

1 **Title: A DNA barcode survey of marine macroalgae from Bergen (Norway).**

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8 **Abstract:** Marine forests are ubiquitous to coastal systems across the globe and are becoming
9 increasingly threatened by climate change. Safeguarding the services provided by marine forests
10 inherently depends on an accurate understanding of macroalgal species diversity. Here, we
11 provide the first DNA barcode survey of marine macroalgae from Norway, with a focus on the
12 Bergen area, and compared our findings to morphological listings for the corresponding area
13 (sector 8; marine area within Hordaland county) as provided by Brattegard & Holte (2001), with
14 updates. Specimens were sampled April 14-20 and June 3-13, 2016, and variously sequenced for
15 several genetic markers, including the five prime end of the cytochrome c oxidase subunit I gene
16 (COI-5P), elongation factor *tufA* in Chlorophyta, and full or partial (three prime end) ribulose-1,
17 5-biphosphate carboxylase large subunit gene (*rbcL* or *rbcL*-3P). We generated 655 new barcode
18 records for COI-5P, 11 for *tufA*, 41 for *rbcL*, and 9 for *rbcL*-3P, representing 51 species of
19 Phaeophyceae, nine species of Chlorophyta, and 74 species of Rhodophyta. Sequence data
20 confirmed 113 morphological species listed for the area. A further 17 genetic groups indicated
21 the presence of new species for sector 8, only six of which were linked to formally described
22 species. The remaining four genetic records were uncertain in terms of morphological species
23 assignment and relation to previous sector 8 records. We recommend further DNA barcoding
24 surveys in the area, as only a third of the listed morphological species were genetically
25 confirmed.

26
27 **Keywords:** Seaweeds, species diversity, marine forests, DNA, Atlantic

28 **Introduction**

29 Marine forests are widespread across the globe, providing numerous services to coastal
30 ecosystems and economies (Wernberg & Filbee-Dexter 2019). Of concern are recently
31 documented and projected changes to marine forests due to climate change, and the
32 accompanying impacts to services they provide (Krumhansl et al. 2016, Assis et al. 2018, Smale
33 et al. 2019). Safeguarding against such changes inherently depends on a thorough understanding
34 of species diversity and biogeographic patterns within marine forests, knowledge that is
35 unfortunately lacking or requires genetic verification in many areas of the globe.

36 Sequence data are critical to enhancing information regarding the distribution of marine
37 macroalgal species diversity. Morphological identifications of macroalgae are frequently
38 hampered by cryptic species diversity, convergent evolution, simple gross morphology, and
39 phenotypic plasticity, issues typically resolved using sequence data (Le Gall & Saunders 2010).
40 DNA barcoding, in particular, utilizes standardized genetic markers to assign morphological
41 species to genetic units (Saunders 2005, Saunders & Kucera 2010). These efforts have led to
42 numerous taxonomic revisions and biogeographic insights (e.g. Melbourne et al. 2017, Kawai et
43 al. 2019a, 2019b, Kupper et al. 2016), and also provide critical baseline information regarding
44 species distributions needed for monitoring ongoing range shifts in marine forests.

45 The coast of Norway covers more than 13 degrees of latitude in a south-north direction,
46 and exhibits conspicuous archipelagos along most of the coast, interrupted by numerous large
47 and small fjords. On the South-West coast of Norway, average surface temperatures in the
48 coastal areas varies from a minimum of 4 °C in February-March to a maximum of around 16 °C
49 in August (Armitage & Sjøtun 2017), and the macroalgal vegetation is that of a typical cold

50 temperate flora. Studies of the algal vegetation on the southwest coast of Norway extend back to
51 the end of the 1800's (Hansteen 1892), and Levring (1937) provided the first extensive inventory
52 of the macroalgal composition around Bergen. Another macroalgal overview from the area
53 around Bergen was published by Jorde (1966), and during the 1950s Jorde and Klavestad (1963)
54 carried out an extensive study of the macroalgae of Hardangerfjord south of Bergen. The main
55 stations of this study were re-investigated 50 years later, and results showed a significant impact
56 of a changing climate in the area (Sjøtun et al. 2015). Warming temperatures are expected to
57 continue impacting the area, with projected poleward shifts in seaweed communities (Bartsch et
58 al. 2012). Some systematic work including DNA sequencing of specimens exists from Norway,
59 especially on members of the red algal order Ceramiales (e.g. Gabrielsen et al. 2003; Skage et al.
60 2005), and corallines (Pardo et al. 2014). However, apart from these limited studies (e.g. Rueness
61 2010; Armitage & Sjøtun 2016) little DNA barcoding of macroalgae from Norway has been
62 done.

63 Our objective was to DNA barcode the marine macroalgal flora in the Bergen area, and
64 compare findings to morphological species listings as reported from the marine area within
65 Hordaland county in Brattegard & Holte (2001). To our knowledge this is the first DNA barcode
66 survey of Norwegian marine macroalgae, marking an important first step towards providing an
67 updated compilation of the species present in the area and genetic data crucial to future
68 biomonitoring and taxonomic work.

