaska and British Columbia shared one haplotype (H15) but they did not share any haplotype with the collection from Washington (Figs 5.3, 5.4 & Tables 5.5, 5.6). The intraspecific variation based on the Tamura–Nei model between the North Atlantic and North Pacific *W. amplissima* populations was between 0.010 and 0.021, and 10 and 16 measured in patristic distances and base pair differences, respectively (data not shown). The variation within the North Atlantic was between 0.000 and 0.010, and 0 and 5 measured in patristic distances and base pair differences, respectively (data not shown). The variation within the North Pacific was between 0.000 and 0.004, and 0 and 4 measured in patristic distances and base pair differences, respectively (data not shown).

The RDP v.4.22 software detected no recombination events in the ITS1 alignment, and therefore the MJ network method could be used. The MJ network revealed two biogeographical groups; one North Atlantic and one North Pacific; the Northeast Atlantic and Northwest Atlantic haplotypes formed one biogeographical group (Fig. 5.4). The SP network (data not shown) revealed the same exact haplotype connections but with better resolution on the missing intermediate haplotypes that are defined as unsampled extant haplotypes or extinct ancestral haplotypes (Posada & Crandall, 2001). In the SP network seven missing intermediate haplotypes connected H8 from the Northwest Atlantic and H15 from the North Pacific, one missing intermediate haplotype connected H8 and H1 from the North Atlantic, and two missing intermediate haplotypes connected H15 and H14 from the North Pacific. The haplotype with the highest outgroup weight and therefore the most likely root haplotype, was found by the TCS software to be H1 that was represented both in the Northeast Atlantic and Northwest Atlantic (marked with an asterisk (*) on Figure 5.4), however the calculated outgroup weight was only 0.25. Haplotype 15 from the North Pacific was connected to the other two haplotypes recovered in the North Pacific, and was also connected to the North Atlantic biogeographic group via H8 recovered from Quebec (Fig. 5.4). All the recovered North Atlantic haplotypes were directly connected to H1, except H2, H4 and H5 from the Faroe Islands, H9 from the Bay of Fundy and H12 from New Hampshire. Haplotype 2 was connected to H1 via both H3 and H6; H5, H9 and H12 were connected to H1 via H6; and H4 was connected to H5 (see Fig. 5.4).

The haplotype diversity (*h*), which is a measure of the uniqueness of a particular haplotype in a given population, and the nucleotide diversity (π), which is a measure of the degree of polymorphism within a population, ranged from 0.5435 to 0.8205 and 0.0020 to 0.0038 in the North Atlantic, respectively, and from 0.000 to 0.2000 and 0.0000 to 0.0014 in the North Pacific, respectively (Table 5.5). The overall haplotype diversity and nucleotide diversity was largest in the Northeast Atlantic and smallest in the Northwest Atlantic, but there was very little difference between the haplotype diversity and nucleotide diversity in the Northwest Atlantic and North Pacific (Table 5.7).

Using the calibration date of 3.5 Ma and the net nucleotide substitution between the North Atlantic and North Pacific sequences (d = 0.01040) the theoretical ITS1 mutation rate in *W. amplissima* was found to be $\mu = 1.49 \times 10^{-9}$ (substitution per site per generation). *Wildemania amplissima* is a spring and summer annual and therefore we would expect it to go through one generation per year. Based on the above estimated theoretical mutation rate for the ITS1 region in *W. amplissima* and the net nucleotide substitution between the Northeast Atlantic and Northwest Atlantic populations (d = 0.00023), the first split between Northeast – and Northwest Atlantic haplotypes occurred within the last 77,404 years.

Discussion

The phylogenetic resolution found in our work, with *Wildemania* resolved in three clades and the phylogenetic position of the clade including *W. norrisii* and two taxa of "*W. schizophylla*" unresolved, corresponds well with the findings in Sutherland *et al*. (2011). Based on morphology and chromosome counts, *W. schizophylla* and *W. norrisii* were reported to differ from the rest of the *Wildemania* species (Conway *et al*., 1975; Mumford & Cole, 1977), but our study and other studies based on *rbc*L and concatenated nrSSU and *rbc*L data resolve *W. schizophylla* and *W. norrisii* within *Wildemania* (Lindstrom & Fredericq, 2003; Sutherland *et al*., 2011). Two different taxonomic entities of "*W. schizophylla*" were resolved in clade II together with *W. norrisii*, and the genetic variation between "*W. schizophylla*" AF452443 and *W. norrisii* was less than between "*W. schizophylla*" AF452443 and "*W. schizophylla*" GU319871. Lindstrom (2008) reported that the more northerly specimens of "*W. schizophylla*" represented a distinct species, and Lindstrom (2009) reported that *W. schizophylla* (as *Porphyra schizophylla*) was restricted to California and north of there *W. schizophylla* was replaced by *W. norrisii*. “*Wildemania schizophylla*” AF452443 should therefore be regarded as *W. norrisii*.

The taxonomy of *W. variegata* and *W. miniata* was unresolved as pointed out in Mols–Mortensen *et al*. (2014). The genetic variation between “*W. variegata*” AF452447 and *W. miniata* was less than between “*W. variegata*” AF452447 and the other *W. variegata* specimens. The identities of both *W. miniata* and *W. variegata* need to be clarified in relation to their respective types, but current data suggest that the same *Wildemania* taxon, identified here as *W. miniata*, is represented both in the North Atlantic and the North Pacific. Lindstrom & Fredericq (2003) pointed out that the genetic variation, based on the *rbc*L gene, between the North Atlantic and North Pacific species pairs *P. amplissima* and *P. cuneiformis*, *P. miniata* and *P. variegata*, and *P. purpurea* and *P. rediviva* was insufficient for recognizing distinct species. Two of these North Atlantic-North Pacific species pairs have been synonymized: *P. amplissima* (*W. amplissima*) and *P. cuneiformis* (*W. cuneiformis*) as *W. amplissima*, and *P. purpurea* and *P. rediviva* as *P. purpurea* (Bray *et al*., 2007; Kucera & Saunders, 2012). *Wildemania miniata* and *W. variegata* are still considered to be distinct species that are North Atlantic and North Pacific counterparts.

Wildemania amplissima was distributed in the North Atlantic and the North Pacific and resolved in clade III together with the unidentified “*W*. sp. Chile”, “*W*. sp. Falkland” and “*W*. sp. Antarctica” from the South Atlantic and Southern Ocean, respectively. A wide geographic range was represented in clade III with species from the North Pacific, North Atlantic, South Atlantic and Southern Ocean, and the species representation from the Southern Hemisphere was higher compared to the Northern Hemisphere. Based on the low genetic variation observed in clade III and broad geographic species distribution with the species diversity centered in the Southern Hemisphere, we hypothesize that a common ancestor to the species in clade III originated in the Southern Ocean and was distributed to the Falkland Islands and the South American continent. The Strait of Magellan creates a seaway connection between the South Atlantic and the South Pacific and therefore the species could have migrated through the strait into the South Pacific, from the South Pacific to the North Pacific and via the Bering Strait and Arctic Ocean into the North Atlantic. Another possibility is that the species migrated from the South Atlantic to the North Atlantic and via the Arctic Ocean and Bering Strait into the North Pacific. However, due to the prevailing species migration direction from the North Pacific to the North Atlantic (Durham & MacNeil, 1967; Lüning, 1990; Lindstrom, 2001; Adey *et al.*, 2008) this route is considered less likely.

The *cox*2–3 was not useful at the intraspecific level in *W. amplissima*, since it only recovered one North Atlantic and two North Pacific haplotypes. The second haplotype recovered from the North Pacific was only detected in one individual and, as this was due to a single transition substitution from A to G, and rather than representing a different haplotype, it could be caused by the single base substitution error rate of *Taq* polymerase during PCR (Tindall & Kunkel, 1988). Teasdale & Klein (2010) also found that the *cox*2–3 spacer was not useful on intraspecific level in *P. umbilicalis* and based on these observations it is likely that *cox*2–3 is not a good choice of marker when studying intraspecific relationships in the Bangiales. The ITS1 spacer was a valuable marker when resolving intraspecific relationships in *W. amplissima* with a total of sixteen haplotypes recovered in the North Atlantic and the North Pacific samples. Teasdale & Klein (2010) also found the ITS region to be useful when resolving intraspecific relationships in *P. umbilicalis*, and they concluded based on the low intra-individual ITS variation (0.00–0.3%), that the marker was suitable for phylogenetic work within *P. umbilicalis*.

The haplotype diversity in the North Atlantic was much greater than in the North Pacific, with thirteen haplotypes recovered in the North Atlantic and only three in the North Pacific. The populations in the North Pacific show characteristics of “stable rear edge” populations that are defined as populations that have persisted at suitable growing sites through changing climate conditions while the species expanded its range (Hampe & Petit, 2005). The intra-population genetic diversity was low in “stable-rear edge” populations but the inter-population diversity was high which lead to high levels of regional genetic diversity (Petit *et al*., 2003; Hampe & Petit, 2005). With only three haplotypes recovered, our study indicated low intra-population genetic diversity in the North Pacific. However, the low intra-population genetic diversity was not reflected at the regional level where both the haplotype diversity and nucleotide diversity in the North Pacific were the same level as in the Northwest Atlantic. The three populations that were sampled by at least ten samples in the North Atlantic, Bay of Fundy, New Hampshire and the Faroe Islands, all had a greater intra-population genetic diversity compared to the North Pacific populations, and the greatest intra-population genetic diversity was recovered in the Faroe Islands. The greatest haplotype diversity and nucleotide diversity was observed in the Northeast Atlantic region.

The two sides of the North Atlantic shared three of the thirteen recovered haplotypes including H1, which was observed to be the most abundant haplotype on both sides of the North Atlantic. In the Northwest Atlantic H1 was by the far the most abundant haplotype, recovered in 62.9% of the samples while it was less abundant in the Northeast Atlantic, recovered in 35.3% of the samples. The three most abundant haplotypes in the Northwest Atlantic (H1, H5 and H6) were those shared with the Northeast Atlantic. All the North Atlantic haplotypes were closely related to each other, and they were all directly or indirectly descended from H1. Interior haplotypes are defined as haplotypes connected to two or more haplotypes in the network in contrast to tip haplotypes that are only connected to one haplotype. Castelloe & Templeton (1994) argued that an interior haplotype had a high root probability whenever it had a high multiplicity or when it was an evolutionary neighbour of a haplotype that had a high multiplicity, either tip or interior. Haplotype 1 was an interior haplotype with high multiplicity and the evolutionary neighbour of seven haplotypes, and therefore H1 was the most obvious candidate in our dataset to have the highest root probability.

The root haplotype analysis did not support the proposed hypothesis that *W. amplissima* was introduced into the North Atlantic from the North Pacific, since the proposed root haplotype (H1) was a North Atlantic haplotype. The SP method was designed for estimating intraspecific haplotype trees, and has great statistical power and accuracy when the number of variable sites is low (Templeton *et al.*, 1992; Clement *et al.*, 2000). Seven missing intermediate haplotypes were between the most closely related North Pacific and North Atlantic haplotypes, equivalent to 52 to 58 variable sites (data not shown). Possibly the ITS1 dataset including both North Pacific and North Atlantic haplotypes was too variable for the SP analysis to handle, and H1 should therefore only be regarded as the root haplotype of the North Atlantic.

Pleistocene glaciation conditions were much more severe in the North Atlantic than in the North Pacific (McIntyre *et al.*, 1976; Lüning, 1990), and southward displacement migration of benthic organisms due to changing climate was less challenging in the North Pacific compared to the North Atlantic. The North Pacific coastline is largely an uninterrupted rocky coast where macroalgae and other benthic species could easily have migrated, whereas the North Atlantic has long, open-sea distances between the North Atlantic islands and the European continental coast, and the Northwest Atlantic coast is primarily sandy shore south of Cape Cod (Lüning, 1990).

The relatively stable conditions in the North Pacific through the Pleistocene could have enabled the evolution of “stable rear edge” populations. Ingolfsson (1992), who compared the rocky shore fauna of Northern Norway, Iceland and the Canadian Maritimes, observed a decrease in the number of species from east to west. He concluded that the rocky shore fauna of Iceland and the Northeast America was largely a result of post-glacial colonization from Europe. Teasdale & Klein (2010) concluded that Northwest Atlantic *Porphyra umbilcalis* populations were extirpated during the LGM and subsequently recolonized from Northeast Atlantic populations. The ITS1 analysis suggested that the time to most recent common ancestor (TMRCA) between Northeast Atlantic and Northwest Atlantic *Wildemania amplissima* populations was within the last 77,404 years, and the populations on the two coasts were therefore already separated in the early Wisconsin (North America; 85,000-11,000 years ago) and Würm (Europe; 110,000-10,000 years ago) glacial periods (Clayton *et al.*, 2006) prior to the LGM, ca. 18,000 years ago. Based on our haplotype data it is likely that the Northwest Atlantic *W. amplissima* populations were partly reintroduced from the Northeast Atlantic populations; the haplotype diversity and the nucleotide diversity in the Northwest Atlantic was lower compared to the Northeast Atlantic and the three most abundant haplotypes in the Northwest Atlantic were also found in the Northeast Atlantic. The rest of the haplotypes recovered in the Northwest Atlantic were all descended from the haplotypes that were identical between the two coasts. Haplotype 8 linked the North Pacific biogeographic group to the North Atlantic biogeographic group via H1 (the likely root haplotype in the North Atlantic) and H8 was only recovered in Quebec in the Northwest Atlantic in our study. Considering H8 as the closest relative to the North Pacific haplotypes then H1 was descendent from H8, and based on our data H1 successfully spread throughout the northern North Atlantic. One scenario for the haplotype relationship between the North

Pacific and the North Atlantic could be that H8 was the closest relative to the North Pacific haplotype that was introduced into the North Atlantic via the Bering Strait and the Arctic Ocean, H8 established in the Northwest Atlantic and spread to the Northeast Atlantic. Haplotype 1 evolved from H8 via an intermediate haplotype and H1 and other descendent haplotypes were introduced to the Northwest Atlantic from the Northeast Atlantic after the LGM. Haplotype 8 must either have survived in the Northwest Atlantic during the last glacial period or another possibility was that H8 was in fact much more abundant in the North Atlantic than the limited sampling showed.

Insufficient sampling limited the biogegraphic conclusions that could be drawn from this study, and therefore the work should be seen as a preliminary report on the phylogeographic relationship in *W. amplissima*. With more complete sampling including populations from the entire distribution of *W. amplissima*, the proposed hypothesis on the origin of *W. amplissima* could in future be tested.

Table 5.1. A list of amplification and sequencing primers used in this study.

	Forward primer & 5’-primer sequence-3’	Reverse primer & 5’-primer sequence-3’	References
3’ *rbc*L + 5’ *rbc*L-S (identification)	RBCL5RC ‘GTGGTATTCATGCTGGTCAAA’	RBCSPC ‘CACTATTCTATGCTCCTTATTKTTAT’	Reverse complement of RBCL in Klein *et al*., 2003; Teasdale *et al*., 2002
*rbc*L (fragment 1)	F67 ‘TACGCTAAAATGGGTTACTG’	R502 ‘TATCCATACGCTCACGTTCTACAA’	Mols-Mortensen *et al*., 2012
*rbc*L (fragment 2)	F461 ‘GTCCTGCAACTGGATTGATTGT’	R901 ‘TACCAGCTCTATGTAAATGTAAAA’	Mols-Mortensen *et al*., 2012
*rbc*L (fragment 3)	F870 ‘TGACATGATTTTACATTTACATAGAC’	R1312 ‘GGCCTTCATTTCTTGCCATAACKTTAT’	Mols-Mortensen *et al*., 2012
ITS1	JBITS7 ‘GTAGGTGAACCTGCGGAAGG’	ITS1-R ‘TATCCACCGTTAAGAGTTGTAT’	Broom *et al*., 2002; Neefus *et al*., 2002
*Cox*2-3	WACOX23-F ‘ATGCAGTTCCCGGTAGATTGA’	WACOX23-R ‘ATGGAAAGGATGTCGTTGTAGC’	This paper

Table 5.2. Clade I: Genetic variation in the *rbc*L gene based on Tamura-Nei genetic distance model and presented as patristic distances (sum of branch lengths) and differences in base pairs.

	W. occidentalis *N* = 1	*W. abyssicola* *N* = 1	*W. variegata* *N* = 3	*W. miniata* *N* = 2	“*W. variegata*” AF452447 *N* = 1
W. occidentalis	*				
W. abyssicola	0.030 (37)	*			
“*W. variegata*”	0.028–0.034 (29–31)	0.031–0.037 (35–37)	0–0.010 (0–13)		
W. miniata	0.027–0.029 (30–33)	0.030–0.031 (34–37)	0.008–0.015 (7–17)	0–0.003 (0–3)	
“*W. variegata*” AF452447	0.028 (34)	0.030 (38)	0.008–0.014 (11–18)	0.001–0.003 (4–7)	*

* Only one sequence.

( ) Base pair differences.

Table 5.3. Clade II: Genetic variation in the *rbc*L gene based on Tamura-Nei genetic distance model and presented as patristic distances (sum of branch lengths) and differences in base pairs.

	"*W. schizophylla*" AF452443 n = 1	*W. norrisii* n = 1	"*W. schizophylla*" GU319871 n = 1
"*W. schizophylla*" AF452443	*		
W. norrisii	0.006 (7)	*	
"*W. schizophylla*" GU319871	0.018 (21)	0.018 (20)	*

* Only one sequence.

( ) Base pair differences.

Table 5.4. Clade III: Genetic variation in the *rbc*L gene based on Tamura-Nei genetic distance model and presented as patristic distances (sum of branch lengths) and differences in base pairs.

	W. amplissima n = 6	"*W.* sp. Chile" n = 3	"*W.* sp. Falkland" n = 1	"*W.* sp. Antarctica" n = 1
W. amplissima	0.000–0.002 (0–1)			
"*W.* sp. Chile"	0.004–0.005 (5–6)	0.000 (0)		
"*W.* sp. Falkland"	0.004–0.005 (8–9)	0.002 (5)	*	
"*W.* sp. Antarctica"	0.009-0.010 (10-11)	0.008 (9)	0.008 (12)	*

* Only one sequence.

( ) Base pair differences.

Table 5.5. *Wildemania amplissima* sampling locations. Map identification numbers for Figure 1, number of individuals per sampling location (N), number of ITS1 haplotypes (N*h*), haplotypes present in population (H*id*), haplotype (*h*) and nucleotide (*π*) diversities.

Location	Code	Map ID	N	N_h	H_{id}	*h*	*π*
Norway	NO	1	2	1	h1	0.0000 ± 0.0000	0.0000 ± 0.0000
Faroe Islands	FO	2	13	6	h1, h2, h3, h4, h5, h6	0.8205 ± 0.0817	0.0038 ± 0.0027
Iceland	IS	3	2	2	h1, h7	1.0000 ± 0.5000	0.0024 ± 0.0034
Canada, Quebec	QE	4	1	1	h8	1.0000 ± 0.0000	0.0000 ± 0.0000
Canada, Bay of Fundy	BF	5	10	4	h1, h9, h10, h11	0.6444 ± 0.1518	0.0023 ± 0.0019
U.S.A., New Hampshire	NH	6	24	5	h1, h5, h6, h12, h13	0.5435± 0.1104	0.0020 ± 0.0016
U.S.A, Alaska	AK	7	10	2	h14, h15	0.2000 ± 0.1541	0.0014 ± 0.0014
Canada, British Columbia	BC	8	2	1	h15	0.0000 ± 0.0000	0.0000 ± 0.0000
U.S.A., Washington	WA	9	9	1	h16	0.0000 ± 0.0000	0.0000 ± 0.0000

Table 5.6. Geographic distribution of haplotypes.

