Molecular genetic diversity of the macro morphological taxon *Ulva* cf. *rigida* along French Atlantic coasts

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Abstract

Green tides are the result of uncontrolled population expansion of green macroalgae in response to coastal eutrophication. Previous studies have proposed that *Ulva* green tides in Brittany (French Atlantic coast) were mainly due to *Ulva armoricana* and *U. rotundata*, leading to multiple taxonomic reappraisal. With the help of DNA barcoding using the chloroplastic gene *tuf*A, we analysed large sample sizes of *Ulva* specimens presenting macro-morphological characters of *U. rigida* collected from three sites, two in Brittany and one in Vendée. Molecular analyses included Museum *Ulva* specimens and the holotype of *U. armoricana*. We identified five different *tuf*A haplotypes, which appeared to be four different taxa, based on Genbank sequences including those of several holotypes and lectotypes: *U. rigida / U. laetevirens*, *U. australis* and *U. fenestrata*. The fourth taxon was putatively attributed to *U. pseudorotundata* using the *rbc*L marker. Our results fully confirm 1) the synonymy of *U. armoricana* with *U. rigida*, based on the genetic analysis of the *U. armoricana* holotype, 2) historical occurrence and long-term presence of *U. australis*, as an introduced species, involved in green tides in Brittany

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and 3) previous molecular determinations of *U. fenestrata* in southern Brittany. The taxonomic history of each taxa is discussed and some taxonomic issues within the genus *Ulva* are highlighted particularly in view of the high molecular similarities between *U. rigida* and *U. laetevirens*.

Keywords: integrative taxonomy, DNA barcoding, phenotypic plasticity, algal bloom, green tides, *Ulva* spp., pseudo-cryptic species, *tuf*A, herbarium, species delimitation

Kommentiert [WF1]: I wonder how many persons will search for “pseudo-cryptic species” in the future…Perhaps “cryptic species” would result in more hits for your paper…

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Introduction

Green tides are the result of a rapid and massive development of green macroalgal biomass following eutrophication (Fletcher, 1996; Coat *et al.*, 1998). The majority of green tides are composed of species of the genus *Ulva* (Fletcher, 1996; Jia *et al.*, 2011). These species are considered as pioneer and opportunistic organisms. This pioneering role is aided by a worldwide distribution and a capacity to produce numerous reproductive spores in a short period of time (Fletcher, 1996). The important volume of algae leads to severely negative ecological, economic and sanitary consequences. It increases sedimentation rates and interferes with oxygen transport.

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During respiration, algae consume oxygen and create an anoxic environment, which leads to decomposition of algal mats and the development of toxic sulfides (Fletcher, 1996; Charlier, Morand & Finkl, 2008). These environmental changes affect benthic and pelagic communities and lead to economic and sanitary impacts on touristic sites (Charlier, Morand & Finkl, 2008). Some cases of human deaths have even been reported because of massive algal mats decomposition (Ménesguen, 2018). In the French Atlantic and especially in Brittany, studies have demonstrated that green tides are caused by eutrophication of coastal waters through the spread of livestock farms effluents on soils (Charlier, Morand & Finkl, 2008) and release into marine environments of excessive nitrogen compounds (Ménesguen, Dussauze & Dumas, 2018).

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Studies of green tides usually begin by understanding which species are involved in these blooms. Because of the phenotypic plasticity of the *Ulva* genus, the use of morphological characters in taxonomy is often inconclusive (Coat *et al.*, 1998 ; Loughnane *et al.*, 2008 ; Lee *et al.*, 2019). Taxonomic studies of this taxon are mainly based on molecular

