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A collections-based approach to the species and their distribution based on the bladed Bangiales (Rhodophyta) of Iceland

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Abstract: An assessment of the 11 species of bladed Bangiales from Iceland in a collection of approximately 1770 specimens collected between 1883 and 2013 was undertaken by combining results from molecular analysis with examination of morphological variation in order to determine their distribution in detail. Seven of the species grow all around Iceland. Of the remaining four species, *Porphyra linearis*, *P. dioica* and *Pyropia leucosticta* have their northern limit of distribution along the south-western and western part of the country, and *Pyropia thulaea*, an arctic species, only grows at the eastern coast, which is the coldest part of the coastline. Detailed reliable records of species distribution are important to detect future changes in the flora due to anthropogenic or natural environmental changes and have implications for conservation policy.

Keywords: *Boreophyllum*; key to genera; North Atlantic; *Porphyra*; *Pyropia*; *Wildemanina*.

Introduction

The bladed Bangiales are a large, cosmopolitan group of red algae that were placed in the genus *Porphyra* until the revision of Sutherland et al. (2011). The morphological identification of these species has been regarded as highly problematic because of the difficulty of finding reliable morphological characters and the variation within and between species. On the basis of a two-gene phylogeny,

Sutherland et al. (2011) split the genus into eight genera: *Boreophyllum*, *Clymene*, *Fuscolium*, *Lysithea*, *Miuraea*, *Porphyra*, *Pyropia* and *Wildemanina*. Since then an additional genus, *Neothemis*, has been discovered (Sánchez et al. 2015a,b). One of the consequences of this revision is that we are now in a position to re-evaluate local and regional Bangiales floras. Although the difficulty of distinguishing species remains, generic circumscriptions enable better placement at the generic level which in turn enables us to focus on species present at the regional and local level.

As a consequence of the difficulty in distinguishing species, names have been misapplied in different parts of the world (e.g. *Porphyra umbilicalis*, Brodie et al. 2008). This in turn causes a misinterpretation of the distribution of species. Reconstructing a biogeography of a species based on all literature reports can only be achieved if every record listed has been checked against a specimen and the identification verified. Determining species distributions requires confidence that specimens have been identified correctly, that these identifications can be verified, i.e. they can be revisited, and that reliable information exists on where each specimen was collected. A specimen represents an individual record of a particular species from a particular location at a particular point in time and any overall distribution will be inferred in the gaps. Here, we use the example of how collections can be used from a defined area, in this case the island of Iceland, to construct reliable distributions based on a robust understanding of species concepts in that region. We have based our taxonomy on a molecular study of the bladed Bangiales in Iceland undertaken to assess their diversity and based on *rbcL* and *cox1* sequences selected from a collection of c. 750 specimens from 158 stations (Mols-Mortensen et al. 2012). This study revealed that there were 11 species (Table 1), five more than the number previously reported by Gunnarsson and Jónsson (2002): *Porphyra amplissima*, *P. dioica*, *P. linearis*, *P. miniata*, *P. purpurea*, *P. umbilicalis*, and belonging to four of the nine genera of bladed Bangiales: *Boreophyllum*, *Porphyra*, *Pyropia* and *Wildemanina*.

The isolated location of Iceland in the northern North Atlantic makes it suitable for detailed studies of species

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Table 1: Numbers of specimens of each species of bladed Bangiales collected from Iceland during different time periods.