	North East Atlantic			North West Atlantic			Nort East Pacific			
Haplotypes	NO	FO	IS	QE	BF	NH	AK	BC	WA	Total
h1	2	3	1	0	6	16	0	0	0	28
h2	0	1	0	0	0	0	0	0	0	1
h3	0	5	0	0	0	0	0	0	0	5
h4	0	1	0	0	0	0	0	0	0	1
h5	0	2	0	0	0	3	0	0	0	5
h6	0	1	0	0	0	3	0	0	0	4
h7	0	0	1	0	0	0	0	0	0	1
h8	0	0	0	1	0	0	0	0	0	1
h9	0	0	0	0	1	0	0	0	0	1
h10	0	0	0	0	2	0	0	0	0	2
h11	0	0	0	0	1	0	0	0	0	1
h12	0	0	0	0	0	1	0	0	0	1
h13	0	0	0	0	0	1	0	0	0	1
h14	0	0	0	0	0	0	1	0	0	1
h15	0	0	0	0	0	0	9	2	0	11
h16	0	0	0	0	0	0	0	0	9	9

Table 5.7. Haplotype – and nucleotide diversity in the North East– and North West Atlantic, and the North Pacific. The samples from Norway, Iceland, Quebec and British Columbia were excluded due to low sample numbers.

	h	*π*
North East Atlantic	0.8205 ± 0.0817	0.0038 ± 0.0027
North West Atlantic	0.5758 ± 0.0966	0.0021 ± 0.0017
North Pacific	0.5789 ± 0.0566	0.0020 ± 0.0017

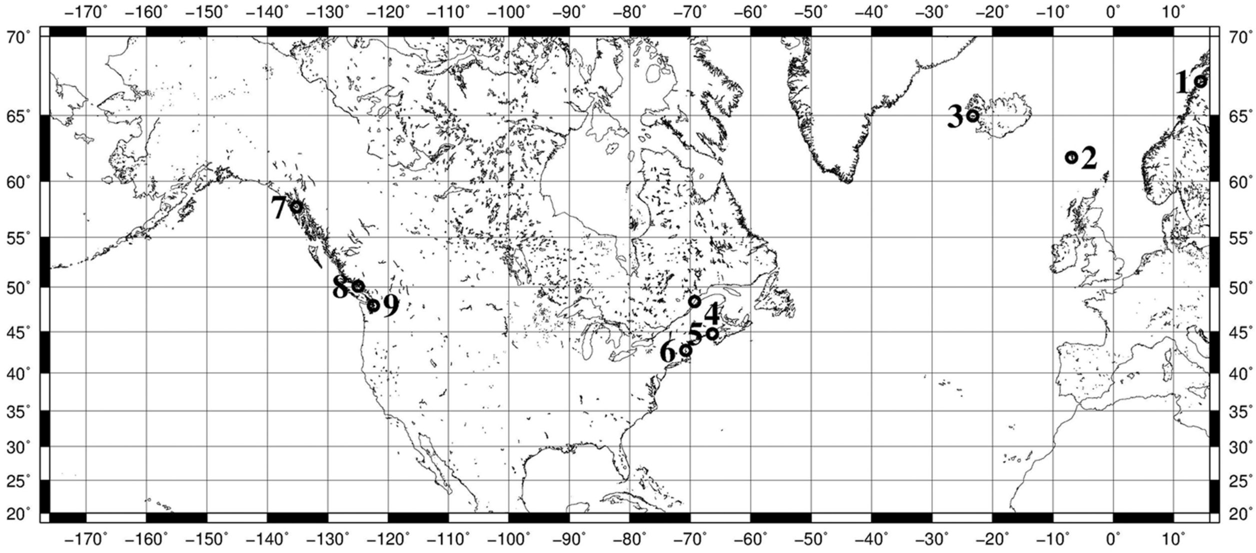

Figure 5.1. Map showing *Wildemania amplissima* sampling locations; 1. Norway2. Faroe Islands, 3. Iceland, 4. Quebec, Canada, 5.Bay of Fundy, Canada, 6. New Hampshire, USA, 7. Alaska, USA, 8. British Columbia, Canada and 9. Washington, USA.

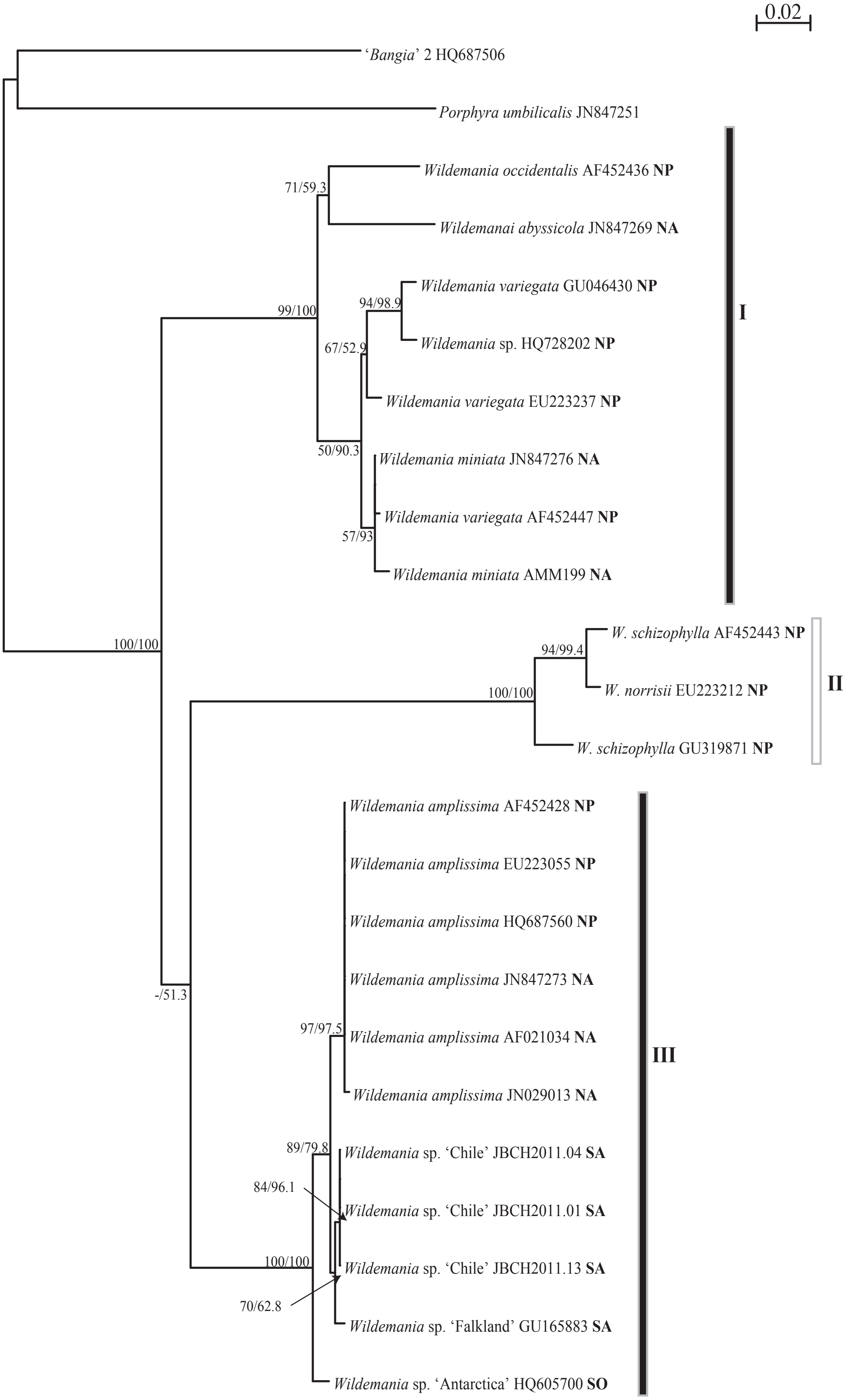

Figure 5.2. Maximum likelihood phylogram based on partial rbcL sequences with ML and NJ bootstrap values (>50%) indicated on the branches (ML/NJ). Abbreviations: NA = North Atlantic, NP = North Pacific, SA = South Atlantic, SO = Southern Ocean.

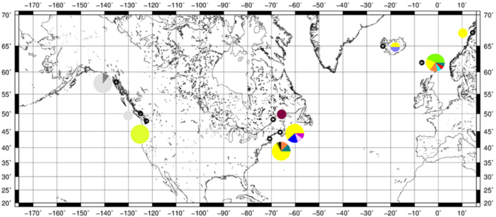

Figure 5.3. Map showing the ITS1 *Wildemania amplissima* haplotypes recovered in the different locations.

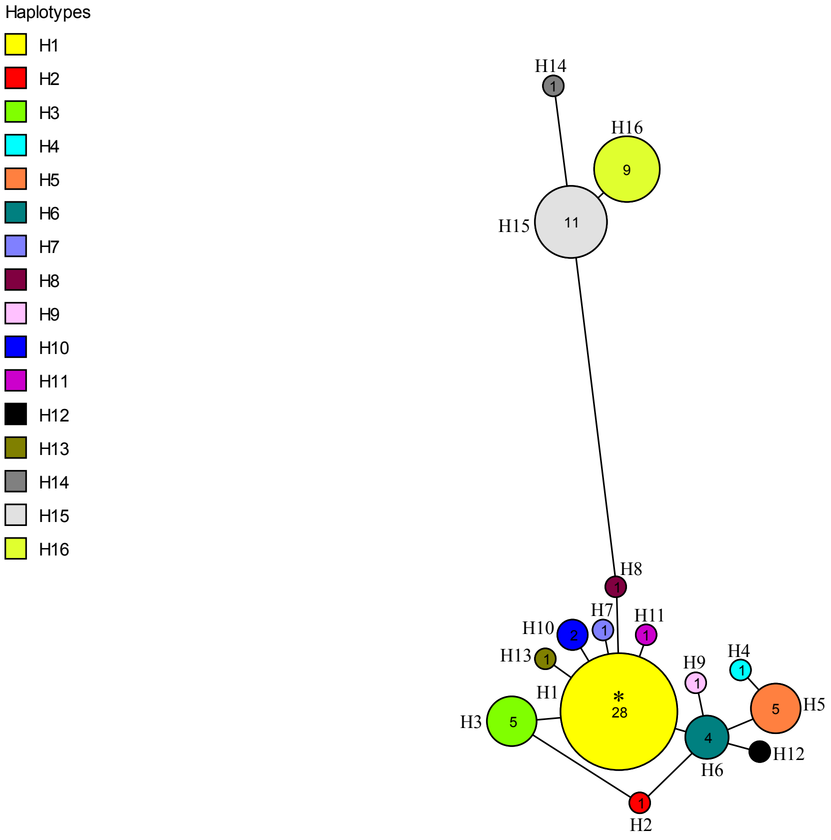

Figure 5.4. Median–Joining ITS1 *Wildemania amplissima* haplotype network.

Conclusion

The work presented in this thesis has documented species diversity and distribution of foliose Bangiales from areas in the North Atlantic that were previously understudied, with special focus on the northern parts of the North Atlantic: Iceland, Faroe Islands and West Greenland. Identifications were based on DNA sequences (*cox*1, *rbc*L, 3’ *rbc*L +5’ *rbc*L-S), and using this approach the work has enabled floristic comparisons between different geographic areas. The mitochondrial *cox*1 marker was useful for identifying foliose Bangiales species, but did not separate the closely related *Porphyra linearis* and *P. umbilicalis*. The chloroplast 3’ *rbc*L +5’ *rbc*L-S marker was found to be a useful tool to differentiate between the North Atlantic foliose Bangiales species. By including both recent collections and herbarium (historic) material, the work demonstrates the value of well preserved historic collections for providing a comparative context for the species diversity and distribution documented by new collections. Four foliose Bangiales genera were recorded from the North Atlantic, and based on both this study and the work of others, 26 foliose Bangiales species are now documented from the North Atlantic. At least three of the foliose Bangiales species in the North Atlantic are recent introductions from the Pacific: *Pyropia katadae*, *Py. yezoensis* (f. *yezoensis* and f. *narawensis*) and *Py. suborbiculata*, with *Py. katadae* and *Py. yezoensis* so far only reported from the Northwest Atlantic and *Py. suborbiculata* reported from both North Atlantic coasts. A close phylogenetic relationship between the North Atlantic and North Pacific foliose Bangiales flora is documented, and phylogeographic results from *Wildemania amplissima* populations in the North Atlantic and North Pacific have provided preliminary insights into the evolutionary history of the species.

The focus on the northern areas of the North Atlantic and inclusion of other relatively understudied areas in the North Atlantic revealed considerably more species diversity and provided new insights into the geographic distribution of the species. The floras in Iceland and the Faroe Islands had the same number of species but with some differences in species composition, and the diversity in West Greenland was less than in Iceland and the Faroe Islands. The Northwest Atlantic and the Northeast Atlantic foliose Bangiales floras were similar in species number but with some differences in species composition. *Pyropia katadae*, *Py. yezoensis* (f. *yezoensis* and f. *narawensis*), "*Py. spatulata*" and "*Py. stamfordensis*" were only documented from the Northwest Atlantic, and *Porphyra dioica*, *P. drachii*, "*Porphyra yezoensis*" *sensu* Kornmann, *Porphyra* sp., *Pyropia* sp. and *Wildemania abyssicola* were only documented from the Northeast Atlantic (including Iceland and the Faroe Islands). *Pyropia njordii* was described from the Faroe Islands with distribution records from Iceland, West Greenland, Northeast Canada and Northeast USA, and *Wildemania abyssicola* was documented from Iceland and northern Norway. *Pyropia thulaea* was reported for the first time from the Northwest Atlantic coast, and *Py. peggicovensis* and "*Py. novae-angliae*" was reported for the first time from the Northeast Atlantic.

A clear difference in the diversity of foliose Bangiales species was observed north and south of Long Island on the Northwest Atlantic coast, with fifteen species found north of Long Island and five south of Long Island. The five species documented south of Long Island were also documented north of Long Island, but south of Long Island they only grew on man-made structures. South of Cape Hatteras, North Carolina, where the warm-temperate biogeographic region begins, only *Pyropia suborbiculata* and *Py. elongata* were documented.

Phylogenetic relationships between the foliose Bangiales floras of the North Atlantic and North Pacific were especially apparent in the West Greenland foliose Bangiales flora. All the foliose Bangiales species reported in the West Greenland study had a close link to North Pacific species, either as closely related sibling species or conspecific populations. Thus, the hypothesis of dispersal of macroalgal species through the Bering Strait potentially followed by allopatric speciation due to subsequent isolation was supported by this work.

Three phylogenetic clades were resolved within *Wildemania*, and *W. amplissima* was resolved in a clade together with three unidentified taxa, including one from Chile. The *cox*2-3 spacer was not found to be useful in resolving phylogeographic patterns in *W. amplissima*, but ITS1 recovered a total of sixteen haplotypes: thirteen from the North Atlantic and three from the North Pacific. Seven missing haplotypes were between the most closely related North Atlantic and North Pacific haplotypes, and together with the low haplotype diversity in the North Pacific populations they were interpreted as "stable rear edge" populations, defined as populations that have persisted at suitable growing sites through changing climatic conditions while the species expanded its range into the North Atlantic. Due to insufficient sampling only preliminary biogeographic conclusions could be made.

The work presented in this thesis has revealed new foliose Bangiales species diversity in the North Atlantic, recorded greater diversity within the studied geographic areas, and documented new distribution records for several of the North Atlantic foliose Bangiales species. It is a contribution to the ongoing study of foliose Bangiales diversity and distribution in the North Atlantic, and it also shows that there is still more work to be done, including formal descriptions of a number of species. Some of these species have only been found once and more information is desirable before they are formally described.

The approach taken in the research of this thesis, using both new collections and herbarium material, provides a model for more detailed studies in other geographic areas. In a world with changing climate conditions, a model that can document both present and historic diversity is valuable. A contribution to a baseline of the North Atlantic foliose Bangiales species is presented, and with this contribution we now have a pretty good understanding of the North Atlantic species and their distribution. The ongoing and future retreat of the Arctic ice will enable species dispersal between the North Pacific and North Atlantic, with the potential for diversity changes in both oceans. A natural next step within the Bangiales is to study the species at the population level, and the work presented in this thesis is a preliminary contribution with the phylogeographic study of *Wildemania amplissima*.

Due to climatic changes and ocean acidification the marine environment is changing, and to survive marine organisms have to adapt. Documenting diversity and determining genetic structure on population level will provide information that can be used to monitor changes and to develop conservation priorities and strategies in a rapidly changing world.

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APPENDICES

Appendix A. Taxa used in the analysis with collecting details and GenBank accession numbers. N/A = not available.

Taxa	**Voucher number**	**Location**	**Date and collector**	**Level and substratum**	**Genbank accession no. *rbc*L**	**Genbank accession no. *cox*1**	**Reference**
'*Bangia*' sp.	WELT A26696	Woodpecker Bay, Paparoa, Wesland, South I, New Zealand	N/A	N/A	EU570051	N/A	Genbank
'*Bangia*' sp.	WELT A026691	14 mile Bluff, Westland, South I, New Zealand	22/08/00 T. Farr, GW	N/A	GU046404	N/A	Broom *et al.*, 2010
Boreophyllum aestivalis	UBCA843442	Ketchikan, AK, U.S.A.	19/08/00 S. Lindstrom	N/A	AF458077	N/A	Lindstrom & Fredericq, 2003
Boreophyllum birdiae	JB431	Hellnar, Iceland	10/07/05 I. Tittley, J. Brodie	Intertidal	N/A	JN847322	This paper
Boreophyllum birdiae	JB448	Hraunhafnartangi, Iceland	20/06/06 J. Brodie, B. Rinkel	Intertidal	JN787100	N/A	This paper
Boreophyllum birdiae	JB449	Hraunhafnartangi, Iceland	20/06/06 J. Brodie, B. Rinkel	Intertidal	JN787101	N/A	This paper
Boreophyllum birdiae	57290	Hvalfjörður, Eyri, Iceland	01/09/04 K. Gunnarsson	Intertidal	JN711446	JN847310	This paper
Boreophyllum birdiae	57291	Hvalfjörður, Eyri, Iceland	01/09/04 K. Gunnarsson	Intertidal	JN703281	N/A	This paper
Boreophyllum birdiae	JB434	Trondheim, Norway	08/1999 F. Lopez	N/A	JN711450	N/A	This paper
Boreophyllum birdiae	Isotype NHA76527	Herring Cove, NS, Canada	21/09/02 C.D. Neefus	Mid intertidal, on rock	AY180909	N/A	Neefus *et al.*, 2002
Boreophyllum birdiae	Holotype NHA76525	Herring Cove, NS, Canada	21/09/02 C. D. Neefus	Mid intertidal, on rock	N/A	JN847321	This paper
Boreophyllum birdiae	AMM235	Forth Stark, NH, U.S.A.	02/08/07 C. D. Neefus, A. Mols-Mortensen, J. Nettleton	Intertidal	N/A	JN847320	This paper
Boreophyllum birdiae	AMM06SF4325	Mølin, Froðba, Trongisvágsfjørður, Faroe Islands	18/07/06 A. Mols-Mortensen	Low intertidal, on rock	JN711449	JN847319	This paper

Boreophyllum birdiae	AMM06SF2347	Tjaldavík, Trongisvágsfjørður, Faroe Islands	19/07/06 A. Mols-Mortensen	Low intertidal, on limpet	JN711447	AM943400	This paper; Brodie *et al.,* 2008
Boreophyllum birdiae	AMM06SF3139	við Hellá, Trongisvágsfjørður, Faroe Islands	20/07/06 A. Mols-Mortensen	Mid intertidal, on rock	JN711448	JN847318	This paper
Clymene coleana	WELT A22181	Leigh, North I, New Zealand	N/A	N/A	FJ263672	N/A	Genbank
Dione arcuata	WELT A23126 Holotype	Ohau Stream, Kaikoura, South I, New Zealand	05/11/02 Neill, T. Farr	Lower intertidal to upper subtidal, on rock	EU570052	N/A	Genbank
Fuscifolium papenfussii	UBC A86209	Seldovia Point, Alaska, U.S.A.	01/07/03 S. Saupe	N/A	EU223120	N/A	GenBank
Minerva aenigmata	WELT A25775 Holotype	Puheke, Northland, North I, New Zealand	08/05/01 W. Nelson, T. Farr	Upper intertidal, on rock	EU570053	N/A	Genbank
Porphyra dioica	JB378	Krossavik, Iceland	10/07/05 J. Brodie, I. Tittley	Intertidal	JN787102	N/A	This paper
Porphyra dioica	AMM06SF4159	Mølin, Froðba, Trongisvágsfjørður, Faroe Islands	18/04/06 A. Mols-Mortensen	Mid intertidal, on rock	JN703282	N/A	This paper
Porphyra dioica	AMM69	Tjaldavík, Trongisvágsfjørður, Faroe Islands	08/01/08 A. Mols-Mortensen	High intertidal, on rock	N/A	JN847311	This paper
Porphyra dioica	AMM78	Saksun, Faroe Islands	04/06/08 A. Mols-Mortensen, M. Sasser	Mid intertidal, on rock	N/A	JN847312	This paper
Porphyra dioica	AMM81	Saksun, Faroe Islands	04/06/08 A. Mols-Mortensen, M. Sasser	Mid intertidal, on rock	N/A	JN847313	This paper
Porphyra dioica	881	North of Aberystwyth, Wales, U.K.	04/04/1998 N/A	N/A	AF081291	N/A	Genbank
Porphyra dioica	JB347	Sidmouth, Devon, England, U.K.	23/07/05 J. Brodie	N/A	N/A	DQ191340	Robba *et al.*, 2006
Porphyra linearis	JB465	Höfnin, Garði, Iceland	11/02/06 K. Gunnarsson	Intertidal	JN787103	N/A	This paper
Porphyra linearis	JB466	Höfnin, Garði, Iceland	11/02/06 K. Gunnarsson	Intertidal	JN787104	N/A	This paper
Porphyra linearis	JB468	Höfnin, Garði, Iceland	11/02/06 K.	Intertidal	JN787105	N/A	This paper