69

70 **Material and Methods**

71 Marine macroalgae were sampled from the Bergen area April 14-20 and June 3-13, 2016.
72 The dataset was also supplemented with publicly available data for *Lithothamnion glaciale*
73 Kjellman, collected May 1, 2008. The macroalgal flora of the area sampled corresponded to the
74 one listed for sector 8 as defined by Brattegard & Holte (1997), an area that represents the coast
75 of Hordaland county, spanning from 59°30' N to 60°51'N. Specimens were haphazardly
76 collected in the intertidal or via scuba up to a max depth of 15 m (though some species were
77 targeted for population genetic analyses separate from the current study, i.e. larger sample sizes
78 in Table 1). Specimens were variously preserved on herbarium sheets and/or as 1 cm² portion of
79 material stored in silica for DNA extraction (Saunders & McDevit 2012). Most of the press
80 material is currently stored at the University of New Brunswick (Canada), with a subset stored at
81 the Herbarium BG at the University of Bergen.

82 Several barcode markers were amplified, including the five prime end of the cytochrome
83 c oxidase subunit I gene (COI-5P) in Rhodophytes and Phaeophyceae as per Saunders & Moore
84 (2013) and Saunders & McDevit (2012), respectively; elongation factor *tufA* in Chlorophytes as
85 per Saunders & Kucera (2010); and full or partial (three prime end) of the ribulose-1, 5-
86 biphosphate carboxylase large subunit gene in Rhodophytes and Phaeophyceae as per Saunders
87 & Moore (2013) and Daugbjerg and Andersen (1997), respectively. Primer information is
88 provided in Table S1. PCR thermocycling regimes for respective markers followed Saunders and
89 Moore (2013), except *tufA* (Saunders and Kucera 2010). Successful PCR products were sent to
90 Genome Quebec for forward and reverse sequencing. Genetic data were edited in Geneious
91 version 8.0 (www.geneious.com; Kearse *et al.* 2012). See Table S2 for a specimen list, markers
92 sequenced, and accompanying GenBank accession numbers. Cryptic genetic groups from other
93 areas of the globe corresponding to some of the morphological species sampled here are also

94 presented in Table S2. Specimen info, including sampling locations, pictures, global
95 geographical coverage of genetic groups, and sequence data can also be accessed through the
96 Barcode of Life Data System (Ratnasingham & Hebert 2013; DOI: [dx.doi.org/10.5883/DS-](https://doi.org/10.5883/DS-NORSE)
97 [NORSE](https://doi.org/10.5883/DS-NORSE)). Species delineations in the brown and red macroalgae were based on the assignment of
98 Barcode Index Numbers using the Barcode of Life Data System. Barcode Index Numbers are
99 defined using an algorithm that approximates species units by analyzing gaps in COI-5P
100 sequence variation, corresponding to intra- and interspecific genetic variation (Ratnasingham &
101 Hebert 2013). A similar concept was applied to the green macroalgae using *tufA* (Saunders &
102 Kucera 2010).

103 A morphological species list was compiled based on listings for sector 8 in Brattegard &
104 Holte (2001). This list was supplemented with other sources; the full morphological species list
105 with key references are provided in Table S3. Inferred species occurrences for sector 8, as per
106 Brattegard & Holte (2001), were not included in the morphological species lists. Morphological
107 listings were then confirmed if sequence data matched the same barcoded species in GenBank,
108 and the genetic group was morphologically consistent with that species. In some cases,
109 morphological listings were linked to newly sampled genetic groups using Rueness (1977),
110 Maggs & Hommersand (1993), Siemer & Pedersen (1995), and Brodie *et al.* (2007; indicated
111 with ¹ in Table 1). These species records are therefore confirmed for sector 8 on the basis of
112 morphology, rather than matching sequence data with previously generated barcodes. Species
113 were considered new records for sector 8 given one of three conditions: 1) genetic data revealed
114 a species not listed in Table S3 (“new records for described species” in Table 1); 2) more
115 genetic groups were recovered than the reported number of species for a given genus from sector
116 8; or 3) a recovered sequence did not correspond to genetic groups previously linked to reported

117 morphospecies for a given genus from sector 8, hence ruling these morphological listings out and
118 indicating the presence of a new record (“new records for species lacking formal description or
119 morphospecies assignment” in Table 1). Note, species could only be considered new records for
120 sector 8 according to the third condition if all reported morphospecies within a given genus were
121 previously linked with genetic groups. Finally, some genetic groups represented species lacking
122 sufficient taxonomic understanding, including sequence data in closely related species, to
123 determine whether or not they corresponded to sector 8 records (listed as “genetic groups of
124 uncertain morphospecies assignment and relation to reported sector 8 flora” in Table 1).

125

126 **Results**

127 In total, we generated 655 new barcode records for COI-5P, 11 for *tufA*, 41 for *rbcL*, and
128 nine for *rbcL*-3P (Table 1). These records represented 51 species of Phaeophyceae, nine species
129 of Chlorophyta, and 74 Rhodophyta. Of these records, there were 113 confirmed morphological
130 species listed in the area, 14 of which represented tentative identifications pending taxonomic
131 work (Table 1). Seventeen species represented new records for sector 8, only six of these records
132 were linked to formal species (Table 1; Fig. 1). The final four species records represented genetic
133 groups whose relation to the sector 8 flora remained unclear (Table 1). Seven genetic groups
134 were linked to morphological species through the current study.

135 **Discussion**

136 Our work represents the first comprehensive survey of Hordaland county macroalgae
137 using DNA barcoding, and has yielded novel insight on levels of biodiversity present in the area.
138 Our work, however, is not without limitations. The most obvious caveat is the varying degree of
139 uncertainty with which genetic groups have been assigned to correct morphological species.

