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S. Steinhagen, R. Karez & F. Weinberger

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Cryptic, alien and lost species: molecular diversity of *Ulva sensu lato* along the German coasts of the North and Baltic Seas

S. Steinhagen^a, R. Karez^b and F. Weinberger^a

^aGEOMAR Helmholtz Centre for Ocean Research Kiel, Marine Ecology Department, Düsternbrooker Weg 20, 24105 Kiel, Germany; ^bState Agency for Agriculture, Environment and Rural Areas, Schleswig-Holstein, Hamburger Chaussee 25, 24220 Flintbek, Germany

ABSTRACT

DNA barcoding analysis, using *tufA*, revealed considerable differences between the expected and observed species inventory of *Ulva sensu lato* in the Baltic and North Sea areas of the German state of Schleswig-Holstein. Of 20 observed genetic entities, at least four (*U. australis, U. californica, U. gigantea* and *Umbraulva dangeardii*) had been introduced recently, whereas three others (one *Ulva* sp. and two *Blidingia* spp.) could not be identified at the species level and could also represent recently introduced species. In addition, the observed distributions of *Kornmannia leptoderma* and *U. rigida* were much more extensive than indicated by historical records, whereas *Blidingia minima* and *Gayralia oxysperma* were absent or much less common than expected. Barcoding analysis also revealed that both *U. tenera* (type material) and *U. pseudocurvata* (historical vouchers) from Helgoland, an off-shore island in the North Sea, actually belong to *U. lactuca*, a species that appears to be restricted to this island. Furthermore, past morphological descriptions of *U. intestinalis* and *U. compressa* have apparently been too restrictive and have been responsible for numerous misidentifications. The same is true for *U. linza*, which, in northern Germany, clusters into two genetically closely related but morphologically indistinguishable entities. One of these entities is present on Helgoland, while the second is present on North Sea and Baltic Sea mainland coasts.

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Introduction

Macroalgae of the orders Ulvales and Ulotrichales are ubiquitous inhabitants of fully marine and brackish coastal waters. Several macroalgal species have recently increased, owing to opportunistic lifestyles and the capacity to benefit from eutrophication and other anthropogenic impacts, and the ability to accurately identify such taxa has become much more important (Charlier et al., 2007, 2008; Smetacek & Zingone, 2013). However, the identification of certain macroalgae, such as the genus Ulva, is notoriously difficult (Koeman & Van den Hoek, 1981, 1982a, 1982b, 1984; Hoeksema & Van den Hoek, 1983; Brodie et al., 2007), with the morphological instability of specific Ulva species being attributed to variation in salinity (Reed & Russell, 1978; Steinhagen et al., 2018b), nutrient concentrations (Blomster et al., 2002; Steinhagen et al., 2018b) and bacterial associations (Spoerner et al., 2012; Wichard, 2015), as well as to an elevated tendency for mutagenesis (Wichard, 2015). As a consequence, morphological plasticity (i.e. multiple morphotypes within species) or cryptic speciation may hinder identification and lead to taxonomic confusion. Such identification problems have been confirmed by DNA barcoding studies (e.g. Blomster et al., 1998, 2002; Tan et al., 1999; Hayden & Waaland, 2002; Hayden et al., 2003; Shimada et al., 2003; Brodie et al., 2007; Heesch et al., 2009; Wolf et al., 2012; Kirkendale et al., 2013), which have reported that the historical separation of Enteromorpha (for tubular 'species') and Ulva (for sheet-like taxa) is artificial and does not reflect phylogenetic relationships, as predicted by Linnaeus (1753; Hayden et al., 2003). The genera Enteromorpha and Ulva were consequently synonymized and the currently accepted genus Ulva includes tubular, sheet-like and mixed-morphology taxa. Thus, allegedly unique morphological characteristics that were indicated in past species descriptions, and subsequently used in identification keys, are often uninformative, whereas molecular methods allow for reliable species differentiation (Blomster et al., 1998, 2002; Hayden et al., 2003; Brodie et al., 2007). In particular, tufA has been reported as a useful marker for identifying green algae (Saunders & Kucera, 2010). However, DNA-based species identification remains ambiguous when reference sequences of type material are missing, as is the case for most of the Ulvales and Ulotrichales. The DNA quality of historical voucher specimens is often low, thereby hampering sequencing efforts (Staats et al., 2011). Therefore, both molecular and morphological methods are still needed to link taxonomic concepts that were originally based on morphology with molecular traits (Hillis, 1987).

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CONTACT S. Steinhagen 🔯 ssteinhagen@geomar.de

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The documentation of seaweeds in northern Germany has been conducted since the mid-19th century, and seaweeds of the small island of Helgoland, located in the SE North Sea, have received much attention from marine botanists and phycologists, making Helgoland among the best-studied seaweed habitats in Europe (Bartsch & Kuhlenkamp, 2000). The solid rock pedestal of Helgoland provides a natural substratum for a macrophytobenthos in a fully marine environment and comprises a unique habitat in Germany (Reinke, 1889; Bartsch & Kuhlenkamp, 2000). However, even the most recent comprehensive descriptions of Helgoland's macroalgae (Kornmann & Sahling, 1977, 1983, 1994) were exclusively based on morphological identification. Bartsch & Kuhlenkamp (2000) also included rare and doubtful species and summarized taxonomic changes. Furthermore, the understanding of macroalgal species diversity on Helgoland is only transferable to a limited extent to Germany's mainland coasts, which differ extensively in ecological conditions.

The tidal Wadden Sea is another fully marine ecosystem (salinity 30-33) within the North Sea, but it mainly consists of extended sand and mud flats, with relatively little hard substrate, and the German coast of the Baltic Sea is brackish, lacks tides, and is mainly composed of stones, gravel and sand (Rönnbäck et al., 2007). Furthermore, except for general identification keys (Rothmaler, 1984; Pankow, 1990), information about the identity and abundance of macroalgae in the Wadden and Baltic Sea areas of Germany is relatively sparse. Based on a summary of literature records, Schories et al. (2009) described the distribution of macroalgae along the coast of Germany. However, the taxonomic concepts underlying historical records are often unclear and records based on molecular species identification are still sparse for the area.

Accordingly, the aim of the present study was to reassess the diversity of *Ulva sensu lato* at geographically separated areas along the coasts of the Baltic and North Seas in the German state of Schleswig-Holstein, as well as on Helgoland. The survey included both DNA barcoding and classical morphological identification approaches, and both field-collected and herbarium specimens were examined which allowed for the detection of several cryptic or newly introduced species and for the identification of several historical misinterpretations.

Materials and methods

Sample collection

Samples of *Ulva sensu lato* were collected from 127 sites throughout the state of Schleswig-Holstein, Germany (Fig. 1), including sites in the Wadden Sea (n = 44), Baltic Sea (n = 73) and on Helgoland (n = 10). The sites represented a variety of habitats, such

as estuaries, overflow basins and drainage channels, within each of the ecosystems. The sites were spread over 536 km along the coast of the Baltic Sea and over 466 km along the coast of the North Sea, with a maximum distance between sites of less than 25 km. Full data on the collection sites are available in Supplementary table S1. To ensure that seasonal species were sampled, collections were conducted during both summer (July-August 2014 and August-September 2015) and spring (April 2015 and March 2016). Single locations were also visited in 2017 and 2018, and only a limited number of sites were visited during winter (November 2014-early March 2015) owing to lower green algal growth. Sites along the coast of the North Sea (mainly groynes, bulwarks, rocks and mudflats) were sampled during low tide, whereas sites along the coast of the Baltic Sea were sampled when water levels were low using waders and an aquascope, which allowed for sampling to a depth of 1.2-1.5 m below mean sea level. Additional sampling (n = 3) was undertaken by divers in August 2014. Representative specimens were collected for each morphotype that was observed at each sample site, and epiphytes were also collected from host specimens. The collected thalli were stored in a cool box (~10°C) and transported to the laboratory.

Morphological analysis

Pre-identification was based on typical morphological characters (e.g. overall thallus morphology, cell form, cell arrangement, number of pyrenoids per cell, etc.) using identification keys (Koeman & Van den Hoek, 1981, 1982a, 1982b, 1984; Hoeksema & Van den Hoek, 1983), and morphological characters were recorded separately at basal, middle and apical-thallus parts using light microscopy. Lugol's solution (iodine-potassium iodide) was used to stain starch-containing compartments, such as pyrenoids. After morphological analysis, epiphyte-free pieces of remaining thallus tissue (1 cm²) or complete smaller thalli were either frozen and lyophilized or dried in silica gel for future molecular analysis.

Molecular analysis

Total DNA was extracted from lyophilized or silicadried samples using the Invisorb Spin Plant Mini Kit (Stratec, Birkenfeld, Germany), according to the manufacturer's protocol, and the plastid-encoded DNA barcoding marker *tuf*A was PCR amplified using the primers tufGF4 (Saunders & Kucera, 2010) and tufAR (Famà *et al.*, 2002). The following conditions for amplification were used: initial denaturation at 94°C for 4 min; 38 cycles of 94°C for 1 min, 55°C for 30 s and 72°C for 1 min; then a final extension of 72°C for 7 min. Both strands of the



Fig. 1. Map of sampling sites in northern Germany. Insets a-j provide higher resolution. Numbers 1–126 cross-reference to Table 2 and Supplementary table S1, whereas numbers 127 and 128 indicate the sampling sites at Winning and Brodersby. The asterisk indicates a previously investigated site in Wohlenberg.

purified amplicons were directly sequenced by GATC Biotech (Konstanz, Germany) and both sequence alignment and reciprocal editing were performed using Sequencher (v. 4.1.4; Gene Codes Co., Ann Arbor, Michigan). The resulting sequences were uploaded to GenBank (Supplementary table 1). Sequence alignment was performed using MAFFT (Katoh *et al.*, 2002), whereas editing was done visually with Sequencher (v. 4.1.4, Gene Codes Corporation, Ann Arbor, Michigan). The alignment represented a 777 bp portion of the *tuf*A gene. An optimal substitution model was determined using MrModeltest software version v. 2.2. (Nylander, 2004) and found to be GTR+G+I. Subsequently, maximum likelihood analysis was performed using RAxML (v. 8; Stamatakis, 2014) with 1000 bootstrap iterations and the suggested substitution model, and Bayesian inference was performed using MrBayes (v. 3.2.2; Ronquist *et al.*, 2012) with four simultaneously running Markov Chain Monte Carlo chains for 5×10^6 generations. The run was ended automatically when the standard deviation of split frequencies dropped below 0.01. Reference sequences from GenBank were also included in the analyses, with preference given to annotated sequences published in peer-reviewed articles. The trees were rooted by an outgroup that contained *Urospora penicilliformis* GenBank code HQ610440 and *Urospora wormskioldii* GenBank code HQ610441. Sequences used in the phylogenetic tree are listed in Table 1.

Comparison of recent species richness to historical findings

To assess the potential misidentification of historical specimens, historical vouchers of Ulvales taxa from the study area and neighbouring regions were obtained from several macroalgae collections and herbaria (Herbarium of the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany (BRM), Herbarium of GEOMAR Helmholtz Centre for Ocean Research, Kiel, Germany (GEO); Herbarium of the Natural History Museum of Denmark, Copenhagen, Denmark (C)) and morphologically compared to specimens collected during the present study. The microand macromorphological characters of the vouchers were assessed using the above-mentioned criteria. When possible, small thallus pieces of the historical voucher specimens were sampled for molecular verification of species identity, as described in Steinhagen et al. (2018a).

Results

A total of 370 *Ulva sensu lato* samples were processed genetically for species discrimination and identification, on the basis of *tufA* sequence data, and the full dataset was subject to phylogenetic analyses (see Supplementary table S1). In addition, an analysis with selected representative sequences was also performed (Fig. 2). The ML and BI analyses yielded congruent consensus trees. The species observed during the present study are described here, with a few particularly conspicuous species discussed in detail, and the majority are discussed in more depth in the Supplementary Information.

The phylogenetic analyses separated the investigated specimens into 20 taxonomic entities, nearly all of which could be resolved on the basis of peer-reviewed reference sequences provided by GenBank. More specifically, the taxa were identified as members of *Ulva*, *Umbraulva*, *Percursaria*, *Blidingia*, *Kornmannia*, *Monostroma* and *Protomonostroma*. One major branch within the consensus tree included members of *Ulva*, *Umbraulva* and *Percursaria* (i.e. the Ulvaceae) and was split into two subgroups, with the larger one containing *Ulva* taxa exclusively and the smaller subgroup containing several *Ulva* taxa (*U. lactuca*, *U. australis*, *U. intestinalis* and *U. compressa*), *Umbraulva dangeardii* and *Percursaria percursa*. However, this topology was only observed when *P. percursa* sequences were included; when *P. percursa* sequences were omitted, *Umbraulva* clustered as a sister group to *Ulva* (Supplementary fig. S1). Most of the species clades obtained full bootstrap and posterior probability support.

All *U. gigantea* sequences were identical to a sequence from New Brunswick, Canada (Fig. 2, Table 2). The specimens of this species were always represented by distromatic blades and were only found in a limited area in the Wadden Sea, except for one specimen in the Baltic Sea (for details see Supplementary Information).

Ulva rigida was always distromatic, and attached specimens were found in all three investigated regions, whereas mats of drifting specimens were only observed in the Wadden Sea (for details see Supplementary Information). The cluster representing *U. rigida* in our phylogenetic tree (Fig. 2) contained reference sequences for *Ulva laetevirens* Areschoug 1854 from Connecticut (JQ048942) and New Brunswick (HQ610428), as well as for *U. rigida* from the Italian Adriatic Sea (HE600178). All sequences were nearly identical, exhibiting divergences from the references of 0–0.26% and were placed in a well-delimited cluster.

Specimens that clustered most closely to *U. shanxiensis* type sequences were genetically more diverse than other taxa, with sequence distances ranging from 0 to 2.8% (Fig. 2). Furthermore, the specimens of *Ulva* sp. sampled during the present study were quite divergent (2.4–2.8%) from the *U. shanxiensis* type sequence. Specimens that belonged to this cluster were observed at all three main study areas and were typically found in areas of intense anthropogenic impact. The specimens were generally tubular but, nonetheless, of variable morphology (for details see Supplementary Information).

The clades delimiting the species *U. flexuosa* and *U. californica* received low to medium support. Both species were observed at all three main study areas. The more fragile and relatively rare species, *U. flexuosa*, exhibited only tubular morphologies and was generally observed unattached. The sequences of specimens in this clade differed from reference sequences from Canada (HQ610296) and South Korea (JN029309) by 0–0.17%. In contrast, the more robust of the two species, *U. californica*, exhibited more variable morphology, ranging from tubular to lanceolate or amorphous forms, and preferentially settled on artificial substrates. The sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from reference sequences of specimens in this clade differed from refere

Table 1. List of green algal samples collected in 2014–2016 in northern Germany and used in the displayed phylogenetic tree.

| ^a Accession | | ^b Voucher | Collection | | | ^c Site | | |
|------------------------|---------------------------------|----------------------|-------------|------------|--------------------------------------------------|-------------------|-------------------------|------------------------|
| no. | Species | no. | date | Region | Location | No. | Lat. | Long. |
| MH475471 | Ulva australis | TD_10 | 24-Jul-2014 | Wadden Sea | Norderfriedrichskoog | 28 | N 54,4136 | E 8,8789 |
| MH475472 | Ulva australis | TD_34 | 15-Aug-2014 | Wadden Sea | St. Peter-Ording | 30 | N 54,2857 | E 8,7032 |
| MH475473 | Ulva australis | TD_36 | 16-Aug-2014 | Wadden Sea | St. Peter-Ording | 29 | N 54,3267 | E 8,5851 |
| MH475450 | Ulva californica | S_106 | 30-Jul-2014 | Wadden Sea | Dagebuell | 11 | N 54,7301 | E 8,6892 |
| MH475454 | Ulva californica | S_791 | 23-Sep-2015 | Helgoland | Helgoland | 48 | N 54,1837 | E 7,8886 |
| MF979651 | Ulva compressa | S_672 | 21-Apr-2015 | Wadden Sea | Finkhaushallig | 27 | N 54,4156 | E 8,9036 |
| MF979652 | Ulva compressa | S_514_B | 19-Sep-2014 | Baltic Sea | W ulfen | 121 | N 54,4089 | E 11,1/31 |
| MF9/9645 | Uiva compressa | 5_14_B | 22-Jul-2014 | Relgoland | Fielgoland | 40 | N 54,1882 | E 7,8742 |
| MH475451 MH475452 | Ulva flexuosa | S 769 | 16-Aug-2014 | Wadden Sea | Dagebuell | 70 | N 54,5556 | E 10,1415 E 8 6892 |
| MH475453 | Ulva flexuosa | S 794 | 23-Sep-2015 | Helgoland | Helgoland | 51 | N 54 1780 | E 7 8887 |
| MH475474 | Ulva gigantea | S 775 | 16-Aug-2015 | Wadden Sea | Dagebuell | 10 | N 54,7304 | E 8.6939 |
| MH475475 | Ulva gigantea | S 564 | 9-Apr-2015 | Wadden Sea | Friedrich-Wilhelm- | 7 | N 54,8333 | E 8,6142 |
| | 00 | _ | Ĩ | | Luebke-Koog, Rhymschlot | | | |
| MH475476 | Ulva gigantea | S 632 | 17-Apr-2015 | Wadden Sea | Dagebuell | 11 | N 54,7301 | E 8.6892 |
| MH475477 | Ulva intestinalis | S_72 | 24-Jul-2014 | Baltic Sea | Gluecksburg | 55 | N 54,8392 | E 9,5176 |
| MH475478 | Ulva intestinalis | S_133 | 31-Jul-2014 | Wadden Sea | Schluettsiel | 13 | N 54,6844 | E 8,7539 |
| MH475479 | Ulva lactuca | S_729 | 24-Apr-2015 | Helgoland | Helgoland | 47 | N 54,1882 | E 7,8801 |
| MH475480 | Ulva lactuca | S_696 | 23-Apr-2015 | Helgoland | Helgoland | 50 | N 54,1797 | E 7,8896 |
| MH475447 | Ulva linza 1 | S_241_U. linza 1 | 18-Aug-2014 | Baltic Sea | Falckenstein | 76 | N 54,3904 | E 10,1922 |
| MH475448 | Ulva linza 1 | S_504_U. linza_1 | 16-Sep-2014 | Wadden Sea | Hamburger Hallig | 18 | N 54,5990 | E 8,8122 |
| MH475449 | Ulva linza 1 | S_64_U. linza_1 | 24-Jul-2014 | Baltic Sea | Gluecksburg | 55 | N54,8392 | E 9,5176 |
| MH475445 | Ulva linza 2 | S_727_U. linza_2 | 24-Apr-2015 | Helgoland | Helgoland | 52 | N 54,1772 | E 7,8930 |
| MH475446 | Ulva linza 2 | S_8_U. linza_2 | 22-Jul-2014 | Helgoland | Helgoland | 46 | N 54,1882 | E 7,8742 |
| MH475481 | Ulva prolifera | S_196 | 12-Aug-2014 | Baltic Sea | Falshoeft | 60 | N 54,7685 | E 9,9653 |
| MH475482 | Ulva prolifera | S_9 | 22-Jul-2014 | Helgoland | Helgoland | 46 | N 54,1882 | E 7,8742 |
| MH475483 | Ulva prolifera | S_466 | 10-Sep-2014 | Wadden Sea | Emmelsbuell | 8 | N 54,7949 | E 8,6581 |
| MH475484 | Ulva rigida | S_449 | 9-Sep-2014 | Wadden Sea | Friedrich-Wilhelm- Luebke-Koog, Rhymschlot | 7 | N 54,8333 | E 8,6142 |
| MH475485 | Ulva rigida | S_123 | 30-Jul-2014 | Wadden Sea | Dagebuell | 11 | N 54,7301 | E 8,6892 |
| MH475486 | Ulva rigida | S_111 | 30-Jul-2014 | Wadden Sea | Dagebuell | 11 | N 54,7301 | E 8,6892 |
| MH475487 | Ulva shanxiensis | S_228 | 13-Aug-2014 | Baltic Sea | Strande | 71 | N 54,4350 | E 10,1702 |
| MH475488 | Ulva shanxiensis | S_269 | 18-Aug-2014 | Baltic Sea | Moenkeberg | 82 | N 54,3465 | E 10,1742 |
| MH475489 | Ulva shanxiensis | S_256 | 18-Aug-2014 | Baltic Sea | Kiel | 78 | N 54,3538 | E 10,1413 |
| MH4/5490 | Ulva shanxiensis | 5_2_A \$ 217 | 22-Jul-2014 | Relgoland | Heigoland Soblandarfar laka | 55 05 | N 54,1698 | E 7,8894 |
| MH475491 MH475492 | Ulva shanxiensis | S 221 | 13-Aug-2014 | Baltic Sea | Strande | 93 70 | N 54,5088 | E 10,0880 E 10,1750 |
| MH475493 | Ulva shanxiensis | S 92 | 24-Jul-2014 | Baltic Sea | Aschau | 65 | N 54 4608 | E 9 9267 |
| MH475494 | Ulva torta | S 81 | 24-Jul-2014 | Baltic Sea | Wackerballig | 59 | N 54,7586 | E 9,8778 |
| MH475495 | Ulva torta | S 231 | 13-Aug-2014 | Baltic Sea | Schilksee | 72 | N 54,4313 | E 10,1693 |
| MH475496 | Ulva torta | S_350 | 25-Aug-2014 | Baltic Sea | Heiligenhafen | 99 | N 54,3787 | E 10,9555 |
| MH475497 | Ulva torta | S_73 | 24-Jul-2014 | Baltic Sea | Gluecksburg | 56 | N 54,8368 | E 9,5231 |
| MH475498 | Umbraulva dangeardii | R_1 | 8-Aug-2014 | Helgoland | Helgoland | 45 | N 54,1874 | E 7,8703 |
| MH475499 | Umbraulva dangeardii | R_2 | 8-Aug-2014 | Helgoland | Helgoland | 45 | N 54,1874 | E 7,8703 |
| MH475464 | Blidingia marginata | S_147_A | 31-Jul-2014 | Wadden Sea | Pellworm | 21 | N 54,4988 | E 8,8087 |
| MH475465 | Blidingia marginata | S_577 | 14-Apr-2015 | Wadden Sea | Brunsbuettel estuary | 41 | N 53,8890 | E 9,1011 |
| KT290281 | Blidingia minima | DA_12 | 18-Jul-2013 | Baltic Sea | Wohlenberg | * | N 53,9446 | E 11,2444 |
| MH475455 | Blidingia sp. 1 | S_828 | 24-Jul-2014 | Wadden Sea | Schobuell | 25 | N 54,5079 | E 8,9956 |
| MH475456 | Blidingia sp. 1 | S_818 | 24-Jul-2017 | Wadden Sea | Husum | 26 | N 54,4712 | E 9,0280 |
| MH4/545/ | Blidingia sp. 1 | 5_815 5_912 | 24-Jul-2017 | Wadden Sea | Finkhaushallig | 27 | N 54,4156 | E 8,9036 |
| MH4/5458 | Bliaingia sp. 1 | 5_813 | 24-Jul-2017 | wadden Sea | Luebke-Koog | 6 | N 54,8374 | E 8,6122 |
| MH475459 | Blidingia sp. 1 | S_179 | 6-Aug-2014 | Wadden Sea | Brunsbuettel estuary | 41 52 | N 53,8890 | E 9,1011 |
| мн475460 Мн75441 | ышпдіа sp. 2 Blidingia cp. 2 | 5_54 S 1 | 25-Jul-2014 | Helgoland | Helgoland | 55 19 | IN 54,1720 N 54 1927 | E 1,8993 E 7 8802 |
| MH475461 | Blidingia on 2 | 5_1 \$ 30 | 22-Jui-2014 | Helgoland | Helgoland | 40 | N 54,1007 | E 7,0000 E 7 8002 |
| MH475463 | Blidingia sp. 2 | S 124 | 30-Jul-2014 | Wadden Sea | Dagebuell | 49 11 | N 54 7301 | E 8,6891 |
| MH475466 | Kornmannia | S 154 | 5-Aug-2014 | Wadden Sea | Finkhaushallig | 27 | N 54.4156 | E 8,9036 |
| MH475467 | leptoderma Kornmannia | S 698 | 23-Apr-2015 | Helgoland | Helgoland | 50 | N 54.1797 | E 7.8896 |
| MH475468 | leptoderma Kornmannia | S 337 | 22-Aug-2014 | Baltic Sea | Heiligenhafen | 101 | N 54.3795 | E 10.9823 |
| | leptoderma | 0_007 | 22 Mug 2017 | Durite Jea | riemgennaten | 101 | 11 51,5775 | 10,7045 |

