

RESEARCH ARTICLE

Incorporating historic specimens to reassess *Ulva* diversity in the Netherlands and Belgium

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Abstract While DNA-assisted identifications have significantly enhanced our understanding of *Ulva* diversity, they have also widened the gap between historical taxonomic and floristic studies based solely on morphology and contemporary studies utilizing DNA sequences. To bridge this gap, we compared historical assessments of *Ulva* sensu lato diversity in the Netherlands and Belgium with molecular-based identifications. By combining DNA barcoding of recent field collections with NGS data from historical herbarium voucher specimens, we confirmed the presence of 17 *Ulva* species using *tufA* barcoding, including three unidentified clades. Additionally, we identified *Blidingia marginata*, *B. minima*, *Monostroma grevillei*, *Umbraulva dangeardii*, and a taxonomic entity that matched reference sequences of both *Gayralia oxy sperma* and *Kormmannia leptoderma*. Of the 24 species previously reported in the southern North Sea based on published literature, only 13 species were molecularly confirmed, highlighting the substantial discrepancy between traditional and DNA-based species identifications in this group of algae. Integrating historical herbarium vouchers into our biodiversity assessment revealed that this mismatch was largely due to misinterpretation of names and to a lesser extent changing species concepts. Plastid genome and nuclear ribosomal DNA assemblies of *Ulva intestinaloides* and *U. pseudolinza* type material showed that their ITS, *rbcL*, and *tufA* sequences were identical or highly similar to reference sequences of *U. compressa* and *U. intestinalis*, respectively, indicating that they are synonyms of these species. Finally, we report four new species records for the southern North Sea: *Ulva capillata* and *Umbraulva dangeardii* that are native to the Northeast Atlantic, and the non-indigenous *Ulva californica* and *U. shanxiensis*. The latter is a freshwater species that has not been recorded outside China until now. The discovery of unidentified clades and non-native species in the southern North Sea emphasizes the importance of molecular monitoring in uncovering cryptic diversity and improving our understanding of *Ulva* biodiversity.

Keywords biodiversity; DNA barcoding; historical vouchers; taxonomy; Ulvales

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Green seaweeds of the genus *Ulva* L. represent one of the most common and most ubiquitous groups of macroalgal species (Mantri & al., 2020). *Ulva* species occur worldwide from tropic to arctic ecosystems, and their high tolerance to environmental variables such as light, salinity, and temperature enables them to thrive in a staggering variety of habitats, rarely seen in other algal genera (Rybak, 2018; Beer, 2023). In coastal ecosystems, *Ulva* serves as an important food source for herbivores (Green & Fong, 2016; Storero & al., 2022) and its commercial cultivation is increasingly gaining interest as a sustainable resource for food, feed, and biomaterials (Bolton & al., 2016; Steinhagen & al., 2022). However, *Ulva*

species are also notorious for developing extensive blooms, known as green tides, posing significant hazards (Fletcher, 1996; Ye & al., 2011). Although *Ulva* has a rich taxonomic history, identifying species of the genus *Ulva* remains challenging even in well-studied regions such as the European coasts (Fort & al., 2021; Tran & al., 2022).

Currently, over 100 taxonomically accepted *Ulva* species are listed in AlgaeBase (Guiry & Guiry, 2024). These species display a tremendous amount of morphological variation and cryptic diversity (Steinhagen & al., 2023b). Morphological identifications of *Ulva* species are based on characteristics such as colour, texture, the presence of blade perforations and marginal dentation, cell size, chloroplast shape, the number of pyrenoids, etc., but these characteristics

are far from reliable. Not only is there a lot of morphological variation within species, there are also a lot of overlapping characteristics between species. In addition, the morphology of the Ulvaceae overlaps with foliose and tubular species from other families (e.g., Gayraliaceae, Kornmanniaceae, Monostromataceae). As a consequence, *Ulva* species are extremely difficult to identify based on morphology. In the recent 20 years, DNA-based studies have significantly improved our understanding of *Ulva* diversity (Hughey & al., 2019, 2021, 2022; Fort & al., 2021; Steinhagen & al., 2023b). Yet, there is still considerable taxonomic confusion, as DNA analyses can only provide a correct identification if based on a solid reference database, preferably including sequences of type material. For example, sequencing the lectotype material of *U. rigida* revealed that none of the DNA sequences deposited in public databases under that name matched the lectotype sequence. Instead, the majority of those sequences were identical to the lectotype of *U. lacinulata* (Hughey & al., 2022). This example shows that a better characterisation of type material through gene sequencing is necessary to avoid the continued misapplication of names.

The Netherlands is arguably one of the most thoroughly studied regions for *Ulva* biodiversity and taxonomy. Extensive collections and species descriptions date back to the early 19th century, with contributions by F.T. Kützing, W.F.R. Suringar, A. Weber-van Bosse, and A.C.J. van Goor, followed by, amongst others, C. den Hartog, P.H. Nienhuis, and H. Stegenga in the 20th century. In the 1980s, Koeman and Van den Hoek provided a comprehensive overview on *Ulva* biodiversity in the Netherlands, resulting in the description of *U. intestinaloides* (Koeman & C.Hoek) H.S.Hayden & al. and *U. pseudolinza* (Koeman & C.Hoek) H.S.Hayden & al. (Koeman & Van den Hoek, 1982a). However, significant changes in *Ulva* taxonomy and species concepts since then warrant a re-evaluation of earlier findings. The Naturalis Biodiversity Center (the Netherlands) and Meise Botanic Garden (Belgium) both house an extensive collection of macroalgae from the southern North Sea collected mainly in the second half of the 20th century, but also including older specimens. Integrating these historic herbarium specimens in current biodiversity assessment is essential to advance our understanding of *Ulva* diversity and taxonomy in the region.

The coasts of the Netherlands and Belgium are naturally characterised by sandy and muddy substrates. However, the construction of artificial structures such as dikes, breakwaters, canals, harbour walls, marinas, and the development of mussel and oyster aquaculture have introduced rocky and other hard substrates to this region, providing additional habitats for diverse macroalgae, including *Ulva*. Seaweed diversity in the region is known to include elements of neighbouring natural rocky shores, in addition to a substantial number of introduced species (Stegenga & al., 1997; Coppejans, 1998; Knoop & al., 2024; Van der Loos & al., 2024). The aim of this study is to provide a comprehensive assessment of *Ulva* s.l. (including morphologically similar *Blidingia*, *Gayralia*, *Kornmannia*, *Monostroma*, and *Umbraulva*) species diversity

in the southern North Sea using DNA barcoding. We combine recent field collections with historic herbarium vouchers dating back to 1845, including the type material of *Ulva intestinaloides* and *U. pseudolinza*, to provide an updated assessment of previously published checklists. This approach facilitates the detection of historical misinterpretations, newly introduced species, and patterns across seasons and habitat, offering new insights into *Ulva* biodiversity.

■ MATERIALS AND METHODS

Sample collection. — Foliose and tubular morphotypes resembling *Ulva* sensu lato (s.l.) were collected in the southern North Sea (Belgium and the Netherlands) between June 2019 and July 2023 (Appendix 1, $n = 274$ samples). In total, 37 sampling sites were visited to cover a variety of habitats, including intertidal artificial rocky shores, harbours/marinas, oyster beds, salt marshes, canals, saltwater lakes, brackish rivers, and freshwater lakes (Fig. 1). Of the 37 sites, eight locations were (re)sampled in both winter (20–23 February 2022) and summer (12–14 July 2022) to investigate seasonal patterns: Goese Sas, Kats, Kreek van Piet, Neeltje Jans pontoon, Neeltje Jans tidal pool, Oostende, Wemeldinge marina, and Yerseke (Fig. 1).

Each site was thoroughly investigated for different *Ulva* s.l. morphotypes across the present substrates. Surveys in tidal waters (e.g., Eastern Scheldt, North Sea coast) were conducted during low tide. Surveys in stagnant waters (e.g., Lake Grevelingen, canals) were conducted with waders to a depth of ~1.0 m below sea level. Representative specimens from all observed populations were photographed in the field, collected, and transported to the laboratory for further processing. In the laboratory, all individuals were photographed again and preserved as herbarium specimens. In addition, subsamples of ~1 cm² tissue were rinsed in fresh water, and conserved in silica for molecular analyses. Herbarium vouchers were deposited in the Meise Botanic Garden herbarium (BR) and the Naturalis Biodiversity Center herbarium (L) (see Appendix 1 for voucher numbers).

Molecular methods and phylogenetic analysis. — Genomic DNA was extracted from silica dried samples using a CTAB method (Doyle & Doyle, 1987). In short, samples were ground in liquid nitrogen and incubated for 60 minutes at 60°C in a CTAB buffer (500 µl cetyl-trimethyl-ammonium-bromide and 5 µl Proteinase-K at a concentration of 20 mg/ml). This was followed by two cleaning cycles with 24:1 chloroform:isoamyl alcohol and a final wash step in 70% ethanol before dissolving the extracted DNA in 50 µl 1× TE buffer. The chloroplast encoded *tufA* gene was amplified using forward primer *tufAF* (5'-TGA AAC AGA AMA WCG TCA TTA TGC-3') and reserve primer *tufAR* (5'-CCT TCN CGA ATM GCR AAW CGC-3') yielding a ~800 bp fragment (Verbruggen & al., 2009). PCR mixtures consisted of 2.5 µl PCR buffer, 2.5 µl dNTP's (200 µM), 1.25 µl forward primer (10 µM), 1.25 µl reverse primer (10 µM), 1 µl BSA

(10 µg/µl), 1.25 µl Taq (1U/µl) and 1 µl sample template. PCRs were run with a thermal profile of 3 min initial denaturation at 94°C, 40 cycles of 1 min at 94°C; 1 min at 45°C; 2 min at 72°C, and 5 min final extension at 72°C. All PCR products were verified by gel electrophoresis and Sanger sequenced by Macrogen (Amsterdam, the Netherlands).

Raw sequences were trimmed and quality checked in BioNumerics v.7 (applied Maths NV). Processed sequences were aligned with MAFFT v.7.154b (Katoh & al., 2002) and trimmed with trimAl v.1.2rev59 using gappout settings (Capella-Gutiérrez & al., 2009) (suppl. Appendix S1). Maximum likelihood phylogenetic trees were generated with IQ-TREE v.1.6.12 using an automated model finder with 1000 ultrafast bootstrap iterations (Nguyen & al., 2015). Species names used in the phylogenetic trees were based on peer-reviewed reference sequences retrieved from NCBI GenBank, following the latest taxonomic revisions by Steinhagen & al. (2023b) and Maggs & al. (2024) as integrated in AlgaeBase (Guiry & Guiry, 2024). The phylogenetic trees include all species relevant to the study area, incorporating available *tufA* sequences of type material.

All sequences, trace files, metadata, and photos were archived in BOLD (Barcode of Life Data System; Project ULVNB with voucher numbers ULVNB001-23 to

ULVNB040-23 and ULVNB091-23 to ULVNB324-24) (Ratnasingham & Hebert, 2007). Sequences are deposited in GenBank (accession numbers PQ733586–PQ733903, Appendix 1).

Historical vouchers. — To be able to compare the observed biodiversity with historical diversity, we additionally sequenced 48 herbarium specimens stored at Meise Botanic Garden (BR) and Leiden Naturalis Biodiversity Centre (L) that were originally collected between 1845 and 2001 (Appendix 2). Of those, 11 were originally collected in Belgium and 37 were originally collected in the Netherlands. The herbarium vouchers included the neotype and isoneotype of *Ulva intestinaloides* (Koeman & C.Hoek) H.S.Hayden & al. (originally described as *Enteromorpha intestinaloides*; L 0050876 and L 0050877) and the neotype of *U. pseudolinza* (Koeman & C.Hoek) H.S.Hayden & al. (originally described as *E. pseudolinza*; voucher L 0050878) collected by Koeman in 1985.

The specimens from the Meise Botanic Garden herbarium (BR) were processed in the Center for Molecular Phylogenetics and Evolution at Ghent University (Belgium) and specimens from the Leiden herbarium (L) were processed in the ancient DNA lab at the Naturalis Biodiversity Center (the Netherlands) following the guidelines proposed by Hughey

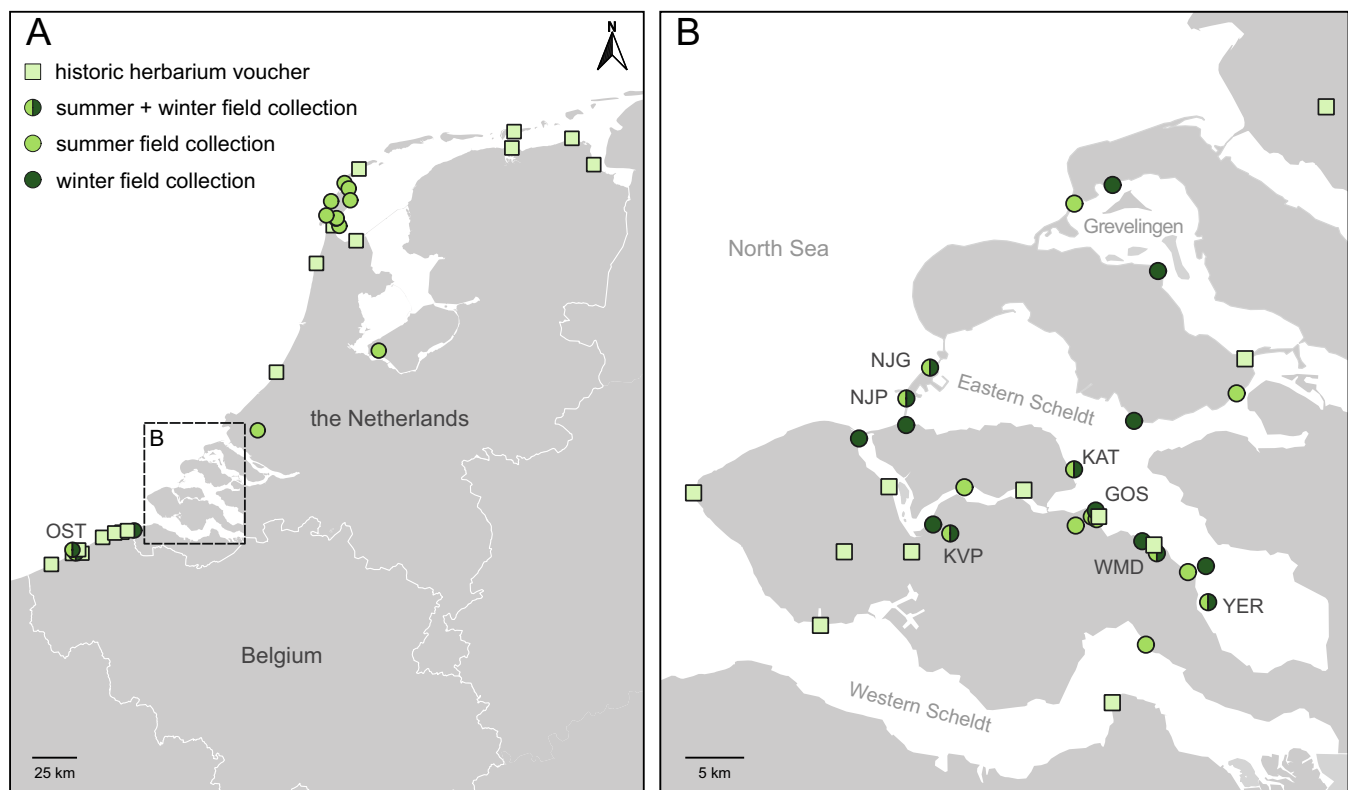


Fig. 1. Overview of the sampling area, with sampling sites visited in Belgium and the Netherlands (A) and the province of Zeeland (B). Symbols represent sampling type: recently visited field sites (circles) and localities of the historic herbarium specimens (squares). For recently visited sites, colours indicate sampling season: summer and winter (light green + dark green), summer only (light green), and winter only (dark green). The eight sites sampled during both summer and winter are labelled: Goese Sas (GOS), Kats (KAT), Kreek van Piet (KVP), Neeltje Jans pontoon (NJP), Neeltje Jans tidal pool (NJG), Oostende (OST), Wemeldinge marina (WMD), and Yerseke (YER).