140 Here, links are primarily based on observations of diagnostic features and by comparison to
141 material from the type localities. However, some of these assignments may be subject to change.
142 As well, due to the limited temporal and spatial coverage of our sampling, we likely missed some
143 species that are otherwise common in certain locations or times of year. For instance, genetic
144 groups corresponding to *Petalonia* and *Scytosiphon* were recovered, but did not correspond to
145 the reported morphospecies *Petalonia fascia* (O.F.Müller) Kuntze and *Scytosiphon lomentaria*
146 (Lyngbye) Link. More extensive sampling may yet recover these morphospecies, and their
147 absence from our study does not necessarily imply their absence from sector 8.

148 Despite the above limitations, several findings can be highlighted from our sampling.
149 First, the molecular data were quite congruent with the morphological listings, with the majority
150 of the species recovered based on molecular data confirming listed morphospecies (113/134).
151 This indicates the morphological work of taxonomists studying this flora (references in
152 Brattegard & Holte 2001) is generally a good representation of the species diversity present in
153 Norway. This stands in contrast to other northern systems wherein DNA barcoding has revealed
154 considerable taxonomic confusion in marine flora, such as in the Arctic basin (e.g., Saunders &
155 McDevit 2013; Bringloe et al. 2017; Bringloe & Saunders 2019). Nonetheless, sequence data
156 revealed new records to sector 8. Some of these species appear to represent cryptic genetic
157 groups within reported morphospecies, and potentially represent unrecognized species (viz.
158 *Petalonia fascia*, *Phycodrys rubens* (Linnaeus) Batters, *Scytosiphon lomentaria*, and
159 *Rhodophyllis divaricata* (Stackhouse) Papenfuss; Table 1). Similarly, many of the tentative
160 molecular confirmations are subject to scrutiny given the presence of cryptic genetic groups in
161 other areas of the globe (viz. *Asperococcus bullosus* J.V. Lamouroux, *Codium fragile* [Suringar]
162 Hariot, *Desmarestia aculeata* [Linnaeus] J.V.Lamouroux, *Ectocarpus siliculosus* [Dillwyn]

163 Lyngbye, *Elachista fucicola* [Velley] Areschoug, *Halosiphon tomentosus* [Lyngbye] Jaasund,
164 *Monostroma grevillei* [Thuret] Wittrock, *Phymatolithon lenormandii* [Areschoug] Adey,
165 *Polysiphonia stricta* [Mertens ex Dillwyn] Greville, *Pterothamnion plumula* [J.Ellis] Nägeli,
166 *Vertebrata fucoides* [Hudson] Kuntze; Table S2). In the previous examples it has yet to be
167 determined which of the genetic partners represents the bona fide species and which requires a
168 different name. In contrast, recent taxonomic work has resolved identifications in some cryptic
169 species groups, including two morphospecies reported here (Phaeophyceans *Chorda filum*
170 [Linnaeus] Stackhouse and *Eudesme borealis* H.Kawai, T.Hanyuda & A.F.Peters; Kawai et al.
171 2019a, 2019b). Alternatively, some of the new species records to sector 8 may correspond to
172 morphological listings from adjacent sectors and, as such, the full list of Norwegian species
173 should be considered during future taxonomic work. Cumulatively, these cases further highlight
174 the utility of sequence data to unmask hidden diversity and inform taxonomic revisions.

175 The need for taxonomic work can be extended to the set of genetic records for which
176 morphological assignment and relation to the sector 8 flora remained uncertain. Further sampling
177 and linking of genetic groups to morphospecies would shed light on these records, some of
178 which are likely to confirm additional morphospecies from sector 8. In particular, the
179 Rhodophyte *Hildenbrandia rubra* (Sommerfelt) Meneghini has its type locality in Nordland
180 (north of Bergen), however, more sampling is required to determine if our genetic group
181 corresponds to this morphospecies, as several dozens of genetic groups throughout the Northern
182 Hemisphere are assignable to *H. rubra* (Table S2). The genetic record tentatively identified as
183 Tilopteridalean sp. further showcases the limited taxonomic understanding in crustose
184 macroalgal species.

185 Interesting biogeographic patterns can also be noted for several Rhodophytes from our
186 sampling. *Coccotylus brodiei* (Turner) Kützing and *Erythrodermis traillii* (Holmes ex Batters)
187 Guiry & Garbary were previously inferred from sector 8 but are verified for the first time here
188 (Fig. 1, Table S2). Known ranges can also be extended northwards in *Fredericqia deveauniensis*
189 Maggs, L.Le Gall, Mineur, Provan & G.W.Saunders and *Meredithia microphylla* (J.Agardh)
190 J.Agardh, which were previously reported from more southerly European locations (Guiry &
191 Guiry 2019). Also worth noting is the presence of several species also reported from the Bering
192 Sea, indicating the Norwegian flora is characterized by a number of broadly distributed cold-
193 tolerant species (viz. *Coccotylus truncatus* [Pallas] M.J.Wynne & J.N.Heine, *E. borealis*, *Fucus*
194 *distichus* Linnaeus, *Haplospora globosa* Kjellman, *Lithothamnion glaciale* Kjellman,
195 *Odonthalia dentata* [Linnaeus] Lyngbye, *Planosiphon zosterifolius* [Reinke] McDevit &
196 G.W.Saunders, *Ulva fenestrata* Postels & Ruprecht previously reported from the Arctic as *Ulva*
197 *lactuca* Linnaeus, *Urospora* sp.; Table 1; Table S2; Saunders & McDevit 2013, Bringloe et al.
198 2019). This pattern was summarized for cold temperate and Arctic floras by Lüning in 1990,
199 however, subsequent genetic surveys indicate substantial population differentiation across these
200 ranges, some of which may represent incipient speciation (Saunders & McDevit 2013, Bringloe
201 & Saunders 2018).