			Gunnarsson				
Porphyra linearis	AMM71	Tjaldavík, Trongisvágsfjørður, Faroe Islands	15/11/07 A. Mols-Mortensen	Mid intertidal, on rock	N/A	JN847315	This paper
Porphyra linearis	AMM83	Tvørábakki, Trongisvágsfjørður, Faroe Islands	24/03/08 A. Mols-Mortensen	High intertidal, on rock	N/A	JN847316	This paper
Porphyra linearis	AMM05SF4020	Mølin, Froðba, Trongisvágsfjørður, Faroe Islands	30/11/05 A. Mols-Mortensen	Mid intertidal, on rock	N/A	JN847314	This paper
Porphyra mumfordii	Topotype AMM152	Orlebar Pt., BC, Canada	03/02/02 S. Lindstrom	N/A	JN787106	N/A	This paper
Porphyra purpurea	JB407	Kálfavík, Iceland	07/06/06 J. Brodie, B. Rinkel	Intertidal	JN787107	N/A	This paper
Porphyra purpurea	57363	Húnaflói, Kollafjörður, Iceland	28/06/05 R. Nielsen	N/A	JN787108	N/A	This paper
Porphyra purpurea	JB450	Kálfavík, Iceland	07/06/06 J. Brodie, B. Rinkel	Intertidal	JN787111	N/A	This paper
Porphyra purpurea	JB446	Somerset, U.K.	23/07/08 J. Brodie	Intertidal	JN787109	N/A	This paper
Porphyra purpurea	JB447 (59185)	Gilleleje, Denmark	16/07/06 R. Nielsen	Intertidal	JN787110	N/A	This paper
Porphyra purpurea	AMM07USA08	Dover Point, NH, U.S.A.	02/08/07 C. D. Neefus, J. Nettleton, A. Mols-Mortensen	Intertidal	N/A	JN847317	This paper
Porphyra umbilicalis	57249	Flekkuvík, Iceland	11/09/93 K. Gunnarsson	Low intertidal	N/A	JN847285	This paper
Porphyra umbilicalis	JB386	Hellnar, Iceland	10/07/05 I. Tittley, J. Brodie	Intertidal	JN787113	N/A	This paper
Porphyra umbilicalis	JB387	Hellnar, Iceland	10/07/05 J. Brodie, I. Tittley	Intertidal	JN787114	N/A	This paper
Porphyra umbilicalis	JB406	Hvítserkur, Iceland	07/06/06 R. Nielsen, S. Egilsdóttir	Intertidal	JN787115	N/A	This paper
Porphyra umbilicalis	JB412	Hrísey, Iceland	14/06/06 R. Nielsen S. Egilsdóttir	Intertidal	JN787116	N/A	This paper

Porphyra umbilicalis	JB428	Hellisnípa, Holmbergi, Iceland	06/07/06 K. Gunnarsson	Intertidal	N/A	JN847303	This paper
Porphyra umbilicalis	JB429	Hellisnípa Holmbergi, Iceland	06/07/06 K. Gunnarsson	Intertidal	N/A	JN847304	This paper
Porphyra umbilicalis	JB430	Siglunes, Iceland	16/06/06 J. Brodie, B. Rinkel	Intertidal	N/A	JN847305	This paper
Porphyra umbilicalis	JB432	Hvítserkur, Iceland	07/06/06 R. Nielsen, S. Egilsdóttir	Low intertidal	N/A	JN847306	This paper
Porphyra umbilicalis	JB467	Höfnin, Garði, Iceland	11/02/06 K. Gunnarsson	High intertidal	JN847249	N/A	This paper
Porphyra umbilicalis	JB469	Höfnin, Garði, Iceland	11/02/06 K. Gunnarsson	Low intertidal	JN847250	N/A	This paper
Porphyra umbilicalis	JB470	Höfnin, Garði, Iceland	11/02/06 K. Gunnarsson	Low intertidal	JN847251	N/A	This paper
Porphyra umbilicalis	JB471	Höfnin, Garði, Iceland	11/02/06 K. Gunnarsson	Low intertidal	JN847252	N/A	This paper
Porphyra umbilicalis	JB472	Garðshagaviti, Iceland	11/02/06 K. Gunnarsson	N/A	JN847253	N/A	This paper
Porphyra umbilicalis	JB435	Skorpa, Norway	04/09/97 T. E. Lein, R. Nielsen	Intertidal	JN847246	JN847307	This paper
Porphyra umbilicalis	JB436	Skorpa, Norway	04/09/97 T. E. Lein, R. Nielsen	Intertidal	JN847247	JN847284	This paper
Porphyra umbilicalis	JB438	Hirsholmene, Frederikshavn, Denmark	05/05/94 J. Plumb	Intertidal	JN847248	JN847308	This paper
Porphyra umbilicalis	AMM0400F409	Mølin, Hvannhagi, Tvøroyri, Faroe Islands	04/07/04 A. Mols-Mortensen, P. Mortensen, N. Mols-Mortensen	Low intertidal	N/A	JN847302	This paper

Porphyra umbilicalis	AMM70	Tjaldavík, Trongisvágsfjørður, Faroe Islands	08/01/08 A. Mols-Mortensen	High intertidal, on rock	N/A	JN847301	This paper
Porphyra umbilicalis	AMM05SF1017	Tjaldavík, Trongisvágsfjørður, Faroe Islands	19/10/05 A. Mols-Mortensen	Low intertidal, on limpet	N/A	JN847286	This paper
Porphyra umbilicalis	AMM06SF1215	Tjaldavík, Trongisvágsfjørður, Faroes	27/04/06 A. Mols-Mortensen	High intertidal, on rock	N/A	JN847287	This paper
Porphyra umbilicalis	AMM06SF1266	Tjaldavík, Trongisvágsfjørður, Faroe Islands	30/04/06 A. Mols-Mortensen	Mid intertidal, on rock	N/A	JN847288	This paper
Porphyra umbilicalis	AMM06SF1269	Tjaldavík, Trongisvágsfjørður, Faroe Islands	30/04/06 A. Mols-Mortensen	Mid intertidal, on rock	N/A	JN847309	This paper
Porphyra umbilicalis	AMM06SF1287	Tjaldavík, Trongisvágsfjørður, Faroe Islands	30/04/06 A. Mols-Mortensen	High intertidal, on rock	N/A	JN847289	This paper
Porphyra umbilicalis	AMM06SF1318	Tjaldavík, Trongisvágsfjørður, Faroe Islands	08/05/06 A. Mols-Mortensen	High intertidal, on rock	N/A	JN847290	This paper
Porphyra umbilicalis	AMM06SF1361	Tjaldavík, Trongisvágsfjørður, Faroe Islands	02/07/06 A. Mols-Mortensen	High intertidal, on rock	N/A	JN847291	This paper
Porphyra umbilicalis	AMM06SF1373	Tjaldavík, Trongisvágsfjord, Faroe Islands	02/07/06 A. Mols-Mortensen	Low intertidal, on rock	N/A	JN847292	This paper
Porphyra umbilicalis	AMM06SF2177	Tjaldavík, Trongisvágsfjørður, Faroe Islands	29/04/06 A. Mols-Mortensen	Low intertidal, on limpet	N/A	JN847293	This paper
Porphyra umbilicalis	AMM06SF2270	Tjaldavík, Trongisvágsfjørður, Faroe Islands	13/07/06 A. Mols-Mortensen	Mid intertidal, on *Fucus*	N/A	JN847294	This paper
Porphyra umbilicalis	AMM06SF2332	Tjaldavík, Trongisvágsfjørður, Faroe Islands	19/07/06 A. Mols-Mortensen	Low intertidal, on limpet	N/A	JN847295	This paper
Porphyra umbilicalis	AMM06SF4180	Mølin, Froðba, Trongisvágsfjørður, Faroe Islands	18/04/06 A. Mols-Mortensen	Mid intertidal, on *Fucus*	N/A	JN847296	This paper
Porphyra umbilicalis	AMM06SF4200	Mølin, Froðba, Trongisvágsfjørður, Faroe Islands	18/04/06 A. Mols-Mortensen	High intertidal, on rock	N/A	JN847297	This paper
Porphyra umbilicalis	AMM06SF4263	Mølin, Froðba, Trongisvágsfjørður, Faroe Islands	08/07/06 A. Mols-Mortensen	Mid intertidal, on rock	N/A	JN847298	This paper
Porphyra umbilicalis	AMM06SF4317	Mølin, Froðba, Trongisvágsfjørður, Faroe Islands	18/07/06 A. Mols-Mortensen	Low intertidal, on rock	N/A	JN847299	This paper
Porphyra umbilicalis	AMM06SF4352	Mølin, Froðba, Trongisvágsfjørðu	20/07/06 A. Mols-	Mid intertidal,	N/A	JN847300	This paper

		r, Faroe Islands	Mortensen	on algae			
Porphyra umbilicalis	JB329	Crawfordsburn, BelfastLough, Co. Down, Northern Ireland, U.K.	25/09/04 C. A. Maggs	N/A	N/A	DQ191334	Robba *et al.*, 2006
Porphyra umbilicalis	JB342	Sidmouth, Devon, England, U.K.	23/04/05 J. Brodie	N/A	N/A	DQ191336	Robba *et al.*, 2006
Porphyra umbilicalis	JB357	Combe Martin, Devon, England, U.K.	24/04/05 J. Brodie, L. Robba	N/A	N/A	DQ191332	Robba *et al.*, 2006
Porphyra umbilicalis	BM000769632 (JB178) Neotype	Easdale, Scotland, U.K.	23/07/98 J. Brodie, P. K. Hayes	Intertidal	N/A	DQ442891	Robba *et al.*, 2006
Porphyra sp. FO	AMM05SF2102	Tjaldavík, Trongisvágsfjørður, Faroe Islands	01/11/05 A. Mols-Mortensen	Low intertidal, on rock	JN787112	N/A	This paper
Pyropia brumalis	UBCA84426	Vancouver, BC, Canada	19/02/99 N/A	N/A	AF452426	N/A	Lindstrom & Fredericq, 2003
Pyropia elongata	NHA76229	Masonboro, NC, U.S.A.	08/02/02 D. W. Freshwater, R. S. Melton	N/A	AY486349	N/A	Genbank
Pyropia elongata	Lectotype	Koster, Bohuslän, Sweden	21/07/1905 Kylin	N/A	FJ817088	N/A	Neefus & Brodie, 2009
Pyropia elongata	AMM06SF1308	Tjaldavík, Trongisvágsfjørður, Faroe Islands	08/05/06 A. Mols-Mortensen	Low intertidal, on limpet	JN847254	AM943399	This paper; Brodie *et al.*, 2008
Pyropia elongata	JB286	Bracklesham Bay, Sussex, England, U.K.	02/05/04 I. Tittley	N/A	N/A	DQ191335	Robba *et al.*, 2006
Pyropia katadae	NHA77880	Mass. Maritime Academy, MA, U.S.A.	15/01/05 T. Bray	N/A	DQ630036	N/A	Neefus *et al.*, 2008
Pyropia '*leucosticta*'A	JB372	Krossavík, Iceland	09/07/05 I. Tittley, J. Brodie	Intertidal	JN847256	JN847325	This paper
Pyropia '*leucosticta*'A	JB477	Stafnes, Iceland	08/08/99 R. Nielsen, K. Gunnarsson,T. E. Lein	Intertidal	JN847257	N/A	This paper
Pyropia '*leucosticta*'A	AMM06SF1200	Tjaldavík, Trongisvágsfjørður, Faroe Islands	27/04/06 A. Mols-Mortensen	Low intertidal, on limpet	N/A	JN847323	This paper
Pyropia '*leucosticta*'A	AMM06SF1240	Tjaldavík, Trongisvágsfjørðu	27/04/06 A. Mols-	Low intertidal,	JN847255	AM943398	This paper; Brodie *et*

		r, Faroe Islands	Mortensen	on limpet			*al*., 2008
Pyropia ‘*leucosticta*’A	AMM06SF2269	Tjaldavík, Trongisvágsfjørður, Faroe Islands	13/07/06 A. Mols-Mortensen	Low intertidal, on *Fucus*	N/A	JN847324	This paper
Pyropia ‘*leucosticta*’B	JB340	Bembridge, Isle of Wight, Hampshire, U.K.	12/04/05 J. Brodie	N/A	N/A	DQ442890	Robba *et al*., 2006
Pyropia njordii	JB214	Hrísey, Iceland	14/06/06 R. Nielsen, S. Egilsdóttir	Intertidal	JN847260	N/A	This paper
Pyropia njordii	JB418	Stokksnes, Iceland	20/06/07 K. Gunnarsson, S. Egilsdóttir	Low intertidal	JN847261	N/A	This paper
Pyropia njordii	JB419	Vattarnes, Iceland	20/06/07 J. Brodie, I. Tittley	Intertidal	JN847262	N/A	This paper
Pyropia njordii	JB420	Vikurbakki, Iceland	13/06/06 R. Nielsen, K. Gunnarsson	Intertidal	JN847263	N/A	This paper
Pyropia njordii	JB421	Merakkaslétta, Iceland	13/06/07 J. Brodie, I. Tittley, S. Egilsdóttir	Intertidal	JN847264	N/A	This paper
Pyropia njordii	Paratype ICEL 11439 1 (JB422)	Stokksnes, Iceland	20/06/07 K. Gunnarsson, S. Egilsdóttir	Mid intertidal	JN847265	N/A	This paper
Pyropia njordii	JB425	Reyðarfjörður, Hruteyri, Slettustrond, Iceland	10/06/07 J. Brodie, I. Tittley	N/A	JN847266	N/A	This paper
Pyropia njordii	Holotype BM001032349 (AMM06SF1255)	Tjaldavík, Trongisvágsfjord, Faroe Islands	27/04/06 A. Mols-Mortensen	Low intertidal, on rock	JN847259	JN847326	This paper
Pyropia njordii	Isotype NHA552091 (AMM06SF1204)	Tjaldavík, Trongisvágsfjørður, Faroe Islands	27/04/06 A. Mols-Mortensen	Low intertidal, on rock	N/A	N/A	This paper
Pyropia njordii	Isotype NHA552091 (AMM06SF1205)	Tjaldavík, Trongisvágsfjørður, Faroe Islands	27/04/06 A. Mols-Mortensen	Low intertidal, on rock	N/A	N/A	This paper

Pyropia njordii	Isotype AMM06SF1206	Tjaldavík, Trongisvágsfjord, Faroe Islands	27/04/06 A. Mols-Mortensen	Low intertidal, on rock	N/A	N/A	This paper
Pyropia njordii	Isotype AMM06SF1262	Tjaldavík, Trongisvágsfjørður, Faroe Islands	27/04/06 A. Mols-Mortensen	Low intertidal, on rock	N/A	N/A	This paper
Pyropia njordii	Isotype ICEL 11437 1 (AMM06SF1207)	Tjaldavík, Trongisvágsfjørður, Faroe Islands	27/04/06 A. Mols-Mortensen	Low intertidal, on rock	N/A	N/A	This paper
Pyropia njordii	Isotype ICEL 11438 1 (AMM06SF1233)	Tjaldavík, Trongisvágsfjørður, Faroe Islands	27/04/06 A. Mols-Mortensen	Mid intertidal, on rock	N/A	N/A	This paper
Pyropia njordii	Isotype AMM06SF1254	Tjaldavík, Trongisvágsfjørður, Faroe Islands	27/04/06 A. Mols-Mortensen	Low intertidal, on rock	N/A	N/A	This paper
Pyropia njordii	Isotype BM001032348 (AMM06SF1226)	Tjaldavík, Trongisvágsfjørður, Faroe Islands	27/04/06 A. Mols-Mortensen	Mid intertidal, on rock	N/A	N/A	This paper
Pyropia njordii	AMM154	Hunde Ejlande, Aasiaat, Greenland	06/09/09 P. M. Pedersen	Low intertidal	JN847258	N/A	This paper
Pyropia olivii	Holotype BM000806050	N. Krini, Thessaloniki Gulf, Greece	16/03/04 S. Orfanidis	N/A	DQ837007	N/A	Brodie *et al.,* 2007
Pyropia pseudolinearis	ALAJ 745, 747	Juneau, AK, U.S.A.	16/04/96 N/A	N/A	AF452441	N/A	Lindstrom & Fredericq, 2003
Pyropia suborbiculata	NHA77881	Little Pond Outlet, Falmouth, MA, U.S.A.	15/01/05 T. Bray	N/A	DQ630041	N/A	Neefus *et al.*, 2008
Pyropia thulaea	Isotype 8463	Nuuk, Greenland	24/08/58 T. Christensen	Low intertidal, on rock	JN847268	N/A	This paper
Pyropia thulaea	56457	Berufjörður, Strokkur, Iceland	09/10/68 I. Munda	N/A	AM94301	N/A	Brodie *et al.*, 2008
Pyropia yezoensis f. *narawensis*	NHA78127	Westport, MA, U.S.A.	9/2/00 C. D. Neefus	N/A	DQ630015	N/A	Neefus *et al.*, 2008
Pyropia yezoensis f. *yezoensis*	NHA78133	Breakwater, Plymouth, MA, U.S.A.	25/4/04 T. Bray, J. Day	Intertidal	DQ535234	N/A	Neefus *et al.*, 2008
Pyropia sp. ‘collinsii’	NHA78139	Millstone Pt., CT, U.S.A.	23/04/04 A. C. Mathieson	N/A	DQ813594	N/A	Genbank

Pyropia sp. ‘*novae-angliae’*	NHA77786	New Meadows River, Brunswick, ME, U.S.A.	12/3/04 T. Bray, A. C. Mathieson	N/A	DQ813607	N/A	Genbank
Pyropia sp. ‘*stamfordensis*’	NHA77883	Falmouth, MA, U.S.A.	15/1/05 T. Bray	N/A	DQ813636	N/A	Genbank
Pyropia sp. ‘*spatulata*’	NHA77916	Westport, MA, U.S.A.	08/02/05 T. Bray, J. Day	N/A	DQ813632	N/A	Genbank
Pyropia sp. DK	JB437	Hirsholmene, Jylland, Denmark	05/05/94 J. Plumb	On rock	JN847267	N/A	This paper
Wildemania abyssicola	JB456	Mariuhorn by Grunnavik, Iceland	2/7/05 K. Gunnarsson, G. Bruntse	Subtidal, 17 m depth	JN847269	N/A	This paper
Wildemania abyssicola	JBIC1	Mariuhorn by Grunnavik, Iceland	2/7/05 K. Gunnarsson, G. Bruntse	Subtidal, 17 m depth	JN847270	N/A	This paper
Wildemania amplissima	AMM77	Kvívík, Faroe Islands	17/06/08 A.Mols-Mortensen, Ø. Patursson	Subtidal, 4 m depth	N/A	JN847327	This paper
Wildemania amplissima	JB460	Holmanes, Iceland	13/6/07 K. Gunnarsson, G. Bruntse	Subtidal, 7 m depth	JN847272	JN847328	This paper
WIldemania amplissima	JB461	Svalbarðseyri, Eyrarbakki, Iceland	19/06/06 R. Nielsen, S. Egilsdóttir	Intertidal	JN847273	JN847329	This paper
Wildemania amplissima	JB462	Vikurbakki, Iceland	13/06/06 R. Nielsen, K. Gunnarsson	Intertidal	JN847274	JN847330	This paper
Wildemania amplissima	JB463	Hellisnípa, Hólmsbergi, Iceland	06/07/06 K. Gunnarsson	Subtidal, 5 m depth	JN847275	N/A	This paper
Wildemania amplissima	JB365 (57406)	Krossavík, Iceland	09/07/05 R. Nielsen, S. Egilsdóttir	Intertidal	JN847271	N/A	This paper
Wildemania cuneiformis	16-Apr-1996	Juneau, AK, U.S.A.	16/04/96 S. Lindstrom	N/A	AF452428	N/A	Genbank
Wildemania miniata	JB416	Krossanes, Iceland	16/06/07 I. Tittley,	Intertidal	JN847276	N/A	This paper

			K. Gunnarsson, S. Egilsdóttir				
Wildemania miniata	JB452	Fálka-Jónsskerr, Fiskimannatangi, Iceland	15/06/07 K. Gunnarsson, R. Nielsen, I. Tittley	Intertidal	JN847277	N/A	This paper
Wildemania miniata	JB453	Selavogur, Iceland	16/06/07 K. Gunnarsson, G. Bruntse	Subtidal, 29 m depth	JN847278	N/A	This paper
Wildemania miniata	JB454	Fálka-Jónsskerr, Iceland	15/06/07 K. Gunnarsson, R. Nielsen, I. Tittley	Intertidal	JN847279	N/A	This paper
Wildemania miniata	JB455	Fálka-Jónsholmi, Iceland	15/06/07 K. Gunnarsson, R. Nielsen, I. Tittley	Rockpool	JB847280	N/A	This paper
Wildemania miniata	JB458	Hellisnípa, Hólmbergi, Iceland	06/07/06 K. Gunnarsson	Subtidal, 3 m depth	JN847281	N/A	This paper
Wildemania miniata	JB459	Kálfavík, Iceland	07/06/06 K. Gunnarsson	Subtidal, 1-3 m depth	JN847282	N/A	This paper
Wildemania miniata	JB464	Sölvabakki, Iceland	08/06/06 R. Nielsen, S. Egilsdóttir	Intertidal	JN847283	N/A	This paper
Wildemania miniata	AMM74	Kvívík, Faroe Islands	17/06/08 A. Mols-Mortensen, Ø. Patursson	Subtidal, 4 m depth	N/A	JN847331	This paper
Wildemania miniata	AMM76	Kvívík, Faroe Islands	17/06/08 A. Mols-Mortensen, Ø. Patursson	Subtidal, 4 m depth	N/A	JN847332	This paper
Wildemania norrisii	UBC A85176, A85177, A85178	Hardling Point, Victoria, BC, Canada	25/04/05 S. Lindstrom	N/A	EU223212	N/A	Genbank
Wildemania	04-Jun-1996	Seldovia, AK,	04/06/96	N/A	AF452447	N/A	Genbank

variegata		U.S.A.	S. Lindstrom				
OUTGROUPS							
Corallina officinalis	3738	Kent, St. Margaret's Bay, U.K.	08/05/04 I. Tittley	N/A	N/A	FM180076	Walker *et al.*, 2009
Phycodrys riggii	N/A	Kittilngook Bay, St. Lawrence Island, Alaska, U.S.A.	05/08/96 S. Lindstrom	N/A	AF257430	N/A	Lin *et al.*, 2001
Phycodrys rubens	N/A	Mouth of Hvamsfjord, Iceland	23/08/99 A. Coleman	N/A	AF257428	N/A	Lin *et al.*, 2001

Appendix B. Taxa used in the analysis with collecting details and GenBank accession numbers. N/A = not available.