& Gabrielson (2012) for working with historical herbarium specimens. In both cases, genomic DNA was extracted using the CTAB method described above. The BR herbarium samples were subsequently amplified by PCRs targeting a ~350 bp fragment of the *tufA* gene using the newly designed primers *tufA*-324F (5'-TGC TGA TGG TCC TAT GCC AC-3') and *tufA*-713R (5'-CCA GTT GCA ACA GTT CCA CG-3'). PCR mixtures consisted of 14.4 µl deionized water, 2.5 µl 10× CL, 0.5 µl dNTP's (2 mM), 1.25 µl forward primer (10 µM), 1.25 µl reverse primer (10 µM), 4 µl Q-solution (5×), 1.25 µl Taq (1 U/µl) and 1 µl sample template. PCRs were run with a thermal profile of 5 min initial denaturation at 94°C, 40 cycles of 1 min at 94°C; 1 min at 55°C; 1 min at 72°C, and 10 min final extension at 72°C. PCR products were Sanger sequenced by MacroGen (Amsterdam, the Netherlands).

The Leiden herbarium samples were prepared for Illumina sequencing. Library preparation was carried out using the NEBNext Ultra II DNA Library Prep Kit for Illumina and the NEBNext Multiplex Oligos for Illumina, following the manufacturer's protocol. Sequencing was performed on a NovaSeq 6000 at BaseClear (Leiden, the Netherlands), yielding a total of 1,257,586,830 reads from a single library. An initial *de novo* assembly was generated using SPAdes v.3.15.5 (Prjibelski & al., 2020) in “careful” mode, followed by a chloroplast assembly with the plasmidSPAdes mode in SPAdes v.3.15.5 (Antipov & al., 2016). Fragments of *tufA* (130–800 bp in size) were extracted from the assembled contigs using a Biopython BLAST script (Altschul & al., 1990; Cock & al., 2009). In addition, *rbcL* and nuclear rDNA ITS fragments were extracted for the type specimens of *Ulva intestinaloides* and *U. pseudolinza*.

DNA sequences were analysed and species identified using the same methods as described above, using MAFFT v.7.154b (Kato & al., 2002) and trimAl v.1.2rev59 (Capella-Gutiérrez & al., 2009) for sequence alignments and IQ-TREE v.1.6.12 (Nguyen & al., 2015) to generate maximum likelihood phylogenetic trees.

All sequences, trace files, metadata, and photos were archived in BOLD (Barcode of Life Data System; Project ULVNB with voucher numbers ULVNB041-23 to ULVNB090-23). Sequences are also available in GenBank (accession numbers PQ733586–PQ733903, Appendix 2).

■ RESULTS

Molecular species identification of recent field-collected samples. — We found a total of 21 taxonomic entities based on the phylogenetic analyses of 274 recent field-collected samples, consisting of two *Blidingia* species, a single *Gayralia* or *Kornmannia* species (genus identification uncertain; see Discussion), a single *Monostroma* species, 16 *Ulva* species, and a single *Umbraulva* species (Figs. 2, 3). Eighteen entities could be identified to species-level based on peer-reviewed reference sequences: *Blidingia marginata* (J. Agardh) P.J.L. Dang. ex Bliding, *Blidingia minima*

(Nägeli ex Kütz.) Kylin, *Monostroma grevillei* (Thur.) Wittr., *Ulva australis* Aresch., *U. californica* Wille, *U. capillata* Steinhagen, *U. compressa* L., *U. fenestrata* Postels & Rupr., *U. flexuosa* Wulfen, *U. intestinalis* L., *U. lacinulata* (Kütz.) Wittr., *U. linza* L., *U. pilifera* (Kütz.) Škaloud & Leliaert, *U. prolifera* O.F. Müll., *U. pseudocurvata* Koeman & C. Hoek, *U. shanxiensis* Le Chen & al., *U. torta* (Mert.) Trevis., and *Umbraulva dangeardii* M.J. Wynne & G. Furnari. A single entity clustered with reference sequences from both *Gayralia oxysperma* (Kütz.) K.L. Vinogr. ex Scagel & al. and *Kornmannia leptoderma* (Kjellm.) Bliding. In addition, we found two unidentified *Ulva* entities in the recent field-collected samples. One clade ($n = 5$ samples) matched with sequences denoted as *Ulva* sp. 6 sensu Steinhagen & al. (2023b). The other entity ($n = 2$), referred to here as *Ulva* sp. 10 to avoid overlap with the clades *Ulva* sp. 1–9 identified in Steinhagen & al. (2023b), did not have any match in the GenBank reference database. *Ulva* sp. 11, a third unidentified *Ulva* entity, was detected exclusively in historical voucher specimens (see section “Molecular species identification of historical vouchers and type specimens”). The phylogenetic trees in Figs. 2 and 3 are based on a subset of specimens with selected representatives of each species. A phylogenetic tree including all specimens is available in suppl. Fig. S1. Observed species morphologies can be found in Fig. 4.

Habitat. — *Ulva* s.l. specimens were found across a wide range of coastal and inland habitats, including the rocky intertidal, oyster beds, salt marshes, stagnant saltwater lakes, marinas, tidal mud flats, and even brackish and freshwater environments (Fig. 5). The highest species diversity was observed on rocky shores in the intertidal, with 17 species recorded. *Blidingia marginata* and *B. minima* dominated the high intertidal, whereas *U. australis*, *U. compressa*, *U. fenestrata*, and *U. lacinulata* were highly abundant in the mid- and lower intertidal. Intertidal oyster reefs likewise harboured high diversity, with 10 species recorded. While species richness was generally low on tidal mud flats due to the limited availability of suitable hard substrates, *Ulva* sp. 6 sensu Steinhagen & al. (2023b) and *U. capillata* were particularly abundant in this habitat throughout summer, forming dense green mats. *Gayralia oxysperma*/*Kornmannia leptoderma* was primarily found in the high intertidal on silt- or clay-covered rocks, particularly in sheltered marinas. *Ulva prolifera* was almost exclusively found in salt marshes. Other common species in salt marshes were *B. marginata* and *U. compressa*. Stagnant saltwater lakes (e.g., Lake Grevelingen, Veerse Meer, Spui kom Oostende) were predominantly inhabited by *U. australis*, *U. intestinalis*, and *U. linza*, but we also found a few records of *Monostroma grevillei*, *U. fenestrata*, and *U. flexuosa*. In brackish environments, *B. marginata*, *U. intestinalis*, *U. lacinulata*, and *U. pilifera* were the most frequently observed species. Finally, *U. shanxiensis* and *Umbraulva dangeardii* were each recorded in only a single location. *Ulva shanxiensis* was found in the freshwater lake Weerwater in Flevoland, the Netherlands, while *Um. dangeardii* was found free-floating in the rocky intertidal in the Eastern Scheldt.

Seasonal patterns. — Species diversity was slightly higher in summer compared to winter. Overall, 14 species were recorded in the winter months (December–February), while 18 species were recorded in the summer period (June–August). Excluding singleton occurrences, 12 species were observed in winter and 17 in summer. Several species were commonly detected during both winter and summer sampling campaigns, including *Blidingia marginata*, *Ulva australis*, *U. compressa*, *U. fenestrata*, *U. intestinalis*, *U. linza*, and *U. prolifera*. In contrast, *B. minima*, *U. pilifera*, *Ulva* sp. 6 sensu Steinhagen & al. (2023b), and *Ulva* sp. 10 were almost exclusively recorded during the summer campaign. *Ulva californica* was present in both winter and summer but was more common in the latter period. At an artificial breakwater in Oostende (Belgium), for example, only two specimens were found in February compared to nine in July. *Ulva lacunculata* was frequently observed in both seasons, with 15 records in winter and 12 in summer. Notably, during summer all specimens were found growing attached to substrates such as pontoons, rocks, or shells, whereas in winter, 9 out of 15 records were found in large drifting masses of seaweeds.

Molecular species identification of historical vouchers and type specimens. — The historical dataset, based on herbarium vouchers, comprised 13 taxonomic entities, of which

11 could be identified using reference sequences: *Blidingia marginata*, *Gayralia oxysperma*/*Kornmannia leptoderma*, *Ulva australis* (a single record dating from the year 2000), *U. compressa*, *U. fenestrata*, *U. flexuosa*, *U. intestinalis*, *U. lacunculata*, *U. linza*, *U. prolifera*, and *U. pseudocurvata*. Two entities remained unidentified, one of which matched to reference sequences of *Ulva* sp. 6 sensu Steinhagen & al. (2023b). The other entity did not match any the GenBank reference database and is referred to here as *Ulva* sp. 11 to avoid overlap with the clades *Ulva* sp. 1–9 identified in Steinhagen & al. (2023b) and *Ulva* sp. 10 identified in this study (Fig. 3).

De novo assembly of the plastid genome of the neotype *Ulva intestinaloides* (voucher L 0050876) resulted in 125 contigs with an N50 of 18,865 bp and max sequence length of 30,614 bp. The isoneotype of *U. intestinaloides* (voucher L 0050877) resulted in 21 contigs with an N50 of 19,204 bp and max sequence length of 57,997 bp. The complete plastid genome contained 96 genes and was 89,239 bp in length (GenBank accession number PQ777151). Gene content included 23 tRNA (*trnL*, *trnM*, and *trnS* occur in duplicate), 21 photosystem (6 *psa* and 15 *psb*), 21 ribosomal proteins (10 *rpl* and 11 *rps*), 6 ATP synthase (*atp*), 5 cytochrome b/f complex (*pet*), 5 hypothetical chloroplast (*ycf*), 4 RNA polymerase (*rpo*), 2 rRNA (1 *rrl*, 1 *rrs*), and 9 other genes involved in plastid function (*accD*, *ccsA*, *cemA*, *chlI*, *clpP*, *ftsH*, *infA*,

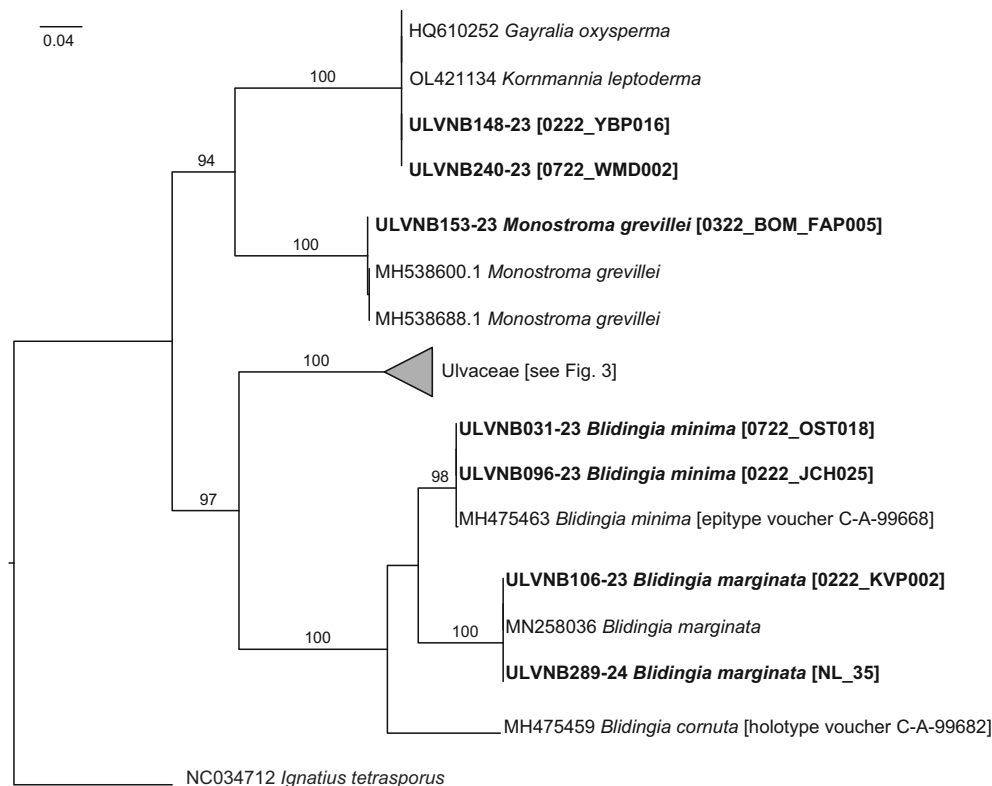


Fig. 2. Maximum likelihood (IQ-TREE) phylogenetic tree of the Ulvales and Ulotrichales species based on *tufA* gene sequences. When available, two sequences per species from this study were included (indicated in bold), with sequence accession number referring to the BOLD identifier and the sample number in brackets. Representative sequences from GenBank are also incorporated. Branch support values are UFBoot2 supports (1000 replicates). Branch lengths are scaled according to the number of nucleotide substitutions per site. The tree is rooted with *Ignatius tetrasporus* as outgroup. The Ulvaceae are collapsed and are visualized in Fig. 3.

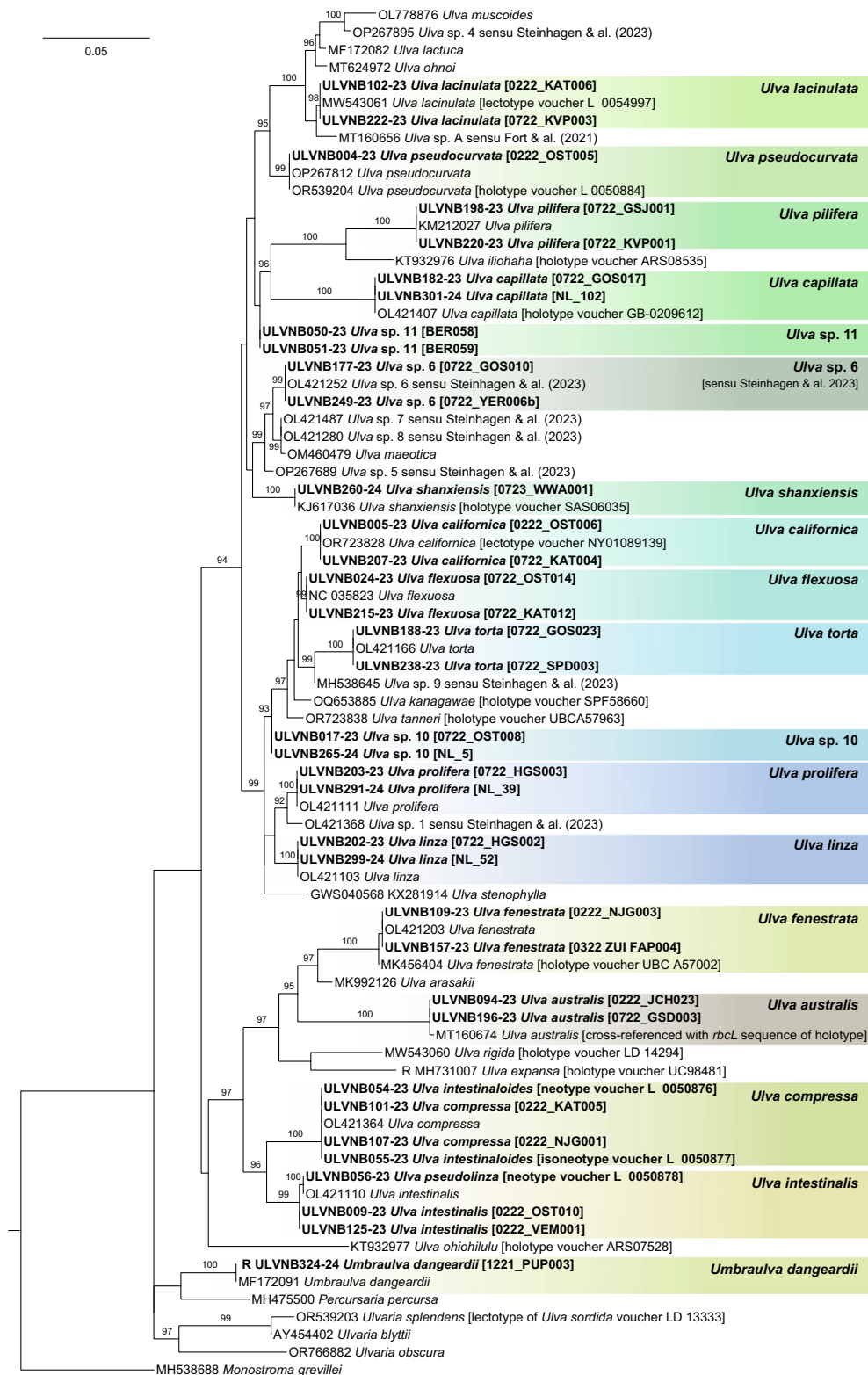


Fig. 3. Maximum likelihood (IQ-TREE) phylogenetic tree of the Ulvaceae species based on *tufA* gene sequences. Clades of species found in this study have been highlighted in colour. When available, two sequences per species from this study were included (indicated in bold), with sequence accession number corresponding to the BOLD identifier and sample number in brackets. Representative sequences from GenBank for species relevant to the study area (North Sea and neighbouring regions) were included, as well as available *Ulva* type material for broader context. Branch support values are UFBoot2 supports (1000 replicates). Branch lengths are scaled according to the number of nucleotide substitutions per site. The tree is rooted with *Monostroma grevillei* as outgroup. See suppl. Fig. S1 for a phylogenetic tree containing all specimens from this study.