202 On a final note, a large portion of the sector 8 marine flora remains to be sequenced.
203 Morphological listings indicated 117 species of Phaeophyceae, 70 species of Chlorophyta, and
204 149 species of Rhodophyta are present in the area (Table S3); of these, we genetically confirmed
205 the presence of 43 brown (37%), seven green (10%), and 62 (42%) red macroalgal species, only
206 a third of all the morphological species listed. Many of the remaining species are microscopic,
207 and will require considerable efforts to sample and possibly cultivate for subsequent DNA

208 analysis. Return efforts to DNA barcode the flora of sector 8, and indeed the entirety of the
209 coastline of Norway, are therefore expected to be productive, further assigning genetic data to
210 morphospecies and unmasking cryptic diversity or species complexes in need of taxonomic
211 revision.

212

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340 Table 1. Summary of results from a DNA barcode survey of marine flora in Bergen and surrounding area (sector 8). An asterisk
 341 indicates species wherein the species name has been updated since Brattegard & Holte 2001; ¹indicates species wherein the genetic
 342 group was linked to the morphological listing through the current study. Note some molecular listings are tentative, pending further
 343 taxonomic work.

Species	Sample sizes and notes
Confirmed morphological listings	
Chlorophyta	
<i>Acrosiphonia arcta</i> (Dillwyn) Gain*	n=1: taxonomic name updated from <i>Spongomorpha arcta</i> (Dillwyn) Kützing.
<i>Codium fragile</i> (Suringar) Hariot	Tentative; n=3: this species occurs as two genetic groups in the North Atlantic. The genetic group sampled here also occurs in the Northwest Atlantic, while a second genetic group is confirmed from the Northeast Atlantic and the Northeast Pacific (Table S2).
<i>Monostroma grevillei</i> (Thuret) Wittrock	Tentative; n=1: this species occurs as two genetic groups, one in the North Pacific and one in the North Atlantic; taxonomic work is needed to determine which is true <i>M. grevillei</i> .
<i>Prasiola furfuracea</i> (Mertens ex Hornemann) Trevisan	Tentative; n=1: taxonomic work is needed to determine if <i>P. furfuracea</i> differs from <i>Prasiola borealis</i> M.Reed (<i>tufA</i> differs at a single site across 574 bp); if these species are the same, <i>P. furfuracea</i> has nomenclatural priority (Moniz <i>et al.</i> 2014).
<i>Spongomorpha aeruginosa</i> (Linnaeus) Hoek	n=1
<i>Ulva intestinalis</i> Linnaeus*	n=1: taxonomic name updated from <i>Enteromorpha intestinalis</i> (Linnaeus) Nees.
<i>Ulothrix flacca</i> (Dillwyn) Thuret	n=1
<i>Ulva fenestrata</i> Postels & Ruprecht*	n=1: specimens from this region were previously incorrectly identified as <i>Ulva lactuca</i> Linnaeus.
Phaeophyceae	
<i>Acrothrix gracilis</i> Kylin	n=1

<i>Alaria esculenta</i> (Linnaeus) Greville	n=21
<i>Ascophyllum nodosum</i> (Linnaeus) Le Jolis	n=1
<i>Asperococcus bullosus</i> J.V. Lamouroux*	Tentative; n=5: data revealed distinct genetic groups assignable to this morphological listing for our collections from Australia versus Norway. Taxonomic name updated from <i>Asperococcus turneri</i> (J.E.Smith) W.J.Hooker.
<i>Asperococcus fistulosus</i> (Hudson) Hooker	n=3
<i>Chaetopterus plumosa</i> (Lyngbye) Kützing*	n=7: taxonomic name updated from <i>Sphacelaria plumosa</i> Lyngbye.
<i>Chorda filum</i> (Linnaeus) Stackhouse	n=7
<i>Chordaria flagelliformis</i> (O.F.Müller) C.Agardh	n=3
<i>Cladostephus spongiosum</i> (Hudson) C.Agardh	n=2
<i>Cutleria multifida</i> (Turner) Greville	n=1
<i>Desmarestia aculeata</i> (Linnaeus) J.V.Lamouroux	Tentative; n=9: two distinct and geographically widespread COI-5P genetic groups are assignable to this morphological species (Table S2). Our Norway collections are assignable to only one of those genetic groups; taxonomic work is needed.
<i>Dictyota dichotoma</i> (Hudson) J.V.Lamouroux	n=5
<i>Ectocarpus fasciculatus</i> Harvey	n=6
<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye	Tentative; n=1: three COI-5P genetic groups are assignable to this morphospecies (Table S2). The Norway specimen joins a genetic group with collections from British Columbia and the Atlantic Provinces, Canada.
<i>Elachista fucicola</i> (Velley) Areschoug	n=1: two COI-5P genetic groups are assignable to this morphological listing, one thus far confined to the northeast Pacific and the other the Canadian Arctic and Atlantic Provinces, as well as New England, USA. This specimen from Norway joins the North Atlantic/Arctic group, which likely represents bona fide <i>E. fucicola</i> .
<i>Fucus distichus</i> Linnaeus	n=1
<i>Fucus serratus</i> Linnaeus	n=2
<i>Fucus spiralis</i> Linnaeus	n=2: recent genomic work continues the ongoing debate regarding recognition of this genetic group at the species level (Alvarez et al. 2018).