Species	Period			
	1883–1900	1901–1960	1961–1990	1991–present
<i>Boreophyllum birdiae</i> (Neefus et A.C. Mathieson) Neefus	1		15	14
<i>Porphyra dioica</i> J. Brodie et L.M. Irvine	1			20
<i>P. linearis</i> Greville				39
<i>P. purpurea</i> (Roth) C. Agardh	3		37	170
<i>P. umbilicalis</i> Kützting	13	1	209	403
<i>Pyropia leucosticta</i> (Thuret) Neefus et J. Brodie	1		28	79
<i>Py. njordii</i> Mols-Mortensen, J. Brodie et Neefus			18	88
<i>Py. thulaea</i> (Munda et P.M. Pedersen) Neefus			21	1
<i>Wildemania abyssicola</i> (Kjellmann) Mols-Mortensen et J. Brodie	2		1	7
<i>W. amplissima</i> Foslie	7		103	174
<i>W. miniata</i> (C. Agardh) Foslie	12	1	74	215
No. of specimens	40	2	506	1210
No. of species	8	2	9	11

distribution. The coastal sea around Iceland is characterized by warm temperatures in the southwest part and cooler temperatures in the northeast and eastern part of the country (Figure 1, Astthorsson et al. 2007). The exposed shoreline of the eastern part of the south coast is made of black volcanic sand that is in constant motion and therefore devoid of seaweeds.

In this paper, we have used the results of Mols-Mortensen et al. (2012) to re-evaluate morphological identification of all the species based on all the bladed Bangiales specimens that have been collected from Iceland since the first expeditions in the 19th century and used that as a basis to describe those species distributions.

We have also provided a key to the genera of bladed Bangiales found in Iceland.

Materials and methods

A comprehensive study was made of all Icelandic specimens of bladed Bangiales held in the Icelandic Institute of Natural history in Reykjavik (ICEL), the Natural History Museum of Denmark, herbarium in Copenhagen (C), and Natural History Museum in London (BM). A summary of the principal collectors, dates and approximate number of specimens are given in Table 2.

Figure 1: Sea surface temperature around Iceland. Contours show mean monthly temperature (°C) for the years 2000–2010 in (A) March and (B) August. Data from the *World Ocean Atlas 2013* (Locarnini et al. 2013).

Table 2: Collections of bladed Bangiales from Iceland. Four periods can be recognized based on collecting effort.

Main collectors	Dates	Where held	Number of specimens
H. Jónsson, C. Ostenfeld	1893–1900	C, ICEL	40
	1901–1960	C, ICEL	2
K. Gunnarsson, S. Jónsson, I. Munda	1961–1990	C, ICEL	506
J. Brodie, G. Bruntse, S. Egilsdóttir, K. Gunnarsson, T.E. Lein, R. Nielsen, I. Tittley	1991–present	ICEL, BM, C	1210
Total			1758

The first collections of bladed Bangiales in Iceland were made in the late 19th century and the start of the 20th century (Table 2). Practically no collections were made after that for 60 years until S. Jónsson and Munda began their collections. After that the bulk of the collections were made by Munda between 1963 and 1980, and our sampling from 158 stations in Iceland as part of a general macroalgal survey initiated in 1999 (southwest coast) and continued in 2005 (west/northwest coasts), 2006 (north coast) and 2007 (northeast and east coasts). Additional details can be found in Mols-Mortensen et al. (2012). Most of these collections were made during the summer months. In specific winter collecting trips, *Porphyra linearis* was collected in south-western and western Iceland. No winter samples exist from other parts of the country.

Morphological identification was reassessed for all the specimens with reference to those for which molecular data were obtained by Mols-Mortensen et al. (2012). Initial identifications were either confirmed or revised. All specimens were databased and the distribution of all those positively identified to species was mapped. Sampling site position was either determined with a GPS device (for all specimens collected after 1999) or by taking positions as latitude/longitude from digital maps (National Land Survey of Iceland) with Lambert conical projection. Maps were created in R (R Core Team 2015).

Results

The distribution of the 11 species found in Iceland is shown in Figures 2 and 3. Most of the bladed Bangiales species are found in all coastal regions with suitable substrata. There is a noticeable lack of records from the eastern part of the south coast due to lack of suitable substrata. *Porphyra dioica*, *P. linearis* and *Pyropia leucosticta* are confined to the south-western part of Iceland. *Porphyra linearis* is almost certainly under-recorded owing to the scarcity of collections in the winter months when this species is present. *Pyropia thulaea* is only found in eastern Iceland, the coldest

part of the coastline. *Boreophyllum birdiae* and *Wildemanian abyssicola* were only found sporadically and there are large gaps in their corresponding distribution maps.