Fig. 4. Morphological overview of the 22 *Ulva* s.l. taxonomic entities identified within this study. All scale bars indicate 3 cm, unless indicated otherwise. Pictures represent press-dried herbarium specimens. (*Continues*)

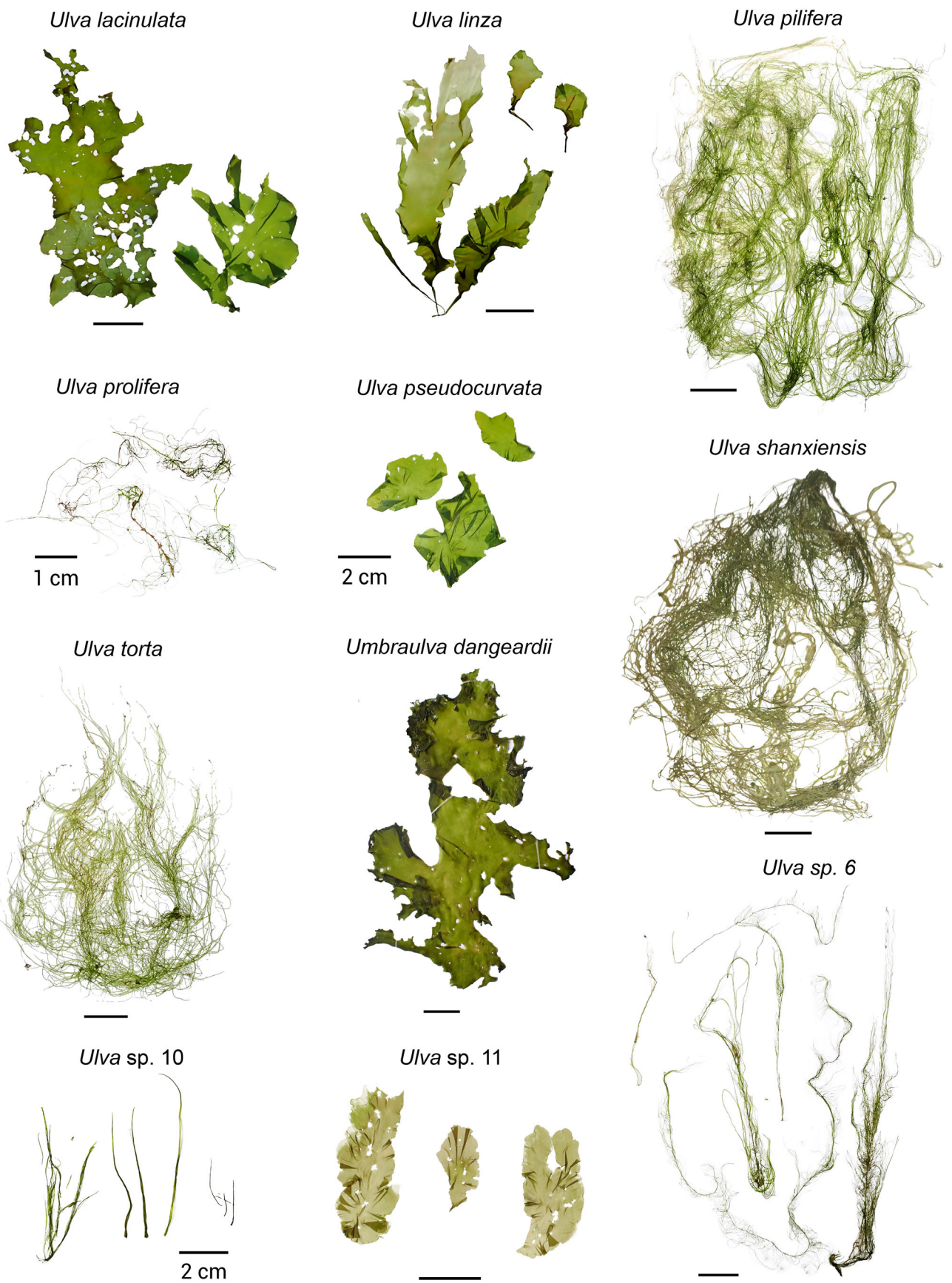


Fig. 4. Continued.

rbcL, *tufA*). The assembly of the neotype did not yield a complete plastid genome, but the three largest plastid contigs (74,116 bp total length) were identical to the isoneotype assembly. The *tufA* sequences of both neotype and isoneotype of *U. intestinaloides* were 100% identical to *tufA* reference sequences of *U. compressa* (GenBank accessions OL421364 and HQ610295) (Fig. 3). The *rbcL* sequences were 99.9%–100% identical to *rbcL* reference sequences of *U. compressa*

(GenBank accessions MW548841 and OR635441) (suppl. Fig. S2), and the ITS sequences exhibited 99.6%–100% similarity to reference sequences (GenBank accession OR734719 and OR428167) (suppl. Fig. S3).

De novo assembly of the plastid genome of the neotype of *Ulva pseudolinza* (voucher L 0050878) resulted in 58 contigs with an N50 of 32,888 bp and max sequence length of 94,905 bp. The complete plastid genome contained 106 genes and



Fig. 5. Examples of foliose and tubular *Ulva* s.l. growing in various habitats. **A**, *Blidingia minima* in the high intertidal on sea dike; **B**, *Ulva* sp. 6 sensu Steinhagen & al. (2023b) on tidal mud flat; **C**, *Blidingia marginata* in the extreme high intertidal on concrete pillars; **D**, Mix of *Blidingia marginata* and *Ulva prolifera* in saltmarsh; **E**, *Ulva australis* in mussel- and oysterbed; **F**, Floating masses of *Ulva pilifera* in marina; **G**, Lower intertidal community of several foliose *Ulva* species; **H**, *Ulva australis* in tidal pool; **I**, Water outlet in canal with *Ulva linza* and *Ulva prolifera*; **J**, *Ulva lacunculata* on the side of a pontoon; **K**, *Ulva linza* on rock in the low intertidal. — Photos: Luna van der Loos.

was 94,778 bp in length (GenBank accession number PQ777150). Gene content included 26 tRNA (*trnG*, *trnL*, *trnR*, and *trnS* occur in duplicate, *trnM* occurs in triplicate), 21 photosystem (6 *psa* and 15 *psb*), 21 ribosomal proteins (10 *rpl* and 11 *rps*), 6 ATP synthase (*atp*), 5 cytochrome b/f complex (*pet*), 11 hypothetical chloroplast and proteins (*ycf*), 4 RNA polymerase (*rpo*), 3 rRNA (1 *rnl*, 1 *rns*, 1 *rrn5*), and 9 other genes involved in plastid function (*accD*, *ccsA*, *cemA*, *chlI*, *clpP*, *ftsH*, *infA*, *rbcL*, *tufA*). The *tufA* sequence of the neotype of *U. pseudolinza* matched with 100% identity to reference sequences of *U. intestinalis* (GenBank accessions MZ561630 and OL421110) (Fig. 3). The *rbcL* sequences were 100% identical to *rbcL* reference sequences of *U. intestinalis* (GenBank accessions AB097616 and HQ603560) (suppl. Fig. S2), and the ITS sequences were 99.8% identical (GenBank accession OR734710) (suppl. Fig. S3).

Our molecular analyses showed that nearly 70% of the herbarium vouchers (31 of 45 specimens identified to species level) were misidentified (Appendix 2). Vouchers identified as *Enteromorpha nana* (Sommerf.) G.Sjöstedt (L.4095667, L.4095670), currently regarded as a synonym of *Blidingia minima*, matched with *B. marginata* based on the molecular data (suppl. Fig. S1). Vouchers of *Monostroma oxyspermum* (Kütz.) Doty (L.4096278, L.4096295), currently accepted as *Gayralia oxysperma* (Kütz.) K.L. Vinogr. ex Scagel & al., aligned with reference sequences of both *G. oxysperma* and *Kornmannia leptoderma*. Specimens originally identified as *Ulva lactuca* grouped with *U. fenestrata* (BR5010111459555V, L.4114447) or *U. pseudocurvata* (L.4114442), while those labelled as *U. rigida* were in fact *U. fenestrata* (L.4114719, L.4114720) or *Ulva* sp. 11 (BR5010111531329V). Vouchers identified as *U. scandinavica* (currently regarded as synonym of *U. laciniolata*) were either *U. fenestrata* (BR5010111537505V) or *U. laciniolata* (BR5010111541335V). Specimens previously identified as *Enteromorpha ramellosa* Kütz. (unresolved taxonomic status; L.4095447, L.4095448) and *E. simplex* (K.L. Vinogr.) Koeman & C. Hoek (regarded currently as synonym of *U. prolifera*; L.4095477, L.4095478, L.4095479) were confirmed as *U. prolifera*. Likewise, vouchers of *U. radiata* (J. Agardh) H.S. Hayden & al. (L.4095600) and *U. ralfsii* (Harv.) Le Jol. (L.4095446) also matched *U. prolifera*. Two vouchers identified as *U. clathrata* or *E. ramulosa* (J. Sm.) Hook. (currently regarded as a synonym of *U. clathrata*) were either *U. prolifera* (L.4316781) or *U. compressa* (L.4095452). Finally, a single voucher identified as *E. erecta* (Lyngb.) J. Agardh, now regarded as synonym of *U. paradoxa* C. Agardh, matched with *Ulva* sp. 6 sensu Steinhagen & al. (2023b).

Comparing molecularly confirmed and reported species richness. — We compared our molecular findings with published accounts of species richness in the Netherlands and Belgium, using inventory lists (Stegenga & al., 1997, 2007; Belgian Register of Marine Species, 2024; Nederlands Soortenregister, 2024), taxonomic studies (Koeman & Van

den Hoek, 1981, 1982a,b), and Floras (Coppejans, 1998) (Table 1). Based on the published literature, a total of 3 *Blidingia* species, 2 *Monostroma* species, 1 *Gayralia* species, and 18 *Ulva* species are recorded from the southern North Sea (Table 1). Our molecular analyses confirmed the presence of 13 of these species. Our findings also showed that two species described from the Netherlands – *U. intestinaloides* and *U. pseudolinza* – are synonymous with *U. compressa* and *U. intestinalis*, respectively. Nine species previously reported in the literature (*B. subsalsa*, *G. oxysperma*, *M. bullosum*, *U. clathrata*, *U. kylinii*, *U. lactuca*, *U. radiata*, *U. ralfsii*, *U. rigida*) were not confirmed in our molecular findings (suppl. Table S1). Furthermore, our analyses identified four new records for the study area: *U. californica*, *U. capillata*, *U. shanxiensis*, and *Umbraulva dangeardii*.

DISCUSSION

Our study reveals a considerable discrepancy between historically reported *Ulva* s.l. diversity and molecularly confirmed diversity in the southern North Sea. This is partly due to the arrival of new species (e.g., *U. californica*, *U. shanxiensis*), but mainly to the consistent misapplication of names and confusion within *Ulva* nomenclature. The taxonomy of *Ulva*, as well as the applied species concepts and known biogeographical distributions, have undergone substantial changes over the past 20 years. Efforts to sequence type specimens, for example, revealed that *U. lactuca* – the generitype of *Ulva* which was thought to have a worldwide distribution – actually is a warm temperate to tropical species, rather than a cold temperate species (Hughey & al., 2019). What was previously referred to as “*Ulva lactuca*” in the Northern Hemisphere, including the southern North Sea, matches the type material of *U. fenestrata*. The same study showed that *U. fasciata* and *U. lobata* are heterotypic synonyms of *U. lactuca* and that *U. stipitata* is a heterotypic synonym of *U. fenestrata* (Hughey & al., 2019). Likewise, the DNA sequence of the material of “*U. rotundata*” (not validly published) from Italy – later described as a new species *U. pseudorotundata* by Cormaci & al. (2014) – was identical to the DNA sequence of *U. lactuca* (Hughey & al., 2022). Accurate morphology-based identification of *Ulva* s.l. is nearly impossible, hampering the interpretation of original and old morphological descriptions, historic specimens, and type material. We therefore integrated historic herbarium vouchers in our molecular analyses, allowing us to better understand how species concepts and the application of names have changed in the southern North Sea.

Species reported in literature awaiting molecular verification. — Of the 24 species reported in the Netherlands and Belgium in published literature, we confirmed the presence of 13 species using molecular methods; however, only four of these were verified against type material (*Blidingia minima*, *Ulva australis*, *U. laciniolata*, *U. pseudocurvata*). Reliable peer-reviewed reference sequences were available

Table 1. Comparison of DNA (*mtl4*)-based species identifications from the present study with previously published checklists (based on morphological identifications) from the study area. Currently accepted species names are marked in bold, whereas heterotypic synonyms used in the investigated literature are listed below each corresponding species. The column “Previously reported in literature” summarizes data from the checklist sources presented in the seven rightmost columns. The column “Netherlands Soortenregister” refers to the Dutch species register (www.nederlandse-soorten.nl). The column “BeRMS” refers to the Belgian Register of Marine Species (<https://www.marinespecies.org/berms/>).

Species name used in the literature	Molecularly identified [this study]	Previously reported in literature	Koeman & Van den Hoek, 1981	Van Stegenga & al., 1997	Stegenga & al., 2007	Netherlands Soortenregister	BeRMS
<i>Blidingia marginata</i> (J.Agardh) P.J.L.Dang. ex Bliding	✓	✓	–	✓	✓	✓	✓
<i>Blidingia minima</i> (Kütz.) Kylin	✓	✓	–	✓	–	✓	✓
<i>Blidingia subsalsa</i> (Kjellm.) Kommann & Sahling ex Scagel, P.W.Gabrielson, Garbary, Golden, M.W.Hawkes, S.C.Lindstr., J.C.Oliveira & Widd.	–	✓	–	–	–	–	✓
<i>Gayralia oxysperma</i> (Kütz.) K.L.Vinogr. ex Scagel, P.W.Gabrielson, Garbary, Golden, M.W.Hawkes, S.C.Lindstr., J.C.Oliveira & Widd.	✓ (?)	✓	–	✓	–	✓	✓
<i>Korumnannia leptoderma</i> (Kjellm.) Bliding	✓ (?)	–	–	–	–	–	–
<i>Monostroma grevillei</i> (Thur.) Witt.	✓	✓	–	✓	–	✓	✓
<i>Monostroma bullosum</i> (Roth) Thur.	–	✓	–	–	–	✓	–
<i>Ulua australis</i> Aresch.	✓	✓	–	–	–	✓	–
<i>Ulua laetevirens</i> Aresch.	–	–	–	–	–	✓	–
<i>Ulua pertusa</i> Kjellm.	–	–	–	–	✓	–	–
<i>Ulua californica</i> Wille	✓	–	–	–	–	–	–
<i>Ulua capillata</i> Steinhagen	✓	–	–	–	–	–	–
<i>Ulua clathrata</i> (Roth) C.Agardh	–	✓	–	✓	–	✓	✓
<i>Enteromorpha crinita</i> Nees	–	–	–	✓	–	–	–
<i>Enteromorpha ramulosa</i> (Sm.) Carmich.	–	–	–	✓	–	–	–
<i>Ulua compressa</i> L.	✓	✓	✓	✓	✓	✓	✓
<i>Enteromorpha usneoides</i> Bonnem. ex J.Agardh	–	–	✓	✓	–	–	–
<i>Ulua curvata</i> (Kütz.) De Toni	–	✓	–	✓	–	✓	✓
<i>Ulua fenestrata</i> Postels & Rupr.	✓	–	–	–	–	–	–
<i>Ulua flexuosa</i> Wulfen	✓	✓	–	✓	✓	✓	✓
“ <i>Enteromorpha linziformis</i> Bliding” (not validly published)	–	–	–	✓	–	–	–
<i>Ulua intestinalis</i> L.	✓	✓	✓	✓	✓	✓	✓

(Continues)

Table 1. Continued.