<i>Fucus vesiculosus</i> Linnaeus	n=2
<i>Halidrys siliquosa</i> (Linnaeus) Lyngbye	n=4
<i>Halosiphon tomentosus</i> (Lyngbye) Jaasund	Tentative; n=1: two COI-5P genetic groups are assignable to this morphological listing (Table S2). One extends from Nome, Alaska to Churchill, Hudson Bay, while the other is found in the Canadian Atlantic Provinces, as well as New England, USA (Bringloe & Saunders 2019). This specimen from Norway joins the North Atlantic group.
<i>Haplospora globosa</i> Kjellman	n=1
<i>Himanthalia elongata</i> (Linnaeus) S.F.Gray ¹	n=2
<i>Hincksia hincksiae</i> (Harvey) P.C.Silva	n=1
<i>Isthmoplea sphaerophora</i> (Carmichael) Gobi	n=1
<i>Laminaria digitata</i> (Hudson) J.V.Lamouroux	n=6
<i>Laminaria hyperborea</i> (Gunnerus) Foslie	n=15
<i>Leathesia marina</i> (Lyngbye) Decaisne*	n=2: taxonomic name updated from <i>Leathesia difformis</i> (Linnaeus) Areschoug.
<i>Mesogloia vermiculata</i> (Smith) S.F.Gray	n=2
<i>Myrionema strangulans</i> Greville	n=1
<i>Pelvetia canaliculata</i> (Linnaeus) Decaisne & Thuret	n=1
<i>Planosiphon zosterifolius</i> (Reinke) McDevit & G.W.Saunders*	n=1: taxonomic name updated from <i>Petalonia zosterifolia</i> (Reinke) Kuntze.
<i>Punctaria latifolia</i> Greville	n=1
<i>Pylaiella littoralis</i> (Linnaeus) Kjellman ¹	n=1
<i>Pylaiella varia</i> Kjellman ¹	n=2
<i>Saccharina latissima</i> (Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W.Saunders*	n=14: taxonomic name updated from <i>Laminaria saccharina</i> (Linnaeus) Lamouroux.
<i>Saccorhiza polyschides</i> (Lightfoot) Batters	n=1
<i>Sargassum muticum</i> (Yendo) Fensholt	n=3

<i>Spermatochnus paradoxus</i> (Roth) Kützing	n=1
<i>Sphacelaria cirrosa</i> (Roth) C.Agardh	n=5
<i>Spongonema tomentosum</i> (Hudson) Kützing	n=3
<i>Stictyosiphon soriferus</i> (Reinke) Rosenvinge	n=1
<i>Striaria attenuata</i> (Greville) Greville	n=2
<hr/>	
Rhodophyta	
<hr/>	
<i>Aglaothamnion tenuissimum</i> (Bonnemaison) Feldmann-Mazoyer	n=1
<i>Ahnfeltia plicata</i> (Hudson) Fries	n=18
<i>Bangia fuscopurpurea</i> (Dwillwyn) Lyngbye*	Tentative; n=1: taxonomic work continues for this genus. Specimens from this region were previously incorrectly identified as <i>Bangia atropurpurea</i> (Roth) C.Agardh.
<i>Bonnemaisonia asparagoides</i> (Woodward) C.Agardh	n=3
<i>Bonnemaisonia hamifera</i> Hariot	n=4
<i>Carradoriella elongata</i> (Hudson) A.M.Savoie & G.W.Saunders*	n=7: taxonomic name updated from <i>Polysiphonia elongata</i> (Hudson) Sprengel.
<i>Catenella caespitosa</i> (Withering) L.M.Irvine ¹	n=1
<i>Ceramium pallidum</i> (Kützing) Maggs & Hommersand	n=5
<i>Ceramium secundatum</i> Lyngbye	n=3
<i>Ceramium shuttleworthianum</i> (Kützing) Rabenhorst	n=1
<i>Ceramium virgatum</i> Roth*	n=5: taxonomic name updated from <i>Ceramium nodulosum</i> (Lightfoot) Ducluzeau.
<i>Chondrus crispus</i> Stackhouse	n=6
<i>Chylocladia verticillata</i> (Lightfoot) Bliding ¹	n=6
<i>Coccotylus truncatus</i> (Pallas) M.J.Wynne & J.N.Heine	n=1

<i>Corallina officinalis</i> Linnaeus	n=5
<i>Cryptopleura ramosa</i> (Hudson) L.Newton	n=5
<i>Cystoclonium purpureum</i> (Hudson) Batters	n=13
<i>Dasysiphonia japonica</i> (Yendo) H.-S.Kim	n=10
<i>Delesseria sanguinea</i> (Hudson) J.V.Lamouroux	n=12
<i>Dilsea carnosa</i> (Schmidel) Kuntze	n=5
<i>Dumontia contorta</i> (S.G.Gmelin) Ruprecht	n=1
<i>Erythrodermis traillii</i> (Holmes ex Batters) Guiry & Garbary	n=3: this species was previously inferred from sector 8 (Brattegard & Holte 2001).
<i>Euthora cristata</i> (C.Agardh) J.Agardh*	n=29: taxonomic name updated from <i>Callophyllis cristata</i> (C.Agardh) Kützing.
<i>Gaillona seposita</i> (Gunnerus) Athanasiadis*	n=1: taxonomic name updated from <i>Aglaothamnion sepositum</i> (Gunnerus) Maggs & Hommersand.
<i>Gelidium spinosum</i> (S.G.Gmelin) P.C.Silva	n=3
<i>Gloiosiphonia capillaris</i> (Hudson) Carmichael	n=1
<i>Griffithisia corallinoides</i> (Linnaeus) Trevisan	n=3
<i>Halarachnion ligulatum</i> (Woodward) Kützing ¹	n=1
<i>Haraldiophyllum bonnemaisonii</i> (Kylin) A.D.Zinova	n=1
<i>Heterosiphonia plumosa</i> (J.Ellis) Batters	n=2
<i>Leptosiphonia brodiei</i> (Dillwyn) A.M.Savoie & G.W.Saunders*	n=2: taxonomic name updated from <i>Polysiphonia brodiei</i> (Dillwyn) Sprengel.
<i>Leptosiphonia fibrillosa</i> (Dillwyn) A.M.Savoie & G.W.Saunders*	n=6: taxonomic name updated from <i>Polysiphonia fibrillosa</i> (C.Agardh) Sprengel.
<i>Lithothamnion glaciale</i> Kjellman	n=4
<i>Lomentaria clavellosa</i> (Lightfoot ex Turner) Gaillon	n=13
<i>Lomentaria orcadensis</i> (Harvey) Collins ¹	n=1
<i>Mastocarpus stellatus</i> (Stackhouse) Guiry	n=5