(Continued)

Table 1. (Continued).

| ^a Accession | | ^b Voucher | Collection | | | ^c Site | | |
|------------------------|------------------------------|----------------------|-------------|------------|---------------|-------------------|-----------|-----------|
| no. | Species | no. | date | Region | Location | No. | Lat. | Long. |
| MH475469 | Monostroma grevillei | S_548 | 8-Apr-2015 | Baltic Sea | Wulfen | 121 | N 54,4089 | E 11,1731 |
| MH475470 | Monostroma grevillei | S_617 | 16-Apr-2015 | Baltic Sea | Heiligenhafen | 101 | N 54,3795 | E 10,9824 |
| MH475500 | Percursaria percursa | S_360 | 25-Aug-2014 | Baltic Sea | Heiligenhafen | 101 | N 54,3795 | E 10,9824 |
| MH475501 | Protomonostroma undulatum | S_733 | 24-Apr-2015 | Helgoland | Helgoland | 49 | N 54,1825 | E 7,8907 |

A sequence of *Blidingia minima* (KT290281) from a former survey at an adjacent site in Mecklenburg-Vorpommern is included as reference. ^a Voucher no. = Accession no. = GenBank accession number for *tuf*A gene. ^b Identification number assigned to the voucher specimen by the GEOMAR Helmholtz Centre for Ocean Research herbarium, Kiel, Germany. ^c Site no. = Referring to number in Fig 1.

from California (KM255003) and Canada (HQ610279 and HQ610280) by 0–1.82% (Fig. 2, Table 2).

Specimens that exhibited the relatively characteristic morphology of Ulva torta (long, narrow, with entangled unbranched tubular thalli and a central lumen of only $3-11 \mu m$) were infrequently observed in either the Baltic or Wadden Seas and were not observed on Helgoland (for details see Supplementary Information). The specimens were clustered with reference sequences from southern Australia (JN029340) British Columbia, Canada and (HQ610437), but with only moderate support (85/ 0.96; Fig. 2), even though the specimens exhibited relatively low genetic divergence from the reference sequences (0.12–0.3%).

Sequences of the U. linza specimens exhibited strong genetic divergence (Fig. 2) and clustered in two strongly supported subgroups, U. linza 1 (100/1) and U. linza 2 (95/1). The U. linza 1 specimens were abundant over the whole study area (except Helgoland), formed a cluster with a genotype from Tasmania (JN029337) and exhibited very low sequence divergence (0-0.0014%). In contrast, the U. linza 2 specimens were exclusively collected from Helgoland, formed a cluster with a reference sequence from the North-east Pacific (KM254997) and exhibited slightly greater sequence divergence (0–0.49%). A historical herbarium voucher, originally identified as Enteromorpha ahlneriana Bliding nom. illeg., could be genetically assigned to Ulva linza sp. 1 (Fig. 2, Table 2). However, the phylogenetic differentiation was not reflected morphologically, and both the U. linza 1 and U. linza 2 specimens exhibited a wide spectrum of tubular to lanceolate and partly distromatic morphologies (for details see Supplementary Information).

The *U. prolifera* reference sequences from Manitoba, Canada (HQ610395) and Labrador, Canada (HQ610394) clustered with specimens from all three main study areas. However, our samples were clearly more similar to one another (-/0.98; Fig. 2), even though their genetic divergence from the reference ranged from 0 to 1.23%. *Ulva prolifera* was always attached when observed, was relatively abundant, exhibited a variety of tubular morphologies

and frequently, but not always, possessed a characteristically twisted stipe-like base (for details see Supplementary Information).

Specimens that formed strongly supported clusters (99/1) with U. lactuca reference specimens from New Brunswick (HQ610341, 0-0.31% divergence) and California (KM255044, 0.12-0.47% divergence) were collected exclusively from Helgoland (Fig. 2). Even though Hughey et al. 2019 have suggested that the oldest available name for the European 'U. lactuca' is U. fenestrata, we will refer to the here mentioned genotype as U. lactuca for reasons of general understanding. They exhibited distromatic thalli of various shapes and were characterized by relatively strong attachment. The specimens were found abundantly within the intertidal zone and grew attached to hard substrata, such as naturally occurring rocks (Fig. 3), stones and mussel beds or artificial breakwaters and piers. Only a few drifting specimens were observed and such drifting thalli exhibited clear indications of recent ruptures in the rhizoidal zone, thereby suggesting that drifting is not tolerated for long time periods. Specimens of this clade were never found in rockpools that were subject to potential desiccation or influence by rainwater. All thalli were distromatic throughout, and their shape varied from rounded to lobed (Fig. 4) or laciniate morphologies that could be straight, petiolate-like (Figs 5, 6) but also strongly curved (Fig. 7). Filled disc-like rhizoidal zones (Fig. 8, 13) were frequently observed at the base of the blade. The margins of the thalli were never toothed (grazing traces were clearly distinguished) and were usually smooth, although the rounded individuals sometimes exhibited ruffled margins. Holes (2-6 mm diameter) were observed infrequently. The thalli reached lengths of 40 cm and widths of 35 cm, but smaller individuals (max. 5 cm length and 2 cm width) were also observed. Longitudinal ridges were observed in the basal regions of most of the investigated specimens but were often absent in young thalli. The thalli were attached by obconically shaped stipe-like structures that terminated in broad rhizoidal zones (Figs 8, 9). The cells of the middle and apical thalli were arranged in curved or short rows, whereas cells of the laciniate thalli were



Fig. 2. Maximum likelihood phylogram of tufA sequences from taxa of *Ulva sensu lato* from northern Germany. Solid triangles indicate herbarium vouchers (see also Table 2). The two shades of grey indicate clades that were present in the study area. Hatched boxes indicate species complexes and, thus, taxonomic entities that could not be clearly resolved phylogenetically. Numbers at nodes indicate bootstrap values (left) and Bayesian posterior probabilities (1000 replicates; right). Poorly supported nodes (< 70% bootstrap and < 0.70 Bayesian support) are not labelled. Branch lengths are proportional to sequence divergence.

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|---------------------------------------------------------|-------------------------------------------------------|------------------------------------------------------|-------------------------------------------|----------------------------------------|-----------------------------------------------------------------------------|---------------------------------------------|-------------------------------------------------------------------------|---------------------------------------------------------|
| Region | Location | Collection date | ^a Herbar. ID | ^b Herbarium | Collector | ^c Accession no. | ^d Morphological identity | ^e Genetic identity tufA |
| Helgoland | Helgoland | 10.04.1991 | BRM001700 | BRM | Kornmann and Sahling | MH720537 | Ulva pseudocurvata | Ulva lactuca |
| Helgoland | Helgoland | 10.04.1991 | BRM001703 | BRM | Kornmann and Sahling | MH720538 | Ulva pseudocurvata | Ulva lactuca |
| Helgoland | Helgoland | 22.10.1988 | BRM007947 | BRM | Kornmann and Sahling | MH720539 | Ulva pseudocurvata | Ulva lactuca |
| Helgoland | Helgoland | 17.07.1978 | BRM007806 | BRM | Kornmann and Sahling | MH720540 | Úlva tenera | Ulva lactuca |
| Baltic Sea (Öresund) | Copenhagen | 27.11.2007 | 73544 | C | Ruth Nielsen and Peer Corfixen | MH720542 | Gayralia oxysperma | Kornmannia leptoderma |
| Baltic Sea (Öresund) | Copenhagen | 17.03.2004 | 40539 | C | Ruth Nielsen and Peer Corfixen | MH720543 | Gayralia oxysperma | Kornmannia leptoderma |
| Baltic Sea | Kiel, Friedrichsort | 19.09.1962 | | GEO | Elfriede Kaminski | MH720544 | Gayralia oxysperma | Kornmannia leptoderma |
| Baltic Sea | Kiel, Friedrichsort | 30.9.1976 | 95 | GEO | Elfriede Kaminski | MH720541 | Enteromorpha aĥlneriana | Ulva linza |
| ^a Herbar. ID = Barcode Herbarium of GEOM/ | of respective Herbarium. \R Helmholtz Centre for (| ^b Herbarium = Abl Ocean Research, Kiel | breviation of the re l, Germany (GEO); | sspective source h Herbarium of the | erbaria (Herbarium of the Alfred Weș 2 Natural History Museum of Denmark | gener Institute for P «, Copenhagen, Dem | olar and Marine Research, Bremark (C)). ^c Accession no. = Ge | merhaven, Germany (BRM); enBank accession number for |
| | | | • | | | , | | |

gene. ^d Morphological identity = Name that was historically assigned to specimen using morphological characters. ^e Genetic identity = Genetic identity obtained using analysis of tufA

tufA

sometimes arranged in longitudinal rows. The cells were polygonal with rounded corners, $12-24 \times 14-31$ µm in surface view, and contained a parietal chloroplast (rarely filling the entire cell) and 1-2 (rarely up to 4) pyrenoids (Figs 10, 11). Cells of the rhizoidal zone contained up to seven pyrenoids, and both the stipe-like region and rhizoidal zone were filled by the elongated tails of the cell bodies, which became visible in microscopic transections. Thalli with these features were not only observed on Helgoland, but also along the mainland coasts, although they were always genetically assigned to *U. compressa*.

The sequence of one of over 100 syntypes of *U.* tenera Kornmann & Sahling – originating from Helgoland and stored at the BRM on Helgoland (voucher ID: BRM007806; Figs 12, 13, Table 2) – clearly clustered with *U. lactuca* (Fig. 2). Additionally, sequences from historical *U. pseudocurvata* vouchers (BRM001703 and BRM001700; Fig. 14), which provided the first evidence of the species' presence on Helgoland and were displayed in the publication of Kornmann & Sahling (1994), were also placed, with full bootstrap support, in the clade representing *U. lactuca* and were identical to the sequences of recently collected *U. lactuca* samples from Helgoland (Fig. 2).

A few specimens from the west coast of Helgoland and an area around the peninsula of Eiderstedt in the Wadden Sea (i.e. fully marine environments) were clustered with an *U. australis* reference sample from Australia (JN029254, genetic dissimilarity 0–0.33%, Fig. 2, Table 2). However, morphological comparison was impossible since only small thallus pieces conserved in silica gel could be obtained from our study area.

Sequences from the U. intestinalis specimens formed a fully supported clade (100/1) with reference specimens from Australia (JN029320) and California (KM255056; Fig. 2) but consistently exhibited slight divergence from both reference sequences (0.12–0.45%). The species was abundantly present at all three main study areas and in salinities that ranged from fresh water to fully marine. All of the specimens investigated exhibited tubular morphology, and most individuals were inflated and unbranched, corresponding to the typical morphology of U. intestinalis. Furthermore, specimens that exhibited branched and unbranched morphologies could not be distinguished genetically (for details see Supplementary Information).

Ulva compressa was abundant in all three main study areas, although only tubular, usually branched individuals were observed on Helgoland, whereas only distromatic sheet-like specimens were found along the Baltic coast. Both morphologies were encountered along the Wadden coast, sometimes even at the same location. Furthermore, individuals exhibiting transition forms between the two



Figs 3–14. Morphology of *Ulva lactuca* specimens from Helgoland, Germany. Fig. 3. *U. lactuca* population growing on the northeast rocky tidal flats. Fig. 4. Typical lobular morphotype. Figs 5, 6. Petiolate-like morphotype. Fig. 7. Strongly curved morphotype, with (Fig. 8) a disk-like rhizoidal zone (cross section) and (Fig. 9) elongated club-shaped cells that extend to the centre of the rhizoidal disc. Fig. 10. Cells of the apical and middle thallus parts, with a hood-shaped chloroplast and one (sometimes two) central or marginal pyrenoids. Fig. 11. Marginal pyrenoid. Fig. 12. *U. tenera* syntypes collected from Helgoland in 1978 (Herbarium of the Alfred Wegener Institute, Bremerhaven; ID BRM007806). (I) However, by sequencing one individual (see also Table 2 and Fig. 2), its genetic affiliation to *U. lactuca* was confirmed. Fig. 14. *U. pseudocurvata* specimens collected from Helgoland in 1988 (Herbarium of the Alfred Wegener Institute, Bremerhaven; ID BRM007947); arrowhead indicates specimen that was genetically identified as *U. lactuca* (see also Table 2 and Fig. 2).

morphologies were only rarely observed (for details see Supplementary Information). However, the morphotypes were not separated during the phylogenetic analyses and remained clustered with a *U. compressa* reference sample from Canada, New Brunswick (HQ610295, genetic dissimilarity 0–0.77%).

Sequences that were identical to those of *Umbraulva dangeardii* reference sequences from southern Italy (MF172090 and MF172091, genetic dissimilarity: 0–0.13%) were only recovered from specimens collected at Helgoland at a depth of 8 m. The specimens were distromatic sheets with a

conspicuous dark olive colour and thin, soft texture, which corresponds to descriptions of specimens from the British Isles (Maggs *et al.*, 2007*a*).

Percursaria percursa was only encountered once in a macroscopically visible state at Heiligenhafen (Baltic Sea), where it grew unattached in dense mats in the supralittoral zone. Microscopic examination confirmed the typical morphology of unbranched biseriate filaments (Maggs & Kelly, 2007) and our sequence was placed in a fully supported cluster with a *P. percursa* reference sequence (AY454403, genetic dissimilarity: 0.13%).

A well-delimited cluster that included *Blidingia* marginata, *B. minima* and *Blidingia* sp. reference sequences formed a sister clade to that including the *Ulva*, *Umbraulva* and *Percursaria* sequences and included four genetic entities (Fig. 2). Two of the four subgroups could not be resolved, since they did not match any references in GenBank, but were putatively identified as *Blidingia* specimens based on sequence similarity, overall morphology and growth habit.

Specimens that exhibited low genetic variability and clustered with a *B. marginata* reference sequence from New Brunswick, Canada (HQ610237, genetic dissimilarity: 0–0.28%) were abundant in all three main study areas. The specimens formed dense populations of variable tubular morphology in the upper intertidal and supralittoral zones and were often encountered as the only macroalgal settlers in microhabitats that are influenced by fresh water and that may fall dry for longer periods (for details see Supplementary Information).

Specimens that belonged to the unresolved entity *Blidingia* sp. 2 were morphologically indistinguishable from *B. marginata* but formed a separate and fully supported cluster with 8–8.2% divergence from the *B. marginata* reference sequence (HQ610237). These specimens were collected from Helgoland and one site in the Wadden Sea (Dagebüll).

Molecular analysis failed to confirm the presence of *B. minima*. However, in a previous project *B. minima* was found at Wohlenberg (Fig. 1, site marked by an asterisk in general map), a site only 30 km to the East in the neighbouring German state of Mecklenburg-Vorpommern. A sample from the previously reported population was included in the phylogenetic tree (KT290281, Fig. 2) and formed a fully supported clade with a *B. minima* reference sequence from Canada (HQ610239).

Specimens that belonged to the unresolved entity *Blidingia* sp. 1 formed a fully supported cluster that was clearly delimited from other *Blidingia* species and genetically dissimilar (4.5–4.8%) from the *B. minima* reference sample (HQ610239). Specimens that belonged to this cluster had a broad distribution and were observed in all three main study areas, at

remote and protected sites as well as in highly trafficked waters (see also Steinhagen *et al.*, 2018*b*). The specimens grew as mats on various substrata in the supralittoral zone and were often found in the close vicinity of freshwater inflows, such as drainage pipes. The *Blidingia* sp. 1 specimens were relatively minute and they often exhibited a characteristic antler-like branched tubular morphology. However, macroscopically visible branches were rarely observed and appeared as spiralled or inflated.

The remaining three clades (Fig. 2) only included specimens with monostromatic blades and formed fully supported clusters with reference sequences of Kornmannia leptoderma, Monostroma grevillei and Protomonostroma undulatum. Kornmannia leptoderma specimens from all three study areas clustered with reference sequences from Canada (HQ610252, dissimilarity: 0-0.38%) and northern Germany (KT290275) and exhibited little to no genetic diversity. Specimens that belonged to this cluster were found in the middle and lower intertidal zones and were typically attached to substrata. The specimens appeared to avoid exposure to direct sunlight and were frequently found on the shaded sides of stones (Fig. 15) or jetties, or under piers. The 1–5 cm (rarely up to 8 cm) long thalli of the K. leptoderma specimens were nearly unrecognizable when the substrate became dry during low tide. The membranous and very soft thalli appeared funnel-shaped (Fig. 17), lanceolate or rosette-like (Fig. 16). Older thalli that had sporulated were amorphous in shape and deeply cut. The rhizoidal zone was not defined by a disc-like structure, and cells proceeded without tapering in a stipe-like region. Cells in the apical and middle thallus parts differed in shape from those in the basal thallus parts. The cells of the upper and middle thallus regions were either polygonal to round or with sharp and clearly defined angular edges, $9-15 \times 11-$ 16 µm in surface view, with a single centrally located pyrenoid and a chloroplast that was either marginal or filling the entire cell (Figs 18, 19). Meanwhile, the cells of the apical and middle thallus regions were thick-walled (Fig. 19), although progressively thinner and larger toward the basal region, and with 1-3 (rarely 4) pyrenoids per cell. In the lower mid-thallus parts, the cells were $11-21 \times 11-27$ (32) µm in surface view and sometimes appeared grainy, whereas others already resembled rhizoidal cells with long drawn-out tips (Figs 20, 21). Cells of the rhizoidal zone were up to 50 µm long, always grainy, with rhizoidal tips extending from the main body, and typically with 1-3 pyrenoids (rarely more; Fig. 21).

All the *M. grevillei* specimens formed a cluster and were often identical to reference sequences from Maine, USA (HQ610262, dissimilarity: 0–0.51%) and New Brunswick, Canada (HQ610259, dissimilarity: 0–0.39%). The species was abundant in the Baltic Sea and



Figs 15–21. Morphology of *Kornmannia leptoderma* specimens from northern Germany. Fig. 15. Typical sampling site along the coast of the Baltic Sea (Aschau lagoon), with *K. leptoderma* growing on the shaded side of a rock. Fig. 16. Rosette-shaped specimens from the Baltic Sea (Aschau lagoon). Fig. 17. Funnel-shaped specimen from the Baltic Sea (coastal inlet, Schlei, Lindaunis). Fig. 18. Cells in apical and middle thallus regions, in rows or pairs. Fig. 19. Marginal chloroplasts and central pyrenoids (one or rarely two). Figs 20, 21. Club-shaped cells of the rhizoidal zone.

also occurred on Helgoland. However, the species was only observed during spring (March to May), and in late spring drifting mats of *M. grevillei* frequently developed in sheltered bays, harbours and lagoons. The cells of the *M. grevillei* specimens were arranged in more distinct rows than those of the *K. leptoderma* specimens.