The growing season for most of the bladed Bangiales species in Iceland is from late May until October with the following exceptions: *Porphyra umbilicalis* and *P. purpurea* are found throughout the year. *Pyropia thulaea* and *B. birdiae* are autumn species found from August until October, *Pyropia njordii* has been recorded only in early summer, from late May to the beginning of July, and *P. linearis* only in January to March.

Porphyra umbilicalis and *P. linearis* grow in the upper littoral zone of exposed coasts. *Wildemanian amplissima*, *W. abyssicola* and *W. miniata* are most frequently found in the sublittoral zone of exposed shores, but occasionally occur in the lowest part of the shore. The other bladed Bangiales species in Iceland are found in the lower littoral of semi-exposed to sheltered coasts. *Porphyra purpurea* can also be found in extremely sheltered shores growing on small pebbles in muddy estuaries.

All the bladed Bangiales species were found growing on rocks or stones but some can also grow epiphytically. *Pyropia leucosticta* is epiphytic on *Mastocarpus stellatus* (Stackhouse) Guiry and occasionally also on other algae (e.g. *Fucus* spp.), *W. abyssicola* was found growing on *Turnerella pennyi* (Harvey) F. Schmitz, and *W. miniata* and *W. amplissima* were found growing on diverse algae or on rocks.

Key to genera of bladed Bangiales in Iceland

1. Blade monostromatic or distromatic, pale pink* to crimson red, thin, 12.5–35 µm in transverse section (TS); monoecious; spermatangial and zygotosporengial sori in separate sectors of the blade or scattered intermixed *Wildemanian*

* Colors mentioned in the key refer to live specimens

Figure 2: Distribution of bladed bangiophytes around Iceland. (A) *Boreophyllum birdiae*, (B) *Porphyra dioica*, (C) *P. linearis*, (D) *P. purpurea*, (E) *P. umbilicalis*. Depth contours for 100 and 200 m are shown.

1. Blade monostromatic, pale brown, olive green, brown-red, purple-red; monoecious or dioecious; spermatangial and zygotosporangial sori in separate, discrete sori	2	
2. Spermatangia in pale yellow lozenge or streak-shaped sori; zygotosporangial sori in separate, reddish patches around the spermatangial sori.....		3. Monoecious or dioecious; blade dark red to brown with a hint of purple; in TS, 48–55 μm wide; with sori forming a broad, prominent zone on lobes along the margin of blade;
		<i>Porphyra</i>
2. Monoecious or dioecious; spermatangial and zygotosporangial sori in separate sectors of the blade		<i>Boreophyllum</i> **
	3	
3. Monoecious; blade olive green to red-brown; in TS, 27–75 μm wide; spermatangia in pale yellow		

** NB: species of *Boreophyllum* can be very difficult to distinguish from *Porphyra*.

Figure 3: Distribution of bladed bangiophytes around Iceland. (A) *Pyropia leucosticta*, (B) *Py. Njordii*, (C) *Py. thulaea*, (D) *Wildemaniana abyssicola*, (E) *W. amplissima*, (F) *W. miniata*. Depth contours for 100 and 200 m are shown.