Species name used in the literature	Molecularly identified [this study]	Previously reported in literature	Koeman & Van den Hoek, 1981	Koeman & Van den Hoek, 1982a,b	Stegenga & al., 1997	Coppejans, Stegenga & al., 2007	Netherlands Soortenregister	BeRMS
<i>Ulva intestinaloides</i> (Koeman & C.Hoek) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	Synonymised with <i>Ulva compressa</i> in current study	Described from the Netherlands	–	✓	–	–	✓	–
<i>Ulva kyllini</i> (Bliding) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	–	✓	–	–	✓	–	–	✓
<i>Ulva lacunculata</i> (Kütz.) Witr.	✓	✓	–	–	–	–	–	–
<i>Ulva scandinavica</i> Bliding	–	–	✓	–	✓	–	–	–
<i>Ulva lactuca</i> L.	–	✓	✓	–	✓	✓	✓	✓
<i>Ulva pseudorotundata</i> Cormaci, G.Furnari & Alongi	–	–	–	–	–	–	✓	–
<i>Ulva tenera</i> Kommann & Sahling	–	–	–	–	–	–	✓	–
<i>Ulva linza</i> L.	✓	✓	–	–	✓	✓	✓	✓
<i>Enteromorpha ahneriana</i> Bliding	–	–	✓	–	–	–	–	–
<i>Ulva pilifera</i> (Kütz.) Škaloud & Leliaert	✓	✓	–	–	–	–	✓	–
<i>Ulva prolifera</i> O.F.Müll.	✓	✓	–	✓	✓	✓	✓	✓
<i>Enteromorpha simplex</i> (K.L.Vinogr.) Koeman & C.Hoek	–	–	✓	–	–	–	–	–
<i>Ulva simplex</i> (K.L.Vinogr.) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	–	–	–	–	–	–	✓	–
<i>Ulva pseudocurvata</i> Koeman & C.Hoek	✓	✓	✓	–	✓	–	✓	✓
<i>Ulva pseudolinza</i> (Koeman & C.Hoek) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	Synonymised with <i>Ulva intestinalis</i> in current study	Described from the Netherlands	–	✓	✓	–	✓	✓
<i>Ulva radiata</i> (J.Agardh) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	–	✓	–	✓	✓	–	✓	✓
<i>Ulva ralfsii</i> (Harv.) Le Jol.	–	✓	–	–	✓	–	✓	✓
<i>Ulva rigida</i> C.Agardh	–	✓	✓	–	✓	–	✓	✓
<i>Ulva shanxiensis</i> L.Chen, J.Feng & S.L.Xie	✓	–	–	–	–	–	–	–
<i>Ulva torta</i> (Mertens) Trevis.	✓	✓	–	✓	✓	–	✓	✓
<i>Umbraulva dangeardii</i> M.J.Wynne & G.Furnari	✓	–	–	–	–	–	–	–

for the remaining nine confirmed species, but without type material sequences. Future taxonomic name changes may be needed if additional type sequences become accessible. In addition, for nine species reported in the literature, we could not confirm their presence, possibly due to their absence in the southern North Sea or the lack of reliable reference sequences for those species. The uncertain taxonomic status of some species further complicates their detection.

Ulva lactuca and *U. rigida* are frequently cited in local Floras and coastal field guides for the southern North Sea. However, Hughey & al. (2019) showed that the name *U. lactuca* has been misapplied to Northern Hemisphere species, which should instead be referred to as *U. fenestrata*. As expected, we were unable to confirm the presence of *U. lactuca* in the southern North Sea, while historic herbarium specimens from this area labelled as *U. lactuca* based on morphology were revealed as *U. fenestrata* or *U. pseudocurvata*. This suggests that *U. lactuca*, a warm-water species, is indeed absent from the southern North Sea. Likewise, recent work on the type specimen of *U. rigida* showed that all sequences in public repositories attributed to this species were misidentified, actually representing various other foliose *Ulva* species (Hughey & al., 2022). This suggests that *U. rigida* is far less common than originally thought. In our dataset, molecular analyses of historic herbarium specimens originally labelled as *U. rigida* identified them as *U. fenestrata* or *Ulva* sp. 11, further supporting the likelihood that *U. rigida* does not occur in the southern North Sea. Reliable reference sequences are lacking or are entirely unavailable in public databases for several species reported in the literature from the southern North Sea, including *U. clathrata*, *U. kylinii*, *U. radiata*, and *U. ralfsii*. As a result, it is possible that the unidentified clades *Ulva* sp. 6, *Ulva* sp. 10, and *Ulva* sp. 11 correspond to some of these unconfirmed species. The morphological description of *Ulva clathrata*, for example, aligns with the thin, highly branched morphology observed in *Ulva* sp. 6, although the historic herbarium vouchers labelled as “*Ulva clathrata*” were found to match reference sequences of *U. prolifera* and *U. compressa*. Similarly, *U. radiata* and *U. ralfsii* are described as thin, tubular, and highly branched species, yet their historic vouchers sequenced in this study were also identified as *U. prolifera*. Bliding suggested that *U. radiata* can be considered a subspecies of *U. prolifera* (Bliding, 1963), raising the possibility that some of these species are synonyms of *U. prolifera*. Solving the identity of the unidentified *Ulva* clades will require further investigation of type specimens.

Our molecular analyses confirmed the presence of a species morphologically resembling *Gayralia oxysperma* in the southern North Sea. However, its precise taxonomic identity remains ambiguous, as identical reference sequences are also archived under the name *Kornmannia leptoderma*. Both the genus *Kornmannia* Bliding and *Gayralia* K.L.Vinogr. were described in 1969. The genus *Kornmannia* is placed within the Ulvales and currently only includes *K. leptoderma*, while *Gayralia* is positioned within the Ulotrichales and comprises three accepted species: *G. brasiliensis*, *G. kurohiensis*, and

G. oxysperma. The genus *Gayralia* was erected primarily on the basis of its typical asexual life cycle and the presence of an initial tube stage in the initial developmental phase (Vinogradova, 1969). However, several studies have questioned the validity of using asexual life cycles as a reliable criterion for genus differentiation and proposed to reinstate the genus *Gayralia* within *Monostroma* (Bast, 2015; Cui & al., 2022; Liao & al., 2024). The described life cycle of *K. leptoderma* resembles that of *G. oxysperma*, but the former produces tetraflagellate zooids that give rise to a discoid structure, while the latter produces biflagellate zooids that develop into a uniseriate filament. It is likely that only one species – either *G. oxysperma* or *K. leptoderma* – occurs in the North-east Atlantic. Given that our sequences cluster within the Ulotrichales, *G. oxysperma* is likely the correct identification. Future research involving sequencing the type specimens of *G. oxysperma* and *K. leptoderma* may provide further clarification and cultivation experiments may shed light on the taxonomic value of the reported developmental differences.

***Ulva intestinaloides* and *U. pseudolinza* are synonyms of *U. compressa* and *U. intestinalis*, respectively.** — Our molecular analyses showed that two species described from the Netherlands, *Ulva intestinaloides* and *U. pseudolinza*, are heterotypic synonyms of *U. compressa* and *U. intestinalis*, respectively. The type locality of *U. intestinaloides* is Westkapelle, the Netherlands, where Koeman originally collected the holotype specimen in April 1976. According to its description, the holotype was deposited at the Rijksherbarium Leiden (number “E339, 11”), with an isotype preserved in the herbarium of the University of Groningen (voucher number not provided) (Koeman & Van den Hoek, 1982a). Similarly, the holotype of *U. pseudolinza* was collected by Koeman in June 1975 at Den Helder, the Netherlands, and deposited at the Rijksherbarium Leiden (number “E92, 4”), with an isotype also at the herbarium of the University of Groningen (no voucher number) (Koeman & Van den Hoek, 1982a). However, any original material of both species appears to have been lost. To replace it, Koeman himself revisited the original type locations in 1985 and collected new specimens. Four specimens collected at Westkapelle on 14 July 1985 are housed at Naturalis in Leiden and are labelled as “isotypes” #1–4 for *U. intestinaloides* (L 0050876 and L 0050877). Additionally, four specimens collected at Den Helder on 1 August 1985 are labelled as “isotypes” #1–4 for *U. pseudolinza* (L 0050878). Although these specimens are labelled as isotypes, they do not meet the definition, as an isotype must be a duplicate of the holotype. Notably, these are the only herbarium specimens of *U. intestinaloides* and *U. pseudolinza* available in the entire Rijksherbarium Leiden collection (now part of the Naturalis Biodiversity Center). Of these, “isotype” #4 of *U. intestinaloides* and “isotype” #1 of *U. pseudolinza* were later assigned neotype status by the Naturalis Biodiversity Center. However, since these designations were never formally published, we hereby officially designate here L 0050876 as the neotype of *U. intestinaloides* and L 0050878 as the neotype for *U. pseudolinza*. Although *Ulva* morphologies can be

highly variable, the morphologies of both neotypes matched well with the typical morphologies we observed in recent collections of *U. compressa* and *U. intestinalis* (Fig. 4).

***Ulva compressa* L., Sp. Pl.: 1163. 1753** – Lectotype (designated by Blomster & al. in J. Phycol. 34: 332. 1998): [illustration in] Dillenius, Hist. Musc.: t. 9 fig. 8. 1742. Epitype (designated by Blomster & al. in J. Phycol. 34: 332. 1998): “8. Tremella marina tenuissima & compressa. The thready and Tape-like Laver”, Dillenian herbarium, sheet 33 (OXF).

= *Enteromorpha intestinaloides* Koeman & C.Hoek in Arch. Hydrobiol. Suppl. 63(3): 321. 1982 ≡ *Ulva intestinaloides* (Koeman & C.Hoek) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland – **Neotype (designated here)**: the Netherlands, Westkapelle, 14 Jul 1985, R.P.T. Koeman s.n. (L barcode L 0050876 [specimen labelled as “isotype 4”]!; isoneotypes: L barcodes L 0050876 [specimen labelled “isotype 3”], L 0050877 [specimens labelled “isotype 1”, “isotype 2”]!). Registration: <http://phycobank.org/106010>

***Ulva intestinalis* L., Sp. Pl.: 1163. 1753** – Lectotype (designated by Blomster & al. in J. Phycol. 34: 332. 1998): [illustration in] Dillenius, Hist. Musc.: t. 9 fig. 7. 1742. Epitype (designated by Blomster & al. in J. Phycol. 34: 332. 1998): “7. Tremella marina tubulosa, intestinorum figura. The Gut Laver.”, Dillenian herbarium, sheet 32 (OXF).

= *Enteromorpha pseudolinza* Koeman & C.Hoek in Arch. Hydrobiol. Suppl. 63(3): 302. 1982 ≡ *Ulva pseudolinza* (Koeman & C.Hoek) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland – **Neotype (designated here)**: the Netherlands, Den Helder, 1 Aug 1985, R.P.T. Koeman s.n. (L barcode L 0050878 [specimen labelled “isotype 1”]!; isoneotypes: L barcode L 0050878 [specimens labelled “isotype 2”, “isotype 3” and “isotype 4”]!). <http://phycobank.org/106011>

New records for the Netherlands and Belgium. — This study revealed the presence of four species previously unrecorded from the Netherlands and Belgium: *Ulva californica*, *U. capillata*, *U. shanxiensis*, and *Umbraulva dangeardii*. Both *U. capillata* and *Um. dangeardii* are native to the Northeast Atlantic Ocean, although the latter has occasionally been considered as non-native as well (Brodie & al., 2016). *Umbraulva dangeardii* is described from Roscoff, France, and has been reported in several countries near the southern North Sea, including Germany (Steinhagen & al., 2019), Great Britain, and Ireland (Maggs & al., 2024). *Umbraulva* species generally occur in the subtidal (Bae & Lee, 2001) and as the specimen in the Netherlands was found free-floating, it is possible that it is more common in the subtidal of the Eastern Scheldt as well. *Ulva capillata* is a relatively recently described species from Sweden (Steinhagen & al., 2023a) that we observed in high abundance throughout summer on tidal mudflats. This

suggests that *U. capillata* may have been present in the southern North Sea for a longer period of time, although we could not confirm its historical presence with the herbarium vouchers that we sequenced. The two other new records, *U. californica* and *U. shanxiensis*, are both non-indigenous species. *Ulva californica*, originally from the Northeast Pacific Ocean, has been recorded as an introduced species in the Northeast Atlantic since at least 1999 (Van der Loos & al., 2024). The presence of *U. shanxiensis*, a species described from a freshwater stream in Shanxi, China (Chen & al., 2015), is here confirmed for the first time outside China using molecular methods. This finding emphasizes the importance of monitoring freshwater habitats to fully assess *Ulva* biodiversity.

Comparing diversity to other European areas. — The substantial morphological variation in *Ulva* species necessitates the use of molecular methods for accurate biodiversity assessments. In the Northeast Atlantic, large-scale molecular studies have primarily focused on the Baltic Sea area (Denmark, Finland, Germany, Norway, Sweden) (Steinhagen & al., 2019, 2023b), Great Britain and Ireland (Maggs & al., 2024), and to a smaller extent Brittany, France (Dartois & al., 2021). The *Ulva* diversity observed in this study is largely congruent with that reported in the forementioned regions. In the Baltic Sea, species richness is slightly higher than in the southern North Sea, mainly due to unidentified clades *Ulva* sp. 1–9 found there. Of these, we detected only *U. capillata* (formerly *Ulva* sp. 2) and *Ulva* sp. 6. We also did not observe *Blidingia cornuta*, which has been described from Germany (Steinhagen & al., 2021). Furthermore, *U. rigida* was absent from both the southern North Sea and the Baltic Sea, but has been confirmed from Great Britain and Ireland (Maggs & al., 2024) and France (Dartois & al., 2021). Interestingly, the non-indigenous species *U. australis* has not been reported from Great Britain or Ireland, yet it is present in France (Dartois & al., 2021; Fort & al., 2021), Norway (Steinhagen & al., 2023b), Portugal (Fort & al., 2021), Spain (Couceiro & al., 2011), and the southern North Sea. To effectively analyse geographic distribution patterns on a wider scale, molecular assessment of *Ulva* biodiversity across Europe will be essential.

■ CONCLUSION

This study aimed to reassess *Ulva* s.l. diversity in the Netherlands and Belgium using DNA barcoding, analysing both recent field collections and historical herbarium vouchers. The findings were compared to pre-DNA diversity assessments previously published. Molecular analysis confirmed only ~50% of the species previously reported, revealing a significant gap between morphological and DNA-based species identifications. We also report the presence of four species new to the Netherlands and Belgium, including one species previously recorded only in China, and demonstrate that *U. intestinaloides* and *U. pseudolinza* are synonyms

of *U. compressa* and *U. intestinalis*, respectively. Our results highlight the critical role of molecular monitoring in uncovering cryptic diversity, addressing historical misinterpretations, and advancing our understanding of *Ulva* biodiversity.

■ AUTHOR CONTRIBUTIONS

LML, FL and ODC designed the study. BD, FP, JK, LML, LVDW, MK, SD, and SST conducted field and lab work. LML and FL conducted all phylogenetic analyses. ODC acquired funding and provided supervision. LML wrote the original manuscript. All other authors commented on and contributed to the manuscript.