The only specimen that clustered with the *P. undulatum* reference sequence (dissimilarity: 0.13%) was found in the lower intertidal zone of Helgoland. As in *M. grevillei*, the cells were often arranged in rows. However, instead of a smooth transition from basal cells to rhizoidal cells, abrupt changes in cell shape were observed, and the rhizoidal cells were longer than those of the *K. leptoderma* specimens (60–90 μ m, up to 110 μ m; Supplementary fig. S2; for details see Supplementary Information).

An additional taxon that might represent Gayralia oxysperma was not detected at any of the study sites, even though Kützing (1843) originally described its basionym, Ulva oxysperma, on the basis of material collected in Schleswig-Holstein at Winning (located at the inner Schlei, a narrow inlet of the Baltic Sea, site 127 in Fig. 1). Unfortunately, the type material of U. oxysperma appears to be lost. However, historical G. oxysperma vouchers from Friedrichsort, Kiel, Germany, that were sampled in 1962 (MH720544) and from Copenhagen, Denmark, that were sampled in 2004 and 2007 (MH720542 and MH720543) were available for sequencing. Notably, all three voucher sequences clustered with K. leptoderma (Fig. 2, Table 2). During subsequent visits (i.e. additional collections in 2017 and 2018), thalli exhibiting the described morphology of G. oxysperma were not detected at Winning (site 127 in Fig. 1, salinity 1) but were collected at the inner Schlei at Brodersby (site 128 in Fig. 1, salinity 7), which is 10 km from Winning, and at Lindaunis (site 61 in Fig. 1, Supplementary table S1), which is 30 km from Winning. However, sequences from these G. oxysperma-like specimens were also placed in the K. leptoderma cluster (MH720545-MH720547; Supplementary table S1).

Discussion

The 20 taxa of green algae that were detected in the present study (Fig. 2) can be identified with variable degrees of certainty. Only one taxon could be assigned to a clade that included a reference sequence from type material, namely for Ulva tenera (Kornmann & Sahling, 1994). However, U. tenera was described relatively recently, and the corresponding cluster in our phylogenetic analysis also encompassed several reference sequences from specimens that were recognized elsewhere as U. lactuca L. Even though only one of the more than 100 U. tenera syntypes was examined, and given that the current concept of U. lactuca has been challenged (Butler, 2007), the phylogenetic analysis presented here strongly suggests that U. tenera is a synonym of U. lactuca. This view is further supported by the observation that young U. lactuca specimens from Helgoland exhibit the described morphology of U. tenera (Kornmann & Sahling, 1994). Other described characteristics of U. tenera are its restriction to the uppermost eulittoral and its exclusively vegetative propagation (i.e. with biflagellate spores; Kornmann & Sahling, 1994); apparently, the authors observed dwarfish forms of U. lactuca that were adapted to extended air exposure. Therefore, U. tenera is here reduced to synonymy with U. lactuca. Other homotypic synonyms of *U. lactuca* cited below are according to Guiry & Guiry (2018).

Ulva lactuca

Linnaeus, C. 1753. Species plantarum, exhibentes plantas rite cognitas, ad gen era relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas. Vol. 2 pp. [i], 561–1200, [1–30, index], [i, err.]. Holmiae [Stockholm]: Impensis Laurentii Salvii.

Homotypic synonyms:

Phyllona lactuca (Linnaeus) F.H.Wiggers 1780 *Monostroma lactuca* (Linnaeus) J.Agardh 1883 *Ulva tenera* Kornmann & Sahling 1994

The genetic-based species identities of several other taxa corresponded to characteristic morphological traits. Indeed, this was the case for U. torta, which usually formed massively intertwined tubular thalli of small diameter; U. prolifera, which mostly exhibited characteristically twisted stipes; and Umbraulva dangeardii, which is characterized by its olive green pigmentation. Meanwhile, the genetic-based species identities of the three monostromatic taxa corresponded to known phenotypic traits. For example, M. grevillei was only observed during spring, which was not the case for any other entity; K. leptoderma exhibited a characteristic heteromorphic life cycle, as reported elsewhere (Weinberger et al., 2018); and P. undulatum, despite only being observed once, exhibited a typical morphology (see Supplementary Information). Furthermore, specimens that clustered with Ulva intestinalis mostly exhibited the tubular and unbranched morphology considered characteristic of the species (Kornmann & Sahling, 1977; Rothmaler, 1984; Pankow, 1990), but branched specimens were occasionally observed, as reported previously (Reed & Russell, 1978; Blomster et al., 1998), probably promoted by low salinity (Steinhagen et al., 2018b).

However, for most cases, genetic-based species identities failed to correspond to characteristic morphological traits. For example, specimens that exhibited the characteristic lanceolate and partly distromatic type morphology of U. linza (Kornmann & Sahling, 1977; Rothmaler, 1984; Pankow, 1990) clustered with U. linza reference sequences, but also with sequences from specimens that exhibited tubular and branched morphologies corresponding to descriptions of U. procera and U. ahlneriana (Kornmann & Sahling, 1977; Rothmaler, 1984; Pankow, 1990) and a sequence from a historical voucher of U. ahlneriana (Fig. 2). This observation supports the previous suggestions that U. procera (Maggs et al., 2007b) and U. ahlneriana(Guiry & Guiry, 2018) are synonyms of U. linza. It was interesting that the cluster representing U. linza in our phylogenetic tree included two lineages which were morphologically

indistinct. One of the lineages was only detected on Helgoland, whereas the second was only detected on mainland coasts. However, more information is needed to determine whether the groups represent distinct species or simply unique genotypes that developed in response to geographic separation.

Meanwhile, the U. compressa specimens also exhibited multiple gross morphologies. One morphotype was only observed on North Sea coasts and corresponded to the morphology of the tubular and branched type material (Linnaeus, 1753). However, as already discussed elsewhere (Steinhagen et al., 2018a), genetically indistinguishable specimens from the Baltic and Wadden Seas exhibited a completely different morphology that was consistently distromatic and sheet-like. Evidently, the distromatic morphology of U. compressa strongly overlaps with the allegedly unique morphology of U. lactuca, thereby causing a considerable amount of historical taxonomic confusion (Steinhagen et al., 2018a). Based on the results of the present study, U. lactuca in northern Germany is only present on Helgoland (Table 2, Supplementary table 2), whereas historical records from the Baltic Sea (Schories et al., 2009) are misidentified U. compressa specimens (Steinhagen et al., 2018a). Notably, historical vouchers from Helgoland (Kornmann & Sahling, 1994) that exhibited the curved morphology of U. pseudocurvata (Hoeksema & Van den Hoek, 1983) yielded sequences that clustered with U. lactuca sequences, whereas specimens that were recently collected from mainland coasts of northern Germany (Steinhagen et al., 2018a) and elsewhere (Tan et al., 1999; Hayden & Waaland, 2004) exhibiting the same morphology yielded sequences that clustered with U. compressa sequences. This clearly challenges the validity of U. pseudocurvata as a taxonomic entity, because its description is based on morphological traits that are clearly not specific, and it also confirms the strong morphological plasticity of U. lactuca on Helgoland and U. compressa, in its distromatic form, on the mainland coasts of northern Germany.

In addition to *U. lactuca* and the distromatic form of *U. compressa*, three additional entities with consistently distromatic blades were also observed in the present study. These specimens clustered with *U. gigantea*, *U. australis*, *U. rigida* and *U. laetevirens* reference specimens (Fig. 2). In these cases, the observed morphologies generally paralleled the corresponding type morphologies. However, based on morphological observations the taxa were not reliably distinguishable from one another, *U. lactuca*, or the distromatic form of *U. compressa*. Furthermore, as recently demonstrated by ITS and *rbcL* analysis (Horta *et al.*, 2018), *U. rigida* and *U. laetevirens* could not be distinguished using *tufA* gene sequences. Therefore, *U. laetevirens* Areschoug 1854 should be considered a synonym of *U. rigida* C. Agardh 1823.

Some clades with tubular morphologies could not be clearly resolved. As reported previously (Heesch *et al.*, 2009; Kraft *et al.*, 2010; Saunders & Kucera, 2010; Kirkendale *et al.*, 2013), there was no clear species boundary between *U. flexuosa* and *U. californica* (Fig. 2). However, despite this observation, Hiraoka *et al.* (2017) used hybridization experiments to confirm the biological separation of *U. flexuosa* and *U. californica* from Japan. Because cross-breeding experiments were not included in the present study, we have chosen to indicate the species' lack of genetic resolution using the term '*Ulva flexuosa/ californica* complex'.

A reference sequence for type material of the tubular species *U. shanxiensis*, which was recently described from a freshwater stream in northern China (Chen *et al.*, 2015), was placed basal to a clade of tubular specimens in the phylogenetic analysis of the present study (Fig. 2). However, the clade encompassing *U. shanxiensis* and the tubular specimens was poorly supported, indicating relatively high sequence divergence (Fig. 2, note branch length). Therefore, the tubular specimens are unlikely to belong to *U. shanxiensis*, and the identity of the clade remains unidentified as a result.

Identities could also not be determined for two genetic entities in the genus Blidingia (Blidingia sp. 1 and Blidingia sp. 2), since they did not match any available reference sequences. Specimens of the Blidingia sp. 2 clade exhibited strong morphological overlap with a second clade encompassing a reference sequence of Blidingia marginata and could only be distinguished molecularly. The morphology of both clades was consistent with that of B. marginata but, perhaps, also with that of B. ramifera (Garbary & Barkhouse, 1987), a species that has not yet been reported from the area and which is, for formal reasons, invalid (Cormaci et al., 2014) and currently regarded as a synonym of B. marginata (Guiry & Guiry, 2018). In contrast, specimens of the relatively abundant Blidingia sp. 1 exhibited unique genetic and morphological traits that clearly distinguished them from other Blidingia taxa in northern Germany. In addition to B. marginata and B. minima, two other Blidingia species (B. chadefaudii and B. subsalsa) have also been reported from the German coasts of the North Sea (Kornmann & Sahling, 1978; Bartsch & Kuhlenkamp, 2000; Schories et al., 2009). However, no molecular reference data were available for B. chadefaudii and B. subsalsa, and morphological identification criteria for the species remain ambiguous and overlapping. Therefore, in order to identify Blidingia sp. 1 and Blidingia sp. 2 and to confirm the identities of B. marginata and B. minima, type material of different Blidingia species

should be analysed by molecular markers and species life cycles should be documented using cultivated material. The same strategy might also facilitate the identification of ambiguous *Ulva* specimens in the future.

Notably, our phylogenetic analyses did not support the monophyly of the genus *Ulva* (Fig. 2). In our study the inclusion of *U. lactuca*, *U. australis*, *U. intestinalis* and *U. compressa* as a sister clade of *Umbraulva* species and *Percursaria percursa* was revealed (Fig. 2), in contrast to previous studies which used other marker genes (Hayden *et al.*, 2003; Heesch *et al.*, 2009; Kirkendale *et al.*, 2013). This topology was not observed when *P. percursa* was excluded from the analysis (Supplementary fig. S1). However, the inclusion of more, rather than fewer, taxa is more likely to yield true phylogenetic relationships.

The species inventory of Ulva sensu lato of the present study diverged considerably from the expected inventory (Schories et al., 2009). Four species (U. australis, U. californica, U. gigantea and Umbraulva dangeardii) were observed in the area for the first time (Fig. 22). Ulva australis was first introduced to southern France and very recently reported from the Dutch Oosterschelde estuary (Fort et al., 2019). Now, the species is also present in the North Friesian Wadden Sea. The same is true for U. gigantea, which, in Europe, had only been reported from Britain and other westerly locations (Maggs et al., 2007b). Single individuals of U. californica were first observed in Germany in 2008 on the Wadden Sea island of Wangerooge in Lower Saxony (Lackschewitz et al., 2015) and, over the next six years, eventually reached the SW Baltic Sea. In the present study, Umbraulva dangeardii was only observed at one site on Helgoland (Table 2, Supplementary table S1). It is interesting that even though Helgoland is a phycological hotspot in Germany, U. dangeardii has never before been included in inventories (Kornmann & Sahling, 1977, 1983, 1994; Bartsch & Kuhlenkamp, 2000), suggesting recent introduction. Yet, the presence of U. dangeardii in Germany may have been ignored for some time, due to the preference of the species for subtidal habitats. In addition to the above-mentioned newly introduced species, three (Blidingia sp. 1, Blidingia sp. 2, Ulva sp.) or even four (if one of the two genetic entities within U. linza is included) additional taxa that were observed in our study probably represent cryptic and perhaps undescribed species that have so far not been recognized.

Despite these new records, the morphologybased species inventories of all three main study areas were expected to be larger than the genetically validated ones (Fig. 22). Altogether, 14 of the species (members of *Ulva, Blidingia, Monostroma,* Gayralia and Ulvaria) that were listed by Schories et al. (2009) and are currently accepted taxonomically (Guiry & Guiry, 2018) were not encountered genetically in the present study. This lack of detection could indicate their absence but might also be attributed to other factors, such as low abundance or lack of molecular reference material. Indeed, no tufA reference sequences are available for 11 of the 14 missing species, and the numerous historical records from the area may be the misidentification result of and taxonomic confusion.

As discussed above, records of Ulva pseudocurvata from northern Germany are often, and perhaps always, due to the misidentification of either U. compressa or U. lactuca. Also, the only record of U. splitiana from our area (as Enteromorpha jugoslavica; Kaminski, 1980) was due to the misidentification of U. linza, as demonstrated through sequencing of the ITS marker gene from the corresponding herbarium voucher (Gesche Bock, pers. comm.). Furthermore, analysis of historical Gayralia oxysperma vouchers from northern Germany and adjacent areas indicated that all the vouchers were genetically identical to Kornmannia leptoderma, which had until now been considered a relatively rare species that was only present on Helgoland (Kornmann & Sahling, 1983) and, therefore, has not been included in identification keys for other parts of Germany (Rothmaler, 1984; Pankow, 1990) or adjacent areas (Brodie et al., 2007). However, K. leptoderma was present in all three main areas of the present study (see also Weinberger et al., 2018). In striking contrast, G. oxysperma was not observed, even at the type locality of its basionym U. oxysperma Kützing (see the Supplementary Information for a description of the relatively complicated nomenclatural history of G. oxysperma). For further details see Doty (1947), Gayral (1965) and Womersley (1984). This apparent absence or rarity of G. oxysperma is surprising because the species should be present across the entire Baltic Sea (Schories et al., 2009). Descriptions of G. oxysperma (Rothmaler, 1984; Pankow, 1990) are in complete agreement with the morphology of K. leptoderma in our area (Figs 15-21, see also Weinberger et al., 2018). The two species have very different life cycles (Vinogradova, 1969), but ontogenetic observations are time consuming, and for this reason most historical records of G. oxysperma are probably based on the morphological traits of field-collected material. As a consequence, it is likely that most records of G. oxysperma are due to the misidentification of K. leptoderma. Similarly, the molecular analysis of G. oxysperma-like specimens from the North-west Atlantic yielded two clusters attributed to

| Snecies | Ralti | c Sea | Wad | den Sea |
|--------------------------------------------------------------------------------------------|-------|-------|------|---------|
| | 2019 | 2009 | 2019 | 2009 |
| Blidingia marginata (J.Agardh) P.J.L.Dangeard ex Bliding 1963 | > | > | > | > |
| Blidingia minima (Nägeli ex Kützing) Kylin 1947 | Х | * | X | > |
| Blidingia chadefaudii (Feldmann) Bliding 1963 | | | | |
| Blidingia subsalsa (Kjellmann) Kornmann & Sahling ex Scagel et al. 1989 | | | | |
| Blidingia sp. 1 | * | X | > | X |
| Blidingia sp. 2 | | | | |
| Kornmannia leptoderma (Kjellmann) Bliding 1969 | 1 | Х | > | > |
| Ulva compressa Linnaeus 1753 | > | > | > | > |
| Ulva pseudocurvata Koeman & Hoek 1981 | | | | |
| Ulva curvata (Kützing) De Toni 1889 | | | X | > |
| Ulva flexuosa Wulfen 1803 | > | > | > | > |
| Enteromorpha flexuosa subsp. linziformis (Bliding) Bliding 1963 | | | X | > |
| Ulva flexuosa subsp. paradoxa (C. Agardh) M.J. Wynne 2005 | | | X | > |
| Ulva californica Wille 1899 | > | X | > | X |
| Ulva intestinalis Linnaeus 1753 | > | > | > | > |
| Ulva lactuca Linnaeus 1753 | X | * | X | > |
| Ulva tenera Kommann & Sahling 1994 | | | X | > |
| Ulva linza Linnaeus 1753 | > | > | > | > |
| Enteromorpha jugoslavica Bliding | X | * | | |
| Ulva prolifera O. F. Müller 1778 | > | > | > | > |
| Ulva torta (Mertens) Trevisan 1841 | > | > | > | > |
| Ulva lobata (Kützing) Harvey 1855 | | | | |
| Ulva radiata (J.Agardh) H.S.Hayden, Blomster, Maggs, P.C.Silva, M.J.Stanhope & J.R.Waaland | | | X | > |
| Ulva ralfsii (Harvev) Le Jolis 1863 | | | X | > |
| Ulva simplex (K.L.Vinogradova) H.S.Hayden, Blomster, Maggs, P.C.Silva, M.J.Stanhope & | Α | > | ~ | > |
| J.R. Waaland 2003 | | | ** | |
| Ulva clathrata (Roth) C. Agardh 1811 | × | > | X | > |
| Ulva rigida C. Agardh 1823 and Ulva scandinavica Bliding 1968 | > | X | > | > |
| Ulva gigantea (Kützing) Bliding 1969 | > | X | > | X |
| Ulva australis Areschoug 1854 | | | > | X |
| Ulva sp. | ~ | Х | > | X |
| Umbraulva dangeardii M.J.Wynne & G.Furnari 2014 | | | | |
| Ulvaria fusca (Postels & Ruprecht) Vinogradova 1967 | X | * | | |
| Percursaria percursa (C. Argardh)Rosenvinge 1893 | ∕ | ~ | X | ~ |
| Monostroma grevillei (Thoret) Wittrock 1866 | ~ | ~ | X | * |
| Monostroma arcticum Wittrock1866 | | | | |
| Protomonostroma undulatum (Wittrock) Vinogradova 1969 | | | | |
| Gayralia oxysperma (Kützing) K.L. Vinogradova ex Scagel et al. 1989 | X | * | | |
| | | | | |

>

2009

2019

> >

5

>

> |>

Helgoland

detected in the present study (2019) from the Baltic Sea, Wadden Sea and Helgoland. $\dot{\mathbf{X}}$, species not observed; \Box , species observed; empty, unexpected by Schories *et al.* (2009) and not observed in present study. Light grey shading indicates agreement. For additional annotations or taxonomic notes by other authors see also Supplementary table S2. Fig. 22. Comparison of molecular (tufA)-based identification from the present study and the inventory list from Schories et al. (2009). List of species predicted by Schories et al. (2009) and

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Monostroma grevillei (Saunders & Kucera, 2010). Therefore, a thorough taxonomic reassessment of *G. oxysperma* and its populations is urgently needed.

Some species that were reported to occur only in parts of northern Germany were found to have broader distributions than expected. For instance, *U. rigida*, which was only expected to occur in the Wadden Sea and on Helgoland, was also observed in the Baltic Sea (Table 2, Supplementary table S1), and *K. leptoderma*, which had only been reported to occur on Helgoland, was observed in both the Baltic and Wadden Seas (Table 2, Supplementary table S1).

In summary, the current morphological concepts that are used for the identification of Ulva species and related taxa in northern Germany are neither in agreement with the species inventory of the area nor with the actual morphology of species that are present. Past morphological descriptions of U. linza, U. intestinalis and U. compressa have been too restrictive, thereby resulting in frequent misidentifications of these abundant taxa. Furthermore, several cryptic and/or newly introduced species, including K. leptoderma, U. australis, U. californica, U. gigantea and Protomonostroma undulatum, are now present in northern Germany, and several genetic entities, namely Ulva sp., Blidingia sp. 1 and Blidingia sp. 2, have yet to be identified. Meanwhile, B. minima and G. oxysperma were either absent or much rarer than expected, and certain other taxa that were expected in the area, namely U. tenera, are actually synonyms. The observations of the present study provide a basis for the development of improved identification keys, although it is unlikely that it will be possible to distinguish all species morphologically owing to the considerable overlap of traits. The DNA barcoding approach used in the present study clearly provides better resolution. However, U. californica and U. flexuosa cannot be clearly distinguished using the analysis of *tufA* alone and more sequences of type material will be needed to improve the identification of species in the future. Furthermore, additional genetic markers should be investigated and cultivation studies should be performed to resolve remaining issues, such as the taxonomic affiliation of the newly found Blidingia species or relations among the genera Ulva, Umbraulva and Percursaria.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Supplementary information

Supplementary Information. (1) Distribution and specific characteristics of observed species, (2) nomenclatural history of *Gayralia oxysperma* and (3) seasonal species variation.

Supplementary table S1. Full collection data.

Supplementary table S2. Comparison of molecular (*tufA*)-based identification from the present study and the inventory list from Schories *et al.* (2009).

Supplementary fig. S1. Maximum likelihood phylogram of *tufA* sequences from taxa of *Ulva sensu lato* from northern Germany.

Supplementary fig. S2. Morphology of *Protomonostroma undulatum* specimens from Helgoland, Germany.