<i>Membranoptera alata</i> (Hudson) Stackhouse	n=7
<i>Metacallophyllis laciniata</i> (Hudson) A.Vergés & L.Le Gall*	n=13: taxonomic name updated from <i>Callophyllis laciniata</i> (Hudson) Kützing.
<i>Nitophyllum punctatum</i> (Stackhouse) Greville	n=2
<i>Odonthalia dentata</i> (Linnaeus) Lyngbye	n=26
<i>Osmundea oederi</i> (Gunnerus) G.Furnari	n=2
<i>Osmundea pinnatifida</i> (Hudson) Stackhouse	n=2
<i>Palmaria palmata</i> (Linnaeus) F.Weber & D.Mohr	n=3
<i>Phycodrys rubens</i> (Linnaeus) Batters	Tentative; n=45: given the presence of two genetic groups potentially corresponding to <i>P. rubens</i> , name assignment is tentative pending taxonomic work. Regardless it should apply to one of the two genetic groups that we have uncovered in this flora (see <i>Phycodrys</i> sp. below).
<i>Phyllophora crispa</i> (Hudson) P.S.Dixon	n=9
<i>Phyllophora pseudoceranoioides</i> (S2.G.Gmelin) Newroth & A.R.A.Taylor ex P.S.Dixon & L.M.Irvine	n=16
<i>Phymatolithon lenormandii</i> (Areschoug) Adey	Tentative; n=1: two COI-5P genetic groups are assignable to this species, this sequence from Norway and sequences for collections from the Northwest Atlantic (Table S2).
<i>Plocamium lyngbyanum</i> Kützing*	n=5: specimens from this region were previously incorrectly identified as <i>Plocamium cartilagineum</i> (Linnaeus) Dixon.
<i>Polyides rotundus</i> (Hudson) Gaillon	n=2
<i>Polysiphonia stricta</i> (Mertens ex Dillwyn) Greville	Tentative; n=7: three COI-5P genetic groups are assignable to this morphospecies with specimens from Norway joining a genetic group confined to the North Atlantic (Table S2). Taxonomic work is needed.
<i>Porphyra umbilicalis</i> Kützing	n=2
<i>Pterothamnion plumula</i> (J.Ellis) Nägeli	Tentative; n=4: two COI-5P genetic groups are assignable to this morphospecies, taxonomic work is needed (Table S2).
<i>Ptilota gunneri</i> P.C.Silva, Maggs & L.M.Irvine	n=39
<i>Pyropia leucosticta</i> (Thuret) Neefus & J.Brodiei*	n=4: taxonomic name updated from <i>Porphyra leucosticta</i> Thuret.
<i>Rhodomela confervoides</i> (Hudson) P.C.Silva	n=25

<i>Rhodomela lycopodioides</i> (Linnaeus) C.Agardh	n=19
<i>Rhodophyllis divaricata</i> (Stackhouse) Papenfuss	Tentative; n=6: four COI-5P genetic groups are potentially assignable to this morphospecies (Table S2), two of which were recovered here. Taxonomic work is needed.
<i>Seirospora interrupta</i> (Smith) F.Schmitz	n=1
<i>Vertebrata byssoides</i> (Goodenough & Woodward) Kuntze*	n=1: taxonomic name updated from <i>Brongniartella byssoides</i> (Goodenough & Woodward) Schmitz.
<i>Vertebrata fucoides</i> (Hudson) Kuntze*	Tentative; n=2: two COI-5P genetic groups are assignable to this morphospecies, one confined to the Northwest Atlantic and the other on both sides of the North Atlantic, the specimens from Norway joining the latter group (Savoie & Saunders 2019; Table S2). Taxonomic name updated from <i>Polysiphonia fucoides</i> (Hudson) Greville.
<i>Vertebrata lanosa</i> (Linnaeus) T.A.Christensen*	n=4: taxonomic name updated from <i>Polysiphonia lanosa</i> (Linnaeus) Tandy.
<i>Wildemanina amplissima</i> (Kjellman) Foslie	n=2
New records for described species	
Phaeophyceae	
<i>Eudesme borealis</i> H.Kawai, T.Hanyuda & A.F.Peters	n=2: though <i>Eudesme virescens</i> (Carmichael ex Berkeley) J.Agardh occurs in sub-boreal European waters, our genetic data matched the newly established and broadly distributed <i>Eudesme borealis</i> H.Kawai, T.Hanyuda, A.F.Peters (Kawai et al. 2019b).
<i>Scytosiphon promiscuus</i> McDevit & G.W.Saunders	n=1: this species was recently described by McDevit & Saunders (2017).
Rhodophyta	
<i>Coccotylus brodiei</i> (Turner) Kützing	n=31: though reported from Northern Norway (Guiry & Guiry 2019), these are the first genetically verified records from the Bergen area.
<i>Fredericqia deveauniensis</i> Maggs, L.Le Gall, Mineur, Provan & G.W.Saunders	n=1: this species was previously reported from more southerly European areas (Guiry & Guiry 2019).
<i>Meredithia microphylla</i> (J.Agardh) J.Agardh	n=1: this species is previously reported from more southerly European areas (Guiry & Guiry 2019).
<i>Titanoderma macrocarpum</i> (J.V.Lamouroux) Nägeli	n=1: see Saunders (2019) for taxonomic notes.
New records for species lacking formal description or morphospecies assignment	