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■ LITERATURE CITED

- Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman, D.J. 1990. Basic local alignment search tool. *J. Molec. Biol.* 215: 403–410. [https://doi.org/10.1016/S0022-2836\(05\)80360-2](https://doi.org/10.1016/S0022-2836(05)80360-2)
- Antipov, D., Hartwick, N., Shen, M., Raiko, M., Lapidus, A. & Pevzner, P.A. 2016. plasmidSPAdes: Assembling plasmids from whole genome sequencing data. *Bioinformatics* 32: 3380–3387. <https://doi.org/10.1093/bioinformatics/btw493>
- Bae, E.H. & Lee, I.K. 2001. *Umbraulva*, a new genus based on *Ulva japonica* (Holmes) Papenfuss (Ulvaaceae, Chlorophyta). *Algae* 16: 217–231.
- Bast, F. 2015. Taxonomic reappraisal of Monostromataceae (Ulvothamnaceae: Chlorophyta) based on multi-locus phylogeny. *Webbia* 70: 43–57. <https://doi.org/10.1080/00837792.2015.1004845>
- Beer, S. 2023. Photosynthetic traits of the ubiquitous and prolific macroalga *Ulva* (Chlorophyta): A review. *Eur. J. Phycol.* 58: 390–398. <https://doi.org/10.1080/09670262.2022.2150894>
- Belgian Register of Marine Species 2024. Belgian Register of Marine Species [Dataset]. <https://www.marinespecies.org/berms/> (accessed 24 Oct 2024)
- Bliding, C. 1963. *A critical survey of European taxa in Ulvales*, part 1, *Capsosiphon*, *Percursaria*, *Blidingia*, *Enteromorpha*. *Opera Botanica* 8(3). Stockholm: Almqvist & Wiksell.
- Bolton, J.J., Cyrus, M.D., Brand, M.J., Joubert, M. & Macey, B.M. 2016. Why grow *Ulva*? Its potential role in the future of aquaculture. *Perspect. Phycol.* 3: 113–120. <https://doi.org/10.1127/pip/2016/0058>
- Brodie, J., Wilbraham, J., Pottas, J. & Guiry, M.D. 2016. A revised check-list of the seaweeds of Britain. *J. Mar. Biol. Assoc. U.K.* 96: 1005–1029. <https://doi.org/10.1017/S0025315415001484>
- Capella-Gutiérrez, S., Silla-Martínez, J.M. & Gabaldón, T. 2009. trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* 25: 1972–1973. <https://doi.org/10.1093/bioinformatics/btp348>
- Chen, L., Feng, J. & Xie, S. 2015. *Ulva shanxiensis* (Ulvaaceae), a new species from Shanxi, China. *Novon* 23: 397–405. <https://doi.org/10.3417/2013021>
- Cock, P.J.A., Antao, T., Chang, J.T., Chapman, B.A., Cox, C.J., Dalke, A., Friedberg, I., Hamelryck, T., Kauff, F., Wilczynski, B. & De Hoon, M.J.L. 2009. Biopython: Freely available Python tools for computational molecular biology and bioinformatics. *Bioinformatics* 25: 1422–1423. <https://doi.org/10.1093/bioinformatics/btp163>
- Coppejans, E. 1998. *Flora van de Noord-Franse en Belgische zeevieren*. Scripta Botanica Belgica 17. Meise: Nationale Plantentuin van België.
- Cormaci, M., Furnari, G. & Alongi, G. 2014. Flora marina bentonica del Mediterraneo: Chlorophyta. *Boll. Accad. Gioenia Sci. Nat. Catania* 47(377): 11–436.
- Couceiro, L., Cremades, J. & Barreiro, R. 2011. Evidence for multiple introductions of the Pacific green alga *Ulva australis* Areschoug (Ulvales, Chlorophyta) to the Iberian Peninsula. *Bot. Mar.* 54: 391–402. <https://doi.org/10.1515/bot.2011.044>
- Cui, J., Chen, C., Tan, H., Huang, Y., Chen, X., Xin, R., Liu, J., Huang, B. & Xie, E. 2022. Taxonomic delimitation of the monostromatic green algal genera *Monostroma* Thuret 1854 and *Gayralia* Vinogradova 1969 (Ulvothamnaceae, Chlorophyta). *Diversity (Basel)* 14: 773. <https://doi.org/10.3390/d14090773>
- Dartois, M., Pante, E., Viricel, A., Becquet, V. & Sauriau, P.-G. 2021. Molecular genetic diversity of seaweeds morphologically related to *Ulva rigida* at three sites along the French Atlantic coast. *PeerJ*. <https://doi.org/10.7717/peerj.11966>
- Doyle, J.J. & Doyle, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull. Bot. Soc. Amer.* 19: 11–15.
- Fletcher, R.L. 1996. The occurrence of “Green Tides”—A review. Pp. 7–43 in: Schramm, W. & Nienhuis, P.H. (eds.), *Marine benthic vegetation*. Ecological Studies 123. Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-61398-2_2
- Fort, A., McHale, M., Cascella, K., Potin, P., Usadel, B., Guiry, M.D. & Sulpice, R. 2021. Foliose *Ulva* species show considerable inter-specific genetic diversity, low intra-specific genetic variation, and the rare occurrence of inter-specific hybrids in the wild. *J. Phycol.* 57: 219–233. <https://doi.org/10.1111/jpy.13079>
- Green, L. & Fong, P. 2016. The good, the bad and the *Ulva*: The density dependent role of macroalgal subsidies in influencing diversity and trophic structure of an estuarine community. *Oikos* 125: 988–1000. <https://doi.org/10.1111/oik.02860>
- Guiry, M.D. & Guiry, G.M. 2024. AlgaeBase. World-wide electronic publication, University of Galway. <https://www.algaebase.org> (accessed 18 Sep 2024)
- Hughes, J.R. & Gabrielson, P.W. 2012. Comment on “Acquiring DNA sequence data from dried archival red algae (Florideophyceae) for the purpose of applying available names to contemporary genetic species: a critical assessment”. *Botany* 90: 1191–1194. <https://doi.org/10.1139/b2012-102>
- Hughes, J.R., Maggs, C.A., Mineur, F., Jarvis, C., Miller, K.A., Shabaka, S.H. & Gabrielson, P.W. 2019. Genetic analysis of the Linnaean *Ulva lactuca* (Ulvales, Chlorophyta) holotype and related type specimens reveals name misapplications, unexpected origins, and new synonymies. *J. Phycol.* 55: 503–508. <https://doi.org/10.1111/jpy.12860>

- Hughey, J.R., Gabrielson, P.W., Maggs, C.A., Mineur, F. & Miller, K.A. 2021. Taxonomic revisions based on genetic analysis of type specimens of *Ulva conglobata*, *U. laetevirens*, *U. pertusa* and *U. spathulata* (Ulvales, Chlorophyta). *Phycol. Res.* 69: 148–153. <https://doi.org/10.1111/pre.12450>
- Hughey, J.R., Gabrielson, P.W., Maggs, C.A. & Mineur, F. 2022. Genomic analysis of the lectotype specimens of European *Ulva rigida* and *Ulva laciniata* (Ulvaceae, Chlorophyta) reveals the ongoing misapplication of names. *Eur. J. Phycol.* 57: 143–153. <https://doi.org/10.1080/09670262.2021.1914862>
- Katoh, K., Misawa, K., Kuma, K.I. & Miyata, T. 2002. MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucl. Acids Res.* 30: 3059–3066. <https://doi.org/10.1093/nar/gkf436>
- Knoop, J., Bouckennooghe, S., Van der Loos, L.M., D'Hondt, S., Karremans, M., Perk, F., Leliaert, F. & De Clerck, O. 2024. DNA barcoding reveals an extensive number of cryptic introductions of bladed Bangiales (Rhodophyta) in the southern North Sea. *Frontiers Mar. Sci.* 11: 1415034. <https://doi.org/10.3389/fmars.2024.1415034>
- Koeman, R.P.T. & Van den Hoek, C. 1981. The taxonomy of *Ulva* (Chlorophyceae) in the Netherlands. *Brit. Phycol. J.* 16: 9–53. <https://doi.org/10.1080/00071618100650031>
- Koeman, R.P.T. & Van den Hoek, C. 1982a. The taxonomy of *Enteromorpha* Link, 1820, (Chlorophyceae) in the Netherlands. I. The section *Enteromorpha*. *Arch. Hydrobiol. Suppl.* 63(3): 279–330.
- Koeman, R.P.T. & Van den Hoek, C. 1982b. The taxonomy of *Enteromorpha* Link, 1820 (Chlorophyceae) in the Netherlands. II. The section *Proliferae*. *Cryptog. Algal.* 3(1): 37–70. <https://doi.org/10.5962/p.309049>
- Liao, J., Wang, S., Lin, K., Huang, Y., Chen, X., Xin, R., Guo, Y. & Xie, E. 2024. Taxonomic identification and life cycle comparison of two populations of the monostromatic green algae *Monostroma nitidum*. *Ecol. Evol.* 14: e11424. <https://doi.org/10.1002/ece3.11424>
- Maggs, C.A., Bunker, A.R., Bunker, F.S.P.D., Harries, D., Kelly, J., Mineur, F., Blomster, J., Díaz-Tapia, P., Gabrielson, P.W., Hughey, J.R. & Brodie, J. 2024. Updating the Ulvaceae in the green seaweeds of Britain and Ireland. *Bot. Mar.* 67: 181–203. <https://doi.org/10.1515/bot-2023-0078>
- Mantri, V.A., Kazi, M.A., Balar, N.B., Gupta, V. & Gajaria, T. 2020. Concise review of green algal genus *Ulva* Linnaeus. *J. Appl. Phycol.* 32: 2725–2741. <https://doi.org/10.1007/s10811-020-02148-7>
- Nederlands Soortenregister 2024. Nederlands Soortenregister [Dataset]. www.nederlandsesoorten.nl (accessed 24 Oct 2024)
- Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molec. Biol. Evol.* 32: 268–274. <https://doi.org/10.1093/molbev/msu300>
- Prjibelski, A., Antipov, D., Meleshko, D., Lapidus, A. & Korobeynikov, A. 2020. Using SPAdes De Novo Assembler. *Curr. Protoc. Bioinf.* 70: e102. <https://doi.org/10.1002/cpbi.102>
- Ratnasingham, S. & Hebert, P.D.N. 2007. BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molec. Ecol. Notes* 7: 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Rybak, A.S. 2018. Species of *Ulva* (Ulvophyceae, Chlorophyta) as indicators of salinity. *Ecol. Indicators* 85: 253–261. <https://doi.org/10.1016/j.ecolind.2017.10.061>
- Stegenga, H., Mol, I., Prud'homme van Reine, W.F. & Lokhorst, G.M. 1997. Checklist of the marine algae of the Netherlands. *Gorteria Suppl.* 4: 1–57. <https://repository.naturalis.nl/pub/528200>
- Stegenga, H., Karremans, M. & Simons, J. 2007. Zeewieren van de voormalige oesterputten bij Yerseke. *Gorteria* 32: 125–143. <https://repository.naturalis.nl/pub/526694>
- Steinhagen, S., Karez, R. & Weinberger, F. 2019. Cryptic, alien and lost species: Molecular diversity of *Ulva* sensu lato along the German coasts of the North and Baltic Seas. *Eur. J. Phycol.* 54: 466–483. <https://doi.org/10.1080/09670262.2019.1597925>
- Steinhagen, S., Düsedau, L. & Weinberger, F. 2021. DNA barcoding of the German green supralittoral zone indicates the distribution and phenotypic plasticity of *Blidingia* species and reveals *Blidingia cornuta* sp. nov. *Taxon* 70: 229–245. <https://doi.org/10.1002/tax.12445>
- Steinhagen, S., Larsson, K., Olsson, J., Albers, E., Undeland, I., Pavia, H. & Toth, G.B. 2022. Closed life-cycle aquaculture of sea lettuce (*Ulva fenestrata*): performance and biochemical profile differ in early developmental stages. *Frontiers Mar. Sci.* 9: 942679. <https://doi.org/10.3389/fmars.2022.942679>
- Steinhagen, S., Kramár, L. & Toth, G.B. 2023a. The unheeded existence of the tubular greens: Molecular analyses reveal the distribution of a new *Ulva* species (Ulvophyceae, Chlorophyta), *Ulva capillata* sp. nov. in the Atlantic-Baltic Sea transect. *J. Appl. Phycol.* 35: 509–522. <https://doi.org/10.1007/s10811-022-02886-w>
- Steinhagen, S., Hoffmann, S., Pavia, H. & Toth, G.B. 2023b. Molecular identification of the ubiquitous green algae *Ulva* reveals high biodiversity, crypticity, and invasive species in the Atlantic-Baltic Sea region. *Algal Res.* 73: 103132. <https://doi.org/10.1016/j.algal.2023.103132>
- Storero, L.P., Avaca, M.S. & Roche, A. 2022. Living under *Ulva* canopy: The case of the scavenger snail *Buccinastrum deformis* in a eutrophic macrotidal bay in Patagonia (Argentina). *Mar. Ecol.* 43: e12718. <https://doi.org/10.1111/maec.12718>
- Tran, L.-A.T., Vieira, C., Steinhagen, S., Maggs, C.A., Hiraoka, M., Shimada, S., Van Nguyen, T., De Clerck, O. & Leliaert, F. 2022. An appraisal of *Ulva* (Ulvophyceae, Chlorophyta) taxonomy. *J. Appl. Phycol.* 34: 2689–2703. <https://doi.org/10.1007/s10811-022-02815-x>
- Van der Loos, L.M., Bafort, Q., Bosch, S., Ballesteros, E., Bárbara, I., Berecibar, E., Blanfuné, A., Bogaert, K., Bouckennooghe, S., Boudouresque, C.-F., Brodie, J., Cecere, E., Díaz-Tapia, P., Engelen, A.H., Gunnarson, K., Shabaka, S.H., Hoffman, R., Huisa, V., Israel, A., Karremans, M., Knoop, J., Le Gall, L., Maggs, C.A., Mineur, F., Parente, M., Perk, F., Petrocelli, A., Rodríguez-Prieto, C., Ruitton, S., Sansón, M., Serrão, E.A., Sfriso, A., Sjøtun, K., Stiger-Pouvreau, V., Surget, G., Taşkın, E., Thibaut, T., Tsiamis, K., Van De Weghe, L., Verlaque, M., Viard, F., Vranken, S., Leliaert, F. & De Clerck, O. 2024. Non-indigenous seaweeds in the Northeast Atlantic Ocean, the Mediterranean Sea and Macaronesia: A critical synthesis of diversity, spatial and temporal patterns. *Eur. J. Phycol.* 59: 127–156. <https://doi.org/10.1080/09670262.2023.2256828>
- Verbruggen, H., Ashworth, M., LoDuca, S.T., Vlaeminck, C., Cocquyt, E., Sauvage, T., Zechman, F.W., Littler, D.S., Littler, M.M. & Leliaert, F. & De Clerck, O. 2009. A multi-locus time-calibrated phylogeny of the siphonous green algae. *Molec. Phylogen. Evol.* 50: 642–653. <https://doi.org/10.1016/j.ympev.2008.12.018>
- Vinogradova, K. 1969. A contribution to the taxonomy of the order Ulvaes. *Bot. Zhurn. S.S.S.R.* 54: 1347–1355. [in Russian with English summary]
- Ye, N.-H., Zhang, X.-W., Mao, Y.-Z., Liang, C.-W., Xu, D., Zou, J., Zhuang, Z.-M. & Wang, Q.-Y. 2011. “Green tides” are overwhelming the coastline of our blue planet: Taking the world’s largest example. *Ecol. Res.* 26: 477–485. <https://doi.org/10.1007/s11284-011-0821-8>

Appendix 1. Voucher information for recent field-collected specimens, presented as follows: species name (molecularly identified), BOLD identifier, country, latitude, longitude, date, collector(s), sample number, herbarium information, GenBank accession number of *tufA* sequence.