Author contributions

S. Steinhagen: experimental design, fieldwork and algae collection, laboratory work, macro- and microscopic observation, phylogenetic analysis, drafting and editing manuscript; R. Karez: experimental design, algae collection, drafting and editing manuscript; F. Weinberger: original concept, collection of specimens, drafting and editing manuscript.

References

- Bartsch, I. & Kuhlenkamp, R. (2000). The marine macroalgae of Helgoland (North Sea): an annotated list of records between 1845 and 1999. *Helgoland Marine Research*, **54**: 160–189.
- Blomster, J., Maggs, C.A. & Stanhope, M.J. (1998). Molecular and morphological analysis of *Enteromorpha intestinalis* and *E. compressa* (Chlorophyta) in the British Isles. *Journal of Phycology*, 34: 319–340.
- Blomster, J., Back, S., Fewer, D.P., Kiirikki, M., Lehvo, A., Maggs, C.A. & Stanhope, M.J. (2002). Novel morphology in *Enteromorpha* (Ulvophyceae) forming green tides. *American Journal of Botany*, 89: 1756–1763.
- Brodie, J., Maggs, C.A., Society, B.P. & John, D.M. (2007). *The Green Seaweeds of Britain and Ireland*. British Phycological Society, London.
- Butler, D. (2007). Ancient algal mixup sorted. *Nature*. https://www.nature.com/news/2007/071220/full/news. 2007.396.html.
- Charlier, R.H., Morand, P., Finkl, C.W. & Thys, A. (2007). Green tides on the Brittany coasts. *Environmental Research, Engineering and Management*, **3**: 52–59.
- Charlier, R.H., Morand, P. & Finkl, C.W. (2008). How Brittany and Florida coasts cope with green tides. *International Journal of Environmental Studies*, **65**: 191–208.
- Chen, L., Feng, J. & Xie, S.-L. (2015). Ulva shanxiensis (Ulvaceae), a new species from Shanxi, China. Novon, 23: 397-405.
- Cormaci, M., Furnari, G., & Alongi, G. (2014). Flora marina bentonica del Mediterraneo: Chlorophyta. Bollettino

dell'Accademia Gioenia di Scienze Naturali di Catania, 47: 11–436

- Doty, M.S. (1947). The marine algae of Oregon. Part 1. Chlorophyta and Phaeophyta. *Farlowia*, **3**: 1–65.
- Famà, P., Wysor, B., Kooistra, W.H.C.F. & Zuccarello, G.C. (2002). Molecular phylogeny of the genus *Caulerpa* (Caulerpales, Chlorophyta) inferred from chloroplast *tuf*A gene. *Journal of Phycology*, **38**: 1040–1050.
- Fort, A., Lebrault, M., Allaire, M., Esteves-Ferreira, A.A., McHale, M., Lopez, F., Fariñas-Franco, J.M., Alseekh, S., Fernie, A.R. & Sulpice, R. (2019). Extensive variations in diurnal growth patterns and metabolism among *Ulva* spp. strains. *Plant Physiology*, **180**: 109–123.
- Garbary, D.J. & Barkhouse, L.B. (1987). *Blidingia ramifera* (Bliding) stat. nov. (Chlorophyta): a new marine alga for eastern North America. *Nordic Journal of Botany*, 7: 359–363.
- Gayral, P. (1965). *Monostroma* Thuret, *Ulvaria* Rupr. emend. Gayral, *Ulvopsis* Gayral. (Chlorophycées, Ulotrichales): structure, reproduction, cycles, position systématique. *Revue générale de botanique*, **72**: 627–638.
- Guiry, M.D. & Guiry, G.M. (2018). *AlgaeBase*. World-wide electronic publication. National University of Ireland, Galway. http://www.algaebase.org.
- Hayden, H.S. & Waaland J.R. (2002). Phylogenetic systematics of the Ulvaceae (Ulvales, Ulvophyceae) using chloroplast and nuclear DNA sequences. *Journal of Phycology*, **38**: 1200–1212.
- Hayden, H.S. & Waaland J.R. (2004). A molecular systematic study of *Ulva* (Ulvaceae, Ulvales) from the northeast Pacific. *Phycologia*, **43**: 364–382.
- Hayden, H.S., Blomster, J., Maggs, C.A., Silva, P.C., Stanhope, M.J. & Waaland, J.R. (2003). Linnaeus was right all along: Ulva and Enteromorpha are not distinct genera. European Journal of Phycology, 38: 277–294.
- Heesch, S., Broom, J.E., Neill, K.F., Farr, T.J., Dalen, J.L. & Nelson, W.A. (2009). *Ulva, Umbraulva* and *Gemina*: genetic survey of New Zealand taxa reveals diversity and introduced species. *European Journal of Phycology*, **44**: 143–154.
- Hillis, D.M. (1987). Molecular versus morphological approaches to systematics. *Annual Review of Ecology and Systematics*, **18**: 23–42.
- Hiraoka, M., Ichihara, K., Zhu, W., Shimada, S., Oka, N., Cui, J., Tsubaki, S. & He, P. (2017). Examination of species delimitation of ambiguous DNA-based *Ulva* (Ulvophyceae, Chlorophyta) clades by culturing and hybridisation. *Phycologia*, 56: 517–532.
- Hoeksema, B.W. & Van Den Hoek, C. (1983). The taxonomy of *Ulva* (Chlorophyceae) from the coastal region of Roscoff (Brittany, France). *Botanica Marina*, 26: 65.
- Horta, P., Bernardes Batista, M., Cunha, R.L. & Castilho, R. (2018). Sea lettuce systematics: lumping or splitting? *In BioRxiv*. https://doi.org/10.1101/413450.
- Hughey, 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. Journal of Phycology, doi: 10.1111/ jpy.12860.
- Kaminski, E. (1980). Über Funde von *Enteromorpha jugoslavica* Bliding in der Kieler Förde (west. Ostsee). *Botanica Marina*, **23**: 309–312.
- Katoh, K., Misawa, K., Kuma, K.-I. & Miyata, T. (2002). MAFFT: a novel method for rapid multiple sequence

alignment based on fast Fourier transform. Nucleic Acids Research, 30: 3059–3066.

- Kirkendale, L., Saunders, G.W. & Winberg, P. (2013). A molecular survey of *Ulva* (Chlorophyta) in temperate Australia reveals enhanced levels of cosmopolitanism. *Journal of Phycology*, **49**: 69–81.
- Koeman, R.P.T. & Van den Hoek, C. (1984). The taxonomy of *Ulva* (Chlorophyceae) in the Netherlands. *British Phycological Journal*, **16**: 9–53.
- Koeman, R. & Van den Hoek, C. (1982a). The taxonomy of *Enteromorpha* Link, 1820, (Chlorophyceae) in the Netherlands I: the section *Enteromorpha*. Archiv für Hydrobiologie, 63: 279–330.
- Koeman, R. & Van den Hoek, C. (1982b). The taxonomy of *Enteromorpha* Link, 1820, (Chlorophyceae) in the Netherlands I. The section Proliferae. *Cryptogamie*, *Algologie*, 3: 37–70.
- Koeman, R. & Van den Hoek, C. (1984). The taxonomy of *Enteromorpha* Link, 1820, (Chlorophyceae) in the Netherlands III. The sections *Flexuosae* and *Clathratae* and an addition to the section *Proliferae*. *Cryptogamie*, *Algologie*, 5: 21–61.
- Kornmann, P. & Sahling, P.-H. (1977). Meeresalgen von Helgoland. Helgoländer wissenschaftliche Meeresuntersuchungen, 29: 1–289.
- Kornmann, P. & Sahling, P.-H. (1978). Die Blidingia-Arten von Helgoland (Ulvales, Chlorophyta). Helgoländer wissenschaftliche Meeresuntersuchungen, 31: 391–413.
- Kornmann, P. & Sahling, P.-H. (1983). Meeresalgen von Helgoland, Ergänzung. Helgoländer wissenschaftliche Meeresuntersuchungen, 36: 1–65.
- Kornmann, P. & Sahling, P.-H. (1994). Marine algae of Helgoland – 2nd Supplement. *Helgoländer Meeresunter*suchungen, 48: 365–406.
- Kraft, L.G.K., Kraft, G.T. & Waller, R.F. (2010). Investigations into southern Australian Ulva (Ulvophyceae, Chlorophyta) taxonomy and molecular phylogeny indicate both cosmopolitanism and endemic cryptic species. Journal of Phycology, 46: 1257–1277.
- Kützing, F.T. (1843). Phycologia generalis: oder, Anatomie, Physiologie und Systemkunde der Tange. Brockhaus, Leipzig.
- Lackschewitz, D., Reise, K., Buschbaum, C. & Karez, R. (2015). Neobiota in deutschen Küstengewässern. Eingeschleppte und kryptogene Tier- und Pflanzenarten an der deutschen Nord- und Ostseeküste. Landesamt für Landwirtschaft, Umwelt und ländliche Räume des Landes Schleswig-Holstein (LLUR).
- Linnaeus, C. (1753). Species Plantarum, Exhibentes Plantas Rite Cognitas Ad Genera Relatas: Cum Differentiis Specificis, Nominibus Trivialibus, Synonymis Selectis, Locis Natalibus, Secundum Systema Sexuale Digestas. Trattner, Stockholm.
- Maggs, C.A. & Kelly, J. (2007). *Percursaria*. In *The Green Seaweeds of Britain and Ireland* (Brodie, J., Maggs, C.A. & John, D., editors). British Phycological Society, London.
- Maggs, C.A., Blomster, J. & Kelly, J. (2007a). Umbraulva. In The Green Seaweeds of Britain and Ireland (Brodie, J., Maggs, C.A. & John, D., editors). British Phycological Society, London.
- Maggs, C.A., Blomster, J., Mineur, F. & Kelly, J. (2007b). Ulva. In The Green Seaweeds of Britain and Ireland (Brodie, J., Maggs, C.A. & John, D., editors). British Phycological Society, London.
- Nylander, J.A.A. (2004). MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

- Pankow, H. (1990). Ostsee-Algenflora. Gustav Fischer Verlag, Jena.
- Reed, R.H. & Russell, G. (1978). Salinity fluctuations and their influence on bottle brush morphogenesis in *Enteromorpha intestinalis* (L) Link. *British Phycological Journal*, 13: 149–153.
- Reinke, J. (1889). Notiz über die Vegetationsverhältnisse in der deutschen Bucht der Nordsee. *Berichte der Deutschen Botanischen Gesellschaft*, 7: 367–369.
- Rönnbäck, P., Kautsky, N., Pihl, L., Troell, M., Soerqvist, T. & Wennhage, H. (2007). Ecosystem goods and services from Swedish coastal habitats: identification, valuation, and implications of ecosystem shifts. *Ambio*, **36**: 534–544.
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61: 539–542.
- Rothmaler, W. (1984). *Exkursionsflora für die Gebiete der* DDR und BRD Band 1: Niedere Pflanzen. Volk und Wissen Volkseigener Verlag, Berlin.
- Saunders, G.W. & Kucera, H. (2010). An evaluation of *rbcL*, *tufA*, UPA, LSU and ITS as DNA barcode markers for the marine green macroalgae. *Cryptogamie*, *Algologie*, **31**: 487–528.
- Schories, D., Selig, U. & Schubert, H. (2009). Species and synonym list of the German marine macroalgae based on historical and recent records. Meeresbiologische Beiträge, University of Rostock.
- Shimada, S., Hiraoka, M., Nabata, S., Iima, M. & Masuda, M. (2003). Molecular phylogenetic analyses of the Japanese Ulva and Enteromorpha (Ulvales, Ulvophyceae), with special reference to the free-floating Ulva. Phycological Research, 51: 99–108.
- Smetacek, V. & Zingone, A. (2013). Green and golden seaweed tides on the rise. *Nature*, **504**: 84–88.
- Spoerner, M., Wichard, T., Bachhuber, T., Stratmann, J. & Oertel, W. (2012). Growth and thallus morphogenesis of *Ulva mutabilis* (Chlorophyta) depends on a combination

of two bacterial species excreting regulatory factor. *Journal of Phycology*, **48**: 1433–1447.

- Staats, M., Cuenca, A., Richardson, J.E., Vrielink-van Ginkel, R., Petersen, G., Seberg, O. & Bakker, F.T. (2011). DNA damage in plant herbarium tissue. *PLoS ONE*, 6: e28448.
- Stamatakis, A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, **30**: 1312–1313.
- Steinhagen, S., Karez, R. & Weinberger, F. (2018a). Molecular analysis of *Ulva compressa* (Chlorophyta, Ulvales) reveals its morphological plasticity, distribution and potential invasiveness on German North Sea and Baltic Sea coasts. *European Journal of Phycology*, 54: 102–114.
- Steinhagen, S., Karez, R. & Weinberger, F. (2018b). Surveying seaweeds from the Ulvales and Fucales in the world's most frequently used artificial waterway, the Kiel Canal. *Botanica Marina*, **62**: 51–61.
- Tan, I.H., Blomster, J., Hansen, G., Leskinen, E., Maggs, C.A., Mann, D.G., Sluimam, H.J. & Stanhope, M.J. (1999).
 Molecular phylogenetic evidence for a reversible morphogenetic switch controlling the gross morphology of two common genera of green seaweeds, *Ulva* and *Enteromorpha*. *Molecular Biology and Evolution*, 16: 1011–1018.
- Vinogradova, K.L. (1969). K. sistematike poryadka Ulvales (Chlorophyta) s.l. A contribution to the taxonomy of the order Ulvales. *Botanicheskij Zhurnal SSSR*, 54: 1347–1355.
- Weinberger, F., Steinhagen, S., Afanasyev, D.F. & Karez, R. (2018). New records from the southern North Sea and first records from the Baltic Sea of *Kornmannia leptoderma*. *Botanica Marina*, **62**: 63–73.
- Wichard, T. (2015). Exploring bacteria-induced growth and morphogenesis in the green macroalga order Ulvales (Chlorophyta). *Frontiers in Plant Science*, **6**.
- Wolf, M.A., Sciuto, K., Andreoli, C. & Moro, I. (2012). Ulva (Chlorophyta, Ulvales) biodiversity in the North Adriatic Sea (Mediterranean, Italy): cryptic species and new introductions. Journal of Phycology, 48: 1510–1521.
- Womersley, H.B.S. (1984). The Marine Benthic Flora of Southern Australia. Government Printer, Adelaide.

Cryptic, alien, and lost species: Molecular diversity of *Ulva sensu lato* along the German coasts of the North and Baltic Seas

S. Steinhagen¹, R. Karez², and F. Weinberger¹

1. GEOMAR Helmholtz Centre for Ocean Research Kiel, Marine Ecology Department, Düsternbrooker Weg 20, 24105 Kiel, Germany

2. State Agency for Agriculture, Environment and Rural Areas, Schleswig-Holstein, Hamburger Chaussee 25, 24220 Flintbek, Germany

(email: ssteinhagen@geomar.de)

Supplement

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1. Distribution and specific characteristics of observed species

The distribution, ecology, and morphology of species observed during the present study are described below.

Ulva gigantea

Specimens of *U. gigantea* were only found in the Wadden Sea around the ferry terminal of Dagebüll and an adjacent area and at one site in the Baltic Sea. The species' distromatic, sheet-like thalli were mostly lobed or rosette-like and rarely lanceolate. Blades were attached by a small rhizoidal zone during the beginning of the growth season (June–July), and mature thalli, with small holes (0.5–3 mm), were mostly found drifting (August). By the end of the vegetation phase, the holes had widened to up to 3 cm. However, in some cases, it was unclear if the holes were naturally occurring or feeding traces. The margins of the lobed or rosette-like thalli lacked microscopic teeth (sometimes possessed macroscopic teeth, probably due to feeding) and were typically frilled or ruffled. The thalli were relatively rigid, ranging from 12 to 42 cm (up to 50 cm) in length. The polygonal (rarely round) cells of the middle and apical regions had rounded corners; were either arranged in short rows, curved, or unordered; $19-23 \times 20-22 \ \mu m$ in surface view; with a marginal chloroplast; and with a single (sometimes 2) pyrenoid. Meanwhile, the elongated cells of the rhizoidal zone contained varying numbers of pyrenoids (1–4).

Ulva rigida

Specimens of *U. rigida* were most prominently found in the northern parts of the Wadden Sea but also occurred at one location in the Baltic Sea (Heiligenhafen) and at multiple sites on Helgoland. In the Wadden Sea, both drifting mats and attached specimens of *U. rigida* were observed, whereas only separate attached individuals were observed on Helgoland and in the Baltic Sea. Individuals inhabited remote sites, strongly trafficked harbours, and tourist-used areas. Mature individuals were generally lanciniate, lobed, or rounded and deeply folded, whereas young thalli often grew as rosettes, and both young and mature specimens were obligately distromatic. A minor portion of the specimens possessed small (1–3 mm) holes, and most specimens possessed microscopic teeth along the outer thallus margins. Teeth were often invisible in mature or drifting thalli. The cells were 8–26 × 8–30 μ m in surface view and either arranged in short, curved rows or irregular and polygonal with rounded corners. The singular chloroplasts were either marginal or cap-like, and most cells contained two (sometimes 3, rarely 1 or >3) pyrenoids. The vegetative thallus parts either passed straight into the rhizoidal zone, with no clear "stipe-like region", or slowly tapered until the cells of the rhizoidal zone were formed. A distinct disc-like structure resembling a holdfast was not observed in the examined specimens.

Ulva sp.

Specimens belonging to this clade were observed at all three main study areas and were usually found in regions of intensive anthropogenic use, such as harbours, marinas, or tourist-trafficked waters. The morphology of these specimens was highly variable. The tubular thalli were either smooth or wrinkled, 5–13 cm in length, and sometimes appeared similar to the unbranched thalli of *U. intestinalis*, whereas the branched specimens possessed first-level, uniseriate branches that overlapped morphologically with young *U. flexuosa* thalli. However, the main-axis of the branched specimens was always apparent. Cells of the middle and apical thallus regions were 9–18 × 12–29 μ m in surface view and either rectangular, quadratic, or polygonal. The singular chloroplasts were either cap-like or filled entire cells, and each contained 1–3 (rarely 4, up to 6 in the rhizoidal zone) pyrenoids.

Ulva flexuosa

Specimens of *U. flexuosa* were observed in all three main study areas but were relatively rare, possibly due to sampling bias from the species' delicate texture and from the inconspicuous nature of drifting specimens. The specimens were observed in both brackish and fully marine habitats, at both remote and highly trafficked sites, and either attached to substrates or more commonly as drifting mats. Due to the species' scarcity, the following description is based on only three individuals. The *U. flexuosa* specimens were always tubular, either as delicate, narrow cords (1mm thick) or as broader tubes (8 mm thick). The thalli were up to 40 cm in length, and first-level branchlets were even observed in the rhizoidal zone, whereas both first-and secondary-level branches were often observed to cover the middle and apical thallus parts. In the broader thallus parts, the cells formed multiseriate rows that sometimes extended through the entire thallus, usually including the rhizoidal zone, whereas uniseriate branchlets had broader bases and ended in filigree tips. Due to strong proliferation, the main axis could not be identified in some specimens. The rectangular cells of the middle and apical thallus region were $7-26 \times 7-32 \ \mu m$ in surface view and contained single cap-like chloroplasts, as well as 1-3 (rarely up to 5, 2-6 in the rhizoidal zone) pyrenoids.

Ulva californica

This species was first observed on Wangerooge, a German island in the North Sea, in 2008 (Lackschewitz et al. 2015) and, six years later (i.e., during the present study), was observed in the Baltic Sea (>180 km [through Kiel Canal] or >1000 km [through Skagerrak] from first introduction), the Wadden Sea (>110 km from first introduction), and on the remote off-shore island of Helgoland (>40 km from first introduction). Accordingly, *U. californica* specimens

were collected from a broad range of salinities. The morphology of the specimens varied from branched to unbranched tubes up to lanceolate thalli or thalli of amorphous shape and were mostly found attached to artificial substrate, such as concrete, groynes, or jetties. The *tuf*A sequences of the *U. californica* specimens were identical to reference sequences from California, USA (KM255003; Fig. 2, Table 2). Even though the cluster representing *U. californica* delimits from other clusters it is not clearly separated from the closely related species *U. flexuosa* (70/-).

Ulva torta

Specimens of *U. torta* were collected infrequently from the Baltic Sea and from a single site in the Wadden Sea (Nordstrand) but not from Helgoland. The specimens were usually found drifting in shallow water or disused areas of harbours but also formed mats of entangled thalli in the upper intertidal zone. The delicate, filigree thalli were $35-80 \mu m$ in width and 12-30cm in length. However, the lengths of individuals were difficult to measure since specimens found in entangled mats often lack rhizoidal zones, probably due to rupture, and are sometimes fragmented. The thalli were unbranched and straight, and the cells were arranged in multiple longitudinal rows, $8-27 \times 4-17 \mu m$ in surface view, rectangular to quadratic with rounded corners, and contained singular parietal chloroplasts, mostly averted from the lumen, as well as singular pyrenoids, which were marginal and embedded in the chloroplasts. The young thalli of *U. torta* specimens could be easily distinguished by a central lumen, which was $3-11 \mu m$ in surface view and observed to run through the complete length of the thallus.