Taxa	**Voucher number**	**Location**	**Date and collector**	**Level and substratum**	**GenBank accession no. 3' *rbc*L + 5' *rbc*L-S**	**GenBank accession no. *rbc*L**	**Reference**
Bangia sp.	N/A	Shannon River, Ireland	N/A	N/A	N/A	AF043371	Sutherland *et al.*, 2011
'Bangia' 1	WELT A26696	Woodpecker Bay, Paparoa, Wesland, South I, NZ	N/A	N/A	N/A	EU570051	Sutherland *et al.*, 2011
'Bangia' 2	WELT A026700	Gentle Annie, Westland, South I, NZ	N/A	N/A	N/A	HQ687506	Sutherland *et al.,* 2011
'Bangia' 3	WELT A026691	14 Mile Bluff, Westland, South I, NZ	22nd Aug. 2000	N/A	N/A	GU046404	Sutherland *et al.*, 2011
Boreophyllum aestivalis	UBCA843442	Ketchikan, AK, U.S.A.	19th Aug. 2000 S. C. Lindstrom	N/A	N/A	AF458077	Lindstrom & Fredericq, 2003
Boreophyllum birdiae	AMM160	At the foot of Nasaasaaq, Sisimiut, Greenland 66º55.181 N; 53º37.617 W	3rd June 2010 A. Mols-Mortensen	On rock, high mid intertidal	KF478670	N/A	This paper
Boreophyllum birdiae	AMM161	Small bay, west side of Sisimiut, Greenland 66º56.360 N; 53º42.193 W	4th June 2010 A. Mols-Mortensen	On rock among Fucus sp.	KF478671	N/A	This paper
Boreophyllum birdiae	AMM163	Small bay, west side of Sisimiut, Greenland 66º56.358 N; 53º42.196 W	4th June 2010 A. Mols-Mortensen	On barnacle	KF478672	N/A	This paper
Boreophyllum birdiae	AMM164	Small bay, west side of Sisimiut, Greenland 66º56.358 N; 53º42.194 W	4th June 2010 A. Mols-Mortensen	On rock among *Fucus* sp.	KF478673	N/A	This paper
Borephyllum birdiae	AMM167	At the foot of Nasaasaaq, Sisimiut, Greenland 66º55.166 N, 53º37.721 W	3rd June 2010 A. Mols-Mortensen	On barnacle, mid intertidal	KF478674	N/A	This paper
Boreophyllum birdiae	AMM169	Nasaasaaq, Sisimiut, Greenland 66º55.178 N; 53º37.629 W	3rd June 2010 A. Mols-Mortensen	On rock, high mid intertidal	KF478675	N/A	This paper
Boreophyllum birdiae	AMM174	Hernhut bay, Nuuk, Greenland	29th July 2010 P. M. Pedersen	On *Fucus* sp., high intertidal	KF478676	N/A	This paper

Boreophyllum birdiae	AMM175	Hernhut bay, Nuuk, Greenland	29th July 2010 P. M. Pedersen	On *Fucus* sp., high intertidal	KF478677	N/A	This paper
Boreophyllum birdiae	AMM176	Small bay, west side of Sisimiut, Greenland 66°56.358 N; 53°42.195 W	4th June 2010 A. Mols-Mortensen	On rock, low intertidal	KF478678	N/A	This paper
Boreophyllum birdiae	AMM177	Sisimiut, Greenland 66°55.844 N; 53°41.104 W	1st June 2010 A. Mols-Mortensen	On rock, high intertidal	KF478679	N/A	This paper
Boreophyllum birdiae	AMM178	Sisimiut, Greenland 66°55.842 N; 53°41.105 W	1st June 2010 A. Mols-Mortensen	On rock, high intertidal	KF478680	N/A	This paper
Boreophyllum birdiae	AMM183	Sisimiut, Greenland 66°55.788 N; 53°41.100 W	2nd June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478681	N/A	This paper
Boreophyllum birdiae	AMM186	Sisimiut, Greenland 66°55.792 N; 53°41.136 W	2nd June 2010 A. Mols-Mortensen	On barnacle, mid intertidal	KF478682	N/A	This paper
Boreophyllum birdiae	AMM191	Arsuk, Greenland 61°10.517 N; 48°27.354 W	17th June 2010 A. Mols-Mortensen	On barnacle, high intertidal	KF478683	N/A	This paper
Boreophyllum birdiae	AMM192	Arsuk, Greenland 61°10.513 N; 48°27.272 W	17th June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478684	KF478753	This paper
Boreophyllum birdiae	AMM198	Nuuk, Greenland 64°10.646 N; 51°43.393 W	20th June 2010 A. Mols-Mortensen	On rock, low mid intertidal	KF478685	N/A	This paper
Boreophyllum birdiae	AMM139	Munkebugten, Qaqatoq, Greenland 60°43.172 N; 46°08.167 W	22nd July 2005 Agnes Mols-Mortensen	N/A	N/A	N/A	This paper
Boreophyllum birdiae	AMM06SF4325	Mølin Froðba, Trongisvágsfjørður, Faroe Islands	18th July 2006 A. Mols-Mortensen	On rock, low intertidal	N/A	JN711449	Mols-Mortensen *et al.*, 2012
Boreophyllum birdiae	57290	Hvalfjörður, Eyri, Iceland	1st Sep. 2004 K. Gunnarsson	Intertidal	N/A	JN711446	Mols-Mortensen *et al.*, 2012
Boreophyllum birdiae	JB434	Trondheim, Norway	August 1999 F. Lopez	N/A	N/A	JN711450	Mols-Mortensen *et al.*, 2012
Boreophyllum birdiae	Isotype NHA76527	Herring Cove, NS, Canada	21st Sep. 2002 C. D. Neefus	Mid intertidal, on rock	N/A	AY180909	Neefus *et al.*, 2002
Clymene coleana	WELT A22181	Leigh, North I, NZ	N/A	N/A	N/A	FJ263672	Sutherland *et al.*, 2011

Dione arcuata	WELT A23126 Holotype	Ohau Stream, Kaikoura, South I, NZ	N/A	N/A	N/A	EU570052	Sutherland *et al.*, 2011
Fuscifolium papenfussii	UBC A86209	Seldovia Point, AK, USA	1st July 2003 S. Saupe	N/A	N/A	EU223120	Sutherland *et al.*, 2011
Lysithea adamsiae	WELT A023233	Orde Lees I, Antipodes Is, NZ	N/A	N/A	N/A	HQ687515	Sutherland *et al.*, 2011
Minerva aenigmata	WELT A25775 Holotype	Puheke, Northland, North I, NZ	N/A	N/A	N/A	EU570053	Sutherland *et al.*, 2011
Miuraea migitae	WELT A023200	Osaka Bay, Osaka, Japan	N/A	N/A	N/A	EU521643	Sutherland *et al.*, 2011
Porphyra corallicola	GWSC014	Maces Bay, Lepreau, Bay of Fundy, Canada 45.1093 N; 66.4817 W	20th Dec. 1999 G. W. Saunders	N/A	N/A	JN028943	Kucera & Saunders, 2012
Porphyra dioica	JB378	Krossavik, Iceland	10th July 2005 J. Brodie, I. Tittley	Intertidal	N/A	JN787102	Mols-Mortensen *et al.*, 2012
Porphyra dioica	AMM06SF4159	Mølin, Froðba, Trongisvágsfjørður, Faroe Islands	18th April 2006 A. Mols-Mortensen	Mid intertidal, on rock	N/A	JN703282	Mols-Mortensen *et al.*, 2012
Porphyra linearis	JB465	Höfnin, Garði, Iceland	11th Feb. 2006 K. Gunnarsson	Intertidal	N/A	JN787103	Mols-Mortensen *et al.*, 2012
Poprhyra mumfordii	AMM152 Topotype	Orlebar Pt., BC, Canada	3rd Feb. 2002 S. C. Lindstrom	N/A	N/A	JN787106	Mols-Mortensen *et al.*, 2012
Porphyra purpurea	AMM193	Eqalugaasuit, Qaqortoq, Greenland 60º46.949 N; 046º08.329 W	11th June 2010 A. Mols-Mortensen	On barnacle, low intertidal	KF478686	N/A	This paper
Porphyra purpurea	AMM195	Kangilleq, Eqalugaasuit, Qaqortoq, Greenland 60º46.948 N; 046º08.326 W	11th June 2010 A. Mols-Mortensen	On rock, low mid intertidal	KF478687	N/A	This paper
Porphyra purpurea	AMM196	Eqalugaasuit, Qaqortoq, Greenland 60º47.025 N; 046º08.758 W	11th June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478688	KF478754	This paper
Porphyra purpurea	AMM134	Kangilinnguit, Greenland 61º14'00'' N; 48º05'55'' W	5th July 2008 P. M. Pedersen	Among *Fucus vesiculosus*	KF478689	N/A	This paper

Porphyra purpurea	AMM483	Sulugssugut, Greenland 64º25’ N; 50º30’ W	1st July 1957 T. Christensen	Mid intertidal	KF478690	N/A	This paper
Porphyra purpurea	AMM485	Eqalugialik, Greenland 64º21’ N; 50º25’ W	16th July 1957 T. Christensen	Not attached	KF478691	N/A	This paper
Porphyra purpurea	JB407	Kálfavík, Iceland	7th June 2006 J. Brodie, B. Rinkel	Intertidal	N/A	JN787107	Mols-Mortensen *et al*., 2012
Porphyra purpurea	JB446	Somerset, U.K.	23rd July 2008 J. Brodie	Intertidal	N/A	JN787109	Mols-Mortensen *et al*., 2012
Porphyra purpurea	JB447 (59185)	Gilleleje, Denmark	16th July 2006 R, Nielsen	Intertidal	N/A	JN787110	Mols-Mortensen *et al*., 2012
Porphyra purpurea	N/A	Fridalgo Bay, WA, U.S.A.	22nd January 2002 S. C. Lindstrom	N/A	N/A	AF514280	GenBank
Porphyra umbilicalis	AMM179	Sisimiut, Greenland 66º55.791 N; 53º41.090 W	2nd June 2010 A. Mols-Mortensen	On barnacle, high intertidal	KF478692	N/A	This paper
Porphyra umbilicalis	AMM181	Sisimiut, Greenland 66º55.793 N; 53º41.070 W	2nd June 2010 A. Mols-Mortensen	On rock, high intertidal	KF478693	N/A	This paper
Porphyra umbilicalis	AMM184	Sisimiut, Greenland 66º55.783 N; 53º41.091 W	20th June 2010 A. Mols-Mortensen	On rock, high intertidal	KF478694	N/A	This paper
Porphyra umbilicalis	AMM200	Nuuk, Greenland 64º10.666 N; 51º45.179 W	19th June 2010 A. Mols-Mortensen	On rock, high intertidal	KF478695	N/A	This paper
Porphyra umbilicalis	AMM208	Nuuk, Greenland 64º10.216 N; 51º45.514 W	19th June 2010 A. Mols-Mortensen	On rock, high intertidal,	KF478696	KF478755	This paper
Porphyra umbilicalis	AMM212	Nuuk, Greenland 64º10.258 N; 51º45.377 W	19th June 2010 A. Mols-Mortensen	On barnacle among *Fucus vesiculosus*, high intertidal	KF478697	N/A	This paper
Porphyra umbilicalis	AMM344	Nuuk, Greenland	26th March 2011 S. Wegeberg	High mid intertidal	KF478698	N/A	This paper
Porphyra umbilicalis	AMM534	Nuuk, Greenland 64º10.215 N; 51º45.516 W	19th June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478699	N/A	This paper
Porphyra umbilicalis	BM000769632 (JB178) Neotype	Easdale, Scotland, U.K.	23rd July 1998 J. Brodie, P. K. Hayes	Intertidal	KF478700	KF478756	This paper

Porphyra umbilicalis	JB438	Hirsholmene, Frederikshavn, Denmark	5th May 1994 J. Plumb	Intertidal	N/A	JN847248	Mols-Mortensen *et al.*, 2012
Porphyra umbilicalis	JB467	Höfnin, Garði, Iceland	11th Feb. 2006 K. Gunnarsson	High Intertidal	N/A	JN847249	Mols-Mortensen *et al.*, 2012
Porphyra umbilicalis	JB435	Skorpa, Norway	4th Sep. 1997 T. E. Lein, R. Nielsen	Intertidal	N/A	JN847246	Mols-Mortensen *et al.*, 2012
Porphyra sp. FO	AMM05SF2102	Tjaldavík, Trongisvágsfjørður, Faroe Islands	1st Nov. 2005 A. Mols-Mortensen	On rock, low intertidal,	N/A	JN787112	Mols-Mortensen *et al.*, 2012
Pyropia abbottiae	12-Apr-1997	Sitka, AK, U.S.A.	12th April 1997 S. C. Lindstrom	N/A	N/A	AF452423	GenBank
Pyropia brumalis	UBC A84426	Vancouver, BC, Canada	19th Feb. 1999	N/A	N/A	AF452426	Lindstrom & Fredericq, 2003
Pyropia californica	GWS008155	Cape Beale, Bamfield, BC, Canada 48.7848 N; 125.216 W	2nd June 2007 L. D. Druehl	N/A	N/A	JN028984	Kucera & Saunders, 2012
Pyropia elongata	Lectotype	Koster, Bohuslän, Sweden	21st July 1905 Kylin	N/A	N/A	FJ817088	Neefus & Brodie, 2009
Pyropia elongata	AMM06SF1308	Tjaldavík, Trongisvágsfjørður, Faroe Islands	8th May 2006 A. Mols-Mortensen	On limpet, low intertidal	N/A	JN847254	Mols-Mortensen *et al.*, 2012
Pyropia fallax	SCL 12637	Surf Bay, Akun Island, AK, U.S.A. 54.15 N; 165.62 W	31st July 2005 S. C. Lindstrom	N/A	N/A	EU223058	GenBank
Pyropia fucicola	SCL 12620	Surf Bay, Akun Island, AK, U.S.A.	31st July 2005 S. C. Lindstrom	N/A	N/A	EU223087	GenBank
Pyropia gardneri	GWS008119	Lands end, Bamfield, BC, Canada	2nd June 2007 B. Clarkston, D. McDevit, K. Roy, H. Kucera	N/A	N/A	JN028972	Kucera & Saunders, 2012
Pyropia hiberna	UBC A87474	Pacific Grove, Monterey County, CA, U.S.A. 36.62 N; 121.91 W	31st Dec. 2007 P. Gabrielson, P. Martone	N/A	N/A	GU319866	Sutherland *et al.*, 2011

Pyropia hollenbergii	WELT A023231	Agua Verde, Baja California Sur, Mexico	N/A	N/A	N/A	HQ687523	Sutherland *et al.*, 2011
Pyropia kanakaensis	SCL 10932	Olympic Peninsula, Clallam County, WA, U.S.A. 48.35 N; 124.54 W	31st May 2003 S. C. Lindstrom	N/A	N/A	EU223099	GenBank
Pyropia katadae	NHA77880	Mass. Maritime Academy, MA, U.S.A.	15th Jan. 2005 T. Bray	N/A	N/A	DQ630036	Neefus *et al.*, 2008
Pyropia kurogii	SCL 9935	Sandy Beach, Sitka Sound, AK, U.S.A. 57.08 N; 135.37 W	20th April 2000 S. C. Lindstrom	N/A	N/A	EU223105	GenBank
Pyropia leucosticta	AMM06SF1240	Tjaldavík, Trongisvágsfjørður, Faroe Islands	27th April 2006 A. Mols-Mortensen	On limpet, low intertidal	N/A	JN847255	Mols-Mortensen *et al.*, 2012
Pyropia njordii	AMM135	Isungua, Greenland 69°14'53.50"N; 53°31'08.97"W	8th August 2006 P. M. Pedersen	High intertidal	N/A	N/A	This paper
Pyropia njordii	AMM165	Nasaasaaq, Sisimiut, Greenland 66º55.146 N; 053º37.768 W	3rd June 2010 A. Mols-Mortensen	On barnacle	KF478701	N/A	This paper
Pyropia njordii	AMM166	Nasaasaaq, Sisimiut, Greenland 66º55.150 N; 053º37.793 W	3rd June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478702	N/A	This paper
Pyropia njordii	AMM168	Nasaasaaq, Sisimiut, Greenland 66º55.164 N; 053º37.759 W	3rd June 2010 A. Mols-Mortensen	On rock, high mid intertidal	KF478703	N/A	This paper
Pyropia njordii	AMM182	Sisimiut, Greenland 66º57.019 N; 053º42.497 W	2nd June 2010 A. Mols-Mortensen	On rock, lower mid intertidal	KF478704	KF478757	This paper
Pyropia njordii	AMM154	Hunde Ejlande, Aasiaat, Greenland	6th Sep. 2009 P. M. Pedersen	Lower intertidal	KF478705	JN847258	Mols-Mortensen *et al.*, 2012
Pyropia njordii	AMM187	Sisimiut, Greenland 66º57.037 N; 053º42.501 W	2nd June 2010 A. Mols-Mortensen	On barnacle, mid intertidal	KF478706	N/A	This paper
Pyropia njordii	AMM188	Sisimiut, Greenland 66º56.634 N; 053º40.443 W	6th June 2010 A. Mols-Mortensen	On barnacle, low intertidal	KF478707	N/A	This paper
Pyropia njordii	AMM189	Maniitsoq, Greenland 65º24.684 N; 052º53.993 W	7th June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478708	N/A	This paper

Pyropia njordii	AMM190	Maniitsoq, Greenland 65°24.685 N; 052°53.992 W	7th June 2010 A. Mols-Mortensen	On barnacle, mid intertidal	KF478709	N/A	This paper
Pyropia njordii	AMM194	Akia, Qaqortoq, Greenland 60°38.523 N; 46°02.307 W	12th June 2010 A. Mols-Mortensen	On barnacle, lower mid intertidal	KF478710	N/A	This paper
Pyropia njordii	AMM197	Qaqortoq, Greenland 60°42.914 N; 46°01.670 W	14th June 2010 A. Mols-Mortensen	On barnacle, mid intertidal	KF478711	N/A	This paper
Pyropia njordii	AMM201	Nuuk, Greenland 64°12.044 N; 51°43.426 W	20th June 2010 A. Mols-Mortensen	On rock, low intertidal	KF478712	N/A	This paper
Pyropia njordii	AMM202	Nuuk, Greenland 64°10.670 N; 51°45.184 W	20th June 2010 A. Mols-Mortensen	On rock, lower mid intertidal	KF478713	N/A	This paper
Pyropia njordii	AMM203	Nuuk, Greenland 64°11.702 N; 51°43.487 W	20th June 2010 A. Mols-Mortensen	On barnacle, upper mid intertidal	KF478714	N/A	This paper
Pyropia njordii	AMM205	Nuuk, Greenland 64°11.708 N; 51°43.499 W	20th June 2010 A. Mols-Mortensen	On rock among *Ulva* sp., mid intertidal	KF478715	N/A	This paper
Pyropia njordii	AMM206	Nuuk, Greenland 64°12.041 N; 51°43.430 W	20th June 2010 A. Mols-Mortensen	On barnacle, mid intertidal	KF478716	N/A	This paper
Pyropia njordii	AMM209	Nuuk, Greenland 64°11.710 N; 51°43.560 W	20th June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478717	N/A	This paper
Pyropia njordii	AMM210	Nuuk, Greenland 64°10.248 N; 51°45.484 W	19th June 2010 A. Mols-Mortensen	On rock, low intertidal	KF478718	N/A	This paper
Pyropia njordii	AMM211	Nuuk, Greenland 64°10.250 N; 51°43.393 W	19th June 2010 A. Mols-Mortensen	On rock	KF478719	N/A	This paper
Pyropia njordii	AMM215	Nuuk, Greenland 64°10.247 N; 51°45.482 W	19th June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478720	N/A	This paper
Pyropia njordii	AMM217	Nuuk, Greenland 64°10.215 N; 51°45.516 W	19th June 2010 A. Mols-Mortensen	On barnacle, mid intertidal	KF478721	N/A	This paper
Pyropia njordii	AMM218	Nuuk, Greenland 64°10.215 N; 51°45.516 W	19th June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478722	N/A	This paper
Pyropia njordii	AMM219	Nuuk, Greenland 64°10.253 N; 51°45.389 W	19th June 2010 A. Mols-Mortensen	On barnacle, mid intertidal	KF478723	N/A	This paper
Pyropia njordii	AMM220	Nuuk, Greenland 64°10.809 N;	19th June 2010 A. Mols-	On rock, on the edge of a high intertidal	KF478724	N/A	This paper