Blidingia marginata (J.Agardh) P.J.L.Dang. ex Bliding, ULVNB319-24, Belgium, 51.363651, 3.35714, 15 Mar 2021, O. De Clerck, L.M. van der Loos, 0321_ZWI003, (BR: BR5010129413440), PQ733605; *Blidingia marginata*, ULVNB321-24, Belgium, 51.363651, 3.35714, 15 Mar 2021, O. De Clerck, L.M. van der Loos, 0321_ZWI005, NA, PQ733604; *Blidingia marginata*, ULVNB129-23, Netherlands, 51.516590, 4.003947, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_WMD001, (L: L.4598342), PQ733595; *Blidingia marginata*, ULVNB098-23, Netherlands, 51.575118, 3.894486, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_KAT002, (L: L.4598346), PQ733598; *Blidingia marginata*, ULVNB103-23, Netherlands, 51.575243, 3.890575, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_KAT009, (L: L.4598345), PQ733597; *Blidingia marginata*, ULVNB106-23, Netherlands, 51.518419, 3.750027, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_KVP002, (L: L.4598344), PQ733599; *Blidingia marginata*, ULVNB118-23, Netherlands, 51.618114, 3.682253, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJP021, (L: L.4598343), PQ733586; *Blidingia marginata*, ULVNB124-23, Netherlands, 51.618114, 3.682253, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJP028, NA, PQ733588; *Blidingia marginata*, ULVNB001-23, Belgium, 51.241033, 2.929862, 23 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_OST001, (BR: BR5010176052456V), PQ733587; *Blidingia marginata*, ULVNB002-23, Belgium, 51.241033, 2.929862, 23 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_OST002, (BR: BR5010176053484V), PQ733596; *Blidingia marginata*, ULVNB035-23, Belgium, 51.238622, 2.925727, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST021, (BR: BR5010176046561V), PQ733594; *Blidingia marginata*, ULVNB216-23, Netherlands, 51.575243, 3.890575, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT013, (L: L.4598320), PQ733591; *Blidingia marginata*, ULVNB217-23, Netherlands, 51.575243, 3.890575, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT014, (L: L.4598398), PQ733589; *Blidingia marginata*, ULVNB236-23, Netherlands, 51.618114, 3.682253, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_NJP006, (L: L.4598397), PQ733590; *Blidingia marginata*, ULVNB275-24, Netherlands, 53.005416, 4.796338, Jun 2019, A. Oerbekke, NL_18, NA, PQ733606; *Blidingia marginata*, ULVNB286-24, Netherlands, 53.183537, 4.840286, Jun 2019, A. Oerbekke, NL_29, NA, PQ733602; *Blidingia marginata*, ULVNB289-24, Netherlands, 53.158161, 4.877851, Jun 2019, A. Oerbekke, NL_35, NA, PQ733607; *Blidingia marginata*, ULVNB293-24, Netherlands, 53.099817, 4.898397, Jun 2019, A. Oerbekke, NL_44, NA, PQ733603; *Blidingia marginata*, ULVNB294-24, Netherlands, 53.099817, 4.898397, Jun 2019, A. Oerbekke, NL_46, NA, PQ733600; *Blidingia marginata*, ULVNB296-24, Netherlands, 53.044271, 4.857548, Jun 2019, A. Oerbekke, NL_49_A, NA, PQ733601; *Blidingia minima* (Kütz.) Kylin, ULVNB096-23, Netherlands, 51.597902, 3.684813, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_JCH025, (L: L.4598347), PQ733611; *Blidingia minima*, ULVNB169-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS002, (L: L.4598390), PQ733615; *Blidingia minima*, ULVNB170-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS003, (L: L.4598387), PQ733623; *Blidingia minima*, ULVNB171-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS004, (L: L.4598391), PQ733616; *Blidingia minima*, ULVNB184-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS019, (L: L.4598394), PQ733622; *Blidingia minima*, ULVNB185-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS020, (L: L.4598266), PQ733613; *Blidingia minima*, ULVNB031-23, Belgium, 51.238622, 2.925727, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST018, (BR: BR501017604440V), PQ733617; *Blidingia minima*, ULVNB239-23, Netherlands, 51.516590, 4.003947, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_WMD001, (L: L.4598388), PQ733620; *Blidingia minima*, ULVNB244-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_YER001, (L: L.4598393), PQ733619; *Blidingia minima*, ULVNB245-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_YER002, (L: L.4598389), PQ733618; *Blidingia minima*, ULVNB204-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT001, (L: L.4598319), PQ733624; *Blidingia minima*, ULVNB209-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT006, (L: L.4598395), PQ733612; *Blidingia minima*, ULVNB210-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT007, (L: L.4598396), PQ733614; *Blidingia minima*, ULVNB231-23, Netherlands, 51.618114, 3.682253, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_NJP001, (L: L.4598392), PQ733621; *Blidingia minima*, ULVNB285-24, Netherlands, 53.183537, 4.840286, Jun 2019, A. Oerbekke, NL_28, NA, PQ733610; *Blidingia minima*, ULVNB308-24, Netherlands, 51.498779, 4.056997, Nov 2021, S. Steinhagen, NL_109, NA, PQ733609; *Blidingia minima*, ULVNB315-24, Netherlands, 51.528363, 3.43293, Nov 2021, S. Steinhagen, NL_116, NA, PQ733608; *Gayralia oxysperma* (Kütz.) K.L. Vinogr. ex Scagel, P.W. Gabrielson, Garbary, Golden, M.W. Hawkes, S.C. Lindstr., J.C. Oliveira & Widd., ULVNB148-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP016, (L: L.4598341), PQ733625; *Gayralia oxysperma*, ULVNB240-23, Netherlands, 51.516590, 4.003947, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_WMD002, (L: L.4598399), PQ733627; *Gayralia oxysperma*, ULVNB241-23, Netherlands, 51.516590, 4.003947, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_WMD003, (L: L.4598400), PQ733629; *Gayralia oxysperma*, ULVNB273-24, Netherlands, 53.005416, 4.796338, Jun 2019, A. Oerbekke, NL_16, NA, PQ733631; *Gayralia oxysperma*, ULVNB290-24, Netherlands, 53.158161, 4.877851, Jun 2019, A. Oerbekke, NL_38, NA, PQ733633; *Gayralia oxysperma*, ULVNB298-24, Netherlands, 53.044271, 4.857548, Jun 2019, A. Oerbekke, NL_51, NA, PQ733632; *Gayralia oxysperma*, ULVNB309-24, Netherlands, 51.528363, 3.43293, Nov 2021, S. Steinhagen, NL_110, NA, PQ733630; *Monostroma grevillei* (Thur.) Wittr., ULVNB153-23, Netherlands, 51.731160, 3.976925, 20 Mar 2022, F. Perk, 0322_BOM_FAP005, (L: L.4598405), PQ733634; *Ulva australis* Aresch., ULVNB130-23, Netherlands, 51.516590, 4.003947, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_WMD002, (L: L.4598348), PQ733683; *Ulva australis*, ULVNB133-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP001, (L: L.4598351), PQ733682; *Ulva australis*, ULVNB143-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP011, (L: L.4598350), PQ733672; *Ulva australis*, ULVNB145-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP013, (L: L.4598302), PQ733670; *Ulva australis*, ULVNB149-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP017, (L: L.4598349), PQ733669; *Ulva australis*, ULVNB092-23, Netherlands, 51.540776, 3.929514, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_GOS002, (L: L.4598354), PQ733648; *Ulva australis*, ULVNB093-23, Netherlands, 51.540776, 3.929514, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_GOS003, (L: L.4598307), PQ733649; *Ulva australis*, ULVNB094-23, Netherlands, 51.597902, 3.684813, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_JCH023, (L: L.4598306), PQ733650; *Ulva australis*, ULVNB100-23, Netherlands, 51.575118, 3.894486, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_KAT004, (L: L.4598305), PQ733651; *Ulva australis*, ULVNB108-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJG002, (L: L.4598304), PQ733646; *Ulva australis*, ULVNB110-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJG004, (L: L.4598352), PQ733685; *Ulva australis*, ULVNB112-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJG006, (L: L.4598303), PQ733645; *Ulva australis*, ULVNB156-23, Netherlands, 51.615764, 3.962783, 20 Mar 2022, F. Perk, 0322_ZUI_FAP002, (L: L.4598404), PQ733668; *Ulva australis*, ULVNB159-23, Netherlands, 51.793692, 3.912480, 20 Apr 2022, L.M. van der Loos, 0422_PHP002, (L: L.4598328), PQ733663; *Ulva australis*, ULVNB173-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS006, (L: L.4598281), PQ733653; *Ulva australis*, ULVNB174-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS007, (L: L.4598280), PQ733652; *Ulva australis*, ULVNB176-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS009, (L: L.4598288), PQ733684; *Ulva australis*, ULVNB180-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS014, (L: L.4598285), PQ733654; *Ulva australis*, ULVNB183-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS018, (L: L.4598403), PQ733658; *Ulva australis*, ULVNB187-23, Netherlands, 51.544188, 3.926503, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS022, (L: L.4598282), PQ733655; *Ulva australis*, ULVNB189-23, Netherlands, 51.543760, 3.924623, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GOS024, (L: L.4598335), PQ733661; *Ulva australis*, ULVNB199-23, Netherlands, 51.538702, 3.926977, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GSJ002, (L: L.4598284), PQ733662; *Ulva australis*, ULVNB200-23, Netherlands, 51.538702, 3.926977, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GSJ003, (L: L.4598277), PQ733664; *Ulva australis*, ULVNB037-23,

Appendix 1. Continued.

Belgium, 51.225272, 2.958835, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST024, (BR: BR5010176048626V), PQ733665; *Ulva australis*, ULVNB039-23, Belgium, 51.225272, 2.958835, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST027, (BR: BR5010176050391V), PQ733666; *Ulva australis*, ULVNB040-23, Belgium, 51.225272, 2.958835, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST028, (BR: BR5010176051428V), PQ733667; *Ulva australis*, ULVNB242-23, Netherlands, 51.516590, 4.003947, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_WMD004, (L: L.4598413), PQ733679; *Ulva australis*, ULVNB246-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_YER003, (L: L.4598247), PQ733676; *Ulva australis*, ULVNB247-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_YER004, (L: L.4598252), PQ733675; *Ulva australis*, ULVNB255-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_YER011, (L: L.4598253), PQ733657; *Ulva australis*, ULVNB256-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_YER012, (L: L.4598251), PQ733656; *Ulva australis*, ULVNB196-23, Netherlands, 51.554434, 3.762467, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GSD003, (L: L.4598249), PQ733659; *Ulva australis*, ULVNB211-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_KAT008, (L: L.4598291), PQ733673; *Ulva australis*, ULVNB212-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_KAT009, (L: L.4598283), PQ733674; *Ulva australis*, ULVNB213-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_KAT010, (L: L.4598408), PQ733677; *Ulva australis*, ULVNB214-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_KAT011, (L: L.4598245), PQ733678; *Ulva australis*, ULVNB227-23, Netherlands, 51.643117, 3.707951, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_NJG004, (L: L.4598287), PQ733647; *Ulva australis*, ULVNB233-23, Netherlands, 51.618114, 3.682253, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_NJP003, (L: L.4598286), PQ733681; *Ulva australis*, ULVNB237-23, Netherlands, 51.777052, 3.867473, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_SPD001, (L: L.4598250), PQ733680; *Ulva australis*, ULVNB164-23, Netherlands, 52.962778, 4.782078, 16 Jul 2022, *F. Perk*, 0722_DHE_FAP048, (L: L.4598259), PQ733660; *Ulva australis*, ULVNB271-24, Netherlands, 53.005416, 4.796338, Jun 2019, *A. Oerbekke*, NL_12, NA, PQ733686; *Ulva californica* Wille, ULVNB111-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_NJG005, (L: L.4598376), PQ733698; *Ulva californica*, ULVNB005-23, Belgium, 51.241033, 2.929862, 23 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_OST006, (BR: BR5010176056577V), PQ733697; *Ulva californica*, ULVNB007-23, Belgium, 51.241033, 2.929862, 23 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_OST008, (BR: BR5010176058632V), PQ733699; *Ulva californica*, ULVNB012-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST002, (BR: BR5010176023456V), PQ733688; *Ulva californica*, ULVNB014-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST004, (BR: BR5010176025511V), PQ733689; *Ulva californica*, ULVNB018-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST009, (BR: BR5010176029632V), PQ733690; *Ulva californica*, ULVNB019-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST009B, (BR: BR5010176030379V), PQ733691; *Ulva californica*, ULVNB022-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST012, (BR: BR5010176033462V), PQ733687; *Ulva californica*, ULVNB025-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST015A, (BR: BR5010176036555V), PQ733692; *Ulva californica*, ULVNB028-23, Belgium, 51.238622, 2.925727, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST016A, (BR: BR5010176039648V), PQ733693; *Ulva californica*, ULVNB030-23, Belgium, 51.238622, 2.925727, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST017, (BR: BR5010176041412V), PQ733694; *Ulva californica*, ULVNB034-23, Belgium, 51.238622, 2.925727, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST020B, (BR: BR5010176045533V), PQ733695; *Ulva californica*, ULVNB250-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_YER007A, (L: L.4598325), PQ733696; *Ulva californica*, ULVNB207-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_KAT004, (L: L.4598324), PQ733700; *Ulva capillata* Steinhagen, ULVNB182-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS017, (L: L.4598321), PQ733702; *Ulva capillata*, ULVNB191-23, Netherlands, 51.543760, 3.924623, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS026, (L: L.4598271), PQ733701; *Ulva capillata*, ULVNB301-24, Netherlands, 51.498779, 4.056997, Nov 2021, *S. Steinhagen*, NL_102, NA, PQ733894; *Ulva capillata*, ULVNB303-24, Netherlands, 51.498779, 4.056997, Nov 2021, *S. Steinhagen*, NL_104, NA, PQ733896; *Ulva compressa* L., ULVNB126-23, Netherlands, 51.524819, 3.984967, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_WKS001, (L: L.4598362), PQ733741; *Ulva compressa*, ULVNB127-23, Netherlands, 51.524819, 3.984967, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_WKS002, (L: L.4598360), PQ733742; *Ulva compressa*, ULVNB128-23, Netherlands, 51.524819, 3.984967, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_WKS003, (L: L.4598361), PQ733743; *Ulva compressa*, ULVNB132-23, Netherlands, 51.516590, 4.003947, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_WMD004, (L: L.4598363), PQ733747; *Ulva compressa*, ULVNB138-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_YBP006, (L: L.4598372), PQ733751; *Ulva compressa*, ULVNB139-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_YBP007, (L: L.4598371), PQ733752; *Ulva compressa*, ULVNB147-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_YBP015, (L: L.4598370), PQ733758; *Ulva compressa*, ULVNB150-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_YBP018, (L: L.4598369), PQ733760; *Ulva compressa*, ULVNB091-23, Netherlands, 51.540776, 3.929514, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_GOS001, (L: L.4598368), PQ733708; *Ulva compressa*, ULVNB095-23, Netherlands, 51.597902, 3.684813, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_JCH024, (L: L.4598367), PQ733707; *Ulva compressa*, ULVNB101-23, Netherlands, 51.575243, 3.890575, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_KAT005, (L: L.4598316), PQ733730; *Ulva compressa*, ULVNB104-23, Netherlands, 51.575118, 3.894486, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_KAT010, (L: L.4598353), PQ733704; *Ulva compressa*, ULVNB107-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_NJG001, (L: L.4598366), PQ733706; *Ulva compressa*, ULVNB113-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_NJG007, (L: L.4598365), PQ733733; *Ulva compressa*, ULVNB115-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_NJG009, (L: L.4598383), PQ733734; *Ulva compressa*, ULVNB117-23, Netherlands, 51.618114, 3.682253, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_NJP020, (L: L.4598382), PQ733735; *Ulva compressa*, ULVNB120-23, Netherlands, 51.618114, 3.682253, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_NJP023, (L: L.4598373), PQ733736; *Ulva compressa*, ULVNB121-23, Netherlands, 51.618114, 3.682253, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_NJP024, (L: L.4598364), PQ733737; *Ulva compressa*, ULVNB003-23, Belgium, 51.241033, 2.929862, 23 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_OST003, (BR: BR5010176054511V), PQ733754; *Ulva compressa*, ULVNB006-23, Belgium, 51.241033, 2.929862, 23 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_OST007, (BR: BR5010176057604V), PQ733705; *Ulva compressa*, ULVNB008-23, Belgium, 51.227544, 2.920811, 23 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_OST009, (BR: BR5010176059660V), PQ733746; *Ulva compressa*, ULVNB010-23, Belgium, 51.241033, 2.929862, 23 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_OST011, (BR: BR5010176061434V), PQ733715; *Ulva compressa*, ULVNB168-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS001, (L: L.4598411), PQ733719; *Ulva compressa*, ULVNB172-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS005, (L: L.4598412), PQ733723; *Ulva compressa*, ULVNB175-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS008, (L: L.4598301), PQ733726; *Ulva compressa*, ULVNB178-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS011, (L: L.4598297), PQ733729; *Ulva compressa*, ULVNB181-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS015, (L: L.4598296), PQ733740; *Ulva compressa*, ULVNB186-23, Netherlands, 51.544188, 3.926503, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS021, (L: L.4598298), PQ733732; *Ulva compressa*, ULVNB192-23, Netherlands, 51.543760, 3.924623, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS027, (L: L.4598300), PQ733728; *Ulva compressa*, ULVNB193-23, Netherlands, 51.543760, 3.924623, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS028, (L: L.4598299), PQ733727; *Ulva compressa*, ULVNB011-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST001, (BR: BR5010176022428V), PQ733725; *Ulva*

Appendix 1. Continued.