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phylogenies. For example, in Brittany, it has been shown that species responsible for green tides include *U. rotundata* Bliding and *U. armoricana* Dion, de Reviers & Coat based on morphological and cytological characters (Dion, de Reviers & Coat, 1998). Following preliminary molecular analyses and comparisons with oversea materials, Coat *et al.* (1998) first highlighted molecular similarities between *U. rotundata* samples from Brittany and *U. australis* Areschoug ITS sequences. This suggestion was further confirmed by Hayden *et al.* (2003), Hayden & Waaland (2004) and Couceiro, Cremades & Barreiro (2011). Similarly, it was suggested that *U. armoricana* and *U. rigida* C. Agardh are probable synonyms (Hayden *et al.*, 2003; Hayden & Waaland, 2004), a view that is today accepted (Brodie, Maggs & John, 2007). As exemplified by these two species, many confusions exist in the taxonomy of the genus *Ulva* (Sfriso, 2010; Hughey *et al.*, 2019). Use of several different genetic markers into the *Ulva* genome add also major difficulties in comparing results and identifying species. For example, *U. rotundata* has been identified ~~on~~ by *rbc*L gene sequencing (Loughnane *et al.*, 2008 ; Wan *et al.*, 2017) and not ~~on~~ ~~*tuf*A~~*tufa* sequencing, although most *Ulva* species have been identified based on *tuf*A. The chloroplastic elongation factor *tuf*A marker has been developed for the routine barcoding of green marine macroalgae (Saunders & Kucera, 2010). Previous studies on *Ulva* spp. using *tuf*A suggest that it is variable enough to allow comparing intra- and inter-specific variation across *Ulva* species, making it a useful molecular barcode for the genus (Kirkendale *et al.*, 2013 ; Kang *et al.*, 2014 ; Lee *et al.*, 2019; Steinhagen, Karez & Weinberger, 2019).

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This paper aims to study the diversity of the *Ulva* cf. *rigida* taxon along the French Atlantic coasts. Our approach consists of a phylogenetic analysis of *tuf*A. We sampled around 360 thalli presenting macro-morphological characters of *U. rigida* on two sites known to harbour green tides in Brittany and one site in Vendée. Our study is the first one to include such large numbers of samples from several sites on the French Atlantic coasts compared to historical (Coat *et al.*, 1998) or recent (e.g. Fort *et al.*, 2020) molecular studies. To clarify the taxonomic confusion between *U. rigida* and *U. armoricana*, we also analysed the *tuf*A sequence of the holotype of *U. armoricana* collected by Dion, de Reviers & Coat (1998).

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Material and methods

Sampling

Green macroalgae matching the macro-morphology of *Ulva rigida* C. Agardh (large and flat thallus, bright green color, stiff base) (Phillips, 1988; Loiseaux-de Goër & Noailles, 2008; Loughnane *et al.*, 2008) were sampled between January the 22th and February the 21st on the intertidal zone at three sites: La Tranche sur Mer (46°20'48.6"N 1°25'19.3"W) in Vendée, and Roscoff (48°43'48.1"N 3°58'57.7"W) and Concarneau (47°51'34.6"N 3°54'47.9"W) in Brittany (Figure 1). Within the Water Directive Framework (WDF), these sites and their surroundings are monitored for green macroalgal blooms by the Centre d'Etude et de Valorisation des Algues (e.g. CEVA, 2015, 2019). At each site, around 120 specimens up to 7 cm^2 were collected, individualized and kept at 4°C. Back in the lab, each individual was rinsed with filtered seawater to remove epiphytes and preserved at -80°C in individual numbered plastic bag. Eleven museum samples, from the cryptogam collection (PC) of the Muséum national d'Histoire naturelle, Paris (France), including the holotype of *U. armoricana*, were added to our samples (Supplementary S1).

DNA extraction and PCR amplifications

Frozen tissue from the thallus was ground up to a powder in liquid nitrogen. Whole genomic DNA was extracted from 0.3 mg of powder using the NucleoSpin Tissue Kit (Macherey-Nagel). The manufacturer's standard protocols for tissues were followed, except for the following steps: (1) we performed an overnight tissue digestion in proteinase K, (2) DNA was eluted in two steps, each consisting in a 3 min incubation with 25 µL of dH$_2$O pre-heated at 70°C, for a final volume of 50 µL. DNA quality and quantity were assessed using a Nanodrop ND-2000 spectrophotometer (Thermo Scientific), a Qubit 1.0 (Thermo Scientific) fluorometer (dsDNA HS Assay Kit), and 1X agarose gel electrophoresis.