		51°45.047 W	Mortensen	rock pool			
Pyropia njordii	AMM221	Nuuk, Greenland 64°12.041 N; 51°43.430 W	20th June 2010 A. Mols-Mortensen	On rock and some on juvenile *Fucus* sp., mid intertidal	KF478725	N/A	This paper
Pyropia njordii	AMM222	Nuuk, Greenland 64°12.040 N; 51°43.429 W	20th June 2010 A. Mols-Mortensen	On rock, high intertidal	KF478726	N/A	This paper
Pyropia njordii	AMM223	Nanortalik, Greenland	9th Oct. 2007 S. Wegeberg	On rock among *Fucus* sp. and *A. nodosum*, high intertidal	KF478727	N/A	This paper
Pyropia njordii	AMM224	Nanortalik, Greenland	9th Oct. 2007 S. Wegeberg	On rock among *Fucus* sp. and *A. nodosum*, high intertidal	KF478728	N/A	This paper
Pyropia njordii	AMM225	Nanortalik, Greenland	9th Oct. 2007 S. Wegeberg	On rock among *Fucus* sp. and *A. nodosum*, high intertidal	KF478729	N/A	This paper
Pyropia njordii	AMM226	Nanortalik, Greenland	9th Oct. 2007 S. Wegeberg	On rock among *Fucus* sp. and *A. nodosum*, high intertidal	KF478730	N/A	This paper
Pyropia njordii	AMM404	Arsuk, Greenland	29th June 1888 L. K. Rosenvinge	N/A	KF478731		This paper
Pyropia njordii	AMM475	Anordliuitsoq, Qaqotoq, Greenland 60°07' N; 44°20' W	7th Aug. 1970 P. M. Pedersen	At low water level	KF478732		This paper
Pyropia njordii	AMM488	Agsanguit, Greenland 60°53' N	8th July 1888 L. K. Rosenvinge	N/A	KF478733		This paper
Pyropia njordii	AMM489	Qaqortoq, Greenland	7th Aug. 1888 L. K. Rosenvinge	Intertidal	KF478734		This paper
Pyropia njordii	Holotype BM001032349 (AMM06SF1255)	Tjaldavík, Trongisvágsfjord, Faroe Islands	27th April 2006 A. Mols-Mortensen	On rock, low intertidal	KF478735	JN847259	Mols-Mortensen *et al.*, 2012
Pyropia olivii	Holotype BM000806050	N. Krini, Thessaloniki Gulf, Greece	16th March 2004 S. Orfanidis	N/A	N/A	DQ837007	Brodie *et al.*, 2007

Pyropia peggicovensis	JB437	Hirsholmene, Jylland, Denmark	5th May 1994 J. Plumb	On rock	N/A	JN847267	Mols-Mortensen *et al.*, 2012
Pyropia pendula	CMMEX 4437	Calerita, Baja Califorbia Sur, Mexico	N/A	N/A	N/A	HQ687530	Sutherland *et al.*, 2011
Pyropia perforata	MATS 162	Punta Popotla, Baja California, Mexico	24th Feb. 1999	N/A	N/A	GU046416	Broom *et al.*, 2010
Pyropia pseudolanceolata	SCL 11885	Perevalnie Passage, Shuyak Island, AK, U.S.A. 58.64 N; 152.37 W	23rd May 2005 S. C. Lindstrom	N/A	N/A	EU223157	GenBank
Pyropia pseudolinearis	01-May-1995	Juneau, AK, U.S.A.	1st May 1995 S. C. Lindstrom	N/A	N/A	AF452441	Lindstrom & Fredericq, 2003
Pyropia smithii	GWS003309	Pachena Beach, BC, Canada 48.786 N; 125.119 W	12th June 2006 G. W. Saunders, B. Clarkston, D. McDevit	N/A	N/A	JN028998	Kucera & Saunders, 2012
Pyropia suborbiculata	NHA77881	Little Pond Outlet, Falmouth, MA, U.S.A.	15th Jan. 2005 T. Bray	N/A	DQ630041	N/A	Neefus *et al.*, 2008
Pyropia thulaea	Isotype 8463	Nuuk, Greenland	24th Aug. 1958 T. Christensen	Low intertidal, on rock	N/A	JN847268	Mols-Mortensen *et al.*, 2012
Pyropia thulaea	AMM156	Kumikume, Greenland 67°18.920 N; 53°51.737 W	8th Sep. 2009 P.M. Pedersen	Intertidal	KF496927	N/A	This paper
Pyropia thulaea	AMM157	Kumikume, Greenland 67°18.920 N; 53°51.737 W	8th Sep. 2009 P.M. Pedersen	Intertidal	KF496928	N/A	This paper
Pyropia thulaea	AMM171	Ilulissat, Greenland	2nd Aug. 2010 P.M. Pedersen	On rock, low intertidal	KF478736	N/A	This paper
Pyropia thulaea	AMM172	Ilulissat, Greenland	2nd Aug. 2010 P.M. Pedersen	On rock, lower intertidal	KF478737	KF478758	This paper
Pyropia thulaea	AMM173	Ilulissat, Greenland	2nd Aug. 2010 P.M. Pedersen	On rock, lower intertidal	KF478738	N/A	This paper
Pyropia thulaea	AMM207	Nuuk, Greenland 64°10.247 N; 51°45.484 W	19th June 2010 A. Mols-Mortensen	On rock among *Acrosiphonia* sp., low intertidal	KF478739	N/A	This paper

Pyropia thulaea	AMM213 Topotype	Nuuk, Greenland 64°10.670 N; 51°45.184 W	20th June 2010 A. Mols-Mortensen	On rock, lower mid intertidal	KF478740	N/A	This paper
Pyropia thulaea	AMM214	Nuuk, Greenland 64°12.044 N; 51°43.426 W	20th June 2010 A. Mols-Mortensen	On rock, low intertidal	KF478741	N/A	This paper
Pyropia thulaea	AMM536	Qaqortoq, Greenland	21st July 2005 A. Mols-Mortensen	N/A	KF478742	N/A	This paper
Pyropia thuretii	GWS010076	Tahsis Island, BC, Canada 49.6145 N; 126.583 W	23rd May 2008 G. W. Saunders, B. Clarkston	N/A	N/A	JN029006	Kucera & Saunders, 2012
Pyropia torta	UBC A85653	Pumicestone Bay, Unalaska Island, AK, U.S.A. 53.53 N; 167.07 W	3rd June 2005 S. C. Lindstrom	N/A	N/A	EU223233	GenBank
Pyropia yezoensis f. *narawensis*	NHA78127	Westport, MA, U.S.A.	9th Feb. 2000 C. D. Neefus	N/A	N/A	DQ630015	Neefus *et al*., 2008
Pyropia yezoensis f. *yezoensis*	NHA78133	Breakwater, Plymouth, MA, U.S.A.	25th April 2004 T. Bray, J. Day	Intertidal	N/A	DQ535234	Neefus *et al*., 2008
Pyropia sp. *‘collinsii’*	NHA78139	Millstone Pt., CT, U.S.A.	23rd April 2004 A. C. Mathieson	N/A	N/A	DQ813594	GenBank
Pyropia sp. ‘*novae-angliae’*	NHA77786	New Meadows River, Brunswick, ME, U.S.A.	12th March 2004 T. Bray, A. C. Mathieson	N/A	N/A	DQ813607	GenBank
Pyropia sp. ‘*stamfordensis*’	NHA77883	Falmouth, MA, U.S.A.	15th Jan. 2005 T. Bray	N/A	N/A	DQ813636	GenBank
Pyropia sp. ‘*spatulata*’	NHA77916	Westport, MA, U.S.A.	8th Feb. 2005 T. Bray, J. Day	N/A	N/A	DQ813632	GenBank
Pyropia peggicovensis	JB437	Hirsholmene, Jylland, Denmark	5th May 1994 J. Plumb	On Rock	N/A	To add	Mols-Mortensen *et al*., 2012
Wildemania abyssicola	JB456	Mariuhorn by Grunnavik, Iceland	2nd July 2005 K. Gunnarsson, G. Bruntse	Subtidal 17m	N/A	JN847269	Mols-Mortensen *et al*., 2012

Wildemania amplissima	JB460	Holmanes, Iceland	13th June 2007 K. Gunnarsson, G. Bruntse	Subtidal 7 m depth	KF478743	JN847272	Mols-Mortensen *et al.*, 2012; This paper
Wildemania amplissima	JB461	Svalbarðseyri, Eyrarbakki, Iceland	19th June 2006 R. Nielsen S. Egilsdóttir	Intertidal	KF478744	JN847273	Mols-Mortensen *et al.*, 2012; This paper
Wildemania amplissima	AMM535	Uppernaviarsuk, Qaqortoq, Greenland 60º44.912 N; 45º53.507 W	19th July 2005 A. Mols-Mortensen	On wooden construction, Just below low water level	KF478745	N/A	This paper
Wildemania amplissima	16-Apr-1996	Juneau, AK, U.S.A.	16th April 1996 S. C. Lindstrom	N/A	N/A	AF452428	Lindstrom & Fredericq, 2003
Wildemania miniata	AMM162	Small bay, west side of Sisimiut, Greenland 66º56.303 N; 53º42.163 W	4th June 2010 A. Mols-Mortensen	Drift	KF478746	N/A	This paper
Wildemania miniata	AMM185	Harbour, Sisimiut, Greenland 66º55.634 N; 53º4.443 W	6th June 2010 A. Mols-Mortensen	On rock, low intertidal	KF478747	N/A	This paper
Wildemania miniata	AMM199	Nuuk, Greenland 64º11.742 N; 51º43.558 W	20th June 2010 A. Mols-Mortensen	On rock, mid intertidal	KF478748	KF478759	This paper
Wildemania miniata	AMM321	Anorliuitsup qeqertaa, Greenland 60º05’00’’ N; 44º12’59’’ W	9th Sep. 2011 P. M. Pedersen	Mid intertidal	KF478749	N/A	This paper
Wildemania miniata	AMM322	Ikigaat, Greenland 59º59’21’’ N; 44º44’34’’ W	11th Sep. 2011 P. M. Pedersen	Subtidal 5-10 m depth	KF478750	N/A	This paper
Wildemania miniata	AMM474	Umiagssat qeqertai, Qaqortoq, Greenland 60º07’ N; 44º20’ W	18th July 1970 P. M. Pedersen	On rock and on *Chaetomorpha melagonium*, Subtidal 10 m depth	KF478751	N/A	This paper
Wildemania miniata	AMM481	Sisimiut, Greenland	3rd August 1886 L. K. Rosenvinge	Intertidal	KF478752	N/A	This paper
Wildemania miniata	JB416	Krissanes, Iceland	16th June 2007 I. Tittley, K. Gunnersson, S. Egilsdóttir	Intertidal	N/A	JN847276	Mols-Mortensen *et al.*, 2012
Wildemania norrisii	UBC A85177	Harling Point, Victoria, BC,	25th April 2005	N/A	N/A	EU223212	GenBank

		Canada	S. C. Lindstrom				
Wildemania occidentalis	15-Apr-1994	Point No Point, BC, Canada	15th April 1994 S. C Lindstrom	N/A	N/A	AF452436	Lindstrom & Fredericq, 2003
Wildemania schizophylla	09-Apr-1997	Sitka, AK, U.S.A.	9th April 1997 S. C. Lindstrom	N/A	N/A	AF452443	Lindstrom & Fredericq, 2003
Wildemania variegata	04-Jun-1996	Seldovia, AK, U.S.A.	4th June 1996 S. C. Lindstrom	N/A	N/A	AF452447	Lindstrom & Fredericq, 2003
Erythrocladia sp.	JAW4480	Ampasi Pohry, Nossi Be, Madagascar	N/A	N/A	N/A	EF660273	GenBank
Smithora naiadum	WELT A24421	Pesquera Zapata, Baja California, Mexico	N/A	N/A	N/A	HQ687545	Sutherland *et al.*, 2011

Appendix C. List of amplification and sequencing primers used in this study.

	Primer name	5′-primer sequence-3′	Reference
3′ *rbc*L + 5′ *rbc*L-S	RBCL5RC (F)	GTGGTATTCATGCTGGTCAAA	Reverse complement of RBCL in Klein *et al.*, 2003
3′ *rbc*L + 5′ *rbc*L-S	RBCSPC (R)	CACTATTCTATGCTCCTTATTKTTAT	Teasdale *et al.*, 2002
*rbc*L (fragment 1)	F67 (F)	TACGCTAAAATGGGTTACTG	Teasdale *et al.*, 2002
*rbc*L (fragment 1)	R502 (R)	TATCCATACGCTCACGTTCTACAA	Mols-Mortensen *et al.*, 2012
*rbc*L (fragment 2)	F461 (F)	GTCCTGCAACTGGATTGATTGT	Mols-Mortensen *et al.*, 2012
*rbc*L (fragment 2)	R901 (R)	TACCAGCTCTATGTAAATGTAAAA	Mols-Mortensen *et al.*, 2012
*rbc*L (fragment 3)	F870 (F)	TGACATGATTTTACATTTACATAGAC	Mols-Mortensen *et al.*, 2012
*rbc*L (fragment 3)	R1312 (R)	GGCCTTCATTTCTTGCCATAACKTTAT	Mols-Mortensen *et al.*, 2012

F = forward; R = reverse

Appendix D. Taxa used in the analysis with collecting details and GenBank accession numbers. N/A = not available.

Taxa	Voucher number	Location	Date and collector	Level and substratum	Genbank accession no. *rbc*L	Genbank accession no. 3' *rbc*L + 5' *rbc*L-S	Reference
Boreophyllum birdiae	AMM06SF4340	Mølin, Froðba, Trongisvág sfjørður, Faroe Islands	July 2006 A. Mols-Mortensen	Mid intertidal on rock	N/A	KP171724	This paper
Boreophyllum birdiae	AMM167	Sisimiut, Greenland 66˚55N 53˚37W	3rd June 2010 A. Mols-Mortensen	Intertidal on barnacle	N/A	KP171725	This paper
Boreophyllum birdiae	AMM183	Sisimiut, Greenland 66˚55N 53˚37W	2nd June 2010 A. Mols-Mortensen	Mid intertidal on rock	N/A	KP171726	This paper
Boreophyllum birdiae	07 8364 1	Vattarnes, Reyðarfjörð, Iceland	31st Aug. 2007 K. Gunnarsson, S. Egilsdóttir	Intertidal	N/A	KP171727	This paper
Boreophyllum birdiae	NRCC3877	Spicer Cove, Cuberland Co., Nova Scotia	30th July 1969 J.McLachlan,T.Edelstein,C.Bird,Crosby	N/A	N/A	KP171728	This paper
Boreophyllum birdiae	AMM91	Bass Harbor Lighthouse, Mt. Desert Island, Maine, USA	12th Oct. 2008 A. Mols-Mortensen, L. Hofmann, H. Day.	Mid intertidal, on rock	N/A	KP171729	This paper
Porphyra dioica	AMM06SF4159	Mølin, Froðba, Trongisvág sfjørður, Faroe Islands	18th April 2006 A. Mols-Mortensen	Mid intertidal on rock	JN703282	KP171730	Mols-Mortensen *et al.* 2012; This paper
Porphyra dioica	AMM05SF2101	Tjaldavík, Trongisvág sfjørður, Faroe Islands	1st Nov. 2005 A. Mols–Mortensen	High intertidal on rock	N/A	KP171731	This paper
Porphyra dioica	AMM81	Saksun, Faroe Islands	4th June 2008 A. Mols-Mortensen, M. Sasser	Mid intertidal on rock	N/A	KP171732	This paper
Porphyra dioica	AMM342	Bodø, Nordaland, Norway	14th April 2011 B.G. Østerkløft	High intertidal on rock	N/A	KP171733	This paper
Porphyra	AMM68	Tjaldavík,	8th Jan.	High	N/A	KP171734	This paper

linearis		Trongisvág sfjørður, Faroe Islands	2008 A. Mols–Mortensen	intertidal on rock			
Porphyra linearis	AMM71	Tjaldavík, Trongisvág sfjørður, Faroe Islands	14th Nov. 2007 A. Mols–Mortensen	Mid intertidal on rock	N/A	KP171735	This paper
Porphyra linearis	AMM72	Mølin, Froðba, Trongisvág sfjørður, Faroe Islands	25th Nov. 2007 A. Mols–Mortensen	High intertidal on rock	N/A	KP171736	This paper
Porphyra linearis	AMM73	Fámjin, Faroe Islands	25th Nov. 2007 A. Mols–Mortensen	High intertidal on rock	N/A	KP171737	This paper
Porphyra linearis	AMM83	Á Dráttinum, Tvøroyri, Faroe Islands	24th March 2008 A. Mols–Mortensen	High intertidal on concrete	N/A	KP171738	This paper
Porphyra linearis	JB622	Sidmouth, Devon, U.K.	27th Feb. 2009 J. Brodie	N/A	N/A	KP171739	This paper
Porphyra linearis	JB625	Sidmouth, Devon, U.K.	27th Feb. 2009 M. Holmes	N/A	N/A	KP171740	This paper
Porphyra linearis	JB625a	Sidmouth, Devon, U.K.	27th Feb. 2009 M. Holmes	N/A	N/A	KP171741	This paper
Porphyra linearis	JB626	Sidmouth, Devon, U.K.	27th Feb. 2009 J. Brodie	N/A	N/A	KP171742	This paper
Porphyra linearis	AMM141	Frederikshavn, Denmark	28th Nov. 2008 P.M. Pedersen	Intertidal	N/A	KP171743	This paper
Porphyra linearis	AMM142	Frederikshavn, Denmark	28th Nov. 2008 P.M. Pedersen	Intertidal	N/A	KP171744	This paper
Porphyra linearis	AMM143	Frederikshavn, Denmark	28th Nov. 2008 P.M. Pedersen	Intertidal	N/A	KP171745	This paper
Porphyra linearis	AMM144	Frederikshavn, Denmark	28th Nov. 2008 P.M. Pedersen	Intertidal	N/A	KP171746	This paper
Porphyra linearis	AMM145	Frederikshavn, Denmark	28th Nov. 2008 P.M. Pedersen	Intertidal	N/A	KP171747	This paper
Porphyra linearis	AMM450	Hirsholm, Denmark	13th Feb. 1981 R. Nielsen	Intertidal	N/A	KP171748	This paper
Porphyra linearis	AMM468	Læsø, Denmark	29th March 2005 R. Nielsen	Inertidal	N/A	KP171749	This paper
Porphyra	AMM521_2	Hirsholm,	13th Feb.	Intertidal	N/A	KP171750	This paper

linearis		Denmark	1981 R. Nielsen				
Porphyra linearis	47303a	Læsø, Denmark	29th March 2005 R. Nielsen	Inertidal	N/A	KP171751	This paper
Porphyra linearis	NRCC8461b	Lawrencetown, Halifax Co., Nova Scotia, Canada	3rd Dec. 1979 C.J. Bird, J.P. van der Meer	High intertidal, on partly sand covered rocks	N/A	KP171752	This paper
Porphyra linearis	AMM131	Fort Stark, New Hampshire, U.S.A.	5th Feb. 2009 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171753	This paper
Porphyra linearis	AMM328	Nobble Lighthouse, New Hampshire, U.S.A.	8th April 2011 A. Mols–Mortensen	Intertidal, on rock	N/A	KP171754	This paper
Porphyra linearis	AMM333	Rye Harbor, New Hampshire, U.S.A.	22nd Nov. 2009 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171755	This paper
Porphyra linearis	AMM338	Odiorne Point, New Hampshire, U.S.A.	22nd April 2010 C. Hinz, A. Piemonte	Intertidal	N/A	KP171756	This paper
Porphyra linearis	AMM339	Odiorne Point, New Hampshire, U.S.A.	22nd April 2010 C. Hinz, A. Piemonte	Intertidal	N/A	KP171757	This paper
Porphyra linearis	AMM109	Rye Harbour, New Hampshire, U.S.A.	1st April 2009 A. Mols–Mortensen, L. Hofmann	High intertidal, on rock	N/A	KP171758	This paper
Porphyra linearis	AMM129	Fort Stark, New Hampshire, U.S.A.	5th Feb. 2009 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171759	This paper
Porphyra linearis	AMM113	Rye Harbour, New Hampshire, U.S.A.	29th Feb. 2009 A. Mols–Mortensen, L. Hofmann	High intertidal, on rock	N/A	KP171760	This paper
Porphyra linearis	AMM106	Rye Harbour, New Hampshire, U.S.A.	1st April 2009 A. Mols–Mortensen, L. Hofmann	High intertidal, on rock	N/A	KP171761	This paper
Porphyra linearis	AMM107	Rye Harbour, New Hampshire, U.S.A.	1st April 2009 A. Mols–Mortensen, L. Hofmann	High intertidal, on rock	N/A	KP171762	This paper
Porphyra linearis	AMM108	Rye Harbour, New Hampshire, U.S.A.	1st April 2009 A. Mols–Mortensen, L. Hofmann	High intertidal, on rock	N/A	KP171763	This paper
Porphyra	AMM110	Rye	1st April	High	N/A	KP171764	This paper

linearis		Harbour, New Hampshire, U.S.A.	2009 A. Mols–Mortensen, L. Hofmann	intertidal, on rock			
Porphyra linearis	AMM125	Fort Stark, New Hampshire, U.S.A.	2nd April 2009 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171765	This paper
Porphyra linearis	AMM126	Fort Stark, New Hampshire, U.S.A.	2nd April 2009 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171766	This paper
Porphyra linearis	1865	Stage Fort Park, Massachusetts, U.S.A.	1st Jan. 2005 C. Neefus	High intertidal	N/A	KP171767	This paper
Porphyra linearis	AMM420	Plymouth, Massachusetts, U.S.A.	22nd April 2001 W. Schneider	High intertidal, on rock	N/A	KP171768	This paper
Porphyra purpurea	AMM05SF3009	við Hellá, Trongisvágsfjørður, Faroe Islands	31st Oct. 2005 A. Mols-Mortensen	Mid intertidal, on rock	N/A	KP171769	This paper
Porphyra purpurea	AMM06SF3129	við Hellá, Trongisvágsfjørður, Faroe Islands	20th July 2006 A. Mols-Mortensen	Mid intertidal, on muscle	N/A	KP171770	This paper
Porphyra purpurea	AMM483 (7294)	Sulugssugut, Greenland 64º25N 50º30W	1st July 1957 T. Christensen	Mid intertidal	N/A	KP171771	Mols-Mortensen *et al.*, 2014; This paper
Porphyra purpurea	AMM196	Kangilleq, Eqalugaasuit, Qaqortoq, Greenland 60º47N 46º80W	11th June 2010 A. Mols-Mortensen	Mid intertidal on rock	KF478754	KF478688	Mols-Mortensen *et al.*, 2014
Porphyra purpurea	AMM485	Eqalugialik, Greenland 64º21N 50º25W	16th July 1957 T. Christensen	Not attached	N/A	KP171772	Mols-Mortensen *et al.*, 2014; This paper
Porphyra purpurea	JB494	Kálfatjarnarkirkja, Iceland	17th July 2005 R. Nielsen	Intertidal	N/A	KP171773	This paper
Porphyra purpurea	AMM509 (LM79001221)	Århus Bay, Denmark	11th June 1979 L. Mathiesen	Intertidal	N/A	KP171774	This paper
Porphyra purpurea	NRCC4745	St. Peters Bay, Richmond Co., Nova Scotia, Canada	11th Aug. 1970 J. McLachlan, T. Edelstein, J. Bailey	N/A	N/A	KP171775	This paper
Porphyra purpurea	AMM123	Dover Point, New	3rd Feb. 2009	Intertidal on wooden	N/A	KP171776	This paper