Ulva linza

Specimens of *U. linza* were observed at all three main sampling areas and in a broad range of habitats, including both remote and strongly trafficked sites. Specimens grew on a variety of

substrates, including hard substrates (e.g., stones, mussel shells, or artificial structures), but were also observed as epiphytes on other phytobenthic species (e.g., Fucus spp., Gracilaria vermiculophylla, Laminariales, etc.) or on intertidal vegetation (e.g., Phragmites sp.). Even though U. linza specimens were usually observed attached to substrates (especially in harbours with low wave movement or in shallow lagoons) drifting, inflated individuals were also observed. The strongest morphological variation among the investigated samples was encountered for specimens of U. linza, the phenotypes of which varied from unbranched tubes to branched individuals and even included mixed morphologies where the basal part was tubular and the apical thallus parts were sheet-like and distromatic. The tubular thalli could appear ruffled with hollow margins (typical "linza-morphology") or progressively tapering from apical to basal thallus parts, with some specimens only exhibiting branches at the basal thallus region. Besides compressed unbranched individuals also "bottle-brush morphologies" of strongly branched thalli were found (similar to "procera-ahlneriana morphology"). In addition, the overall size of U. linza thalli ranged from 1-8 cm in length and 0.5-1 cm in width in small epiphytes to greater than 160 cm in length and 10 cm in width in specimens found in sheltered bays, calm inlets, and ditches. The cells were arranged in longitudinal and transverse rows throughout, $13-19 \times 13-25 \mu m$ in surface view, and apical cells were mostly quadrangular or rectangular, although sometimes polygonal, whereas cells in the middle thallus section were either rectangular or quadrangular. Cells of the apical and middle thallus sections contain singular (rarely 2) pyrenoids and singular marginal chloroplasts that were not necessarily orientated in same direction in all cells, and the rhizoidal cells also contained singular (less frequently 2) pyrenoids observed. The phylogenetic analysis of U. linza is discussed in the main text.

Ulva prolifera

Specimens of *U. prolifera* were abundant in the intertidal zones of all three main study areas. The specimens were always found attached, never drifting. The thalli were mostly compressed and frequently branched, with both uniseriate and multiseriate branches of varying length. Unbranched individuals were less frequent and sometimes possessed thalli constrictions. Specimens ranged from 1 to 25 cm in length and from 0.5 to 2 cm in width. Even though the stipe-like region was characteristically twisted and "corkscrew-like" in some specimens, other specimens exhibited straight basal regions. Some individuals exhibited a basal part that was slowly tapering and ends in a small (sometimes very reduced) rhizoidal zone. Cells were often paired, rectangular to polygonal, $8-22 \times 8-26 \ \mu m$ in surface view and arranged in distinct longitudinal and transverse rows (rarely short rows). A prominent central pyrenoid (rarely two) and a parietal or cell-filling chloroplast were observed in each cell. Most samples possessed only a few rhizoidal cells, and those cells were similar in both the size and number of pyrenoids to those of the apical and middle thallus regions. Cells with elongated tails, as frequently observed in other species, were nearly absent.

Ulva lactuca

Please see main document.

Ulva intestinalis

Specimens of *U. intestinalis* were abundant in all three main study areas and in a variety of ecosystems, including fully marine, brackish, and freshwater ecosystems and were often observed as epiphytes on perennial seaweeds (e.g., *Fucus* spp.). *U. intestinalis* was a dominant species in overflow basins, rock pools, and water bodies with salinities of <5 PSU and formed dense communities in areas of fresh water inflow to the sea (small streams or

8

drainage ditches). Notably, the texture of thalli collected from areas of low salinity was rigid and inelastic, thereby corresponding to descriptions of var. *crispa* Roth (Greville), which is listed in the species inventory by Schories *et al.* (2009), but differing strongly from the rather soft and fragile texture of *U. intestinalis* specimens at fully marine sites. All the specimens from the study sites were obligately tubular, and the thalli were usually inflated, although sometimes compressed, with tubes that either appeared to be corrugated with ruffled margins, smooth with pale margins, or with multiple constrictions. Meanwhile, the majority of the specimens were unbranched, although several specimens were highly branched and, thus, differed from the unbranched type material. Furthermore, even though the branched specimens were usually found in low salinity environments, they were also observed haphazardly in fully marine habitats.

The thalli ranged from 4 to 35 cm in length in unsheltered or wave-exposed habitats and up to 140 cm in length in sheltered lagoons or overflow basins. Cells of the apical and middle thallus regions were $12-21 \times 14-28$ cm in surface view, rectangular, quadratic, or polygonal, and either arranged in short, longitudinal rows or unordered. The chloroplasts were either parietal and arranged in the same direction in every cell or filled the entire cells. One pyrenoid, often marginal, was observed in each cell. The apical thallus part often ended in a tapered stipe-like section that transitioned into the rhizoidal zone. Cells of the rhizoidal zone were cone-shaped and possessed 1–3 pyrenoids.

Ulva compressa

Specimens of *U. compressa* were abundant at all three main study areas and inhabited a variety of habitats, ranging from sheltered and remote locations to strongly trafficked harbours, drain channels, and overflow basins, and a variety of salinities, ranging from

brackish (9 PSU) to fully marine (32 PSU). The thalli were highly variable in overall morphology. For example, only tubular, mostly branched, and generally attached individuals were observed on Helgoland, whereas only distromatic, sheet-like and generally attached specimens were found along the Baltic coast. Meanwhile, in the Wadden Sea, both morphologies were observed, and sheet-like specimens could be encountered drifting or attached. The different morphotypes were not separated by the phylogenetic analysis of *tuf*A sequences. For further details about the morphology of *U. compressa* see Steinhagen *et al.* (2018a). During the summer (July–August), the species strongly proliferated in sheltered lagoons of the Baltic Sea and formed "green tide-like" states in the Wadden Sea (see also Steinhagen *et al.*, 2018a).

Umbraulva dangeardii

Specimens of *U. dangeardii* were only found on Helgoland at a depth of 8 m, where they grew attached to the solid rock pedestal in communities with other annual and perennial algae. Specimens were conspicuous, owing to their dark olive colour and typical thin, soft texture (Brodie et al. 2007). The *tuf*A sequences of the species were identical to a reference sequences from southern Italy (MF172091; Fig. 2, Table 2).

Percursaria percursa (Morphological data was recorded at one population only)

Specimens of *P. percursa* were only observed at one site in the Baltic Sea (Heiligenhafen), where it grew unattached in dense mats of entangled specimens in the supralittoral zone. The length of single individuals was hard to determine, but single disentangled thalli ranged from 3 to 6 cm in length. Rhizoidal zones were not observed. The thalli were mostly biseriate, with opposing, quadratic cells that were 5–14 μ m in surface view and that contained singular 10

chloroplasts along the interior cell wall and 1–3 pyrenoids. Additional populations should be surveyed in order to assess the species' morphological variation.

Blidingia marginata

Specimens of *B. marginata* were observed at all three main study areas, and the species was observed to grow as dense populations in the upper intertidal and supralittoral zones. Especially in freshwater-influenced microhabitats that were not directly connected to the sea and that fell dry for longer periods (e.g., in the immediate vicinity of beach showers or rain water drainages), specimens of B. marginata and sometimes U. intestinalis were found. Blidingia marginata grew on a variety of substrates, ranging from stones, concrete, and plastic sheathings of pillars to wood and, at some sites, was observed as an epiphyte on beach vegetation, such as on roots of higher plants or on *Phragmites* sp. The species was abundant at remote sites and protected areas as well as in harbours and highly frequented marinas. Specimens were either observed growing as single individuals or in tufts. The thalli were either corrugated, with slightly to strongly ruffled margins, or straight and compressed and varied from thin compressed tubes of no more than 200 μ m in width and 1–3 cm in height to broad, inflated thalli of 0.5-1 cm in width and 5-18 cm in length. Different forms were also observed in the same populations. In addition to the most commonly observed unbranched specimens, individuals with small microscopic branchlets or with macroscopic branches were also observed. The cells were rectangular to polygonal with rounded corners, 3-8 µm in diameter, arranged in distinct longitudinal or sometimes short, curved rows, and possessed both a central, cell-filling chloroplast and a central pyrenoid. Seemingly randomly occurring large round cells (5–9 μ m) were also observed.

Blidingia minima, Blidingia sp. 1 and Blidingia sp. 2

Please see main document

Monostroma grevillei (gametophyte)

This species was abundant in the Baltic Sea and occurred on Helgoland. However, the species was only observed during spring (March-May), and in late spring, drifting mats of M. grevillei frequently developed in sheltered bays, harbours, and lagoons. The thalli were 2-13 cm (rarely >20 cm) in length, monostromatic, and sac-like, lanceolate, or amorphous, and especially in May, individuals began to rupture and appeared deeply cut. The specimens lacked a stipe-region, but the microscopic rhizoidal zone was clearly separated from the basal thallus region. Cell shape and size varied with the respective thallus position. The apical cells were quadrangular to round with rounded corners, $5-20 \times 5-26 \mu m$ in surface view, and arranged in distinct cell rows, often forming tetrads. In addition, each cell contained a single central pyrenoid and a chloroplast that mostly filled the cell. Thickened cell walls were more prominent in cells of the distal thallus regions than in the other regions but were also observed in cells of the middle thallus region. The cells of the mid-region cells were rectangular to quadrangular, sometimes polygonal, with distinct angular corners, and arranged in distinct rows. Each of the cells contained a single pyrenoid (rarely 2) and a cell-filling chloroplast. The basal cells were distinctly angular, elongated into drawn-out rectangles of $5-12 \times 15-32$ (46) µm, and were arranged in small but distinct rows. The rhizoidal cells were club-shaped, restricted to the rhizoidal zone, and directed proximal.

Protomonostroma undulatum

Only *P. undulatum* specimens from Helgoland were genetically validated. These specimens were predominately observed growing on stone but were also found on piers in the lower and middle intertidal zone. The thalli were monostromatic, lobed, and rosette-like or round and ranged from 2 to 18 cm in length and from 4 to 13 cm in width. The cells of the apical and middle thallus parts were angular, polygonal, $6-16 \times 6-24 \mu m$ in surface view and arranged in packs of 2–8 in distinct rows. In some individuals, the cell walls were thickened, similar to those of *K. leptoderma* specimens. The cells also contained 1–3 pyrenoids and a marginal to cell-filling chloroplast. Instead of a smooth transition zone between the basal and rhizoidal cells, abrupt changes in cell shape were observed. Cells of the rhizoidal zone generally ranged from 60 to 90 μm in length, with some individuals reaching 110 μm , extended basally as rhizoids and contained 1–3 pyrenoids.

Kornmannia leptoderma

Please see main document and Weinberger et al., (2018).

2. The nomenclatural history of Gayralia oxysperma

The basionym of *Gayralia oxysperma* is *Ulva oxysperma*, which was described by Kützing (1843) on the basis of material from the Schlei (Winning [Schaalby], Schleswig-Holstein, Germany, site 127 in Fig. 1). Today, this type locality is a freshwater habitat (salinity 1 PSU) that is characterised by extensive stands of *Phalaris arundinacea* and the presence of *Ulva intestinalis* var. *crispa*. Similar environmental conditions certainly existed 150 years ago, since no important geological changes have occurred since then. Kützing characterized the

morphology of U. oxysperma as follows: "U. late expansa, plicato-crispa, foraminibus irregularibus perforata; cellularum interaneis monogonimicis, homogeneis, turgidis, primo globosis, demum in spermatia elongate basi acuminata transeuntibus. Ostsee: Schleybusen bei Winning: Frölich (als Ulva lactuca)" [translation: A wide spread Ulva, being multiply folded, perforated by irregularly appearing holes, cells in rows, of uniform shape, then turgid (probably referring to thickened cell walls), initially round (unclear, perhaps referring to early crust-like thallus stages), then changing into an elongated fertile thallus with a tapering, elongated base. Baltic Sea; Schlei near Winning: Frölich (as Ulva lactuca)]. Two years later, Kützing (1845) synonymized the validly published species U. oxysperma with U. oxycocca Kützing nom. illeg., notably in opposition of taxonomic rules, which require the use of the first legitimate epithet, in this case U. oxysperma. More than one century later, Doty (1947) changed the affiliation to Monostroma oxyspermum, and Bliding (1968) later moved M. oxyspermum to the genus Ulvaria on the basis of its single-row filament, which is similar to representatives of the family Ulvaceae. However, Vinogradova (1968) introduced the nomen novum Gayralia oxysperma and placed the species in a newly introduced family, the Gayraliaceae, within the independent genus Gayralia. As stated by Vinogradova (1969), this taxonomic replacement was widely based on the morphologic observations made by Gayral (1965). Vinogradova (1969) also considered Bliding's transfer of the species to the Ulvaceae as incorrect due to major differences in spore release. Probably because the original type material of Ulva oxysperma was lost, a lectotype that was collected from the coast of Calvados, France, was established (Womersley, 1984). Since the annotations made by Scagel et al. (1989), the species Gayralia oxysperma (Kützing) K.L. Vinogradova ex Scagel Helgoland. is validly established.

3. Seasonal species variation

The species composition of the study sites investigated in the present study was found to vary by season (Supplementary Table S1). During the summer (June–September), representatives of *Ulva sensu lato* were observed at nearly all the study sites and formed conspicuous intertidal or subtidal communities, whereas, during the winter (November–March), only reduced algal growth was observed and, if any, only small remaining pieces or fragments of thallus were found. Maximum vegetation was only observed during the summer (June– August). In early April, the typical spring algal blooms of *Monostroma grevillei* were observed in the Baltic Sea and on Helgoland but not along the mainland coasts of the North Sea. The bloom of monostromatic thalli from this species lasted for 3–4 weeks, and individuals were only recorded until the end of May (Supplementary Table S1), which indicates the brevity of the species' lifecycle.

4. Full collection data

| Table S1: Ulva sensu lato samples collected from northern Germany (Accession No. = GenBank accession |
|-------------------------------------------------------------------------------------------------------|
| number; Voucher = Identification number of voucher specimen; Station map = Numbers used in Figure 1). |

| Acces sion No. | Species | Voucher | Date | Region | Country | Lat | Lon | Stati on map |
|----------------------|---------------------------|---------------|--------------------|---------------|-------------------------------------------------------------------|---------------------|---------------------|--------------------|
| MH53 8542 | Blidingia marginata | S_129 | 30. Jul 2014 | Wadden Sea | Germany: Schleswig-Holstein, Schluettsiel | N 54,6813 333 | E 8,7544 167 | 14 |
| MH53 8543 | Blidingia marginata | S_147_B | 31. Jul 2014 | Wadden Sea | Germany: Schleswig-Holstein, Schobuell | N 54,5078 167 | E 8,9955 667 | 25 |
| MH53 8544 | Blidingia marginata | S_6 61 | 21. Apr 2015 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4707 167 | E 8,8068 333 | 23 |
| MH53 8545 | Blidingia marginata | S_708 | 23. Apr 2015 | Helgoland | Germany: Helgoland | N 54,1780 333 | E 7,8887 167 | 51 |
| MH53 8546 | Blidingia marginata | S_ 474 | 12. Sep 2014 | Wadden Sea | Germany: Schleswig-Holstein, Schluettsiel | N 54,6843 5 | E 8,7538 5 | 13 |
| MH53 8547 | Blidingia marginata | S_737 | 24. Apr 2015 | Helgoland | Germany: Helgoland | N 54,1825 | E 7,8906 167 | 49 |
| MH53 8548 | Blidingia marginata | S_156 | 05. Aug 2014 | Wadden Sea | Germany: Schleswig-Holstein, Woehrden | N 54,1173 167 | E 8,9359 333 | 35 |
| MH53 8549 | Blidingia marginata | S_327 | 25. Aug 2014 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3765 333 | E 10,980 0667 | 103 |
| MH47 5464 | Blidingia marginata | S_147_A | 31. Jul 2014 | Wadden Sea | Germany: Schleswig-Holstein, Pellworm | N 54,4988 2 | E 8,8087 | 21 |
| MH47 5465 | Blidingia marginata | S_577 | 14. Apr 2015 | Wadden Sea | Germany: Schleswig-Holstein, Brunsbuettel estuary | N 53,889 | E 9,1011 33 | 41 |
| MH53 8691 | <i>Blidingia</i> sp. 1 | S_93 | 24. Jul 2014 | Wadden Sea | Germany:Schleswig-Holstein, Aschau | N 54,4608 | E 9,9266 5 | 65 |
| MH53 8692 | <i>Blidingia</i> sp. 1 | S_622 | 16. Apr 2015 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3787 167 | E 10,955 45 | 99 |
| MH53 8693 | <i>Blidingia</i> sp. 1 | S_21 | 23. Jul 2014 | Helgoland | Germany: Helgoland | N 54,1825 | E 7,8906 17 | 49 |
| MH47 5455 | <i>Blidingia</i> sp. 1 | S_828 | 24. Jul 2014 | Wadden Sea | Germany: Schleswig-Holstein, Schobuell | N 54,5078 2 | E 8,9955 67 | 25 |
| MH47 5456 | <i>Blidingia</i> sp. 1 | S_818 | 24. Jul 2017 | Wadden Sea | Germany: Schleswig-Holstein, Husum | N 54,4711 3 | E 9,0279 17 | 26 |
| MH47 5457 | <i>Blidingia</i> sp. 1 | S_815 | 24. Jul 2017 | Wadden Sea | Germany: Schleswig-Holstein, Finkhaushallig | N 54,4155 8 | E 8,9036 33 | 27 |
| MH47 5458 | Blidingia sp. 1 | S_813 | 24. Jul 2017 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8373 5 | E 8,6122 | 6 |

| MH47 5459 | <i>Blidingia</i> sp. 1 | S_179 | 06. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Brunsbuettel estuary | N 53,889 | E 9,1011 33 | 41 |
|--------------|---------------------------|--------------|--------------------|---------------|------------------------------------------------------|---------------------|---------------------|-----|
| MH47 5460 | <i>Blidingia</i> sp. 2 | S_ 34 | 23. Jul 2014 | Helgoland | Germany: Helgoland | N 54,1719 5 | E 7,8993 | 53 |
| MH47 5461 | <i>Blidingia</i> sp. 2 | S_1 | 22. Jul 2014 | Helgoland | Germany: Helgoland | N 54,1836 7 | E 7,8886 33 | 48 |
| MH47 5462 | <i>Blidingia</i> sp. 2 | S_39 | 23. Jul 2014 | Helgoland | Germany: Helgoland | N 54,1825 | E 7,8906 17 | 49 |
| MH47 5463 | <i>Blidingia</i> sp. 2 | S_124 | 30. Jul 2014 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7300 7 | E 8,6891 67 | 11 |
| MH72 0546 | Kornmannia leptoderma | Lin_1 | 08. Jul 2018 | Baltic Sea | Germany:Schleswig-Holstein, Lindaunis | N 54,5852 67 | E 69,8173 833 | 61 |
| MH72 0547 | Kornmannia leptoderma | Lin_2 | 08. Jul 2018 | Baltic Sea | Germany: Schleswig-Holstein, Lindaunis | N 54,5852 667 | E 9,8173 833 | 61 |
| MH72 0545 | Kornmannia leptoderma | Lin_3 | 08. Jul 2018 | Baltic Sea | Germany: Schleswig-Holstein, Lindaunis | N 54,5852 667 | E 9,8173 833 | 61 |
| MH53 8551 | Kornmannia leptoderma | S_204 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiekut | N 54,4476 | E 9,8716 833 | 64 |
| MH53 8552 | Kornmannia leptoderma | S_223 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4369 167 | E 10,173 4667 | 69 |
| MH53 8553 | Kornmannia leptoderma | S_248 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Falckenstein | N 54,3903 667 | E 10,192 2 | 76 |
| MH53 8554 | Kornmannia leptoderma | S_334 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3794 5 | E 10,982 3833 | 101 |
| MH53 8555 | Kornmannia leptoderma | S_337 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3821 31 | E 10,963 75 | 100 |
| MH53 8556 | Kornmannia leptoderma | S_342 | 22. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3758 | E 10,987 4167 | 110 |
| MH53 8557 | Kornmannia leptoderma | S_376 | 27. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Grossenbrode | N 54,3566 167 | E 11,061 0167 | 123 |
| MH53 8558 | Kornmannia leptoderma | S_382 | 27. Sep 14 | Baltic Sea | Germany: Schleswig-Holstein, Wulfen | N 54,4089 167 | E 11,173 1333 | 121 |
| MH53 8559 | Kornmannia leptoderma | S_525 | 17. Sep 14 | Baltic Sea | Germany: Schleswig-Holstein, Grossenbrode | N 54,3581 | E 11,065 5 | 122 |
| MH53 8560 | Kornmannia leptoderma | S_535 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Brodten | N 54,9911 667 | E 10,832 2833 | 127 |
| MH53 8561 | Kornmannia leptoderma | S_698 | 23. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Aschau | N 54,4608 | E 9,9266 5 | 65 |
| MH53 8562 | Kornmannia leptoderma | S_705 | 23. Apr | Helgoland | Germany: Helgoland | N 54,1780 | E 7,8887 | 51 |