compressa, ULVNB013-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST003, (BR: BR5010176024484V), PQ733724; *Ulva compressa*, ULVNB016-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST007, (BR: BR5010176027577V), PQ733722; *Ulva compressa*, ULVNB026-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST015B, (BR: BR5010176037583V), PQ733720; *Ulva compressa*, ULVNB027-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST015C, (BR: BR5010176038610V), PQ733717; *Ulva compressa*, ULVNB029-23, Belgium, 51.238622, 2.925727, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST016B, (BR: BR5010176040385V), PQ733716; *Ulva compressa*, ULVNB033-23, Belgium, 51.238622, 2.925727, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST020A, (BR: BR5010176044505V), PQ733713; *Ulva compressa*, ULVNB243-23, Netherlands, 51.516590, 4.003947, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_WMD005, (L: L.4598338), PQ733750; *Ulva compressa*, ULVNB248-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_YER005b, (L: L.4598332), PQ733759; *Ulva compressa*, ULVNB251-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_YER007B, (L: L.4598290), PQ733712; *Ulva compressa*, ULVNB252-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_YER008, (L: L.4598339), PQ733714; *Ulva compressa*, ULVNB254-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_YER010, (L: L.4598340), PQ733721; *Ulva compressa*, ULVNB205-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT002, (L: L.4598410), PQ733711; *Ulva compressa*, ULVNB208-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT005, (L: L.4598336), PQ733709; *Ulva compressa*, ULVNB218-23, Netherlands, 51.575243, 3.890575, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT015, (L: L.4598337), PQ733738; *Ulva compressa*, ULVNB230-23, Netherlands, 51.643117, 3.707951, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_NJG007, (L: L.4598295), PQ733703; *Ulva compressa*, ULVNB232-23, Netherlands, 51.618114, 3.682253, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_NJP002, (L: L.4598294), PQ733748; *Ulva compressa*, ULVNB167-23, Netherlands, 52.962584, 4.731242, 16 Jul 2022, F. Perk, 0722_DHE_FAP054, (L: L.4598414), PQ733718; *Ulva compressa*, ULVNB269-24, Netherlands, 53.087917, 4.739333, Jun 2019, A. Oerbekke, NL_10, NA, PQ733768; *Ulva compressa*, ULVNB270-24, Netherlands, 53.087917, 4.739333, Jun 2019, A. Oerbekke, NL_11, NA, PQ733769; *Ulva compressa*, ULVNB262-24, Netherlands, 53.015639, 4.708444, Jun 2019, A. Oerbekke, NL_2, NA, PQ733765; *Ulva compressa*, ULVNB287-24, Netherlands, 53.183537, 4.840286, Jun 2019, A. Oerbekke, NL_30, NA, PQ733770; *Ulva compressa*, ULVNB288-24, Netherlands, 53.183537, 4.840286, Jun 2019, A. Oerbekke, NL_33, NA, PQ733771; *Ulva compressa*, ULVNB264-24, Netherlands, 53.015639, 4.708444, Jun 2019, A. Oerbekke, NL_4, NA, PQ733767; *Ulva compressa*, ULVNB295-24, Netherlands, 53.099817, 4.898397, Jun 2019, A. Oerbekke, NL_48, NA, PQ733762; *Ulva compressa*, ULVNB297-24, Netherlands, 53.044271, 4.857548, Jun 2019, A. Oerbekke, NL_50, NA, PQ733763; *Ulva compressa*, ULVNB267-24, Netherlands, 53.087917, 4.739333, Jun 2019, A. Oerbekke, NL_7, NA, PQ733766; *Ulva compressa*, ULVNB314-24, Netherlands, 51.528363, 3.43293, Nov 2021, S. Steinhagen, NL_115, NA, PQ733764; *Ulva compressa*, ULVNB316-24, Netherlands, 51.528363, 3.43293, Nov 2021, S. Steinhagen, NL_117, NA, PQ733761; *Ulva fenestrata* Postels & Rupr., ULVNB109-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJG003, (L: L.4598377), PQ733776; *Ulva fenestrata*, ULVNB114-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJG008, (L: L.4598379), PQ733777; *Ulva fenestrata*, ULVNB116-23, Netherlands, 51.643117, 3.707951, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJG010, (L: L.4598378), PQ733779; *Ulva fenestrata*, ULVNB157-23, Netherlands, 51.615764, 3.962783, 20 Mar 2022, F. Perk, 0322_ZUI_FAP004, (L: L.4598331), PQ733781; *Ulva fenestrata*, ULVNB161-23, Netherlands, 51.584572, 3.628692, 30 Apr 2022, F. Perk, 0422_VEM_FAP025, (L: L.4598260), PQ733786; *Ulva fenestrata*, ULVNB225-23, Netherlands, 51.643117, 3.707951, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_NJG002, (L: L.4598289), PQ733785; *Ulva fenestrata*, ULVNB226-23, Netherlands, 51.643117, 3.707951, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_NJG003, (L: L.4598402), PQ733782; *Ulva fenestrata*, ULVNB228-23, Netherlands, 51.643117, 3.707951, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_NJG005, (L: L.4598279), PQ733783; *Ulva fenestrata*, ULVNB229-23, Netherlands, 51.643117, 3.707951, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_NJG006, (L: L.4598401), PQ733772; *Ulva fenestrata*, ULVNB234-23, Netherlands, 51.618114, 3.682253, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_NJP004, (L: L.4598278), PQ733778; *Ulva fenestrata*, ULVNB165-23, Netherlands, 52.964403, 4.782402, 16 Jul 2022, F. Perk, 0722_DHE_FAP052, (L: L.4598258), PQ733775; *Ulva fenestrata*, ULVNB166-23, Netherlands, 52.962584, 4.731242, 16 Jul 2022, F. Perk, 0722_DHE_FAP053A, (L: L.4598330), PQ733784; *Ulva flexuosa* Wulfen, ULVNB024-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST014, (BR: BR5010176035527V), PQ733636; *Ulva flexuosa*, ULVNB038-23, Belgium, 51.225272, 2.958835, 13 Jul 2022, L.M. van der Loos, J. Knoop, 0722_OST026, (BR: BR5010176049654V), PQ733643; *Ulva flexuosa*, ULVNB215-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT012, (L: L.4598322), PQ733638; *Ulva intestinalis* L., ULVNB131-23, Netherlands, 51.516590, 4.003947, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_WMD003, (L: L.4598315), PQ733801; *Ulva intestinalis*, ULVNB105-23, Netherlands, 51.518419, 3.750027, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_KVP001, (L: L.4598359), PQ733799; *Ulva intestinalis*, ULVNB125-23, Netherlands, 51.524093, 3.728200, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_VEM001, (L: L.4598358), PQ733800; *Ulva intestinalis*, ULVNB009-23, Belgium, 51.225272, 2.958835, 23 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_OST010, (BR: BR5010176060406V), PQ733794; *Ulva intestinalis*, ULVNB160-23, Netherlands, 51.793692, 3.912480, 20 Apr 2022, L.M. van der Loos, 0422_PHP003, (L: L.4598329), PQ733802; *Ulva intestinalis*, ULVNB162-23, Netherlands, 51.584572, 3.628692, 30 Apr 2022, F. Perk, 0422_VEM_FAP027, (L: L.4598406), PQ733803; *Ulva intestinalis*, ULVNB163-23, Netherlands, 51.914415, 4.250449, 3 May 2022, F. Perk, 0522_MAS_FAP028, (L: L.4598407), PQ733793; *Ulva intestinalis*, ULVNB221-23, Netherlands, 51.518419, 3.750027, 12 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KVP002, (L: L.4598385), PQ733807; *Ulva intestinalis*, ULVNB194-23, Netherlands, 51.554434, 3.762467, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GSD001, (L: L.4598386), PQ733804; *Ulva intestinalis*, ULVNB197-23, Netherlands, 51.554434, 3.762467, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_GSD004, (L: L.4598267), PQ733805; *Ulva intestinalis*, ULVNB206-23, Netherlands, 51.575118, 3.894486, 14 Jul 2022, L.M. van der Loos, J. Knoop, 0722_KAT003, (L: L.4598265), PQ733806; *Ulva intestinalis*, ULVNB259-23, Netherlands, 51.643076, 4.085409, 6 Sep 2022, M. Karremans, 0922_BRU_MK009, (L: L.4598261), PQ733808; *Ulva intestinalis*, ULVNB274-24, Netherlands, 53.005416, 4.796338, Jun 2019, A. Oerbekke, NL_17, NA, PQ733811; *Ulva intestinalis*, ULVNB276-24, Netherlands, 53.00289, 4.791057, Jun 2019, A. Oerbekke, NL_19, NA, PQ733810; *Ulva intestinalis*, ULVNB281-24, Netherlands, 53.00289, 4.791057, Jun 2019, A. Oerbekke, NL_24, NA, PQ733812; *Ulva intestinalis*, ULVNB312-24, Netherlands, 51.528363, 3.43293, Nov 2021, S. Steinhagen, NL_113, NA, PQ733813; *Ulva intestinalis*, ULVNB313-24, Netherlands, 51.528363, 3.43293, Nov 2021, S. Steinhagen, NL_114, NA, PQ733809; *Ulva laciniolata* (Kütz.) Wittr., ULVNB134-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP002, (L: L.4598313), PQ733847; *Ulva laciniolata*, ULVNB135-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP003, (L: L.4598312), PQ733846; *Ulva laciniolata*, ULVNB136-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP004, (L: L.4598311), PQ733845; *Ulva laciniolata*, ULVNB137-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP005, (L: L.4598310), PQ733843; *Ulva laciniolata*, ULVNB141-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP009, (L: L.4598356), PQ733840; *Ulva laciniolata*, ULVNB144-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP012, (L: L.4598309), PQ733838; *Ulva laciniolata*, ULVNB146-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP014, (L: L.4598355), PQ733837; *Ulva laciniolata*, ULVNB151-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP019, (L: L.4598255), PQ733834; *Ulva laciniolata*, ULVNB152-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_YBP020, (L: L.4598308), PQ733830; *Ulva laciniolata*, ULVNB102-23, Netherlands, 51.575118, 3.894486, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_KAT006, (L: L.4598257), PQ733833; *Ulva laciniolata*, ULVNB119-23, Netherlands, 51.618114, 3.682253, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJP022, (L: L.4598357), PQ733832; *Ulva laciniolata*, ULVNB122-23, Netherlands, 51.618114, 3.682253, 22 Feb 2022, L.M. van der Loos, J. Knoop, L. Van De Weghe, 0222_NJP025, (L: L.4598256), PQ733831; *Ulva laciniolata*, ULVNB123-23,

Appendix 1. Continued.

Netherlands, 51.618114, 3.682253, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_NJP027, (L: L.4598314), PQ733848; *Ulva lacinulata*, ULVNB154-23, Netherlands, 51.509918, 4.065071, 18 Mar 2022, *M. Karremans*, 0322_SYE_MART507, (L: L.4598333), PQ733850; *Ulva lacinulata*, ULVNB155-23, Netherlands, 51.509918, 4.065071, 18 Mar 2022, *M. Karremans*, 0322_SYE_MART508, (L: L.4598334), PQ733849; *Ulva lacinulata*, ULVNB201-23, Netherlands, 51.532520, 3.902192, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_HGS001, (L: L.4598317), PQ733851; *Ulva lacinulata*, ULVNB222-23, Netherlands, 51.518419, 3.750027, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_KVP003, (L: L.4598384), PQ733852; *Ulva lacinulata*, ULVNB223-23, Netherlands, 51.518419, 3.750027, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_KVP006, (L: L.4598263), PQ733829; *Ulva lacinulata*, ULVNB015-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST006, (BR: BR5010176026549V), PQ733842; *Ulva lacinulata*, ULVNB023-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST013, (BR: BR5010176034490V), PQ733835; *Ulva lacinulata*, ULVNB253-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_YER009, (L: L.4598318), PQ733836; *Ulva lacinulata*, ULVNB235-23, Netherlands, 51.618114, 3.682253, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_NJP005, (L: L.4598246), PQ733841; *Ulva lacinulata*, ULVNB261-24, Netherlands, 53.015639, 4.708444, Jun 2019, *A. Oerbekke*, NL_1, NA, PQ733817; *Ulva lacinulata*, ULVNB272-24, Netherlands, 53.005416, 4.796338, Jun 2019, *A. Oerbekke*, NL_15, NA, PQ733818; *Ulva lacinulata*, ULVNB277-24, Netherlands, 53.00289, 4.791057, Jun 2019, *A. Oerbekke*, NL_20, NA, PQ733819; *Ulva lacinulata*, ULVNB278-24, Netherlands, 53.00289, 4.791057, Jun 2019, *A. Oerbekke*, NL_21, NA, PQ733820; *Ulva lacinulata*, ULVNB279-24, Netherlands, 53.00289, 4.791057, Jun 2019, *A. Oerbekke*, NL_22, NA, PQ733821; *Ulva lacinulata*, ULVNB280-24, Netherlands, 53.00289, 4.791057, Jun 2019, *A. Oerbekke*, NL_23, NA, PQ733822; *Ulva lacinulata*, ULVNB282-24, Netherlands, 53.00289, 4.791057, Jun 2019, *A. Oerbekke*, NL_25, NA, PQ733823; *Ulva lacinulata*, ULVNB283-24, Netherlands, 53.00289, 4.791057, Jun 2019, *A. Oerbekke*, NL_26, NA, PQ733824; *Ulva lacinulata*, ULVNB284-24, Netherlands, 53.00289, 4.791057, Jun 2019, *A. Oerbekke*, NL_27, NA, PQ733825; *Ulva lacinulata*, ULVNB263-24, Netherlands, 53.015639, 4.708444, Jun 2019, *A. Oerbekke*, NL_3, NA, PQ733815; *Ulva lacinulata*, ULVNB266-24, Netherlands, 53.087917, 4.739333, Jun 2019, *A. Oerbekke*, NL_6, NA, PQ733816; *Ulva lacinulata*, ULVNB268-24, Netherlands, 53.087917, 4.739333, Jun 2019, *A. Oerbekke*, NL_8, NA, PQ733814; *Ulva lacinulata*, ULVNB306-24, Netherlands, 51.498779, 4.056997, Nov 2021, *S. Steinhagen*, NL_107, NA, PQ733826; *Ulva lacinulata*, ULVNB307-24, Netherlands, 51.498779, 4.056997, Nov 2021, *S. Steinhagen*, NL_108, NA, PQ733827; *Ulva lacinulata*, ULVNB311-24, Netherlands, 51.528363, 3.43293, Nov 2021, *S. Steinhagen*, NL_112, NA, PQ733828; *Ulva linza* L., ULVNB140-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_YBP008, (L: L.4598380), PQ733857; *Ulva linza*, ULVNB142-23, Netherlands, 51.482596, 4.071364, 20 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_YBP010, (L: L.4598381), PQ733856; *Ulva linza*, ULVNB158-23, Netherlands, 51.793692, 3.912480, 20 Apr 2022, *L.M. van der Loos*, 0422_PHP001, (L: L.4598327), PQ733859; *Ulva linza*, ULVNB202-23, Netherlands, 51.532520, 3.902192, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_HGS002, (L: L.4598409), PQ733854; *Ulva linza*, ULVNB020-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST010, (BR: BR5010176031406V), PQ733860; *Ulva linza*, ULVNB021-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST011, (BR: BR5010176032434V), PQ733861; *Ulva linza*, ULVNB032-23, Belgium, 51.238622, 2.925727, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST019, (BR: BR5010176043478V), PQ733866; *Ulva linza*, ULVNB036-23, Belgium, 51.225272, 2.958835, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST023, (BR: BR5010176047599V), PQ733867; *Ulva linza*, ULVNB195-23, Netherlands, 51.554434, 3.762467, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GSD002, (L: L.4598292), PQ733858; *Ulva linza*, ULVNB142-23, Netherlands, 51.643117, 3.707951, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_NJG001, (L: L.4598293), PQ733861; *Ulva linza*, ULVNB258-23, Netherlands, 51.446444, 3.999762, 30 Sep 2022, *M. Karremans*, 0922_HWE_MK006, (L: L.4598326), PQ733855; *Ulva linza*, ULVNB299-24, Netherlands, 53.044271, 4.857548, Jun 2019, *A. Oerbekke*, NL_52, NA, PQ733869; *Ulva linza*, ULVNB300-24, Netherlands, 51.498779, 4.056997, Nov 2021, *S. Steinhagen*, NL_101, NA, PQ733870; *Ulva linza*, ULVNB305-24, Netherlands, 51.498779, 4.056997, Nov 2021, *S. Steinhagen*, NL_106, NA, PQ733872; *Ulva linza*, ULVNB310-24, Netherlands, 51.528363, 3.43293, Nov 2021, *S. Steinhagen*, NL_111, NA, PQ733871; *Ulva pilifera* (Kütz.), Škaloud & Leliaert, ULVNB198-23, Netherlands, 51.538702, 3.926977, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GSJ001, (L: L.4598272), PQ733873; *Ulva pilifera*, ULVNB220-23, Netherlands, 51.518419, 3.750027, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_KVP001, (L: L.4598273), PQ733874; *Ulva prolifera* O.F.Müll., ULVNB317-24, Belgium, 51.363651, 3.35714, 4 Feb 2021, *O. De Clerck, Q. Bafort*, 0221_ZWI001, (BR: BR5010129396583), PQ733889; *Ulva prolifera*, ULVNB318-24, Belgium, 51.363651, 3.35714, 4 Feb 2021, *O. De Clerck, Q. Bafort*, 0221_ZWI002, (BR: BR5010129398648), PQ733890; *Ulva prolifera*, ULVNB320-24, Belgium, 51.363651, 3.35714, 15 Mar 2021, *O. De Clerck, L.M. van der Loos*, 0321_ZWI004, (BR: BR5010129415505), PQ733892; *Ulva prolifera*, ULVNB322-24, Belgium, 51.363651, 3.35714, 15 Mar 2021, *O. De Clerck, L.M. van der Loos*, 0321_ZWI006, (BR: BR5010129420363), PQ733886; *Ulva prolifera*, ULVNB323-24, Belgium, 51.363651, 3.35714, 15 Mar 2021, *O. De Clerck, L.M. van der Loos*, 0321_ZWI007, (BR: BR5010129422428), PQ733887; *Ulva prolifera*, ULVNB097-23, Netherlands, 51.575243, 3.890575, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_KAT001, (L: L.4598375), PQ733883; *Ulva prolifera*, ULVNB099-23, Netherlands, 51.575243, 3.890575, 22 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_KAT003, (L: L.4598374), PQ733884; *Ulva prolifera*, ULVNB203-23, Netherlands, 51.532520, 3.902192, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_HGS003, (L: L.4598264), PQ733885; *Ulva prolifera*, ULVNB291-24, Netherlands, 53.158161, 4.877851, Jun 2019, *A. Oerbekke*, NL_39, NA, PQ733891; *Ulva prolifera*, ULVNB292-24, Netherlands, 53.158161, 4.877851, Jun 2019, *A. Oerbekke*, NL_40, NA, PQ733888; *Ulva pseudocurvata* Koeman & C.Hoek, ULVNB004-23, Belgium, 51.241033, 2.929862, 23 Feb 2022, *L.M. van der Loos, J. Knoop, L. Van De Weghe*, 0222_OST005, (BR: BR5010176055549V), PQ733790; *Ulva shanxiensis* L.Chen, J.Feng & S.L.Xie, ULVNB260-24, Netherlands, 52.357853, 5.217385, 7 Jul 2023, *L.M. van der Loos*, 0723_WWA001, (L: L.4598262), PQ733893; *Ulva* sp. 6, ULVNB177-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS010, (L: L.4598274), PQ733635; *Ulva* sp. 6, ULVNB179-23, Netherlands, 51.540776, 3.929514, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS012, (L: L.4598275), PQ733644; *Ulva* sp. 6, ULVNB190-23, Netherlands, 51.543760, 3.924623, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS025, (L: L.4598276), PQ733640; *Ulva* sp. 6, ULVNB249-23, Netherlands, 51.482596, 4.071364, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_YER006b, (L: L.4598323), PQ733642; *Ulva* sp. 6, ULVNB257-23, Netherlands, 51.504210, 4.043758, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_YER013, (L: L.4598248), PQ733639; *Ulva* sp. 10, ULVNB017-23, Belgium, 51.241033, 2.929862, 13 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_OST008, (BR: BR5010176028604V), PQ733641; *Ulva* sp. 10, ULVNB265-24, Netherlands, 53.015639, 4.708444, Jun 2019, *A. Oerbekke*, NL_5, NA, PQ733895; *Ulva torta* (Mertens) Trevis., ULVNB188-23, Netherlands, 51.544188, 3.926503, 12 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_GOS023, (L: L.4598270), PQ733900; *Ulva torta*, ULVNB219-23, Netherlands, 51.575243, 3.890575, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_KAT016, (L: L.4598269), PQ733899; *Ulva torta*, ULVNB238-23, Netherlands, 51.770752, 3.867473, 14 Jul 2022, *L.M. van der Loos, J. Knoop*, 0722_SPD003, (L: L.4598268), PQ733898; *Ulva torta*, ULVNB302-24, Netherlands, 51.498779, 4.056997, Nov 2021, *S. Steinhagen*, NL_103, NA, PQ733901; *Ulva torta*, ULVNB304-24, Netherlands, 51.498779, 4.056997, Nov 2021, *S. Steinhagen*, NL_105, NA, PQ733902; *Umbraulva dangeardii* M.J.Wynne & G.Furnari, ULVNB324-24, Netherlands, 51.545203, 3.925117, 11 Dec 2021, *F. Perk*, 1221_PUP003, (L: L.4598254), PQ733903.