		Hampshire, USA	A. Mols-Mortensen, A. C. Mathieson	piling			
Porphyra purpurea	AMM372	Nobska Pt. Woods Hole, Massachusetts, USA	13th Aug. 1928 W.R. Taylor	NA	N/A	KP171777	This paper
Porphyra purpurea	AMM446	Thimble Island, Connecticut, USA	12th June 2012 A. Mols-Mortensen, C. Neefus, C. Yarish	High intertidal on rock	N/A	KP171778	This paper
Porphyra umbilicalis	AMM534	Nuuk, Greenland 64°10N 51°45W	19th June 2010 A. Mols-Mortensen	Mid intertidal on rock	N/A	KP171779	This paper
Porphyra umbilicalis	09 10947 1	Flekkuvík, Reykjanes, Iceland	30th April 2009 S. Egilsdóttir	Intertidal	N/A	KP171780	This paper
Porphyra umbilicalis	AMM343	Bodø, Nordaland, Norway	14th April 2011 B.G. Østerkløft	High intertidal on rock	N/A	KP171781	This paper
Porphyra umbilicalis	SL3600101 4	Korsør harbour, Denmark 55°20'N 11°08'E	5th May 1936 S. Lund	Intertidal	N/A	KP171782	This paper
Porphyra umbilicalis	BM000769632 (JB178) Neotype	Easdale, Scotland	23rd July 1998 J. Brodie, P.K. Hayes	Intertidal	KF478756	KF478700	Mols-Mortensen *et al.*, 2014
Porphyra umbilicalis	AMM263	Ribadeo, Spain	Oct. 1895 M.C. Sauvageau	N/A	N/A	KP171783	This paper
Porphyra umbilicalis	AMM112	Rye Harbor, New Hampshire, USA	29th Feb. 2009 A. Mols-Mortensen, L.C. Hofmann	High intertidal on rock	N/A	KP171784	This paper
Porphyra umbilicalis	AMM127	Fort Stark, New Hampshire, U.S.A.	2nd April 2009 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171785	This paper
Porphyra umbilicalis	NRCC8461a	Lawrencetown, Halifax Co., Nova Scotia, Canada	3rd Dec. 1979 C.J. Bird, J.P. van der Meer	High intertidal, on partly sand covered rocks	N/A	KP171786	This paper
Porphyra umbilicalis	AMM534	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171787	This paper
Porphyra umbilicalis	AMM179	Sisimiut, Greenland	2nd June 2010 A. Mols–Mortensen	High intertidal, on barnacle	N/A	KP171788	This paper

Porphyra umbilicalis	AMM181	Sisimiut, Greenland	2nd June 2010 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171789	This paper
Porphyra umbilicalis	AMM184	Sisimiut, Greenland	2nd June 2010 A. Mols–Mortensen	Mid intertidal, on barnacle	N/A	KP171790	This paper
Porphyra umbilicalis	AMM200	Nuuk, Greenland	20th June 2010 A. Mols–Mortensen	Hig intertidal, on rock	N/A	KP171791	This paper
Porphyra umbilicalis	AMM208	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171792	This paper
Porphyra umbilicalis	AMM212	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	High intertidal, on barnacle	N/A	KP171793	This paper
Porphyra umbilicalis	AMM344	Nuuk, Greenland	26th March 2011 S. Wegeberg	High intertial	N/A	KP171794	This paper
Porphyra umbilicalis	7955	Skagen, Denmark	12th April 1906 K. Rosenvinge	N/A	N/A	KP171795	This paper
Porphyra umbilicalis	AMM06SF3035	við Hellá, Trongisvág sfjørður, Faroe Islands	19th April 2006 A. Mols–Mortensen	Mid intertidal, on Mytilus edulis	N/A	KP171796	This paper
Porphyra umbilicalis	AMM06SF1338	Tjaldavík, Trongisvág sfjørður, Faroe Islands	2nd July 2006 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171797	This paper
Porphyra umbilicalis	AMM99	Mølin, Froðba, Trongisvág sfjørður, Faroe Islands	16th Nov. 2008 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171798	This paper
Porphyra umbilicalis	AMM06SF1340	Tjaldavík, Trongisvág sfjørður, Faroe Islands	2nd July 2006 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171799	This paper
Porphyra umbilicalis	AMM05SF2109	Tjaldavík, Trongisvág sfjørður, Faroe Islands	2nd Nov. 2005 A. Mols–Mortensen	Mid intertidal	N/A	KP171800	This paper
Porphyra umbilicalis	AMM05SF2123	Tjaldavík, Trongisvág sfjørður, Faroe Islands	2nd Nov. 2005 A. Mols–Mortensen	Mid intertidal	N/A	KP171801	This paper
Porphyra umbilicalis	AMM06SF2134	Tjaldavík, Trongisvág sfjørður, Faroe	3rd Jan. 2006 A. Mols-Mortensen	Mid intertidal	N/A	KP171802	This paper

		Islands					
Porphyra umbilicalis	AMM06SF4246	Mølin, Froðba, Trongisvág sfjørður, Faroe Islands	8th July 2006 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171803	This paper
Porphyra umbilicalis	AMM70	Tjaldavík, Trongisvág sfjørður, Faroe Islands	8th Jan. 2008 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171804	This paper
Porphyra umbilicalis	AMM95	Svínáir, Faroe Islands	2nd July 2008 A. Mols–Mortensen, Ø. Patursson	On aquaculture net	N/A	KP171805	This paper
Porphyra umbilicalis	AMM0400F409	Hvannhagi, Mølin, Faroe Islands	4th July 2004 A Mols–Mortensen, N. Mols–Mortensen, P. Mortensen	Intertidal	N/A	KP171806	This paper
Porphyra umbilicalis	AMM05SF4086	Mølin, Froðba, Trongisvág sfjørður, Faroe Islands	4th Nov. 2005 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171807	This paper
Porphyra umbilicalis	SL3600101_4	Korsør, Denmark	5th May 1936 S. Lund	Intertidal	N/A	KP171808	This paper
Porphyra umbilicalis	SL3700201	Svendborg, Denmark	18th Sep. 1937 S. Lund	Intertidal	N/A	KP171809	This paper
Porphyra umbilicalis	AK5801504	Tuborg Havn, Copenhagen, Denmark	29th Oct. 1958 Aa. Kristiansen	Intertidal	N/A	KP171810	This paper
Porphyra umbilicalis	AMM457_2 (7943)	Thyborøn, Denmark	21st March 1906 L.K. Rosenvinge	N/A	N/A	KP171811	This paper
Porphyra umbilicalis	AMM516 (RN0040 04)	Frederikshavn, Denmark	17th June 2000 R. Nielsen	Intertidal	N/A	KP171812	This paper
Porphyra umbilicalis	LM89024_2	Ebeltoft, Vig, Denmark	12th April 1989 L. Mathiesen	Intertidal	N/A	KP171813	This paper
Porphyra umbilicalis	LM6400102	Frederikshavn, Denmark	9th July 1964 L. Mathiesen	Intertidal	N/A	KP171814	This paper
Porphyra umbilicalis	LM6903101	Hirsholmene, Denmark	28th June 1969 L. Mathiesen	Intertidal	N/A	KP171815	This paper
Porphyra umbilicalis	LM7500157	Århus, Denmark	12th June 1975 L. Mathiesen	Intertidal	N/A	KP171816	This paper
Porphyra umbilicalis	LM9300105	Kalø Vig, Egå Marina,	1st Feb. 1993 L.	Intertidal	N/A	KP171817	This paper

		Denmark	Mathiesen				
Porphyra umbilicalis	SL3600101_5	Korsør, Denmark	5th May 1936 S. Lund	Intertidal	N/A	KP171818	This paper
Porphyra umbilicalis	SL4800201	Skovshoved, Denmark	26th August 1948 S. Lund	Intertidal	N/A	KP171819	This paper
Porphyra umbilicalis	07 8306 1c	Dalatangi, Iceland	30th Aug. 2007 S. Egilsdóttir, K. Gunnarsson	Intertidal	N/A	KP171820	This paper
Porphyra umbilicalis	AMM326	Fort Stark, New Hampshire, U.S.A.	29th Nov. 2009 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171821	This paper
Porphyra umbilicalis	AMM130	Fort Stark, New Hampshire, U.S.A.	5th Feb. 2009 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171822	This paper
Porphyra umbilicalis	AMM132	Fort Stark, New Hampshire, USA	5th March 2009 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171823	This paper
Porphyra umbilicalis	AMM263	Ribadeo, Spain	17th Oct. 1881 M.C. Sauvageau	N/A	N/A	KP171824	This paper
Porphyra sp.	AMM05SF2102	Tjaldavík, Trongisvág sfjørður, Faroe Islands	1st Nov. 2005 A. Mols–Mortensen	Low intertidal, on rock	JN787112	KP171825	Mols-Mortensen *et al.*, 2012; This paper
Pyropia elongata	AMM395	Pivers Island, Beaufort, NC, U.S.A	8th-9th Dec. 1981 C.W. Schneider	Low intertidal and upper subtidal, on oyster	N/A	KP171826	This paper
Pyropia elongata	NHA76229	Masonboro, NC, U.S.A.	8th Feb. 2002 D.W. Freshwater, R.S. Melton	N/A	AY486349	AY486349	GenBank
Pyropia elongata	Lectotype	Koster, Bohuslän, Sweden	21st July 1905 Kylin	N/A	FJ817088	FJ817088	Neefus & Brodie, 2009
Pyropia njordii	AMM154	Hunde Ejlande, Aasiaat, Greenland	6th Sep. 2009 P.M. Pedersen	Low intertidal	JN847258	KP171827	Mols-Mortensen *et al.*, 2012; This paper
Pyropia njordii	AMM155	Hunde Ejlande, Aasiaat, Greenland	6th Sep. 2009 P.M. Pedersen	Low intertidal	N/A	KP171828	This paper
Pyropia njordii	AMM165	Sisimiut, Greenland	3rd June 2010 A. Mols–Mortensen	On barnacle	N/A	KP171829	This paper
Pyropia njordii	AMM166	Sisimiut, Greenland	3rd June 2010 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171830	This paper

Pyropia njordii	AMM168	Sisimiut, Greenland	3rd June 2010 A. Mols–Mortensen	High mid intertidal, on rock	N/A	KP171831	This paper
Pyropia njordii	AMM182	Sisimiut, Greenland	2nd June 2010 A. Mols–Mortensen	Low mid intertidal, on rock	N/A	KP171832	This paper
Pyropia njordii	AMM187	Sisimiut, Greenland	2nd June 2010 A. Mols–Mortensen	Mid intertidal, on barnacle	N/A	KP171833	This paper
Pyropia njordii	AMM189	Maniitsoq harbour, Greenland	7th June 2010 A. Mols–Mortensen	Mid intertidal, on barnacle	N/A	KP171834	This paper
Pyropia njordii	AMM190	Maniitsoq harbour, Greenland	7th June 2010 A. Mols–Mortensen	Mid intertidal, on barnacle	N/A	KP171835	This paper
Pyropia njordii	AMM194	Akia, Qaqortoq, Greenland	12th June 2010 A. Mols–Mortensen	Low mid intertidal, on barnacle	N/A	KP171836	This paper
Pyropia njordii	AMM197	Qaqortoq, Greenland	14th June 2010 A. Mols–Mortensen	Mid intertidal, on barnacle	N/A	KP171837	This paper
Pyropia njordii	AMM201	Nuuk, Greenland	20th June 2010 A. Mols–Mortensen	Low intertidal, on rock	N/A	KP171838	This paper
Pyropia njordii	AMM202	Nuuk. Old shipyard, Greenland	20th June 2010 A. Mols–Mortensen	Low mid intertidal, on rock	N/A	KP171839	This paper
Pyropia njordii	AMM203	Nuuk, Greenland	20th June 2010 A. Mols–Mortensen	High mid intertidal, on barnacle	N/A	KP171840	This paper
Pyropia njordii	AMM205	Nuuk, Greenland	20th June 2010 A. Mols–Mortensen	Mid intertidal,on rock	N/A	KP171841	This paper
Pyropia njordii	AMM206	Nuuk, Greenland	20th June 2010 A. Mols–Mortensen	Mid intertidal, on barnacle	N/A	KP171842	This paper
Pyropia njordii	AMM209	Nuuk, Greenland	20th June 2010 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171843	This paper
Pyropia njordii	AMM210	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	Low intertidal, on rock	N/A	KP171844	This paper
Pyropia njordii	AMM211	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	Intertidal, on rock	N/A	KP171845	This paper
Pyropia njordii	AMM215	Nuuk, Greenland	19th June 2010 A. Mols–	Mid intertidal, on rock	N/A	KP171846	This paper

			Mortensen				
Pyropia njordii	AMM217	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	Mid intertidal, on barnacle	N/A	KP171847	This paper
Pyropia njordii	AMM218	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171848	This paper
Pyropia njordii	AMM219	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	Mid intertidal, on barnacle	N/A	KP171849	This paper
Pyropia njordii	AMM220	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	High intertidal rock pool, on rock	N/A	KP171850	This paper
Pyropia njordii	AMM221	Nuuk, Greenland	20th June 2010 A. Mols–Mortensen	Mid intertidal, on rock and on juvenile Fucus sp.	N/A	KP171851	This paper
Pyropia njordii	AMM222	Nuuk, Greenland	20th June 2010 A. Mols–Mortensen	High intertidal, on rock	N/A	KP171852	This paper
Pyropia njordii	AMM223	Nanortalik, Greenland	9th Oct. 2007 S. Wegeberg	Mid intertidal	N/A	KP171853	This paper
Pyropia njordii	AMM224	Nanortalik, Greenland	9th Oct. 2007 S. Wegeberg	Mid intertidal	N/A	KP171854	This paper
Pyropia njordii	AMM225	Nanortalik, Greenland	9th Oct. 2007 S. Wegeberg	Mid intertidal	N/A	KP171855	This paper
Pyropia njordii	AMM226	Nanortalik, Greenland	9th Oct. 2007 S. Wegeberg	Mid intertidal	N/A	KP171856	This paper
Pyropia njordii	AMM404	Arsuk, Greenland	29th June 1888 L.K. Rosenvinge	N/A	N/A	KP171857	This paper
Pyropia njordii	AMM475	Anordliuitsoq, north of Qaqortoq, Greenland	7th Aug. 1970 P.M. Pedersen	Subtidal, 1 m depth	N/A	KP171858	This paper
Pyropia njordii	AMM488	Agsangiut, Greenland	8th July 1888 L.K. Rosenvinge	N/A	N/A	KP171859	This paper
Pyropia njordii	AMM489	Ilulissat, Greenland	7th Aug. 1888 L.K. Rosenvinge	Intertidal	N/A	KP171860	This paper
Pyropia njordii	07 8306 1a	Dalatangi, Iceland	30th Aug. 2007 S.	Intertidal	N/A	KP171861	This paper

			Egilsdóttir, K. Gunnarsson				
Pyropia njordii	07 10914 1	Melrakkanes, Iceland	13th June 2007 J. Brodie, I. Tittley, S. Egilsdóttir	Intertidal	N/A	KP171862	This paper
Pyropia njordii	JB417	Hvítserkur, Iceland	7th June 2006 R. Nielsen, S. Egilsdóttir	Intertidal	N/A	KP171863	This paper
Pyropia njordii	AMM06SF1324	Tjaldavík, Trongisvágsfjørður, Faroe Islands	15th May 2006 A. Mols–Mortensen	High intertidal	N/A	KP171864	This paper
Pyropia njordii	AMM06SF4161	Á Møl, Froðba, Trongisvágsfjørður, Faroe Islands	18th April 2006 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171865	This paper
Pyropia njordii	AMM257_1	Northern Norway	1886 M. Foslie	N/A	N/A	KP171866	This paper
Pyropia njordii	AMM466	Gilleleje, Denmark	24th Feb. 1993 H. Götzsche, R. Nielsen	Intertidal, on harbour jetty	N/A	KP171867	This paper
Pyropia njordii	AMM514	Hirsholm, Denmark	25th June 1985 R. Nielsen	Intertidal, on harbour jetty	N/A	KP171868	This paper
Pyropia njordii	NRCC8195	Dinner Head, Campobello Island, Charlotte Co., NB, Canada	21st June 1978 C. Bird, S. Wilson, E. Fraser	N/A	N/A	KP171869	This paper
Pyropia njordii	NRCC4043	Fink Cove, Halifax Co., Nova Scotia, Canada	25th Feb.1970 C. Bird, M. Greenwell	N/A	N/A	KP171870	This paper
Pyropia njordii	NRCC6377a	Fink Cove, Halifax Co., Nova Scotia, Canada	18th Dec. 1969 C. Bird, M. Greenwell	Low intertidal, on rock	N/A	KP171871	This paper
Pyropia peggicovensis	AMM482 (LM780041)	Bohus Län, Mörholmen, Sweden	1st July 1978 M. Værn	Intertidal	N/A	KP171872	This paper
Pyropia peggicovensis	AMM452_2 (LM8904802)	Ebeltoft vig, Denmark	22nd Feb. 1989 L. Mathiesen	High intertidal	N/A	KP171873	This paper
Pyropia peggicovensis	AMM453_1 (LM8905501)	Aarhus bay, Demnark	11th Feb. 1989 B. Olesen	N/A	N/A	KP171874	This paper
Pyropia	AMM453_2	Aarhus bay,	11th Feb.	N/A	N/A	KP171875	This paper

peggicovensis	(LM8905501)	Demnark	1989 B. Olesen				
Pyropia peggicovensis	AMM458 040	Læsø, Kattegat, Denmark	1st April 1988 R. Nielsen	High intertidal	N/A	KP171876	This paper
Pyropia peggicovensis	AMM459 LM8700100	Grenen, Skagen, Denmark	8th May 1987 L. Mathiesen	N/A	N/A	KP171877	This paper
Pyropia peggicovensis	AMM462 48360	Ebeltoft vig, Denmark	22nd Feb. 1989 L. Mathiesen	N/A	N/A	KP171878	This paper
Pyropia peggicovensis	AMM470 LM9200127	Aarhus bay, Demnark	8th April 1992 E. Soekendarsi	N/A	N/A	KP171879	This paper
Pyropia peggicovensis	AMM491 10791 & 8564	Frederikshavn, Denmark	13th July 1928 L.K. Rosenvinge	N/A	N/A	KP171880	This paper
Pyropia peggicovensis	AMM515 RN78027 01	Hirsholm, Denmark	21st July 1978 R. Nielsen	On harbour jetty	N/A	KP171881	This paper
Pyropia peggicovensis	NRCC8714	Fairfield, Kings Co., Prince Edward Island, Canada	11th Dec. 1981 M. Greenwell	High intertidal	N/A	KP171882	This paper
Pyropia peggicovensis	NRCC4021	Herring Cove, Nova Scotia, Canada	2nd May 1970 C. Bird, T.E. Edelstein, M. Greenwell	High intertidal	N/A	KP171883	This paper
Pyropia peggicovensis	NRCC4133	Fink Cove, Halifax Co., Nova Scotia, Canada	28th May 1970 J. McLachlan, C. Bird	Intertidal	N/A	KP171884	This paper
Pyropia suborbiculata	AMM304	Belmar Jetty, NJ, U.S.A.	24th May 2011 A. Mols–Mortensen, S. Solmunde	High mid intertidal, on rock	N/A	KP171885	This paper
Pyropia suborbiculata	AMM306	Rehoboth Bay, Delaware, U.S.A.	27th May 2011 A. Mols–Mortensen, S. Solmunde	Intertidal, on rock	N/A	KP171886	This paper
Pyropia suborbiculata	AMM315	Surf City, NJ, U.S.A.	31st May 2011 A. Mols–Mortensen, S. Solmunde	On barnacle sitting on piling	N/A	KP171887	This paper