| | | | 15 | | | 333 | 167 | |
|--------------|--------------------------|---------------|------------------|---------------|------------------------------------------------|---------------------|---------------------|-----|
| MH53 8563 | Kornmannia leptoderma | S_715 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1771 67 | E 7,8929 44 | 52 |
| MH53 8564 | Kornmannia leptoderma | S_ 716 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1771 67 | E 7,8929 44 | 52 |
| MH47 5466 | Kornmannia leptoderma | S_154 | 05. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Finkhaushallig | N 54,4155 8 | E 8,9036 33 | 27 |
| MH47 5467 | Kornmannia leptoderma | SH_698 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1796 7 | E 7,8895 83 | 50 |
| MH47 5468 | Kornmannia leptoderma | S_337 | 22. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3794 5 | E 10,982 38 | 101 |
| MH53 8580 | Monostroma grevillei | S_529 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Neustadt | N 54,1107 167 | E 10,813 5333 | 126 |
| MH53 8581 | Monostroma grevillei | S_530 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Neustadt | N 54,1107 167 | E 10,813 5333 | 126 |
| MH53 8582 | Monostroma grevillei | S_533 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Neustadt | N 54,1107 167 | E 10,813 5333 | 126 |
| MH53 8583 | Monostroma grevillei | S_537 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Brodten | N 54,9911 667 | E 10,832 2833 | 127 |
| MH53 8584 | Monostroma grevillei | S_5 41 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Grossenbrode | N 54,3566 167 | E 11,061 0167 | 123 |
| MH53 8585 | Monostroma grevillei | S_ 543 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Grossenbrode | N 54,3554 667 | E 11,086 3667 | 124 |
| MH53 8586 | Monostroma grevillei | S_545 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Grossenbrode | N 54,3554 667 | E 11,086 3667 | 124 |
| MH53 8587 | Monostroma grevillei | S_548 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Wulfen | N 54,4089 167 | E 11,173 1333 | 121 |
| MH53 8588 | Monostroma grevillei | S_550 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Wulfen | N 54,4089 167 | E 11,173 1333 | 121 |
| MH53 8589 | Monostroma grevillei | S_554 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Hohwacht | N 54,3181 5 | E 10,680 7333 | 94 |
| MH53 8590 | Monostroma grevillei | S_585 | 15. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Moenkeberg | N 54,3526 667 | E 10,177 9 | 84 |
| MH53 8591 | Monostroma grevillei | S_587 | 15. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Moenkeberg | N 54,3526 667 | E 10,177 9 | 84 |
| MH53 8592 | Monostroma grevillei | S_593 | 15. Apr 15 | Baltic Sea | Germany:Schleswig-Holstein, Aschau | N 54,4608 | E 9,9266 5 | 65 |
| MH53 8593 | Monostroma grevillei | S_599 | 15. Apr 15 | Baltic Sea | Germany:Schleswig-Holstein, Eckernfoerde | N 54,4732 167 | E 9,8330 833 | 63 |
| MH53 | Monostroma | S_604 | 15. | Baltic Sea | Germany:Schleswig-Holstein, | Ν | Е | 56 |

| 8594 | grevillei | | Apr | | Gluecksburg | 54,8367 | 9,5230 | |
|--------------|----------------------------------|---------------|------------------------|---------------|------------------------------------------------------|----------------------|---------------------|-----|
| MH53 8595 | Monostroma grevillei | S_605 | 15 15. Apr 15 | Baltic Sea | Germany:Schleswig-Holstein, Gluecksburg | N 54,8392 04 | E 9,5175 77 | 55 |
| MH53 8596 | Monostroma grevillei | S_616 | 16. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3794 5 | E 10,982 3833 | 101 |
| MH53 8597 | Monostroma grevillei | S_ 614 | 16. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3765 333 | E 10,980 0667 | 103 |
| MH53 8598 | Monostroma grevillei | S_623 | 16. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3759 333 | E 10,979 7333 | 104 |
| MH53 8599 | Monostroma grevillei | S_624 | 16. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3787 167 | E 10,955 45 | 99 |
| MH53 8600 | Monostroma grevillei | S_627 | 16. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3787 167 | E 10,955 45 | 99 |
| MH53 8688 | Monostroma grevillei | FM 6 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1719 5 | E 7,8993 | 53 |
| MH53 8689 | Monostroma grevillei | FM 1 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1796 667 | E 7,8895 833 | 50 |
| MH53 8690 | Monostroma grevillei | FM 5 | 24. Apr 15 | Helgoland | Germany: Helgoland | N 54,1881 667 | E 7,8742 333 | 46 |
| MH47 5469 | Monostroma grevillei | S_548 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Wulfen | N 54,4089 2 | E 11,173 13 | 121 |
| MH47 5470 | Monostroma grevillei | S_617 | 16. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3794 5 | E 10,982 38 | 101 |
| MH47 5500 | Percursaria percursa | S_360 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3794 5 | E 10,982 38 | 101 |
| MH47 5501 | Protomonost roma undulatum | S_ 733 | 24. Apr 15 | Helgoland | Germany: Helgoland | N 54,1825 | E 7,8906 17 | 49 |
| MH53 8642 | Ulva australis | R_9 | 13. Aug 14 | Helgoland | Germany: Helgoland | N 54,1719 5 | E 7,8993 | 53 |
| MH53 8643 | Ulva australis | R_ 10 | 13. Aug 14 | Helgoland | Germany: Helgoland | N 54,1719 5 | E 7,8993 | 53 |
| MH53 8644 | Ulva australis | TD_11 | 24. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Wesselburenerkoog | N 54,2382 3661 | E 8,7856 8942 | 33 |
| MH47 5471 | Ulva australis | TD_10 | 24. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Norderfriedrichskoog | N 54,4136 2 | E 8,8789 22 | 28 |
| MH47 5472 | Ulva australis | TD_34 | 15. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, St. Peter-Ording | N 54,2857 | E 8,7032 04 | 30 |
| MH47 5473 | Ulva australis | TD_36 | 16. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, St. Peter-Ording | N 54,3269 5 | E 8,5850 63 | 29 |

| MH53 8645 | Ulva californica | S_233 | 13. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Schilksee | N 54,4278 | E 10,171 7167 | 73 |
|--------------|---------------------|---------------|-------------------|---------------|--------------------------------------------------------------------------------|---------------------|---------------------|-----|
| MH53 8646 | Ulva californica | TD_67 | 23. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Buesum | N 54,1253 667 | E 8,8730 5 | 34 |
| MH47 5454 | Ulva californica | S_ 791 | 23. Sep 15 | Helgoland | Germany: Helgoland | N 54,1836 7 | E 7,8886 33 | 48 |
| MH47 5450 | Ulva californica | S_106 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7300 7 | E 8,6891 67 | 11 |
| MF97 9360 | Ulva compressa | S_112 | 30. Jul 14 | Wadden Sea | Germany:Schleswig-Holstein, Dagebuell 1 | N 54,7300 67 | E 8,6891 667 | 11 |
| MF97 9645 | Ulva compressa | S_14_B | 22. Jul 14 | Helgoland | Germany:Helgoland | N 54,1881 667 | E 7,8742 333 | 46 |
| MF97 9646 | Ulva compressa | S_29 | 23. Jul 14 | Helgoland | Germany: Helgoland | N 54,1698 167 | E 7,8894 167 | 53 |
| MF97 9647 | Ulva compressa | S_115 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell 1 | N 54,7300 67 | E 8,6891 667 | 11 |
| MF97 9648 | Ulva compressa | S_254 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiel | N 54,3538 | E 10,141 25 | 78 |
| MF97 9649 | Ulva compressa | S_459 | 16. Mar. 16 | Wadden Sea | Germany: Schleswig-Holstein, Emmelsbuell | N 54,7948 667 | E 8,6580 667 | 8 |
| MF97 9650 | Ulva compressa | S_ 305 | 20. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Stein | N 54,4177 5 | E 10,264 5 | 91 |
| MF97 9651 | Ulva compressa | S_672 | 21. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Finkhaushallig | N 54,4155 83 | E 8,9036 3 | 27 |
| MF97 9652 | Ulva compressa | S_514_B | 19. Sep 14 | Baltic Sea | Germany: Schleswig-Holstein, Wullfen | N 54,4089 167 | E 11,173 13 | 121 |
| MF97 9653 | Ulva compressa | S_ 356 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen inland lake | N 54,3787 167 | E 10,955 45 | 99 |
| MF97 9654 | Ulva compressa | S_361 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen natural reserve ´´Graswader´´ | N 54,3792 5 | E 11,005 0167 | 111 |
| MF97 9655 | Ulva compressa | S_ 381 | 27. Sep 14 | Baltic Sea | Germany: Schleswig-Holstein, Wullfen | N 54,4089 167 | E 11,173 13 | 121 |
| MF97 9656 | Ulva compressa | S_383 | 27. Sep 14 | Baltic Sea | Germany: Schleswig-Holstein, Wullfen | N 54,4089 167 | E 11,173 13 | 121 |
| MF97 9657 | Ulva compressa | S_113 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell 1 | N 54,7300 67 | E 8,6891 667 | 11 |
| MF97 9658 | Ulva compressa | S_6 | 22. Jul 14 | Helgoland | Germany: Helgoland | N 54,1698 167 | E 7,8894 167 | 53 |
| MF97 9659 | Ulva compressa | S_563 | 09. Apr | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- | N 54,8333 | E 8,6142 | 7 |

| | | | 15 | | Koog | | | |
|--------------|-------------------|---------------|------------------|---------------|-----------------------------------------------------------------------|---------------------|--------------------|-----|
| MF97 9661 | Ulva compressa | S_79 | 24. Jul 16 | Baltic Sea | Germany: Schleswig-Holstein, Wackerballig | N 54,7586 3 | E 9,8778 3 | 59 |
| MG57 5234 | Ulva compressa | S_107 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell 1 | N 54,7300 67 | E 8,6891 667 | 11 |
| MG57 5235 | Ulva compressa | S_120 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell 1 | N 54,7300 67 | E 8,6891 667 | 11 |
| MG57 5236 | Ulva compressa | S_128_pl u | 31. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Schluettsiel | N 54,6813 | E 8,7544 167 | 14 |
| MG57 5237 | Ulva compressa | S_151 | 31. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Schobuell | N 54,5078 167 | E 8,9955 667 | 25 |
| MG57 5238 | Ulva compressa | S_155 | 05. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Woehrden | N 54,1173 167 | E 8,9359 3 | 35 |
| MG57 5239 | Ulva compressa | S_157 | 05. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Woehrden | N 54,1173 167 | E 8,9359 3 | 35 |
| MG57 5240 | Ulva compressa | S_166 | 05. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Meldorf | N 54,0776 33 | E 8,9681 17 | 38 |
| MG57 5241 | Ulva compressa | S_171_A | 06. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrichskoog-Spitze | N 54,0374 3 | E 8,8448 5 | 39 |
| MG57 5242 | Ulva compressa | S_182 | 11. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8824 83 | E 8,6031 | 4 |
| MG57 5243 | Ulva compressa | S_183 | 11. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8824 83 | E 8,6031 | 4 |
| MG57 5244 | Ulva compressa | S_188 | 12. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Rickelsbuellerkoog, Hindenburgdamm | N 54,8911 3 | E 8,6068 3 | 3 |
| MG57 5245 | Ulva compressa | S_ 443 | 08. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8567 | E 8,6034 3 | 5 |
| MG57 5246 | Ulva compressa | S_447 | 09. Sep 14 | Wadden Sea | Germany:Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MG57 5247 | Ulva compressa | S_ 452 | 09. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MG57 5248 | Ulva compressa | S_468 | 10. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Galmsbuellkoog | N 54,7611 5 | E 8,6967 | 9 |
| MG57 5249 | Ulva compressa | S_473 | 10. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Galmsbuellkoog | N 54,7611 5 | E 8,6967 | 9 |
| MG57 5250 | Ulva compressa | S_506 | 16. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Hamburger Hallig | N 54,5989 83 | E 8,8121 67 | 18 |
| MG57 5251 | Ulva compressa | S_514_C | 18. Sep 14 | Baltic Sea | Germany: Schleswig-Holstein, Wullfen | N 54,4089 167 | E 11,173 13 | 121 |
| MG57 | Ulva | S_631 | 17. | Wadden | Germany: Schleswig-Holstein, | Ν | Е | 11 |

| 5252 | compressa | | Apr | Sea | Dagebuell 1 | 54,7300 | 8,6891 | |
|------|-----------|---------------|-------------|-------------|------------------------------|------------------|--------------|----|
| | | | 15 | | | 67 | 667 | |
| MG57 | Ulva | G (50 | 21. | Wadden | Germany: Schleswig-Holstein, | N | E | |
| 5253 | compressa | S_65 2 | Apr | Sea | Nordstrand | 54,4707 | 8,8068 | 23 |
| | 1 | | 16 | | | 167 | 3 | |
| MG57 | Ulva | 0 710 | 23. | ** 1 1 1 | | N | E | 50 |
| 5254 | compressa | S_/13 | Apr | Helgoland | Germany: Helgoland | 54,1771 | 7,8929 | 52 |
| | 1 | | 15 | | | 56 | 52 | |
| MG57 | Ulva | 0.740 | 01. | Wadden | Germany: Schleswig-Holstein, | N | E 0.0107 | 22 |
| 5255 | compressa | S _/42 | Sep | Sea | Nordstrand | 54,4860 | 8,8185 | 22 |
| | * | | 15 | | | 52 N | /4 | |
| MG57 | Ulva | 0 742 4 | 01. | Wadden | Germany: Schleswig-Holstein, | N | E | 22 |
| 5256 | compressa | 5_745_A | Sep | Sea | Nordstrand | 54,4800 | 8,8185 | 22 |
| | | | 15 | | | JZ N | /4 E | |
| MG57 | Ulva | S 744 | 02. Son | Wadden | Germany: Schleswig-Holstein, | IN 54 4860 | E 0 0105 | 22 |
| 5257 | compressa | 3_/44 | 3ep | Sea | Nordstrand | 52 | 0,010J 74 | 22 |
| | | | 04 | | | JZ N | 74 E | |
| MG57 | Ulva | S 748 A | 04. Sen | Wadden | Germany: Schleswig-Holstein, | 54 4604 | E 8 8445 | 24 |
| 5258 | compressa | 5_740_A | 15 | Sea | Nordstrand | 17 | 67 | 24 |
| | | | 05 | | | N | | |
| MG57 | Ulva | \$ 749 | Sen | Wadden | Germany: Schleswig-Holstein, | 54 4604 | 8 8445 | 24 |
| 5259 | compressa | 5_/4/ | 15 | Sea | Nordstrand | 17 | 67 | 24 |
| | | | 27 | | | N | F | |
| MG57 | Ulva | \$ 803 | Sen | Helgoland | Germany: Helgoland | 54 1881 | 7 8742 | 46 |
| 5260 | compressa | 5_005 | 15 | riengolalia | Germany: Heigenand | 7 | 33 | 10 |
| | | | 17 | | | , N | E | |
| MG57 | Ulva | CL 1 A | Inl | Wadden | Germany: Schleswig-Holstein, | 54 4711 | 9 0279 | 26 |
| 5261 | compressa | CL_1_M | 15 | Sea | Husum | 33 | 17 | 20 |
| | | | 17 | | | N | E | |
| MG57 | Ulva | CL 1 B | Jul | Wadden | Germany: Schleswig-Holstein, | 54.4711 | 9.0279 | 26 |
| 5262 | compressa | | 15 | Sea | Husum | 33 | 17 | |
| MOST | T 71 | | 16. | W/. 11. | | 55 0252 | Е | |
| MG5/ | Ulva | FLS_1_A | Jun | Wadden | Germany: Schleswig-Holstein, | 55.0352 | 8,4001 | 1 |
| 5265 | compressa | | 15 | Sea | Syn | 05 | 6 | |
| MC57 | Illera | | 16. | Waddan | Commony Schloswig Holstoin | 55 0252 | Е | |
| MG57 | Olva | FLS_1_B | Jun | wadden | Germany: Schleswig-Holstein, | 55.0552 05 | 8,4001 | 1 |
| 3204 | compressa | | 15 | Sea | Syn | 05 | 6 | |
| MG57 | Ulha | | 16. | Waddan | Cormany: Schlaswig Holstoin | 55 0352 | Е | |
| 5265 | ormprassa | FLS_2(1) | Jun | Soo | Sult | 05 05 | 8,4001 | 1 |
| 5205 | compressu | | 15 | Sea | Syn | 05 | 6 | |
| MG57 | Ulha | | 16. | Waddan | Cormany: Schlaswig Holstoin | 55 0183 | E | |
| 5266 | compressa | FLS_3(3) | Jun | Sea | Svlt | 2 2 2 2 | 8,4395 | 2 |
| 5200 | compressu | | 15 | Bea | - Syn | 2 | 8 | |
| MG57 | Ulva | | 06. | Wadden | Germany: Schleswig-Holstein | Ν | Е | |
| 5267 | compressa | S_171_B | Aug | Sea | Friedrichskoog-Spitze | 54,0374 | 8,8448 | 39 |
| 5207 | compressa | | 14 | Beu | | 3 | 5 | |
| MG57 | Ulva | | 30. | Wadden | Germany: Schleswig-Holstein. | N | E | |
| 5268 | compressa | S_104 | Jul | Sea | Dagebuell 1 | 54,7300 | 8,6891 | 11 |
| | | | 14 | ~ | | 67 | 667 | |
| MG57 | Ulva | 0.107 | 31. | Wadden | Germany: Schleswig-Holstein. | Ν | Е | 10 |
| 5269 | compressa | S_125 | Jul | Sea | Dagebuell 2 | 54,7304 | 8,6939 | 10 |
| | · | | 14 | | ~ | | | |
| MG57 | Ulva | 0 104 | 31. T | Wadden | Germany: Schleswig-Holstein, | Ν | Е | 10 |
| 5270 | compressa | S_126 | | Sea | Dagebuell 2 | 54,7304 | 8,6939 | 10 |
| | _ | | 14 | | - | NT | E | |
| MG57 | Ulva | C 10 | 22. 1.,1 | Halgaland | Cormony Holesland | IN 5/1 1001 | E 7 0740 | 16 |
| 5271 | compressa | 5_12 | 1 <i>1</i> | rieigoialiu | Germany. nergolanu | 54,1001 67 | 7,0742 | 40 |
| | | l | 14 | | | 07 | 5 | |

| MG57 5272 | Ulva compressa | S_134 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Amsinck Haus | N 54,6153 67 | E 8,8668 83 | 16 |
|--------------|-------------------|---------------|------------------|---------------|--------------------------------------------------------------------------------|---------------------|---------------------|-----|
| MG57 5273 | Ulva compressa | S_135 | 31. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Amsinck Haus | N 54,6153 67 | E 8,8668 83 | 16 |
| MG57 5274 | Ulva compressa | S_137 | 01. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,5166 3 | E 8,8543 67 | 20 |
| MG57 5275 | Ulva compressa | S_ 141 | 02. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Pellworm | N 54,4988 167 | E 8,8087 | 21 |
| MG57 5276 | Ulva compressa | S_ 143 | 02. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Pellworm | N 54,4988 167 | E 8,8087 | 21 |
| MG57 5277 | Ulva compressa | S_144_A | 02. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Pellworm | N 54,4988 167 | E 8,8087 | 21 |
| MG57 5278 | Ulva compressa | S_158 | 05. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Woehrden | N 54,1173 167 | E 8,9359 3 | 35 |
| MG57 5279 | Ulva compressa | S_159 | 05. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Woehrden | N 54,1173 167 | E 8,9359 3 | 35 |
| MG57 5280 | Ulva compressa | S_ 160 | 05. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Woehrden | N 54,1173 167 | E 8,9359 3 | 35 |
| MG57 5281 | Ulva compressa | S_172 | 06. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrichskoog-Spitze | N 54,0374 3 | E 8,8448 5 | 39 |
| MG57 5282 | Ulva compressa | S_174_A | 07. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrichskoog-Spitze | N 54,0374 3 | E 8,8448 5 | 39 |
| MG57 5283 | Ulva compressa | S_174_C | 08. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrichskoog-Spitze | N 54,0374 3 | E 8,8448 5 | 39 |
| MG57 5284 | Ulva compressa | S_177 | 08. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Kaiser-Wilhelm-Koog | N 53,9360 33 | E 8,9052 5 | 40 |
| MG57 5285 | Ulva compressa | S_185 | 11. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Rickelsbuellerkoog, Hindenburgdamm | N 54,8911 3 | E 8,6068 3 | 3 |
| MG57 5286 | Ulva compressa | S_ 190 | 13. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhem-Luebke- Koog | N 54,8373 5 | E 8,6122 | 6 |
| MG57 5287 | Ulva compressa | S_ 192 | 13. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhem-Luebke- Koog | N 54,8373 5 | E 8,6122 | 6 |
| MG57 5288 | Ulva compressa | S_ 193 | 13. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhem-Luebke- Koog | N 54,8373 5 | E 8,6122 | 6 |
| MG57 5289 | Ulva compressa | S_335 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen inland lake | N 54,3794 5 | E 10,982 383 | 101 |
| MG57 5290 | Ulva compressa | S_340 | 22. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen natural reserve ´´Graswader´´ | N 54,3789 83 | E 10,987 2167 | 105 |
| MG57 5291 | Ulva compressa | S_346 | 25. Aug | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen inland lake | N 54,3833 | E 10,950 | 98 |