Discussion

This is the first time we have been able to determine the distribution of bladed Bangiales species based on morphology and molecular analysis for an entire region. Combining molecular analysis and morphological studies, we have examined individual specimens from a large collection sampled in Iceland between 1893 and 2013. During the present study, 11 species were positively identified occurring on the coast of Iceland. Similar species-diversity with 10 species has been found in the Faroes (Mols-Mortensen et al. 2012). Only five species have been recorded in Norway (Norwegian Seaweeds Network 2016) and in Greenland

(Mols-Mortensen et al. 2014). Even though there is a relatively large collection of bladed Bangiales specimens from the coast of Iceland, evidence of cryptic diversity within the order (Lindstrom 2008) suggests that there are still more species to be discovered in the area. *Pyropia thulaea* was first described in 1978 (Munda and Petersen 1978) based on specimens from eastern Iceland and Greenland. It was not picked up in the 2007 expedition when the east coast was visited. The species is confined to a few shores on the east coast and has only been reported from August to October which was outside the collecting dates for 2007. It seems to be an arctic species confined to the coldest region in Iceland.

Pyropia njordii is a newly described species from the area (Mols-Mortensen et al. 2012). It is conspicuous, therefore that the lack of specimens prior to 2005 and its abundance during this period suggests that it could be a new arrival in Iceland. Molecular data indicate that it is very closely related to *Pyropia brumalis* (Mols-Mortensen et al. 2012, fig. 12), a species described from the Canadian Pacific. Thus, there is the possibility that *Py. njordii* is a relatively recent arrival from the Pacific, although the species has been verified in historic collections from Greenland dating back to 1888 (Mols-Mortensen et al. 2014).

Boreophyllum birdiae has disrupted distribution records and is probably under-recorded and/or misidentified owing to confusion with *Porphyra purpurea* (Neefus et al. 2002). Similarly, distribution records for *Wildemania abyssicola* are disrupted and, because there are relatively few collections from deep water where it is known to occur, this species is also probably under-recorded. Knowledge of the distribution of both species would benefit from further collecting.

Porphyra dioica is only found in the southwest and probably has its northern distribution limit in Iceland as it has been recorded in the Faroes but not in Greenland (Mols-Mortensen et al. 2012, 2014). The distribution of *Pyropia leucosticta* coincides with the areas in the southwest, where its principal host species *Mastocarpus stellatus* forms dense stands on the lower shore. *Mastocarpus stellatus* is found sporadically along the north and the east coast where *Py. leucosticta* is not found. Brodie et al. (1998) suggested that *Py. leucosticta* might be an introduced species in the North Atlantic; in Sutherland et al. (2011), *Py. leucosticta* is resolved in a clade with taxa from the Pacific, lending weight to this suggestion. A few specimens collected from all sections of the coast, morphologically resembled *Pyropia elongata* (Kylin) Neefus et J. Brodie (cf. Brodie et al. 2007) but their identity has to await confirmation as no molecular data are available.

Another factor that may affect the biodiversity in the region is the current increase in sea surface temperature. Southern species are likely to extend their distribution into the area (Muller et al. 2009). In addition, we can expect longer seasonal ice-free periods in the Bering Strait and the Northwest Passage, with a potential increase in the number of introduced species from the Pacific (Reid et al. 2007).

Conclusions

Our work demonstrates the value of collections in determining a reliable and verifiable distribution in a defined area and enables a greater understanding of the overall

biogeography of a species with implications for diversity, endemism and the presence of non-natives in a region. It also provides a baseline from which temporal change can be assessed and the time of arrival of new species into a geographical area can be determined (cf. Brodie et al. 2007). This work also highlights the problem of the misapplication of names and the importance of applying a robust taxonomy which has enabled us to establish the presence of species in the Icelandic flora which previously had been overlooked. The data are also valuable in relation to conservation policy and have implications for the overall distribution of the species studied.

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Juliet Brodie is Research Leader in Phycology at the Natural History Museum, London, specializing in genomic approaches to macroalgal biology and their microbiomes, seaweeds in a time of rapid environmental change and taxonomy, phylogenetics and conservation of algae. She is a leading authority on the Bangiales, a cosmopolitan order of red seaweeds including nori and laver. Her research also addresses the impact of ocean acidification on calcified red algae and the effects of climate change on large brown habitat-forming seaweeds. She is currently the President of the International Phycological Society.

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