Appendix 2. Voucher information for historical specimens newly sequenced, presented as follows: species name (molecularly identified), species name (original label herbarium specimen), BOLD identifier, country, latitude, longitude, date, collector(s), sample number, herbarium information, GenBank accession number of *tufA* sequence.

Blidingia marginata (J.Agardh) P.J.L.Dang. ex Bliding, *Enteromorpha nana* (Sommerf.) Sjöstedt, ULVNB066-23, Netherlands, 52.899605, 4.970173, 28 Jun 1949, C. den Hartog, NAT025, (L: L.4095667), PQ733592; *Blidingia marginata*, *Enteromorpha nana* (Sommerf.) Sjöstedt, ULVNB067-23, Netherlands, 52.899605, 4.970173, 28 Jun 1949, C. den Hartog, NAT026, (L: L.4095670), PQ733593; *Gayralia oxysperma* (Kütz.) K.L.Vinogr. ex Scagel, P.W.Gabrielson, Garbary, Golden, M.W.Hawkes, S.C.Lindstr., J.C.Oliveira & Widd., *Monostroma oxyspermum* (Kütz.) Doty, ULVNB077-23, Netherlands, 51.497525, 3.622778, 10 Apr 1943, C. Brakman, NAT046, (L: L.4096278), PQ733628; *Gayralia oxysperma*, *Monostroma oxyspermum* (Kütz.) Doty, ULVNB078-23, Netherlands, 52.965662, 4.770015, 6 Sep 1956, C. van den Hoek, NAT047, (L: L.4096295), PQ733626; *Ulva australis* Aresch., *Ulva* sp., ULVNB052-23, Belgium, 51.349225, 3.259919, 18 Sep 2000, H. Engledow, A. Volckaert, BER080, (BR: BR5010111706505V), PQ733671; *Ulva compressa* L., *Ulva curvata* (Kütz.) De Toni, ULVNB049-23, Belgium, 51.154733, 2.723395, 18 Apr 2001, H. Engledow, A. Volckaert, BER055, (BR: BR5010111517484V), PQ733757; *Ulva compressa*, *Enteromorpha* sp., ULVNB044-23, Belgium, 51.219844, 2.882464, 1 Aug 1988, C. Hanssens, BER023, (BR: BR5010111575484V), PQ733710; *Ulva compressa*, *Enteromorpha intestinaloides* Koeman & C.Hoek, ULVNB054-23, Netherlands, 51.532076, 3.432760, 14 Jul 1985, R.P.T. Koeman, NAT002, (L: L.0050876), PQ733756; *Ulva compressa*, *Enteromorpha intestinaloides* Koeman & C.Hoek, ULVNB055-23, Netherlands, 51.532076, 3.432760, 14 Jul 1985, R.P.T. Koeman, NAT003, (L: L.0050877), PQ733755; *Ulva compressa*, *Enteromorpha ramulosa* Hook., ULVNB061-23, Netherlands, 52.771984, 4.655859, 14 Apr 1950, C. den Hartog, NAT015, (L: L.4095452), PQ733753; *Ulva compressa*, *Enteromorpha linza* (L.) J.Agardh, ULVNB073-23, Netherlands, 53.346866, 6.910948, 14 Aug 1856, S.E. Stratingh, NAT041, (L: L.4095753), PQ733749; *Ulva compressa*, *Ulva gigantea* (Kütz.) Bliding, ULVNB081-23, Netherlands, 51.556083, 3.835304, 1 Nov 1845, unknown, NAT053, (L: L.4108061), PQ733745; *Ulva compressa*, *Enteromorpha compressa* (L.) Grev., ULVNB082-23, Netherlands, 53.259187, 4.951689, 11 Jul 1950, C. den Hartog, NAT054, (L: L.4108125), PQ733744; *Ulva compressa*, *Enteromorpha compressa* (L.) Grev., ULVNB084-23, Netherlands, 51.522691, 3.999558, 21 Jul 1975, G.M. Lokhorst, NAT056, (L: L.4108148), PQ733739; *Ulva compressa*, *Ulva plicata* O.F.Müll., ULVNB087-23, Netherlands, unknown, unknown, NA, Herb Kützing, F.T., NAT062, (L: L.4114661), PQ733731; *Ulva fenestrata* Postels & Rupr., *Ulva lactuca* L., ULVNB047-23, Netherlands, 51.541278, 3.930302, 15 Jan 1975, G.M. Lokhorst, BER043, (BR: BR5010111459555V), PQ733780; *Ulva fenestrata*, *Ulva scandinavica* Bliding, ULVNB043-23, Belgium, 51.342084, 3.203657, 4 Sep 2000, H. Engledow, A. Volckaert, BER016, (BR: BR5010111537505V), PQ733773; *Ulva fenestrata*, *Ulva lactuca* L., ULVNB086-23, Netherlands, 51.541278, 3.930302, 15 Jan 1975, G.M. Lokhorst, NAT060, (L: L.4114447), PQ733774; *Ulva fenestrata*, *Ulva rigida* C.Agardh, ULVNB088-23, Netherlands, 51.669878, 4.092202, 8 Jun 1975, R.P.T. Koeman, NAT064, (L: L.4114719), PQ784082; *Ulva fenestrata*, *Ulva rigida* C.Agardh, ULVNB089-23, Netherlands, 51.669878, 4.092202, 8 Jun 1975, R.P.T. Koeman, NAT065, (L: L.4114720), PQ733787; *Ulva flexuosa* Wulfen, *Enteromorpha linza* (L.) J.Agardh, ULVNB071-23, Netherlands, 51.541278, 3.930302, 28 Jun 1976, H. Stegenga, NAT037, (L: L.4095733), PQ733637; *Ulva intestinalis* L., *Enteromorpha compressa* (L.) Grev., ULVNB045-23, Belgium, 51.359438, 3.303312, 14 Sep 2000, H. Engledow, A. Volckaert, BER036, (BR: BR5010111485462V), PQ733795; *Ulva intestinalis*, *Enteromorpha pseudolinza* Koeman & C.Hoek, ULVNB056-23, Netherlands, 52.965662, 4.770015, 1 Aug 1985, R.P.T. Koeman, NAT004, (L: L.0050878), PQ733796; *Ulva intestinalis*, *Enteromorpha intestinalis* (L.) Link, ULVNB072-23, Netherlands, 52.899605, 4.970173, 28 Aug 1954, C. den Hartog, NAT040, (L: L.4095741), PQ733797; *Ulva intestinalis*, *Enteromorpha compressa* (L.) Grev., ULVNB083-23, Netherlands, 52.213497, 4.395826, 20 Feb 1949, J.A.W. Lucas, NAT055, (L: L.4108136), PQ733798; *Ulva laciniolata* (Kütz.) Wittm., *Ulva scandinavica* Bliding, ULVNB048-23, Belgium, 51.238993, 2.920490, 24 May 1984, E. Coppejans, BER051, (BR: BR5010111541335V), PQ733839; *Ulva laciniolata*, *Ulva pseudocurvata* Koeman & C.Hoek, ULVNB042-23, Belgium, 51.154733, 2.723395, 27 Apr 1999, E. Coppejans, F. Leliaert, M. De Mey, M. De Mol, J. Nuytinck, BER013, (BR: BR5010111555462V), PQ733844; *Ulva linza* L., *Enteromorpha intestinalis* (L.) Link, ULVNB046-23, Belgium, 51.238993, 2.920490, 28 Aug 2000, H. Engledow, A. Volckaert, BER037, (BR: BR5010111487527V), PQ733853; *Ulva linza*, *Enteromorpha prolifera* (O.F.Müll.) J.Agardh, ULVNB068-23, Netherlands, 53.410810, 6.218992, 17 Jul 1975, R.P.T. Koeman, NAT033, (L: L.4095684), PQ733868; *Ulva linza*, *Enteromorpha flexuosa* (Wulfen) J.Agardh, ULVNB075-23, Netherlands, 53.493181, 6.230344, 5 Jul 1975, R.P.T. Koeman, NAT044, (L: L.4095919), PQ733865; *Ulva linza*, *Enteromorpha flexuosa* (Wulfen) J.Agardh, ULVNB076-23, Netherlands, 53.493181, 6.230344, 5 Jul 1975, R.P.T. Koeman, NAT045, (L: L.4095920), PQ784081; *Ulva linza*, *Enteromorpha* cf. *linza*, ULVNB079-23, Netherlands, 51.400222, 3.964683, 14 May 1958, W.G. Beeftink, NAT049, (L: L.4108041), PQ733864; *Ulva linza*, *Enteromorpha* cf. *linza* (L.) J.Agardh, ULVNB080-23, Netherlands, 51.866368, 4.166912, 12 May 1957, C. van den Hoek, NAT050, (L: L.4108042), PQ733863; *Ulva prolifera* O.F.Müll., *Enteromorpha ralfsii* Harv., ULVNB058-23, Netherlands, 51.866368, 4.166912, 30 Aug 1961, W.G. Beeftink, NAT010, (L: L.4095446), PQ733878; *Ulva prolifera*, *Enteromorpha ramellosa* Kütz., ULVNB059-23, Netherlands, 51.541278, 3.930302, NA, R.B. van den Bosch, NAT011, (L: L.4095447), PQ733877; *Ulva prolifera*, *Enteromorpha ramellosa* Kütz., ULVNB060-23, Netherlands, 51.541278, 3.930302, 1 Jul 1846, R.B. van den Bosch, NAT012, (L: L.4095448), PQ733876; *Ulva prolifera*, *Enteromorpha simplex* (K.L.Vinogr.) Koeman & C.Hoek, ULVNB062-23, Netherlands, 53.410810, 6.218992, 17 Jul 1975, R.P.T. Koeman, NAT019, (L: L.4095477), PQ733875; *Ulva prolifera*, *Enteromorpha simplex* (K.L.Vinogr.) Koeman & C.Hoek, ULVNB063-23, Netherlands, 53.473750, 6.718386, 29 Jun 1975, R.P.T. Koeman, NAT020, (L: L.4095478), PQ784079; *Ulva prolifera*, *Enteromorpha simplex* (K.L.Vinogr.) Koeman & C.Hoek, ULVNB064-23, Netherlands, 53.493181, 6.230344, 6 Jul 1975, R.P.T. Koeman, NAT021, (L: L.4095479), PQ784080; *Ulva prolifera*, *Enteromorpha radiata* J.Agardh, ULVNB065-23, Netherlands, 53.473750, 6.718386, 5 Jun 1975, R.P.T. Koeman, NAT024, (L: L.4095600), PQ733879; *Ulva prolifera*, *Enteromorpha prolifera* (O.F.Müll.) J.Agardh, ULVNB069-23, Netherlands, 53.493181, 6.230344, 6 Jul 1975, R.P.T. Koeman, NAT034, (L: L.4095685), PQ733880; *Ulva prolifera*, *Enteromorpha juergensii* Kütz., nom. illeg., ULVNB070-23, Netherlands, 51.501892, 3.704827, 15 May 1942, C. Brakman, NAT035, (L: L.4095729), PQ733881; *Ulva prolifera*, *Enteromorpha clathrata* (Roth) Grev., ULVNB090-23, Netherlands, 51.440039, 3.601667, 2 Jun 1952, J.A.W. Lucas, NAT068, (L: L.4316781), PQ733882; *Ulva pseudocurvata* Koeman & C.Hoek, *Ulva pseudocurvata* Koeman & C.Hoek, ULVNB041-23, Belgium, 51.342084, 3.203657, 26 Apr 1999, E. Coppejans, F. Leliaert, B. Janssens, M. Raman, E. Demeulenaere, BER012, (BR: BR5010111557527V), PQ733791; *Ulva pseudocurvata*, *Ulva lactuca* L., ULVNB085-23, Netherlands, 51.549914, 3.670414, 7 Apr 1961, W.G. Beeftink, NAT059, (L: L.4114442), PQ733789; *Ulva* sp. 6, *Enteromorpha erecta* (Lyngb.) J.Agardh, ULVNB074-23, Netherlands, 52.965662, 4.770015, 9 Jun 1933, J.S. Zaneveld, NAT043, (L: L.4095906), PQ733897; *Ulva* sp. 11, *Ulva pseudocurvata* Koeman & C.Hoek, ULVNB050-23, Belgium, 51.314448, 3.110378, 18 Apr 2000, Claerbout, Delarue, Waumans, Menu, Cocquyt, De Backer, Vanderschaeve, Engledow, Leliaert, BER058, (BR: BR5010111529555V), PQ733788; *Ulva* sp. 11, *Ulva rigida* C.Agardh, ULVNB051-23, Belgium, 51.359438, 3.303312, 14 Sep 2000, H. Engledow, A. Volckaert, BER059, (BR: BR5010111531329V), PQ733792.