| | | | 14 | | | 67 | 2167 | |
|--------------|-------------------|---------------|------------------|---------------|--------------------------------------------------------------------------------|---------------------|---------------------|-----|
| MG57 5292 | Ulva compressa | S_348 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen inland lake | N 54,3833 67 | E 10,950 2167 | 98 |
| MG57 5293 | Ulva compressa | S_353 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen inland lake | N 54,3833 67 | E 10,950 2167 | 98 |
| MG57 5294 | Ulva compressa | S_362 | 26. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen natural reserve ´´Graswader´´ | N 54,378 | E 11,008 583 | 112 |
| MG57 5295 | Ulva compressa | S_368 | 26. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen inland lake | N 54,1825 | E 7,8906 167 | 49 |
| MG57 5296 | Ulva compressa | S_37_plus | 23. Jul 14 | Helgoland | Germany: Helgoland | N 54,1825 | E 7,8906 167 | 49 |
| MG57 5297 | Ulva compressa | S_4_plus | 22. Jul 14 | Helgoland | Germany: Helgoland | N 54,1698 167 | E 7,8894 167 | 53 |
| MG57 5298 | Ulva compressa | S_450 | 25. Aug 17 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MG57 5299 | Ulva compressa | S_478 | 12. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Schluettsiel | N 54,6843 5 | E 8,7538 5 | 13 |
| MG57 5300 | Ulva compressa | S_507 | 16. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Hamburger Hallig | N 54,5989 83 | E 8,8121 67 | 18 |
| MG57 5301 | Ulva compressa | S_511 | 17. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Hamburger Hallig | N 54,5989 83 | E 8,8122 | 18 |
| MG57 5302 | Ulva compressa | S_512 | 18. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Hamburger Hallig | N 54,5989 83 | E 8,8122 | 18 |
| MG57 5303 | Ulva compressa | S_ 513 | 19. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Hamburger Hallig | N 54,5989 83 | E 8,8122 | 18 |
| MG57 5304 | Ulva compressa | S_549 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Wullfen | N 54,4089 167 | E 11,173 13 | 121 |
| MG57 5305 | Ulva compressa | S_651 | 21. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4707 167 | E 8,8068 3 | 23 |
| MG57 5306 | Ulva compressa | S_540 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Großenbrode | N 54,3930 3 | E 11,110 2 | 114 |
| MG57 5307 | Ulva compressa | S_626 | 16. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen inland lake | N 54,3787 167 | E 10,955 45 | 99 |
| MG57 5308 | Ulva compressa | S_670 | 21. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Finkhaushallig | N 54,4155 83 | E 8,9036 3 | 27 |
| MG57 5309 | Ulva compressa | S_ 707 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1780 333 | E 7,8887 167 | 51 |
| MG57 5310 | Ulva compressa | S_739_A | 31. Aug 15 | Baltic Sea | Germany: Schleswig-Holstein, Wullfen | N 54,4089 167 | E 11,173 13 | 121 |
| MG57 | Ulva | S_741 | 31. | Baltic Sea | Germany: Schleswig-Holstein, | Ν | Е | 121 |

| 5311 | compressa | | Aug | | Wullfen | 54,4089 | 11,173 | |
|--------------|-------------------|---------------|------------------------|---------------|-------------------------------------------------------------------|---------------------------|--------------------|-----|
| MG57 5312 | Ulva compressa | S_740 | 15 31. Aug 15 | Baltic Sea | Germany: Schleswig-Holstein, Wullfen | N 54,4089 167 | E 11,173 13 | 121 |
| MG57 5313 | Ulva compressa | S_743_B | 01. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4860 52 | E 8,8185 74 | 22 |
| MG57 5314 | Ulva compressa | S_743_C | 01. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4860 52 | E 8,8185 74 | 22 |
| MG57 5315 | Ulva compressa | S_745 | 02. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4860 52 | E 8,8185 74 | 22 |
| MG57 5316 | Ulva compressa | S_746 | 03. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4860 52 | E 8,8185 74 | 22 |
| MG57 5317 | Ulva compressa | S_752 | 06. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4604 167 | E 8,8445 67 | 24 |
| MG57 5318 | Ulva compressa | S_754 | 07. Sep 15 | Wadden Sea | Germany:Schleswig-Holstein, Nordstrand | N 54,4604 167 | E 8,8445 67 | 24 |
| MG57 5319 | Ulva compressa | S_756_A | 08. Sep 15 | Wadden Sea | Germany:Schleswig-Holstein, Nordstrand | N 54,4604 167 | E 8,8445 67 | 24 |
| MG57 5320 | Ulva compressa | S_756_B | 09. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4604 167 | E 8,8445 67 | 24 |
| MG57 5321 | Ulva compressa | S_760_A | 16. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8824 83 | E 8,6031 | 4 |
| MG57 5322 | Ulva compressa | S_77 0 | 17. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell 1 | N 54,7300 67 | E 8,6891 667 | 11 |
| MG57 5323 | Ulva compressa | S_ 771 | 18. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell 1 | N 54,7300 67 | E 8,6891 667 | 11 |
| MG57 5324 | Ulva compressa | S_778 | 19. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell 1 | N 54,7300 67 | E 8,6891 667 | 11 |
| MG57 5325 | Ulva compressa | S_779 | 20. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell 1 | N 54,7300 67 | E 8,6891 667 | 11 |
| MG57 5326 | Ulva compressa | S_780A | 09. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4604 167 | E 8,8445 67 | 24 |
| MG57 5327 | Ulva compressa | S_782 | 10. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4604 167 | E 8,8445 67 | 24 |
| MG57 5328 | Ulva compressa | S_788 | 23. Sep 15 | Helgoland | Germany: Helgoland | N 54,1836 <u>67</u> | E 7,8886 39 | 49 |
| MG57 5329 | Ulva compressa | S_790 | 24. Sep 15 | Helgoland | Germany: Helgoland | N 54,7586 3 | E 9,8778 3 | 59 |
| MG57 5330 | Ulva compressa | S_795 | 25. Sep 15 | Helgoland | Germany: Helgoland | N 54,1836 67 | E 7,8886 39 | 48 |

| MG57 5331 | Ulva compressa | S_797 | 26. Sep 15 | Helgoland | Germany: Helgoland | N 54,1780 3 | E 7,8887 167 | 51 |
|--------------|-------------------|---------------|---------------------|---------------|-------------------------------------------------------------------------------|---------------------|---------------------|-----|
| MG57 5332 | Ulva compressa | S_747 | 01. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4860 52 | E 8,8185 74 | 22 |
| MG57 5333 | Ulva compressa | S_805 | 27. Sep 15 | Helgoland | Germany: Helgoland | N 54,1881 7 | E 7,8742 33 | 46 |
| MG57 5334 | Ulva compressa | S_799 | 28. Sep 15 | Helgoland | Germany: Helgoland | N 54,1780 3 | E 7,8887 167 | 51 |
| MG57 5335 | Ulva compressa | S_146_B | 31. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Schobuell | N 54,5078 167 | E 8,9955 67 | 25 |
| MG57 5336 | Ulva compressa | S_454 | 09. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MG57 5337 | Ulva compressa | S_ 479 | 12. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Schluettsiel | N 54,6843 5 | E 8,7538 5 | 13 |
| MG57 5338 | Ulva compressa | S_1003 | 16. Mar. 16 | Wadden Sea | Germany: Schleswig-Holstein, Emmelsbuell | N 54,7948 667 | E 8,6580 667 | 8 |
| MG57 5340 | Ulva compressa | S_1001 | 05. Jul 16 | Baltic Sea | Germany: Schleswig-Holstein, Wulfen | N 54,4089 167 | E 11,173 1333 | 121 |
| MG57 5341 | Ulva compressa | S_1000 | 17- Mar- 2016 | Wadden Sea | Germany: Schleswig-Holstein, Emmelsbuell | N 54,7948 667 | E 8,6580 667 | 8 |
| MG57 5342 | Ulva compressa | S_441 | 08. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8567 | E 8,6034 333 | 5 |
| MG57 5339 | Ulva compressa | S_1002 | 16. Nov 15 | Baltic Sea | Germany: Schleswig-Holstein, Moenkeberg | N 54,3526 667 | E 10,177 9 | 84 |
| MH47 5451 | Ulva flexuosa | S_257 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiel | N 54,3538 | E 10,141 25 | 78 |
| MH47 5452 | Ulva flexuosa | S_769 | 16. Aug 15 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7300 7 | E 8,6891 67 | 11 |
| MH47 5453 | Ulva flexuosa | S_794 | 23. Sep 15 | Helgoland | Germany: Helgoland | N 54,1780 3 | E 7,8887 17 | 51 |
| MH53 8550 | Ulva gigantea | S_102 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7300 667 | E 8,6891 667 | 11 |
| MH53 8696 | Ulva gigantea | S_87_A | 24. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Eckernfoerde | N 54,4732 167 | E 9,8330 833 | 63 |
| MH47 5474 | Ulva gigantea | S_775 | 16. Aug 15 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7304 | E 8,6939 | 10 |
| MH47 5475 | Ulva gigantea | S_564 | 09. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog, Rhymschlot | N 54,8333 | E 8,6142 | 7 |
| MH47 5476 | Ulva gigantea | S_632 | 17. Apr | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7300 | E 8,6891 | 11 |

| | | | 15 | | | 7 | 67 | |
|--------------|----------------------|---------------|------------------|---------------|------------------------------------------------------|---------------------|------------------------------|-----|
| MH53 8514 | Ulva intestinalis | S_200 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiekut | N 54,4476 | E 9,8716 833 | 64 |
| MH53 8515 | Ulva intestinalis | S_38_A | 23. Jul 14 | Helgoland | Germany: Helgoland | N 54,1825 | E 7,8906 167 | 49 |
| MH53 8516 | Ulva intestinalis | S_294 | 19. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Laboe | N 54,3972 5 | E 10,212 6333 | 88 |
| MH53 8517 | Ulva intestinalis | S_195 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Falshoeft | N 54,7684 5 | E 9,9653 333 | 60 |
| MH53 8518 | Ulva intestinalis | S_ 94 | 24. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Aschau | N 54,4608 | E 9,9266 5 | 65 |
| MH53 8519 | Ulva intestinalis | S_95 | 24. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Aschau | N 54,4608 | E 9,9266 5 | 65 |
| MH53 8520 | Ulva intestinalis | S_569 | 14. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Brokdorf | N 53,8611 667 | E 9,3231 333 | 44 |
| MH53 8521 | Ulva intestinalis | S_642 | 21. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Schobuell | N 54,5078 167 | E 8,9955 667 | 25 |
| MH53 8522 | Ulva intestinalis | S_ 181 | 06. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Brunsbuettel estuary | N 53,889 | E 9,1011 333 | 41 |
| MH53 8523 | Ulva intestinalis | S_ 191 | 11. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Neukirchen | N 54,8018 333 | E 9,7554 833 | 58 |
| MH53 8524 | Ulva intestinalis | S_214 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4442 | E 10,181 25 | 67 |
| MH53 8525 | Ulva intestinalis | S_251 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiel-Wik | N 54,3662 | E 10,148 8333 | 77 |
| MH53 8526 | Ulva intestinalis | S_271 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Moenkeberg | N 54,3464 667 | E 10,174 2 | 82 |
| MH53 8527 | Ulva intestinalis | S_303_B | 20. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Stein | N 54,4177 5 | E 10,264 5 | 91 |
| MH53 8528 | Ulva intestinalis | S_ 307 | 20. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Marina Wendtorf | N 54,4205 5 | E 10,289 9 | 92 |
| MH53 8529 | Ulva intestinalis | S_ 316 | 22. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Hohwacht | N 54,3181 5 | E 10,680 7333 | 94 |
| MH53 8530 | Ulva intestinalis | S_322 | 22. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3759 333 | E 10,979 7 <u>33</u> 3 | 104 |
| MH53 8531 | Ulva intestinalis | S_325 | 22. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3759 333 | E 10,979 7333 | 104 |
| MH53 8532 | Ulva intestinalis | S_343 | 22. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3783 167 | E 10,991 25 | 107 |
| MH53 | Ulva | S_359 | 25. | Baltic Sea | Germany: Schleswig-Holstein, | Ν | Е | 107 |

| 8533 | intestinalis | | Aug | | Heiligenhafen | 54,3783 | 10,991 | |
|--------------|--------------|--------------|-------------|------------|------------------------------|---------------|----------------|-----|
| | | | 14 | | | 167 | 25 | |
| MH53 | Ulva | 0 201 | 27. | Dali's Gas | Germany: Schleswig-Holstein, | N | E | 101 |
| 8534 | intestinalis | S_381 | Sep | Baltic Sea | Wulfen | 54,4089 | 11,1/3 | 121 |
| | | | 14 | | | 107 | 1555 E | |
| MH53 | Ulva | S 415 | 02. Son | Poltio Soo | Germany: Schleswig-Holstein, | Ν | E 10.004 | 109 |
| 8535 | intestinalis | 5_415 | 3ep | Dallie Sea | Heiligenhafen | 54,3773 | 10,994 8667 | 108 |
| | | | 14 | | | N | 0007 E | |
| MH53 | Ulva | S 126 | 05. Som | Doltio See | Germany: Schleswig-Holstein, | IN 54 1027 | E 11.070 | 105 |
| 8536 | intestinalis | 5_420 | 3ep | Dallie Sea | Kellenhusen | 54,1927 | 11,070 8167 | 123 |
| | | | 14 | | | J | 8107 E | |
| MH53 | Ulva | S 420 | 05. Som | Doltio See | Germany: Schleswig-Holstein, | IN 54 1107 | E 10.912 | 126 |
| 8537 | intestinalis | 3_430 | 3ep | Dallie Sea | Neustadt | 167 | 5222 | 120 |
| | | | 14 | | | 107 N | - 3333 E | |
| MH53 | Ulva | S 520 | 08. Apr | Poltio Soo | Germany: Schleswig-Holstein, | IN 54 2566 | E 11.061 | 122 |
| 8538 | intestinalis | 5_339 | 15 | Dallie Sea | Grossenbrode | 167 | 0167 | 123 |
| | | | 15 | | | 107 N | 0107 E | |
| MH53 | Ulva | \$ 607 | Δpr | Baltic Sea | Germany: Schleswig-Holstein, | 5/ 8367 | 0 5230 | 56 |
| 8539 | intestinalis | 5_007 | 15 | Danie Sea | Gluecksburg | 5 | 333 | 50 |
| | | | 21 | | | N | 555 F | |
| MH53 | Ulva | S 662 | Δnr | Wadden | Germany: Schleswig-Holstein, | 5/ /155 | 8 9036 | 27 |
| 8540 | intestinalis | 5_002 | 15 | Sea | Finkhaushallig | 833 | 333 | 27 |
| | | | 23 | | | N | F | |
| MH53 | Ulva | S 700 | Apr | Helgoland | Germany: Helgoland | 54 1796 | 7 8895 | 50 |
| 8541 | intestinalis | 5_700 | 15 | Theigoland | Germany: Heigoland | 667 | 833 | 50 |
| | | | 24 | | | 007 | F | |
| MH47 | Ulva | S 72 | 24. Jul | Baltic Sea | Germany: Schleswig-Holstein, | Ν | 9 5175 | 55 |
| 5477 | intestinalis | 5_72 | 14 | Danie Sea | Gluecksburg | 54,8392 | 77 | 55 |
| | | | 31 | | | N | E | |
| MH47 | Ulva | S 133 | Jul | Wadden | Germany: Schleswig-Holstein, | 54.6843 | 8.7538 | 13 |
| 5478 | intestinalis | | 14 | Sea | Schluettsiel | 5 | 5 | _ |
| 10150 | | | 22. | | | N | Е | |
| MH53 | Ulva lactuca | S 5 | Jul | Helgoland | Germany: Helgoland | 54,1836 | 7,8886 | 48 |
| 8565 | | — | 14 | U | , , | 67 | 33 | |
| 10150 | | | 22. | | | Ν | Е | |
| MH53 | Ulva lactuca | S_10 | Jul | Helgoland | Germany: Helgoland | 54,1881 | 7,8800 | 47 |
| 8366 | | | 14 | C | | 72 | 24 | |
| MILES | | | 22. | | | Ν | Е | |
| NH55 9567 | Ulva lactuca | S_11 | Jul | Helgoland | Germany: Helgoland | 54,1881 | 7,8742 | 46 |
| 8307 | | | 14 | | | 667 | 333 | |
| MU52 | | | 22. | | | Ν | Е | |
| 8568 | Ulva lactuca | S_20 | Jul | Helgoland | Germany: Helgoland | 54,1836 | 7,8886 | 48 |
| 0500 | | | 14 | | | 67 | 33 | |
| MH53 | | | 23. | | | Ν | Е | |
| 8569 | Ulva lactuca | S_673 | Apr | Helgoland | Germany: Helgoland | 54,1881 | 7,8800 | 47 |
| 0507 | | | 15 | | | 72 | 24 | |
| MH53 | | | 23. | | | Ν | E | |
| 8570 | Ulva lactuca | S_678 | Apr | Helgoland | Germany: Helgoland | 54,1881 | 7,8800 | 47 |
| 0070 | | | 15 | | | 72 | 24 | |
| MH53 | | | 23. | | | N | E | |
| 8571 | Ulva lactuca | S_679 | Apr | Helgoland | Germany: Helgoland | 54,1881 | 7,8742 | 46 |
| - | | | 15 | | | 667 | 333 | |
| MH53 | | a | 23. | | | N | E | |
| 8572 | Ulva lactuca | S_681 | Apr | Helgoland | Germany: Helgoland | 54,1881 | 7,8742 | 46 |
| | | | 15 | | | 667 | 333 | |
| MH53 | T 71 T | 0 | 23. | TT 1 1 - | | N | E | 50 |
| 8573 | Ulva lactuca | S_696 | Apr | Heigoland | Germany: Helgoland | 54,1796 | /,8895 | 50 |
| | | | 15 | | | 00/ | 833 | |

| MH53 8574 | Ulva lactuca | S_72 1 | 24. Apr 15 | Helgoland | Germany: Helgoland | N 54,1881 667 | E 7,8742 333 | 46 |
|--------------|--------------|---------------|------------------|---------------|-------------------------------------------------------------------|---------------------|--------------------|----|
| MH53 8575 | Ulva lactuca | S_725 | 24. Apr 15 | Helgoland | Germany: Helgoland | N 54,1881 667 | E 7,8742 333 | 46 |
| MH53 8576 | Ulva lactuca | S_728 | 24. Apr 15 | Helgoland | Germany: Helgoland | N 54,1881 667 | E 7,8742 333 | 46 |
| MH53 8577 | Ulva lactuca | S_729 | 24. Apr 15 | Helgoland | Germany: Helgoland | N 54,1825 | E 7,8906 167 | 49 |
| MH53 8578 | Ulva lactuca | S_734 | 24. Apr 15 | Helgoland | Germany: Helgoland | N 54,1825 | E 7,8906 167 | 49 |
| MH53 8579 | Ulva lactuca | S_735 | 24. Apr 15 | Helgoland | Germany: Helgoland | N 54,1796 667 | E 7,8895 833 | 50 |
| MH47 5479 | Ulva lactuca | S_729 | 24. Apr 15 | Helgoland | Germany: Helgoland | N 54,1881 7 | E 7,8800 24 | 47 |
| MH47 5480 | Ulva lactuca | S_696 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1796 7 | E 7,8895 83 | 50 |
| MH53 8647 | Ulva linza 1 | S_6 3 | 24. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Gluecksburg | N 54,8367 5 | E 9,5230 333 | 56 |
| MH53 8648 | Ulva linza 1 | S_64 | 24. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Gluecksburg | N 54,8367 5 | E 9,5230 333 | 56 |
| MH53 8649 | Ulva linza 1 | S_65 | 24. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Gluecksburg | N 54,8367 5 | E 9,5230 333 | 56 |
| MH53 8650 | Ulva linza 1 | S_132 | 30. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Schluettsiel | N 54,6813 333 | E 8,7544 167 | 14 |
| MH53 8651 | Ulva linza 1 | S_192 | 12. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8373 5 | E 8,6122 | 6 |
| MH53 8652 | Ulva linza 1 | S_197_B | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Schoenhagen | N 54,6361 167 | E 10,031 25 | 62 |
| MH53 8653 | Ulva linza 1 | S_198 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Schoenhagen | N 54,6361 167 | E 10,031 25 | 62 |
| MH53 8654 | Ulva linza 1 | S_199 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Schoenhagen | N 54,6361 167 | E 10,031 25 | 62 |
| MH53 8655 | Ulva linza 1 | S_201 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiekut | N 54,4476 | E 9,8716 833 | 64 |
| MH53 8656 | Ulva linza 1 | S_203 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiekut | N 54,4476 | E 9,8716 833 | 64 |
| MH53 8657 | Ulva linza 1 | S_206 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiekut | N 54,4476 | E 9,8716 833 | 64 |
| MH53 8658 | Ulva linza 1 | S_207 | 12. Aug | Baltic Sea | Germany: Schleswig-Holstein, Kiekut | N 54,4476 | E 9,8716 | 64 |

| | | | 14 | | | | 833 | |
|--------------|--------------|-------|------------------|------------|----------------------------------------------|---------------------|---------------------|----|
| MH53 8659 | Ulva linza 1 | S_209 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4442 | E 10,181 25 | 67 |
| MH53 8660 | Ulva linza 1 | S_211 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4442 | E 10,181 25 | 67 |
| MH53 8661 | Ulva linza 1 | S_212 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4362 333 | E 10,175 0167 | 70 |
| MH53 8662 | Ulva linza 1 | S_217 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4362 333 | E 10,175 0167 | 70 |
| MH53 8663 | Ulva linza 1 | S_220 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4362 333 | E 10,175 0167 | 70 |
| MH53 8664 | Ulva linza 1 | S_222 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4362 333 | E 10,175 0167 | 70 |
| MH53 8665 | Ulva linza 1 | S_224 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4369 167 | E 10,173 4667 | 69 |
| MH53 8666 | Ulva linza 1 | S_226 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4349 833 | E 10,170 15 | 71 |
| MH53 8667 | Ulva linza 1 | S_229 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4349 833 | E 10,170 15 | 71 |
| MH53 8668 | Ulva linza 1 | S_237 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Falckenstein | N 54,3903 667 | E 10,192 2 | 76 |
| MH53 8669 | Ulva linza 1 | S_240 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Falckenstein | N 54,3990 39 | E 10,190 814 | 75 |
| MH53 8670 | Ulva linza 1 | S_243 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Falckenstein | N 54,3990 39 | E 10,190 814 | 75 |
| MH53 8671 | Ulva linza 1 | S_250 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiel-Wik | N 54,3662 | E 10,148 8333 | 77 |
| MH53 8672 | Ulva linza 1 | S_255 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiel | N 54,3538 | E 10,141 25 | 78 |
| MH53 8673 | Ulva linza 1 | S_260 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiel-Wik | N 54,3514 667 | E 10,143 2 | 79 |
| MH53 8674 | Ulva linza 1 | S_262 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiel | N 54,3478 833 | E 10,150 3 | 80 |
| MH53 8675 | Ulva linza 1 | S_267 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiel | N 54,3463 5 | E 10,152 6333 | 81 |
| MH53 8676 | Ulva linza 1 | S_279 | 19. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heikendorf | N 54,3766 833 | E 10,195 8667 | 85 |
| MH53 8677 | Ulva linza 1 | S_284 | 19. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heikendorf | N 54,3827 | E 10,202 5833 | 86 |
| MH53 | Ulva linza 1 | S_288 | 19. | Baltic Sea | Germany: Schleswig-Holstein, | Ν | Е | 87 |