Chlorophyta	
<i>Urospora</i> sp.	n=1: the genetic group recovered did not match <i>Urospora penicilliformis</i> (Roth) Areschoug, the only species of <i>Urospora</i> reported for the area; rather, this genetic group most closely matched <i>Urospora wormskioldii</i> (Mertens ex Hornemann) Rosenvinge (97%). This genetic group was previously reported as <i>Urospora</i> sp. 2Nome from Nome, Alaska (Bringloe and Saunders 2019; Table S2); taxonomic work is needed.
Phaeophyceae	
<i>Ectocarpus</i> sp.	n=1: a third <i>Ectocarpus</i> genetic group was recovered, despite only two being listed in the flora.
<i>Myriotrichia</i> sp.	n=1: this newly sampled genetic group does not match <i>Myriotrichia clavaeformis</i> Harvey, leaving only <i>Myriotrichia repens</i> Hauck, also reported in the area, as a putative match. However, microscopic examination of the host brown alga did not reveal the latter species leaving the identification uncertain but indicating the presence of a new record.
<i>Petalonia</i> sp.	n=1: this genetic group does not correspond to <i>Petalonia fascia</i> , the only species of <i>Petalonia</i> reported and genetically confirmed in the area (AB860189). Taxonomic work is needed to assign a species name.
<i>Scytosiphon</i> sp.	n=3: another <i>Scytosiphon</i> genetic group was recovered, which also did not correspond to <i>Scytosiphon lomentaria</i> (Lyngbye) Link, the only reported species of <i>Scytosiphon</i> reported from the area. Considerably more sampling is necessary given the diversity of <i>Scytosiphon</i> spp. in the North Atlantic (McDevit & Saunders 2017).
Rhodophyta	
<i>Ceramium</i> spp.	n=2: a further two new genetic groups for <i>Ceramium</i> were recovered. Based on <i>rbcL</i> data, one is closely related to <i>C. secundatum</i> (99%; also reported from France as <i>Ceramium</i> sp. MAR5), while the other is a close match to <i>Ceramium pallidum</i> (Kützinger) Maggs & Hommersand (98%). The genetic groups recovered here also do not match published <i>rbcL</i> data for the other species of <i>Ceramium</i> listed for the area (Gabrielsen <i>et al.</i> 2003; Wolf <i>et al.</i> 2011; Hughey & Boo 2016). As such, two new records for <i>Ceramium</i> are inferred here, but taxonomic work is needed to assign a species name or description.

<i>Lomentaria</i> sp.	n=1: this genetic group is a close match to <i>L. clavellosa</i> (based on COI-5P; 97%). <i>Lomentaria articulata</i> (Hudson) Lyngbye is listed for the area (Brattegard & Holte 2001), but is currently linked to a different genetic group, indicating the presence of a new species.
<i>Phycodrys</i> sp.	n=22: this genetic group was originally reported from Europe by van Oppen et al. (1995). Taxonomic work is needed to assign a species name, and to determine whether the genetic group above has been correctly assigned to <i>P. rubens</i> .
<i>Polysiphonia</i> sp.	n=6: this genetic group corresponds to <i>Polysiphonia</i> sp. 23GWS, which was previously limited to two specimens from Rhode Island, USA, and one from the Bay of Fundy, New Brunswick, Canada (Savoie & Saunders 2019). In addition to <i>P. stricta</i> , <i>Polysiphonia hemisphaerica</i> Areschoug is also reported from sector 8, however, our sequence is a distant match to published COI-5P and <i>rbcL</i> data for this species (Rueness 2010; Díaz-Tapia et al. 2018). As such, a new record for <i>Polysiphonia</i> is inferred here, but taxonomic work is needed to assign a species name or description.
<i>Rhodophyllis</i> sp.	n=5: as with <i>Phycodrys</i> , multiple genetic groups corresponding to a single morphological listing were recovered, in this case potentially corresponding to <i>R. divaricata</i> . Taxonomic work is needed to assign a species name to the multiple groups listed in Table S2, and to determine whether the correct genetic group has been assigned to <i>R. divaricata</i> .

Genetic groups of uncertain morphospecies assignment and relation to reported sector 8 flora

Phaeophyceae

<i>Lithoderma</i> sp.	n=2: <i>Pseudolithoderma extensum</i> (P.Crouan & H.Crouan) S.Lund has been reported from Norway, but our genetic group allies closer to species that we have tentatively assigned to <i>Lithoderma</i> (Table S2). This genetic group is potentially assignable to <i>Lithoderma fatiscens</i> Areschoug, which is reported from Swedish and Arctic waters (Rueness 1977). Taxonomic work is needed.
Tilopteridalean sp.	n=1: it remains unclear whether or not this crustose specimen corresponds to any of the species listed by Brattegard & Holte (2001).