Pyropia suborbiculata	AMM316	Surf City, NJ, U.S.A.	31st May 2011 A. Mols–Mortensen, S. Solmunde	On barnacle sitting on piling	N/A	KP171888	This paper
Pyropia suborbiculata	AMM317	Wrightsville Beach, Wilmington, NC, U.S.A.	1st June 2011 A. Mols–Mortensen, S. Solmunde	On barnacle sitting on piling	N/A	KP171889	This paper
Pyropia suborbiculata	AMM318	Wrightsville Beach, Wilmington, NC, U.S.A.	1st June 2011 A. Mols–Mortensen, S. Solmunde	On concrete piling	N/A	KP171890	This paper
Pyropia suborbiculata	AMM319	Myrtle Beach, SC, U.S.A.	1st June 2011 A. Mols–Mortensen, S. Solmunde	On wooden piling	N/A	KP171891	This paper
Pyropia suborbiculata	AMM320	Myrtle Beach, SC, U.S.A.	1st June 2011 A. Mols–Mortensen, S. Solmunde	On barnacle sitting on wooden piling	N/A	KP171892	This paper
Pyropia thulaea	AMM156	Kumikume, Greenland	8th Sep. 2009 P.M. Pedersen	Intertidal	KF496927	KP171893	Mols–Mortensen *et al.*, 2014; This paper
Pyropia thulaea	AMM157	Kumikume, Greenland	8th Sep. 2009 P.M. Pedersen	Intertidal	KF496928	KP171894	Mols–Mortensen *et al.*, 2014; This paper
Pyropia thulaea	AMM171	Ilulissat, Greenland	2nd Aug. 2010 P.M. Pedersen	Low intertidal, on rock	N/A	KP171895	This paper
Pyropia thulaea	AMM172	Ilulissat, Greenland	2nd Aug. 2010 P.M. Pedersen	Low intertidal, on rock	N/A	KP171896	This paper
Pyropia thulaea	AMM173	Ilulissat, Greenland	2nd Aug. 2010 P.M. Pedersen	Low intertidal, on rock	N/A	KP171897	This paper
Pyropia thulaea	AMM207	Nuuk, Greenland	19th June 2010 A. Mols–Mortensen	Low intertidal, on rock	N/A	KP171898	This paper
Pyropia thulaea	AMM213	Old shipyard, Nuuk, Greenland (Py. thulaea type location)	20th June 2010 A. Mols–Mortensen	Low mid intertidal, on rock	N/A	KP171899	This paper
Pyropia thulaea	AMM536	Qaqortoq, Greenland	21st July 2005	Intertidal	N/A	KP171900	This paper

			A. Mols–Mortensen				
Pyropia thulaea	AMM394	Near Torbay, Newfoundland, Canada	21st-26st Aug. 1901 M.A. Howe	Intertidal, on stones	N/A	KP171901	This paper
Pyropia thulaea	NRCC8118	South Head, Grand Manan Is., Charlotte Co., New Brunswick, Canada	21st June 1978 D. Smith, E. Fraser	Subtidal	N/A	KP171902	This paper
Pyropia yezoensis f. *yezoensis*	AMM115	Dover Point, NH, U.S.A.	1st April 2009 A.C. Mathieson	Intertidal, under the bridge	N/A	KP171903	This paper
Pyropia yezoensis f. *yezoensis*	AMM119	Dover Point, NH, U.S.A.	3rd Feb. 2009 A. Mols–Mortensen, A.C. Mathieson	High mid intertidal, on Fucus vesiculosus	N/A	KP171904	This paper
Pyropia yezoensis f. *yezoensis*	AMM121	Dover Point, NH, U.S.A.	3rd Feb. 2009 A. Mols–Mortensen, A.C. Mathieson	Mid intertidal, on rock	N/A	KP171905	This paper
Pyropia yezoensis f. *yezoensis*	AMM290	Light-house Point, New Haven, CT, U.S.A.	21st May 2011 A. Mols–Mortensen, S. Solmunde	High intertidal, on barnacle	N/A	KP171906	This paper
Pyropia yezoensis f. *narawensis*	AMM295	Avery Point, UCONN, CT, U.S.A.	21st May 2011 A. Mols–Mortensen, S. Solmunde	High intertidal, on Fucus sp.	N/A	KP171907	This paper
Pyropia yezoensis f. *narawensis*	AMM297	Lavallette Jetty, NJ, U.S.A.	24th May 2011 A. Mols–Mortensen, S. Solmunde	Mid intertidal, on rock	N/A	KP171908	This paper
Pyropia yezoensis f. *narawensis*	AMM299	Belmar Jetty, NJ, U.S.A.	24th May 2011 A. Mols–Mortensen, S. Solmunde	Mid intertidal, on rock	N/A	KP171909	This paper
Pyropia yezoensis f. *narawensis*	AMM300	Barneget Lighthouse, NJ, U.S.A.	24th May 2011 A. Mols–Mortensen, S. Solmunde	High intertidal, on rock	N/A	KP171910	This paper
Pyropia yezoensis f. *narawensis*	AMM301	Barneget Lighthouse, NJ, U.S.A.	24th May 2011 A. Mols–	Mid intertidal, on rock and barnacle	N/A	KP171911	This paper

			Mortensen, S. Solmunde				
Pyropia yezoensis f. *narawensis*	AMM302	Belmar Jetty, NJ, U.S.A.	24th May 2011 A. Mols–Mortensen, S. Solmunde	High mid intertidal, on rock	N/A	KP171912	This paper
Pyropia yezoensis f. *narawensis*	AMM305	Surf City, NJ, U.S.A.	25th May 2011 A. Mols–Mortensen, S. Solmunde	High mid intertidal, on rock	N/A	KP171913	This paper
Pyropia yezoensis f. *yezoensis*	AMM308	Cape May Lighthouse, NJ, U.S.A.	27th May 2011 A. Mols–Mortensen, S. Solmunde	Intertidal, on barnacle sitting on jetty	N/A	KP171914	This paper
Pyropia yezoensi f. *yezoensis*	AMM309	Cape May Lighthouse, NJ, U.S.A.	27th May 2011 A. Mols–Mortensen, S. Solmunde	On muscle sitting on jetty	N/A	KP171915	This paper
Pyropia yezoensis f. *yezoensis*	AMM312	Atlantic City, NJ, U.S.A.	26th May 2011 A. Mols–Mortensen, S. Solmunde	Mid intertidal, on rock	N/A	KP171916	This paper
Pyropia yezoensis f. *yezoensis*	AMM313	Longport, NJ, U.S.A.	26th May 2011 A. Mols–Mortensen, S. Solmunde	On barnacles and muscles sitting on wood and iron construction	N/A	KP171917	This paper
Pyropia yezoensis f. *yezoensis*	AMM314	Longport, NJ, U.S.A.	26th May 2011 A. Mols–Mortensen, S. Solmunde	On barnacles and muscles sitting on wood and iron construction	N/A	KP171918	This paper
"*Pyropia collinsii*"	AMM527_2 RN08008 04	Gilleleje harbour, Denmark	3rd May 2008 R. Nielsen	1 m depth	N/A	KP171919	This paper
"*Pyropia collinsii*"	AMM527_5 RN08008 04	Gilleleje harbour, Denmark	3rd May 2008 R. Nielsen	1 m depth	N/A	KP171920	This paper
"*Pyropia collinsii*"	RN9300106	Lynæs, Denmark	15th Feb. 1993 H. Götzsche, P. Corfixen, R. Nielsen	Intertidal	N/A	KP171921	This paper
"*Pyropia collinsii*"	AMM114	Dover Point, NH, U.S.A.	22nd March 2009 A.C. Mathieson	Intertidal, on Gracilaria tikvahiae	N/A	KP171922	This paper
"*Pyropia*	AMM124	Dover	22nd March	Intertidal, on	N/A	KP171923	This paper

collinsii”		Point, NH, U.S.A.	2009 A.C. Mathieson	Gracilaria tikvahiae			
“*Pyropia collinsii*”	AMM293	Avery Point, UCONN, CT, U.S.A.	21st May 2011 A. Mols–Mortensen, S. Solmunde	Low mid intertidal, on other algae	N/A	KP171924	This paper
“*Pyropia collinsii*”	AMM294	Avery Point, UCONN, CT, U.S.A.	21st May 2011 A. Mols–Mortensen, S. Solmunde	Low mid intertidal, on other algae	N/A	KP171925	This paper
“*Pyropia collinsii*”	AMM296	Avery Point, UCONN, CT, U.S.A.	21st May 2011 A. Mols–Mortensen, S. Solmunde	High intertidal	N/A	KP171926	This paper
“*Pyropia collinsii*”	AMM425 (787)	Bridgeport, CT, U.S.A.	18th April 1887 J. Holden	N/A	N/A	KP171927	This paper
“*Pyropia collinsii*”	AMM403 (10140)	Point Conaskonck, Raritan Bay, Union Beach, NJ, U.S.A.	7th March 1958 E.T. Moul	N/A	N/A	KP171928	This paper
“*Pyropia collinsii*”	AMM409 (7326)	Keanburg, Monmouth Co., NJ, U.S.A.	14th April 1951 E.T. Moul, W. Crotty	N/A	N/A	KP171929	This paper
“*Pyropia collinsii*”	AMM310	Ocean City, NJ, U.S.A.	26th May 2011 A. Mols–Mortensen, S. Solmunde	On concrete floating dock	N/A	KP171930	This paper
“*Pyropia leucosticta*”	JB385	Hellnar, Iceland	10th July 2005	Intertidal	N/A	KP171931	This paper
“*Pyropia leucosticta*”	JB389	Hellnar, Iceland	10th July 2005	Intertidal	N/A	KP171932	This paper
“*Pyropia leucosticta*”	JB474	Selvogul, Gullbringu, Iceland	10th Aug. 1999	Intertidal	N/A	KP171933	This paper
“*Pyropia leucosticta*”	AMM84	Tjaldavík, Trongisvágsfjørður, Faroe Islands	5th July 2008 A. Mols–Mortensen	Mid intertidal, on Corallina officinalis	N/A	KP171934	This paper
“*Pyropia leucosticta*”	AMM85	Tjaldavík, Trongisvágsfjørður, Faroe Islands	15th June 2008 A. Mols–Mortensen	Low mid intertidal, on limpet	N/A	KP171935	This paper
“*Pyropia leucosticta*”	AMM86	Tjaldavík, Trongisvágsfjørður, Faroe	15th June 2008 A. Mols–Mortensen	Low intertidal, on Mastocarpus stellatus	N/A	KP171936	This paper

		Islands					
“*Pyropia leucosticta*”	AMM540	Hoyvík, Tórshavn, Faroe Islands	13th July 2012 A. Mols–Mortensen, M. Mols–Mortensen	Subtidal, 2 m depth	N/A	KP171937	This paper
“*Pyropia leucosticta*”	AMM06SF4299	Á Møl, Froðba, Trongisvág sfjørður, Faroe Islands	18th July 2006 A. Mols–Mortensen	Low intertidal, on limpet	N/A	KP171938	This paper
“*Pyropia leucosticta*”	RN8100804	Skiveren, Denmark	14th June 1981 R. Nielsen	Drift	N/A	KP171939	This paper
“*Pyropia leucosticta*”	NRCC10787	Gulliver Cove, Digby Co., Nova Scotia, Canada	4th June 1989 J. McLachlan	Low intertidal, on rocks and coarse low intertidal algae	N/A	KP171940	This paper
“*Pyropia leucosticta*”	AMM87	Odiorne Point, Portsmouth, NH. U.S.A.	21st Sep. 2008 A. Mols–Mortensen	Low mid intertidal, on Fucus vesiculosus	N/A	KP171941	This paper
“*Pyropia leucosticta*”	AMM88	Odiorne Point, Portsmouth, NH. U.S.A.	21st Sep. 2008 A. Mols–Mortensen	Low mid intertidal, on Fucus vesiculosus	N/A	KP171942	This paper
“*Pyropia leucosticta*”	AMM93	Mt. Desert Island, maine, U.S.A.	12th Oct. 2008 A. Mols–Mortensen, L. Hofmann, H. Day	Mid intertidal, on Fucus vesiculosus	N/A	KP171943	This paper
“*Pyropia leucosticta*”	AMM111	Fort Stark, NH, U.S.A.	2nd April 2009 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171944	This paper
“*Pyropia leucosticta*”	AMM128	Fort Stark, NH, U.S.A.	2nd April 2009 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171945	This paper
“*Pyropia leucosticta*”	AMM133	Fort Stark, NH, U.S.A.	5th March 2009 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KP171946	This paper
“*Pyropia leucosticta*”	AMM329	Fort Stark, NH, U.S.A.	17th May 2010 A. Mols–Mortensen, R. Eriksen	Low mid intertidal, on Fucus sp.	N/A	KP171947	This paper
“*Pyropia leucosticta*”	AMM330	Fort Stark, NH, U.S.A.	17th May 2010 A. Mols–Mortensen, R. Eriksen	Mid intertidal, on Polysiphonia lanosa (on Ascophyllum nodosum)	N/A	KP171948	This paper
“*Pyropia novae–angliae*”	AK5700201	Tuborg Havn, Copenhage	7th Oct. 1957 Aa.	Intertidal, on jetty	N/A	KP171949	This paper

		n, Denmark	Kristiansen				
“*Pyropia novae–angliae*”	LM89024_1	Ebeltoft Vig, Natohavn, Denmark	12th April 1989 L. Mathiesen	Intertidal	N/A	KP171950	This paper
“*Pyropia novae–angliae*”	LM89041b56	Lillebælt, Årøsund, Denmark	20th May 1989 L. Mathiesen	Intertidal, on Fucus serratus	N/A	KP171951	This paper
“*Pyropia novae–angliae*”	LM89050205	Strib lystbådehavn, Denmark	26th April 1989 L. Mathiesen	Intertidal	N/A	KP171952	This paper
“*Pyropia novae–angliae*”	SL3600101_1	Korsør Harbour, Denmark	5th May1936 S. Lund	Intertidal	N/A	KP171953	This paper
“*Pyropia novae–angliae*”	SL3600101_3	Korsør Harbour, Denmark	5th may 1936 S. Lund	Intertidal	N/A	KP171954	This paper
“*Pyropia novae–angliae*”	SL4800102	Helsingør, Nordhavn, Demnark	2nd June 1948 S. Lund	Intertidal	N/A	KP171955	This paper
“*Pyropia novae–angliae*”	AMM506 (042)	Læsø, Kattegat, Denmark	1st April 1988 R. Nielsen	High intertidal	N/A	KP171956	This paper
“*Pyropia novae–angliae*”	AMM117	Dover Point, NH, U.S.A.	1st April 2009 A.C. Mathieson	Intertidal	N/A	KP171957	This paper
Pyropia sp.	AMM324_1	Hoyvík, Tórshavn, Faroe Islands	12th Sep. 2011 A. Mols–Mortensen, M. Mols–Mortensen	Subtidal, 2 m depth	N/A	KP171958	This paper
Wildemania abyssicola	JB486	Mariuhorn, Iceland	2nd July 2005 K. Gunnarsson, G. Bruntse	Subtidal, 17 m depth	N/A	KP171959	This paper
Wildemania abyssicola	JB487	Selavogur, Iceland	15th June 2007	Subtidal, 29 m depth	N/A	KP171960	This paper
Wildemania abyssicola	JB491	Suður-bar, Iceland	7th July 2005 K. Gunnarsson, G. Bruntse	Subtidal, 14 m depth	N/A	KP171961	This paper
Wildemania abyssicola	AMM247_2	Northern Norway	21st June 1887	N/A	N/A	KP171962	This paper
Wildemania abyssicola	AMM283_2	Kjøllefjord, Norway	1887 M. Foslie	N/A	N/A	KP171963	This paper
Wildemania amplissima	AMM535	Uppernaviarsuk, Qaqortoq area, Greenland	19th July 2005 A. Mols–Mortensen	On wooden construction just below low water level	N/A	KF478745	Mols-Mortensen *et al.*, 2014
Wildemania amplissima	JB488	Sudur-Bar, Iceland	7th June 2005 K.	Subtidal, 14 m depth	N/A	KP171964	This paper

			Gunnarsson, G. Bruntse				
Wildemania amplissima	AMM77	Kvívík, Faroe Islands	17th June2008 A. Mols–Mortensen, Ø. Patursson	Subtidal, 4 m depth	N/A	KP171965	This paper
Wildemania amplissima	AMM158	Kollafjørður, Faroe Islands	23rd June 2008 A. Mols–Mortensen, Ø. Patursson	Subtidal, from aquaculture net	N/A	KP171966	This paper
Wildemania amplissima	AMM159	Gøtuvík, Faroe Islands	30th June 2008 A. Mols–Mortensen, Ø. Patursson	Subtidal, from aquaculture net	N/A	KP171967	This paper
Wildemania amplissima	AMM539_1	Kvívík, Faroe Islands	18th July 2012 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A	KP171968	This paper
Wildemania amplissima	AMM247_1	Northern Norway	21st June 1887 (from Foslies Herbarium)	N/A	N/A	KP171969	This paper
Wildemania amplissima	AMM248	Northern Norway	N/A (from Foslies Herbarium)	N/A	N/A	KP171970	This paper
Wildemania amplissima	AMM258_1	Tromsø, Norway	3rd Aug. 1886 M. Foslie	N/A	N/A	KP171971	This paper
Wildemania amplissima	AMM258_2	Tromsø, Norway	3rd Aug. 1886 M. Foslie	N/A	N/A	KP171972	This paper
Wildemania amplissima	AMM278_1	Northern Norway	16th July1887 M. Foslie	N/A	N/A	KP171973	This paper
Wildemania amplissima	AMM278_2	Northern Norway	16th July 1887 M. Foslie	N/A	N/A	KP171974	This paper
Wildemania amplissima	AMM282_2	Kjelvik, Finmark, Norway	8th Aug. 1891 M. Foslie	N/A	N/A	KP171975	This paper
Wildemania amplissima	AMM283_1	Kjolfjord, Norway	1887 M. Foslie	N/A	N/A	KP171976	This paper
Wildemania amplissima	AMM323	Osundet, Øygarden, Norway	3rd Aug. 2011 K. Sjøtun	N/A	N/A	KP171977	This paper
Wildemania amplissima	RN8700301	Krogen Hirsholm, Denmark	3rd July 1987 R. Nielsen	Intertidal	N/A	KP171978	This paper