| 8678 | | | Aug | | Heikendorf | 54,3828 | 10,202 | |
|--------------|-------------------|---------------------|------------|---------------|----------------------------------------------|----------------|----------------|-----|
| МН53 | | | 14 | | Germany: Schleswig-Holstein | N | в В | |
| 8679 | Ulva linza 1 | S_290 | Aug 14 | Baltic Sea | Laboe | 54,4035 333 | 10,215 9167 | 89 |
| MH53 | Ulva linza 1 | S 301 | 20. | Baltic Sea | Germany: Schleswig-Holstein, | N 54 4177 | E 10.264 | 01 |
| 8680 | | 3_301 | 14 | Danie Sea | Stein | 5 | 5 | 91 |
| MH53 8681 | Ulva linza 1 | S_ 314 | 22. Aug | Baltic Sea | Germany: Schleswig-Holstein, Hohwacht | N 54,3181 | E 10,680 | 94 |
| M1152 | | | 14 22. | | Company Schlagwig Halstein | 5 N | 7333 E | |
| 8682 | Ulva linza 1 | S_341 | Aug 14 | Baltic Sea | Heiligenhafen | 54,3783 833 | 10,987 9667 | 106 |
| MH53 | Ulva linza 1 | S 364 | 26. | Baltic Sea | Germany: Schleswig-Holstein, | N 54 3792 | E 11.005 | 111 |
| 8683 | | 5_504 | 14 | Danie Sea | Heiligenhafen | 5 | 0167 | 111 |
| MH53 | Ulva linza 1 | S_39 0 | 01. Sep | Baltic Sea | Germany: Schleswig-Holstein, | N 54,3783 | Е 10,987 | 106 |
| 000- | | | 14 18. | | | 833 N | 9667 E | |
| MH47 5447 | Ulva linza 1 | S_241_U. linza 1 | Aug | Helgoland | Germany: Schleswig-Holstein, Falckenstein | 54,3903 7 | 10,192 | 76 |
| MH47 | X XI I: 1 | S 504 U. | 16. | | Germany: Schleswig-Holstein, | N | E | 10 |
| 5448 | Ulva linza 1 | linza_1 | Sep 14 | Baltic Sea | Hamburger Hallig | 54,5989 8 | 8,8122 | 18 |
| MH47 | Ulva linza 1 | S_64_U.li | 24. Jul | Wadden | Germany: Schleswig-Holstein, | N54,83 | E 9,5175 | 55 |
| 5449 | | nza_1 | 14 | Sea | Gluecksburg | 92 N | 77 E | |
| MH53 8685 | Ulva linza 2 | S_726 | Apr | Helgoland | Germany: Helgoland | 54,1780 | E 7,8887 | 51 |
| МН53 | | | 15 22. | | | 333 N | 167 E | |
| 8686 | Ulva linza 2 | S_12 | Jul 14 | Helgoland | Germany: Helgoland | 54,1881 667 | 7,8742 333 | 46 |
| MH53 | Ulwa linza ? | S 710 | 24. | Helgoland | Germany: Helgoland | N 54 1881 | E 7 8742 | 46 |
| 8687 | 0110 111120 2 | 5_/19 | 15 | Theigotand | Germany. Heigoland | 667 | 333 | 40 |
| MH47 | Ulva linza 2 | S_727_U. | 24. Apr | Helgoland | Germany: Helgoland | N 54,1771 | E 7,8929 | 52 |
| 5445 | | IIIIZa_2 | 15 22 | | | 7 N | 44 E | |
| MH47 5446 | Ulva linza 2 | S_8_U.lin za_2 | Jul | Helgoland | Germany: Helgoland | 54,1881 | 7,8742 | 46 |
| МН53 | Ulwa | | 14 22. | | | / N | 55 E | |
| 8601 | prolifera | S_9 | Jul 14 | Helgoland | Germany: Helgoland | 54,1881 72 | 7,8800 24 | 47 |
| MH53 | Ulva | S 78 | 24. Jul | Baltic Sea | Germany: Schleswig-Holstein, | N 54 7586 | E 9 8778 | 59 |
| 8602 | prolifera | 5_76 | 14 | Danie Sea | Wackerballig | 333 | 333 | 39 |
| MH53 | Ulva | S_ 114 | 30. Jul | Wadden | Germany: Schleswig-Holstein, | N 54,7300 | E 8,6891 | 11 |
| 0003 | proujera | | 14 31 | Sea | Dageouell | 667 N | 667 F | |
| MH53 8604 | Ulva prolifera | S_136 | Jul | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | 54,5166 | 8,8543 | 20 |
| MU52 | I II | | 14 31. | Woddon | Cormony Sobleswig Helstein | 333 N | 667 E | |
| 8605 | prolifera | S_139 | Jul 14 | Sea | Nordstrand | 54,5166 333 | 8,8543 667 | 20 |

| MH53 8606 | Ulva prolifera | S_142 | 31. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Pellworm | N 54,4988 167 | E 8,8087 | 21 |
|--------------|-------------------|---------------|------------------|---------------|-------------------------------------------------------------------|---------------------|---------------------|-----|
| MH53 8607 | Ulva prolifera | S_168_A | 05. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Meldorf | N 54,0776 333 | E 8,9681 167 | 38 |
| MH53 8608 | Ulva prolifera | S_196 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Falshoeft | N 54,7684 5 | E 9,9653 333 | 60 |
| MH53 8609 | Ulva prolifera | S_358 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3787 167 | E 10,955 45 | 99 |
| MH53 8610 | Ulva prolifera | S_424_B | 02. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Burg | N 54,4146 333 | E 11,211 45 | 119 |
| MH53 8611 | Ulva prolifera | S_440 | 08. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8567 | E 8,6034 333 | 5 |
| MH53 8612 | Ulva prolifera | S_444 | 08. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MH53 8613 | Ulva prolifera | S_446 | 08. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MH53 8614 | Ulva prolifera | S_461 | 10. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Emmelsbuell | N 54,7948 667 | E 8,6580 667 | 8 |
| MH53 8615 | Ulva prolifera | S_464 | 10. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Emmelsbuell | N 54,7948 667 | E 8,6580 667 | 8 |
| MH53 8616 | Ulva prolifera | S_466 | 10. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Emmelsbuell | N 54,7948 667 | E 8,6580 667 | 8 |
| MH53 8617 | Ulva prolifera | S_ 470 | 10. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Galmsbuellkoog | N 54,7611 5 | E 8,6967 | 9 |
| MH53 8618 | Ulva prolifera | S_488 | 12. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Großengaarde | N 54,6636 833 | E 8,7909 667 | 15 |
| MH53 8619 | Ulva prolifera | S_508 | 16. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Hamburger Hallig | N 54,5989 833 | E 8,8121 667 | 18 |
| MH53 8620 | Ulva prolifera | S_509 | 16. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Hamburger Hallig | N 54,5989 833 | E 8,8121 667 | 18 |
| MH53 8621 | Ulva prolifera | S_532 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Neustadt | N 54,1107 167 | E 10,813 5333 | 126 |
| MH53 8622 | Ulva prolifera | S_532_B | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Neustadt | N 54,1107 167 | E 10,813 5333 | 126 |
| MH53 8623 | Ulva prolifera | S_537_A | 08. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Brodten | N 54,9911 667 | E 10,832 2833 | 127 |
| MH53 8624 | Ulva prolifera | S_546 | 08. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Wulfen | N 54,4089 167 | E 11,173 1333 | 121 |
| MH53 8625 | Ulva prolifera | \$_552 | 08. Apr | Baltic Sea | Germany: Schleswig-Holstein, Hohwacht | N 54,3181 | E 10,680 | 94 |

| | | | 15 | | | 5 | 7333 | |
|--------------|-------------------|---------------|------------------|---------------|-------------------------------------------------------------------|----------------------|----------------------|-----|
| MH53 8626 | Ulva prolifera | S_555 | 09. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MH53 8627 | Ulva prolifera | S_619 | 16. Apr 15 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3794 5 | E 10,982 3833 | 101 |
| MH53 8628 | Ulva prolifera | S_639 | 17. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Schluettsiel | N 54,6843 5 | E 8,7538 5 | 13 |
| MH53 8629 | Ulva prolifera | S_680 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1881 72 | E 7,8800 24 | 47 |
| MH53 8630 | Ulva prolifera | S_ 709 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1719 5 | E 7,8993 | 53 |
| MH53 8631 | Ulva prolifera | TD_43 | 18. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, St. Peter Ording | N 54,2857 0206 | E 8,7032 04001 | 30 |
| MH53 8632 | Ulva prolifera | TD_65 | 23. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Grothusenkoog | N 54,2885 8739 | E 8,7368 4072 | 31 |
| MH47 5481 | Ulva prolifera | S_196 | 12. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Falshoeft | N 54,7684 5 | E 9,9653 33 | 60 |
| MH47 5482 | Ulva prolifera | S_9 | 22. Jul 14 | Helgoland | Germany: Helgoland | N 54,1881 7 | E 7,8742 33 | 46 |
| MH47 5483 | Ulva prolifera | S_466 | 10. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Emmelsbuell | N 54,7948 7 | E 8,6580 67 | 8 |
| MH53 8633 | Ulva rigida | R_13 | 13. Aug 14 | Helgoland | Germany: Helgoland | N 54,1719 5 | E 7,8993 | 53 |
| MH53 8634 | Ulva rigida | S_116 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7300 667 | E 8,6891 667 | 11 |
| MH53 8635 | Ulva rigida | S_121 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7300 667 | E 8,6891 667 | 11 |
| MH53 8636 | Ulva rigida | S_189 | 11. Aug 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8373 5 | E 8,6122 | 6 |
| MH53 8637 | Ulva rigida | S_442 | 08. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8567 | E 8,6034 333 | 5 |
| MH53 8638 | Ulva rigida | S_453_A | 09. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MH53 8639 | Ulva rigida | S_558 | 09. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MH53 8640 | Ulva rigida | S_560 | 09. Apr 15 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8333 | E 8,6142 | 7 |
| MH53 8641 | Ulva rigida | S_701 | 23. Apr 15 | Helgoland | Germany: Helgoland | N 54,1796 667 | E 7,8895 833 | 50 |
| MH53 | Ulva rigida | S_613 | 16. | Baltic Sea | Germany: Schleswig-Holstein, | N | Е | 111 |

| 8695 | | | Apr | | 54,3792 | 11,005 | | |
|--------------|-------------------------|--------------|------------------|---------------|-------------------------------------------------------------------------------|---------------------|--------------------|----|
| MH47 5484 | Ulva rigida | S_449 | 09. Sep 14 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog, Rhymschlot | N 54,8333 | E 8,6142 | 7 |
| MH47 5485 | Ulva rigida | S_123 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7300 7 | E 8,6891 67 | 11 |
| MH47 5486 | Ulva rigida | S_111 | 30. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Dagebuell | N 54,7300 7 | E 8,6891 67 | 11 |
| MH53 8697 | <i>Ulva</i> sp. | S_773 | 16. Sep 15 | Wadden Sea | Germany: Schleswig-Holstein, Friedrich-Wilhelm-Luebke- Koog | N 54,8373 5 | E 8,6122 | 6 |
| MH47 5487 | <i>Ulva</i> sp. | S_228 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4349 8 | E 10,170 15 | 71 |
| MH47 5488 | <i>Ulva</i> sp. | S_269 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Moenkeberg | N 54,3464 7 | E 10,174 2 | 82 |
| MH47 5489 | <i>Ulva</i> sp. | S_256 | 18. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Kiel | N 54,3538 | E 10,141 25 | 78 |
| MH47 5490 | <i>Ulva</i> sp. | S_2_A | 22. Jul 14 | Helgoland | Germany: Helgoland | N 54,1698 2 | E 7,8894 17 | 53 |
| MH47 5491 | <i>Ulva</i> sp. | S_317 | 22. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Sehlendorfer lake | N 54,3088 2 | E 10,688 63 | 95 |
| MH47 5492 | <i>Ulva</i> sp. | S_221 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Strande | N 54,4362 3 | E 10,175 02 | 70 |
| MH47 5493 | <i>Ulva</i> sp. | S_92 | 24. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Aschau | N 54,4608 | E 9,9266 5 | 65 |
| MH53 8694 | Ulva torta | S_138 | 31. Jul 14 | Wadden Sea | Germany: Schleswig-Holstein, Nordstrand | N 54,4707 167 | E 8,8068 333 | 23 |
| MH47 5494 | Ulva torta | S_81 | 24. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Wackerballig | N 54,7586 3 | E 9,8778 33 | 59 |
| MH47 5495 | Ulva torta | S_231 | 13. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Schilksee | N 54,4313 2 | E 10,169 33 | 72 |
| MH47 5496 | Ulva torta | S_350 | 25. Aug 14 | Baltic Sea | Germany: Schleswig-Holstein, Heiligenhafen | N 54,3787 2 | E 10,955 45 | 99 |
| MH47 5497 | Ulva torta | S_73 | 24. Jul 14 | Baltic Sea | Germany: Schleswig-Holstein, Gluecksburg | N 54,8367 5 | E 9,5231 | 56 |
| MH47 5498 | Umbraulva dangeardii | R_1 | 08. Aug 14 | Helgoland | Germany: Helgoland | N 54,1874 3 | E 7,8703 | 45 |
| MH47 5499 | Umbraulva dangeardii | R_2 | 08. Aug 14 | Helgoland | Germany: Helgoland | N 54,1874 3 | E 7,8703 | 45 |

Table S 2: Comparison of molecular (*tufA*)-based identification from the present study and the inventory list from Schories *et al.* (2009). List of species predicted by Schories et al. (2009) and detected in the present study (2019) from the Baltic Sea, Wadden Sea, and Helgoland.

| Species | Baltic Sea | | Wadden Sea | | Helgoland | | Taxonomic notes | |
|----------------------------------|------------|--------------|------------|------|--------------|------|---------------------|--|
| | 2019 | 2009 | 2019 | 2009 | 2019 | 2009 | | |
| Blidingia marginata (J.Agardh) | | | | | | | | |
| P.J.L.Dangeard ex Bliding 1963 | ✓ | \checkmark | ✓ | ✓ | \checkmark | ✓ | | |
| | | | | | | | | |
| Blidingia minima (Nägeli ex | | | | | | | | |
| Kützing) Kylin 1947 | X | ✓ | X | ✓ | X | ✓ | | |
| | | | | | | | | |
| Blidingia chadefaudii (Feldmann) | | | | | | | On Helgoland, B. | |
| Bliding 1963 | | | | | | , | on the basis of dev | |
| | | | | | X | √ | thickened inner ce | |
| | | | | | | | Helgoland's popul | |

On Helgoland, *B. chadefaudii* was taxonomically separated from *B. minima* on the basis of developmental differences, habit and zonation. However, a thickened inner cell wall, distinctive for *B. chadefaudii*, was absent from Helgoland's populations (Kornmann & Sahling, 1978)



First listed as subspecies of *B. marginata* (*Blidingia marginata* subsp. *subsalsa* [Kjellmann] Bliding), *B. subsalsa* was given the rank as a species (Kornmann & Sahling, 1978) on the basis of developmental differences observed on specimens from Helgoland.

Indicated as rare species and absent from Helgoland since 1975 (Kornmann & Sahling, 1977)

Highly variable in overall morphology (Blomster *et al.*, 1998; Maggs *et al.*, 2007*b*; Steinhagen *et al.*, 2018a; Tan *et al.*, 1999); Observation of different morphotypes in northern Germany (Steinhagen *et al.*, 2018a)

Different studies highlight conspecificity of U. pseudocurvata and U. compressa (Tan et al., 1999, Loughnane et al., 2008; Steinhagen et al.,

Ulva curvata (Kützing) De Toni

1889

Ulva flexuosa Wulfen 1803

Enteromorpha flexuosa subsp.

linziformis (Bliding) Bliding 1963

Ulva flexuosa subsp. paradoxa (C.

Agardh) M.J. Wynne 2005

Ulva californica Wille 1899



2018a), but material from Helgoland is shown in this study to be conspecific with *U. lactuca*.

Specimens formerly identified as *U. curvata* on Helgoland, were later assigned to the species *U. pseudocurvata*, due to morphological reconsiderations (Kornmann & Sahling, 1977; Kornmann & Sahling, 1994) "Clearly multiple closely related species" (Kirkendale *et al.*, 2013). ITS based species boundaries are ambiguous. Observation of life history and hybridization experiments clarified species boundaries of the "flexuosacomplex" (Hiraoka *et al.*, 2017)

Regarded as synonym of Ulva flexuosa var. linziformis Guiry & Guiry, 2018)

Regarded as synonym of U. paradoxa C. Agardh1817

Closely related to U. flexuosa. complex that is "clearly composed of multiple

Ulva intestinalis Linnaeus 1753

Ulva lactuca Linnaeus 1753

Ulva tenera Kornmann & Sahling

1994

Ulva linza Linnaeus 1753

Enteromorpha jugoslavica Bliding

Ulva prolifera O. F. Müller 1778



closely related species"(Kirkendale et al., 2013).

Aberrant morphologies induced by various factors (Bliding, 1963; Blomster *et al.*, 2002; Reed and Russell, 1978; Steinhagen *et al.*, 2018b) Based on missing morphological characters Kornmann & Sahling (1994) conclude *that U. lactuca* is absent from Helgoland. Later, its presence was verified by Bartsch & Kuhlenkamp (2000).

Shown in the present work to be conspecific with U. lactuca

Gross morphology highly variable (from sheets to proliferous tubes). Several studies stated different closely related genetic groups in the "linza-ahlneriana-procera" cluster (Kirkendale *et al.*, 2013; Kraft *et al.*, 2010), others support the conspecificty of *U. linza* and *U. procera* (Maggs *et al.*, 2007*b*). Records from the area are conspecific with *U. linza* (Gesche Bock, pers.

comm.)

Ulva torta (Mertens) Trevisan 1841

Ulva lobata (Kützing) Harvey 1855

Ulva radiata (J.Agardh)

H.S.Hayden, Blomster, Maggs,

P.C.Silva, M.J.Stanhope &

J.R.Waaland 2003

Ulva ralfsii (Harvey) Le Jolis 1863

Ulva simplex (K.L.Vinogradova) H.S.Hayden, Blomster, Maggs, P.C.Silva, M.J.Stanhope &



J.R.Waaland 2003

Ulva clathrata (Roth) C. Agardh 1811

Ulva rigida C. Agardh 1823 and Ulva scandinavica Bliding 1968

Ulva gigantea (Kützing) Bliding 1969

Ulva australis Areschoug 1854

Ulva sp.



Type locality: Fehmarn, SW Baltic (original material missing) (Guiry & Guiry 2018)

U. rigida, *U. scandinavica* and *U. armoricana* are considered as conspecific (Loughnane *et al.*, 2008)

"*U. gigantea* is notoriously difficult to separate from *U. pseudocurvata* on morphological grounds alone"(Loughnane *et al.*, 2008). First Observations in Ireland and Britain byLoughnane *et al.* (2008).

U. australis and *U. pertusa* can be regarded as conspecific (Kirkendale *et al.*, 2013). Likely to be a NIS in Australia (Kirkendale *et al.*, 2013).



The name *Umbraulva dangeardii* was proposed to replace the invalid names *Ulva olivascens* J.P.L.Dangeard nom. inval. and *Umbraulva olivascens* (P.J.L.Dangeard) G. Furnari nom. inval.

X

 \checkmark

Samples identified as *M. grevillei* segregated into two clusters in phylogenetic analyses of (Saunders & Kucera, 2010), suggesting crypticity.

Regarded as a synonym of *Monostroma grevillei* var. *arcticum* (Guiry & Guiry, 2018)



Type locality: Winning, SW Baltic (original material missing)

Annotations or taxonomic notes by other authors are marked respectively. X, species not observed; ✓, species observed; empty, unexpected and not

observed. Green shading indicates agreement between Schories et al. (2009) and the present study, whereas red shading indicates disagreement.

5. Supplementary Figure Legends

Figure S1: Maximum likelihood phylogram of *tuf*A sequences from taxa of *Ulva sensu lato* from northern Germany. Solid triangles indicate herbarium vouchers (see also Table 2). The two shades of grey indicate clades that were present in the study area. Hatched boxes indicate species complexes and, thus, taxonomic entities that could not be clearly resolved phylogenetically. Numbers at nodes indicate bootstrap values (left) and Bayesian posterior probabilities (1000 replicates; right). Poorly supported nodes (<70% bootstrap and <0.70 Bayesian support) are not labelled. Branch lengths are proportional to sequence divergence.

Figure S2: Morphology of *Protomonostroma undulatum* specimens from Helgoland, Germany. (A) Monostromatic thallus, with (i) close-up of the rhizoidal zone. (B) Elongated cells of the rhizoidal zone. (C) Transition zone between cells of the rhizoidal zone and the basal thallus. (D) Cell rows of the middle and apical thallus regions, with vein-like thickened cell walls. (E) Rectangular- to polygonal-shaped cells, each with 1–3, mostly centrally arranged, pyrenoids.