Rhodophyta

<i>Hildenbrandia</i> sp.	n=1: several dozens of COI-5P genetic groups are assignable to
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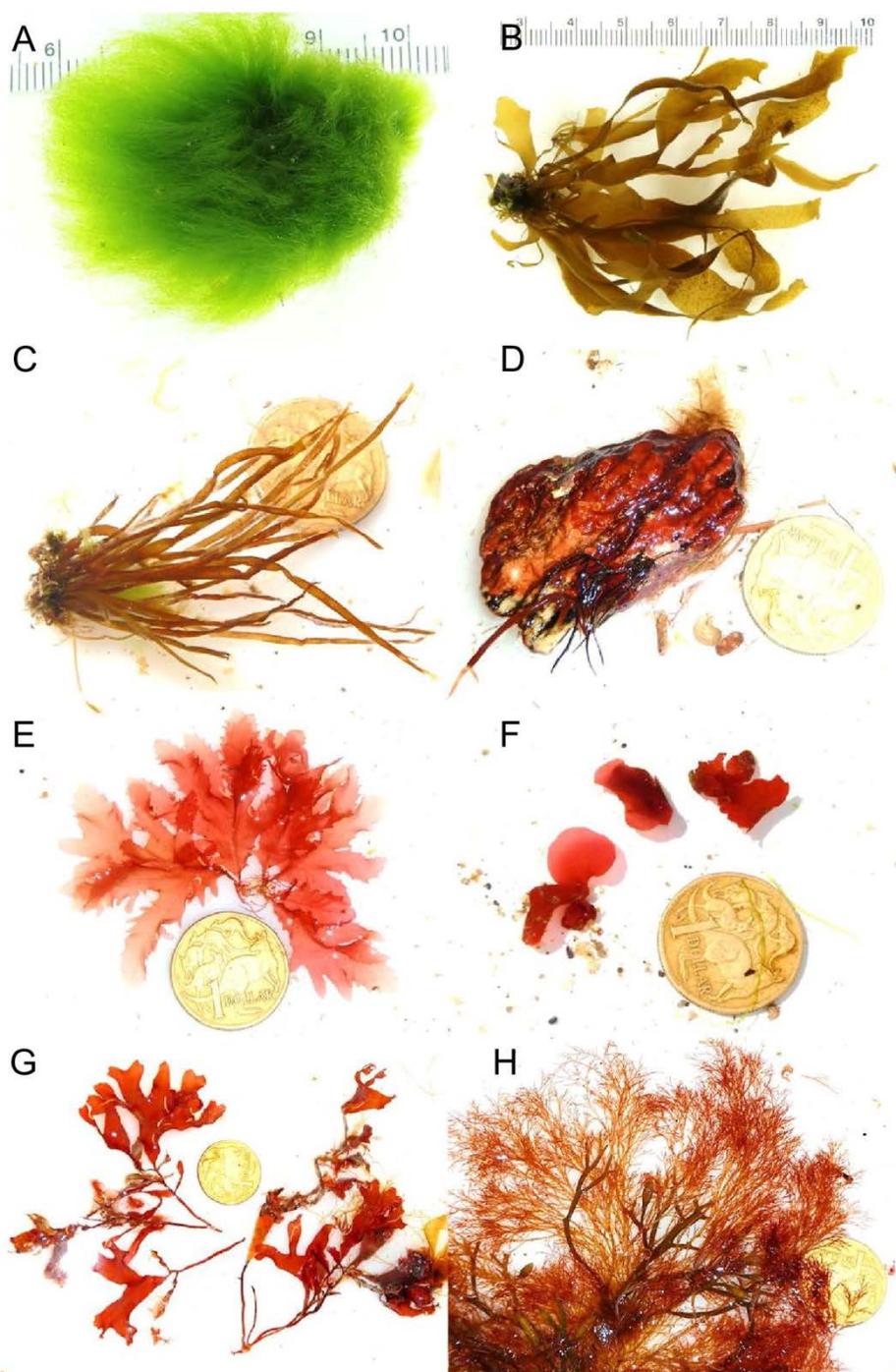
Hildenbrandia rubra (Sommerfelt) Meneghini (examples provided in Table S2). As such, we cannot be certain if this genetic group corresponds to *H. rubra* or represents a new record for sector 8. We do note, however, that *H. rubra* has its type locality in Nordland (north of Bergen; Guiry & Guiry 2019). More sampling and substantial taxonomic work is needed in this genus.

Rhodomelacean sp.

n=4: this genetic group allies to the tribe Pterosiphoniae based on both COI-5P and *rbcL*, but insufficient sequence data and taxonomic information exists to determine if this genetic group corresponds to any of the species listed by Brattegard & Holte (2001).

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347 Figure 1. Marine macroalgae sampled from sector 8, Bergen area, April 14-20 and July 3-13,
 348 2016. Confirmed record: A) *Acrosiphonia arcta* (2016_BIO309A_61); new records: B)
 349 *Petalonia* sp. (2016_BIO309A_57); C) *Scytosiphon* sp. (GWS040911); D) *Hildenbrandia* sp.
 350 (GWS040997); E) *Phycodrys* sp. (GWS040070); F) *Meredithia microphylla* (GWS040886); G)
 351 *Coccotylus brodiei* (GWS040736); H) *Ceramium* sp. (GWS040811). A cm ruler is used for
 352 scale, or otherwise an Australian dollar (diameter of 2.5 cm).