Wildemania amplissima	AMM07USA 019	Blueberry Hill, ME, U.S.A.	19th August 2007 N. Blouin	Subtidal	N/A	KP171979	This paper
Wildemania amplissima	AMM236_1	Mingo Rock, Isles of Shoals, NH, USA	22nd April 2011 A. Mols-Mortensen	Subtidal, 10 m depth	N/A	KP171980	This paper
Wildemania amplissima	AMM288_1	Marine Costal Laboratory Pier, Newcastlen NH, USA	1st May 2011 Agnes Mols-Mortensen	Subtidal, 2 m depth	N/A	KP171981	This paper
Wildemania amplissima	AMM288_3	Marine Costal Laboratory Pier, Newcastlen NH, USA	1st May 2011 Agnes Mols-Mortensen	Subtidal, 2 m depth	N/A	KP171982	This paper
Wildemania amplissima	AMM288_4	Marine Costal Laboratory Pier, Newcastlen NH, USA	1st May 2011 Agnes Mols-Mortensen	Subtidal, 2 m depth	N/A	KP171983	This paper
Wildemania amplissima	AMM331	Fort Stark Newcastle, NH, U.S.A.	17th May 2010 A. Mols–Mortensen, R. Erikssen	Mid intertidal, in rock pool	N/A	KP171984	This paper
Wildemania amplissima	AMM332_1	Dover Point, NH, U.S.A.	17th May 2010 A. Mols-Mortensen, R. Eriksen	Shallow Subtidal, on algae	N/A	KP171985	This paper
Wildemania amplissima	AMM407_1	Dover Point, NH, U.S.A.	3rd May 2012 L. Green	N/A	N/A	KP171986	This paper
Wildemania amplissima	AMM408_1	Dover Point, NH, U.S.A.	4th May 2012 L. Green	N/A	N/A	KP171987	This paper
Wildemania amplissima	AMM151_1	Dover Point, NH, U.S.A.	28th April 2009 A. Mathieson	N/A	N/A	KP171988	This paper
Wildemania amplissima	AMM386	Atlantic City, NJ, U.S.A.	S.R. Morse	N/A	N/A	KP171989	This paper
Wildemania amplissima	AMM388	Atlantic City, NJ, U.S.A.	S.R. Morse	N/A	N/A	KP171990	This paper
Wildemania miniata	AMM138	Greenland	A. Mols–Mortensen	Subtidal	N/A	KP171991	This paper
Wildemania miniata	AMM162	Sisimiut, Greenland	4th June 2010 A. Mols–Mortensen	Drift	N/A	KF478746	Mols–Mortensen *et al.*, 2014
Wildemania miniata	AMM185	Sisimiut, Greenland	6th June 2010 A. Mols–Mortensen	Mid intertidal, on rock	N/A	KF478747	Mols–Mortensen *et al.*, 2014
Wildemania	AMM199	Nuuk,	20th June	Mid intertidal,	KF478759	KF478748	Mols–

miniata		Greenland	2010 A. Mols–Mortenen	on rock			Mortensen *et al.*, 2014
Wildemania miniata	AMM321	Anorliuitsup qeqertaa, Greenland	9th Sep. 2011 P.M. Pedersen	Mid intertidal	N/A	KF478749	Mols–Mortensen *et al.*, 2014
Wildemania miniata	AMM322	Ikigaat, Greenland	11th Sep. 2011 P.M. Pedersen	Subtidal, 5-10 m depth	N/A	KF478750	Mols–Mortensen *et al.*, 2014
Wildemania miniata	AMM474	Umiagssat qeqertai, Qaqortoq, Greenland	18th July 1970 P.M. Pedersen	Subtidal, 10 m depth, On rock and on Chaetomorpha melagonuim	N/A	KF478751	Mols–Mortensen *et al.*, 2014
Wildemania miniata	AMM481	Holsteinsborg (Sisimiut), Greenland	3rd Aug. 1886 L.K. Rosenvinge	Intertidal	N/A	KP171992	This paper
Wildemania miniata	07 8327 1	Vattarnes, Reyðarfjørður, Iceland	31st Aug. 2007 S. Egilsdóttir, K. Gunnarsson	Intertidal	N/A	KP171993	This paper
Wildemania miniata	07 8328 1	Vattarnes, Reyðarfjørður, Iceland	31st Aug 2007 S. Egilsdóttir, K. Gunnarsson	Intertidal	N/A	KP171994	This paper
Wildemania miniata	AMM74	Kvivík, Faroe Islands	17th June 2008 A. Mols–Mortensen, Ø. Patursson	Subtidal, 4 m depth	N/A	KP171995	This paper
Wildemania miniata	AMM236_3	Mingo Rock, Isles of Shoals, NH, U.S.A.	22nd April 2011 A. Mols-Mortensen	Subtidal, 10 m depth	N/A	KP171996	This paper
Wildemania miniata	AMM237	Seal Cove, Isles of Shoals, NH, U.S.A.	22nd April 2011 A. Mols–Mortensen	Subtidal, 7 m depth	N/A	KP171997	This paper
Wildemania miniata	AMM238	Seal Cove, Isles of Shoals, NH, U.S.A.	22nd April 2011 A. Mols–Mortensen	Subtidal, 7 m depth	N/A	KP171998	This paper
Wildemania miniata	AMM289_1	Star Island, Isles of Shoals, NH, U.S.A.	8th May 2011 A. Mols–Mortensen	Subtidal, 7 m depth	N/A	KP171999	This paper

Appendix E. Intra- and interspecific variation in the 3’ *rbc*L + 5’ *rbc*L-S dataset using the Tamura-Nei genetic distance model.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
	N=4	N=2	N=5	N=4	N=7	N=1	N=3	N=3	N=4	N=2	N=3	N=8	N=7	N=7	N=2	N=1	N=2	N=7	N=3
1	**0.000-0.004**	0.077-0.081	0.077-0.086	0.080-0.087	0.080-0.087	0.081-0.085	0.097-0.101	0.085-0.091	0.085-0.089	0.106-0.109	0.084-0.088	0.084-0.093	0.087-0.096	0.089-0.099	0.089-0.093	0.099-0.102	0.100-0.104	0.069-0.079	0.089 0.092
2		**0.000**	0.037-0.041	0.055-0.060	0.040-0.043	0.041	0.104	0.092-0.094	0.092	0.112	0.091	0.091-0.096	0.094-0.099	0.096-0.102	0.096	0.105	0.107	0.077-0.083	0.096
3			**0.000-0.005**	0.056-0.065	0.012-0.020	0.007-0.012	0.105-0.109	0.092-0.099	0.093-0.097	0.113-0.118	0.091-0.096	0.092-0.101	0.094-0.104	0.097-0.107	0.096-0.101	0.106-0.111	0.108-0.112	0.078-0.088	0.096 0.101
4				**0.000-0.004**	0.058-0.066	0.059-0.064	0.107-0.111	0.094-0.101	0.095-0.099	0.115-0.119	0.094-0.098	0.094-0.103	0.096-0.106	0.099-0.109	0.098-0.103	0.108-0.112	0.110-0.114	0.079-0.089	0.098 0.102
5					**0.000-0.005**	0.015-0.019	0.108-0.111	0.095-0.100	0.095-0.099	0.116-0.119	0.094-0.097	0.094-0.103	0.097-0.106	0.099-0.108	0.099-0.102	0.109-0.112	0.110-0.114	0.080-0.089	0.099 0.102
6						**0.000**	0.109	0.096-0.098	0.096	0.117	0.095	0.095-0.100	0.098-0.103	0.101-0.106	0.100	0.110	0.111	0.081-0.087	0.100
7							**0.000**	0.059-0.061	0.060	0.080	0.058	0.030-0.035	0.032-0.038	0.035-0.041	0.035	0.044	0.100	0.068-0.074	0.089
8								**0.000-0.003**	0.030-0.032	0.067-0.069	0.029-0.031	0.046-0.053	0.049-0.056	0.051-0.059	0.051-0.053	0.060-0.062	0.088-0.090	0.056-0.064	0.076 0.078
9									**0.000**	0.068	0.004	0.046-0.051	0.049-0.054	0.051-0.057	0.051	0.061	0.088	0.057-0.063	0.076
10										**0.000**	0.066	0.066-0.072	0.069-0.075	0.072-0.077	0.071	0.081	0.108	0.077-0.083	0.097
11											**0.000**	0.045-0.050	0.048-0.053	0.050-0.056	0.050	0.059	0.087	0.056-0.062	0.075
12												**0.000-0.005**	0.019-0.030	0.022-0.032	0.021-0.026	0.031-0.036	0.087-0.092	0.055-0.066	0.075 0.080
13													**0.000-0.006**	0.024-0.035	0.024-0.029	0.034-0.039	0.089-0.095	0.057-0.069	0.078 0.083
14														**0.000-0.006**	0.027-0.032	0.011-0.016	0.092-0.098	0.061-0.072	0.081 0.086
15															**0.000**	0.036	0.092	0.060-0.066	0.080
16																**0.000**	0.101	0.069-0.075	0.090
17																	**0.000**	0.050-0.056	0.014
18																		**0.000-0.006**	0.038 0.044
19																			**0.000**

1. *Boreophyllum birdiae*, 2. *Porphyra dioica*, 3. *Porphyra linearis*, 4. *Porphyra purpurea*, 5. *Porphyra umbilicalis*, 6. *Porphyra* sp., 7. *Pyropia elongata*, 8. *Pyropia njordii*, 9. *Pyropia peggicovensis*, 10. *Pyropia suborbiculata*, 11. *Pyropia thulaea*, 12. *Pyropia yezoensis*, 13. “*Pyropia collinsii*”, 14. “*Pyropia leucosticta*”, 15. *Pyropia novae-angliae*”, 16. *Pyropia* sp., 17. *Wildemania abyssicola*, 18. *Wildemania amplissima*, 19. *Wildemania miniata*.

Appendix F. Taxa used in the analysis with collecting details and GenBank accession numbers. N/A = not available.

Taxa	**Voucher number**	**Location**	**Date and collector**	**Level and substratum**	**GenBank accession no. *rbc*L**	**Reference**
Wildemania abyssicola	JB456	Mariuhorn by Grunavik, Iceland	2/7/05 K. Gunnarsson G. Bruntse	Subtidal 17m depth	JN847269	Mols-Mortensen *et al.*, 2012
Wildemania amplissima	AMM341	Bodø, Nordland; Norway	10/05/11 Bernt-Gunnar Østerkløft	On *D. contorta* in a rock pool	N/A	
Wildemania amplissima	AMM278_2	North Norway	16/07/1887 M. Foslie	N/A	N/A	
Wildemania amplissima	AMM158	Kollafjørður, Faroe Islands	23/06/08 A. Mols-Mortensen, Ø. Patursson	Subtidal	N/A	
Wildemania amplissima	AMM159	Gøtuvík, Faroe Islands	30/06/08 A. Mols-Mortensen, Ø. Patursson	1 m depth	N/A	
Wildemania amplissima	AMM539_1	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A	
Wildemania amplissima	AMM539_2	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A	
Wildemania amplissima	AMM539_3	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A	
Wildemania amplissima	AMM539_4	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A	
Wildemania amplissima	AMM539_5	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A	
Wildemania amplissima	AMM539_6	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde,	1-3 m depth	N/A	

			T. Sólarnarsson		
Wildemania amplissima	AMM539_7	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A
Wildemania amplissima	AMM539_8	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A
Wildemania amplissima	AMM539_9	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A
Wildemania amplissima	AMM539_10	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A
Wildemania amplissima	AMM539_11	Kvívík, Faroe Islands	18/07/12 A. Mols-Mortensen, S. Solmunde, T. Sólarnarsson	1-3 m depth	N/A
Wildemania amplissima	JB488	Suður-Bar, Iceland	07/07/05 K. Gunnarsson, G. Bruntse	14 m depth	N/A
Wildemania amplissima	JB490	Suður-Bar, Iceland	07/07/05 K. Gunnarsson, G. Bruntse	14 m depth	N/A
Wildemania amplissima	GWS006180	Escoumins, Quebec, Canada	G. W. Saunders	On mussel, low intertidal	N/A
Wildemania amplissima	GWS002653	Letete, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On rock, low intertidal	N/A
Wildemania amplissima	GWS002654	Letete, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On rock, low intertidal	N/A
Wildemania amplissima	GWS003696	Letete, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On rock, low intertidal	N/A

Wildemania amplissima	GWS003697	Letete, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On rock, low intertidal	N/A	
Wildemania amplissima	GWS005929	Letete, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On rock, low intertidal	N/A	
Wildemania amplissima	GWS005930	Letete, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On rock, low intertidal	N/A	
Wildemania amplissima	GWS006183	Maces Bay, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On *Dumontia contorta*, low intertidal pool	N/A	
Wildemania amplissima	GWS006184	Maces Bay, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On limpet, low intertidal pool	N/A	
Wildemania amplissima	GWS003684	Letete, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On rock and reds, low intertidal	N/A	
Wildemania amplissima	GWS003693	Letete, Bay of Fundy, New Brunswick, Canada	G. W. Saunders	On Fucus, low intertidal	JN029013	Kucera & Saunders, 2012
Wildemania amplissima	AMM236_1	Mingo Rock, Isles of Shoals, NH, USA 43º00.024 N, 070º37.079W	22/04/11 A. Mols-Mortensen	10m depth	N/A	
Wildemania amplissima	AMM236_2	Mingo Rock, Isles of Shoals, NH, USA 43º00.024 N, 070º37.079W	22/04/11 A. Mols-Mortensen	10m depth	N/A	

Wildemania amplissima	AMM236_5	Mingo Rock, Isles of Shoals, NH, USA 43º00.024 N, 070º37.079W	22/04/11 A. Mols-Mortensen	10m depth	N/A
Wildemania amplissima	AMM236_14	Mingo Rock, Isles of Shoals, NH, USA 43º00.024 N, 070º37.079W	22/04/11 A. Mols-Mortensen	10m depth	N/A
Wildemania amplissima	AMM236_15	Mingo Rock, Isles of Shoals, NH, USA 43º00.024 N, 070º37.079W	22/04/11 A. Mols-Mortensen	10m depth	N/A
Wildemania amplissima	AMM236_20	Mingo Rock, Isles of Shoals, NH, USA 43º00.024 N, 070º37.079W	22/04/11 A. Mols-Mortensen	10m depth	N/A
Wildemania amplissima	AMM288_1	Marine Costal Laboratory Pier, Newcastlen NH, USA	01/05/11 Agnes Mols-Mortensen	2m depth	N/A
Wildemania amplissima	AMM288_4	Marine Costal Laboratory Pier, Newcastlen NH, USA	01/05/11 Agnes Mols-Mortensen	2m depth	N/A
Wildemania amplissima	AMM288_5	Marine Costal Laboratory Pier, Newcastlen NH, USA	01/05/11 Agnes Mols-Mortensen	2m depth	N/A
Wildemania amplissima	AMM288_7	Marine Costal Laboratory Pier, Newcastlen NH,	01/05/11 Agnes Mols-Mortensen	2m depth	N/A

		USA			
Wildemania amplissima	AMM288_11	Marine Costal Laboratory Pier, Newcastlen NH, USA	01/05/11 Agnes Mols-Mortensen	2m depth	N/A
Wildemania amplissima	AMM288_12	Marine Costal Laboratory Pier, Newcastlen NH, USA	01/05/11 Agnes Mols-Mortensen	2m depth	N/A
Wildemania amplissima	AMM151_1	Hilton Park, Dover Point, NH, USA	28/04/2009 A. Mathieson	N/A	N/A
Wildemania amplissima	AMM151_3	Hilton Park, Dover Point, NH, USA	28/04/2009 A. Mathieson	N/A	N/A
Wildemania amplissima	AMM407_1	Hilton Park, Dover Point, NH, USA	03/05/2012 L. Green	N/A	N/A
Wildemania amplissima	AMM407_2	Hilton Park, Dover Point, NH, USA	03/05/2012 L. Green	N/A	N/A
Wildemania amplissima	AMM407_3	Hilton Park, Dover Point, NH, USA	03/05/2012 L. Green	N/A	N/A
Wildemania amplissima	AMM407_4	Hilton Park, Dover Point, NH, USA	03/05/2012 L. Green	N/A	N/A
Wildemania amplissima	AMM408_1	Hilton Park, Dover Point, NH, USA	04/05/2012 L. Green	N/A	N/A
Wildemania amplissima	AMM408_2	Hilton Park, Dover Point, NH, USA	04/05/2012 L. Green	N/A	N/A
Wildemania amplissima	AMM332_1	Hilton Park, Dover Point, NH, USA	17/05/10 A. Mols-Mortensen, R. Eriksen	Shallow Subtidal	N/A

Wildemania amplissima	AMM332_2	Hilton Park, Dover Point, NH, USA	17/05/10 A. Mols-Mortensen, R. Eriksen	Shallow Subtidal	N/A
Wildemania amplissima	AMM332_3	Hilton Park, Dover Point, NH, USA	17/05/10 A. Mols-Mortensen, R. Eriksen	Shallow Subtidal	N/A
Wildemania amplissima	AMM332_4	Hilton Park, Dover Point, NH, USA	17/05/10 A. Mols-Mortensen, R. Eriksen	Shallow Subtidal	N/A
Wildemania amplissima	AMM363_1	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	AMM363_2	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	AMM363_3	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	AMM363_4	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	AMM363_5	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	AMM363_6	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	AMM363_7	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	AMM363_8	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	AMM363_9	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	AMM363_10	Sunshine Cove, Alaska, USA	19/04/11 S. C. Lindstrom	N/A	N/A
Wildemania amplissima	GWS009728	Manson's Landing Lagoon, Cortes	G. W. Saunders	On rock, low intertidal	N/A

		Island, British Columbia, Canada			
Wildemania amplissima	GWS009729	Manson’s Landing Lagoon, Cortes Island, British Columbia, Canada	G. W. Saunders	On rock, low intertidal	N/A
Wildemania amplissima	SCL14667_1	Penn Cove, Coupeville, Whidbey, Washington, USA (*W. cuneiformis* type locality)	06/05/2011 S. C. Lindstrom	On pebbles and shells, low intertidal	N/A
Wildemania amplissima	SCL14667_2	Penn Cove, Coupeville, Whidbey, Washington, USA (*W. cuneiformis* type locality)	06/05/2011 S. C. Lindstrom	On pebbles and shells, low intertidal	N/A
Wildemania amplissima	SCL14667_3	Penn Cove, Coupeville, Whidbey, Washington, USA (*W. cuneiformis* type locality)	06/05/2011 S. C. Lindstrom	On pebbles and shells, low intertidal	N/A
Wildemania amplissima	SCL14667_5	Penn Cove, Coupeville, Whidbey, Washington, USA (*W. cuneiformis* type locality)	06/05/2011 S. C. Lindstrom	On pebbles and shells, low intertidal	N/A
Wildemania amplissima	SCL14667_6	Penn Cove, Coupeville, Whidbey, Washington, USA (*W. cuneiformis* type locality)	06/05/2011 S. C. Lindstrom	On pebbles and shells, low intertidal	N/A

Wildemania amplissima	SCL14667_8	Penn Cove, Coupeville, Whidbey, Washington, USA (*W. cuneiformis* type locality)	06/05/2011 S. C. Lindstrom	On pebbles and shells, low intertidal	N/A	
Wildemania amplissima	SCL14667_9	Penn Cove, Coupeville, Whidbey, Washington, USA (*W. cuneiformis* type locality)	06/05/2011 S. C. Lindstrom	On pebbles and shells, low intertidal	N/A	
Wildemania amplissima	SCL14667_10	Penn Cove, Coupeville, Whidbey, Washington, USA (*W. cuneiformis* type locality)	06/05/2011 S. C. Lindstrom	On pebbles and shells, low intertidal	N/A	
Wildemania amplissima	58186, 58171	Cobscook Bay, Maine, U.S.A.	08/07/1995	N/A	AF021034	GenBank
Wildemania amplissima	JB461	Svalbarðseyri, Eyrarbakki, Iceland	19/06/06 R. Nielsen, S. Egilsdóttir	Intertidal	JN847273	Mols-Mortensen *et al.*, 2012
Wildemania amplissima	UBCA85669	Kake Ferry Terminal, Alaska, U.S.A.	21/04/07 S.C. Lindstrom	N/A	EU223055	GenBank
Wildemania amplissima	16-Apr-1996	Juneau, Alaska, U.S.A.	16/04/96 S.C. Lindstrom	N/A	AF452428	GenBank
Wildemania amplissima	Welt A023167	Nosappu, Nemuro, Hokkaido, Japan	N/A	N/A	HQ687560	Sutherland *et al.*, 2011
Wildemania miniata	AMM199	Nuuk, Greenland	20/06/10 A. Mols–Mortensen	On rock, mid intertidal	KF478748	Mols-Mortensen *et al.*, 2014
Wildemania miniata	JB416	Krossanes, Iceland	16/06/07 I. Tittley, K. Gunnarsson, S. Egilsdóttir	Intertidal	JN847276	Mols-Mortensen *et al.*, 2012
Wildemania norrisii	UBC A85176, A85177, A85178	Hardling Point, Victoria, BC, Canada	25/04/05 S.C. Lindsrton	N/A	EU223212	GenBank

Wildemania occidentalis	15-Apr-1994	Point No Point, BC, Canada	15/04/1994	N/A	AF452436	GenBank
Wildemania schizophylla	09-Apr-1997	Sitka, Alaska, U.S.A.	09/04/1997	N/A	AF452443	GenBank
Wildemania schizophylla	UBC A87692	Van Damme State Park, CA, U.S.A.	09/04/08 S.C. Lindstrom	N/A	GU319871	GenBank
Wildemania variegata	ALEUT06_308	Kagamil Island, Alaska, U.S.A.	16/07/06 M. Lindeberg	N/A	EU223237	GenBank
Wildemania variegata	4-Jun-1996	Seldovia, Alaska, U.S.A.	04/06/96 S.C. Lindstrom	N/A	AF452447	GenBank
Wildemania sp.	JBCH2011-1 (AMM353)	Buque Quemada, Punta Arenas, Chile	20/01/2011 J. Brodie	Intertidal	N/A	
Wildemania sp.	JBCH2011.04	Buque Quemada, Punta Arenas, Chile	20/01/2011 J. Brodie	Intertidal		
Wildemania sp.	JBCH2011.13 (AMM345)	Buque Quemada, Punta Arenas, Chile	20/01/2011 J. Brodie	Intertidal	To add	This paper
Wildemania sp.	A023563	Hill Cove, Falkland Islands, UK	08/01/03	N/A	GU165883	Sutherland *et al.*, 2011
Wildemania sp.	SPF56431	Antarctica	N/A	N/A	HQ605700	Sutherland *et al.*, 2011
Wildemania sp.	HM080	Songjiho, Gangwondo, Korea	N/A	N/A	HQ728202	Sutherland *et al.*, 2011
OUTGROUPS						
'*Bangia*' 2	WELT A026700	Gentle Annie, Westland, NZ	N/A	N/A	HQ687506	Sutherland *et al.*, 2011
Porphyra umbilicalis	JB470	Höfnin, Garði, Iceland	11/02/06 K. Gunnarsson	Low intertidal	JN847251	Mols–Mortensen *et al.*, 2012