The chloroplast gene *tuf*A was targeted to barcode our specimens. Primers were designed based on Saunders and Kucera (2010) (Table 1), as to reduce the number of ambiguities, based on available chloroplast genomes available for *Ulva* on Genbank (*Ulva* sp. KP720616.1, *U. flexuosa* KX579943.1, NC_035823.1, *U. prolifera* NC_036137.1, KX342867.1, *U. ohnoi*

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AP018696.1, *U. lactuca* NC_042255.1, MH730972.1, *U. linza* KX058323.1, NC_030312.1, *U. fasciata* NC_029040.1, KT882614.1). Sequence~~s~~ primers are presented in Table 1. PCR ~~were~~ was carried out with a Sensoquest labcycler using a TaKara ExTaq reaction kit (Takara Bio). PCR amplicons were checked on a 1X agarose gel electrophoresis prior to purification and Sanger sequencing in both forward and reverse directions by Eurofins Genomics (Ebersberg, Germany).

All *tuf*A sequences (plus one *rbc*L sequence) from our specimens, as well as MNHN specimens, were deposited on Genbank (Supplementary S1).

Data analysis

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Chromatograms were cleaned manually with Geneious Prime 2019.1.2 (www.geneious.com); primer sequences were trimmed, sequences were checked for the presence of ambiguities and stop codons, and forward and reverse chromatograms were assembled. All *tuf*A sequences produced in this study were aligned to the 1122 available *Ulva* spp. sequences from Genbank using Muscle 3.8.425 (Edgar, 2004). Three *Umbraulva japonica* sequences, 14 *Umbraulva* sp. and one *Umbraulva dangeardii* were added to constitute an outgroup. Identical sequences from the same species were represented by a single *tuf*A haplotype for further phylogenetic analyses.

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Uncorrected-p distances (hereon called p distances) were calculated using PAUP* v.4.0 (Swofford, 2002) based on full *tuf*A sequences of 774 bp, ~~as~~ which are available on Genbank for Kirkendale, Saunders & Winberg (2013) and truncated sequences of 500 bp, ~~as~~ to allow for alignment with other Ulva sequences available on GenBank. A Maximum Likelihood tree o~~n~~f *tuf*A genes among *Ulva* species was inferred using IQtree 2.0.5 (Ming *et al*., 2020) with ultrafast bootstrapping (1000 pseudoreplicates) (Hoang *et al.*, 2018) and a TPM3+F+I+G4 model of evolution (Kalyaanamoorthy et al., 2017). The resulting tree was edited using iTOL 5.6.3 (Letunic and Bork 2006). Because of the large number of species included in this tree and in order to be consistent with our analysis, we only kept species with a large and flat thallus, and excluded species with tubular forms (ex-*Enteromorpha* spp.) such as *Ulva compressa*, *U. flexuosa*, *U. intestinalis*, *U. linza*, *U. prolifera*, *U. stenophylla*, *U. torta* and *Ulva* sp. (we also reduced the outgroup to *Um. japonica*). The reduced tree presented in our results is based on 979 sequences (53 haplotypes) and supports the same ~~information~~ interpretation as the full dataset (Supplementary S2).

Haplotype richness (*R*), Shannon's diversity index (*H*) and Pielou's evenness (*J*) were calculated in vegan 2.5-4 (Oksanen *et al.*, 2019) in R 3.6.0 (R Core Team, 2020). We used the same package to perform species rarefaction based on sample numbers, and fit a Preston's veil model (method: maximized likelihood to log2 abundances) to our data (sites pooled) (Preston, 1948; Williamson & Gaston, 2005).

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Results

*tuf*A *analysis*

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*Tuf*A was sequenced for 339 o~~n~~f the 360 samples and for only 3 o~~n~~f the 11 museum specimens, because of amplification or sequencing difficulties. Five haplotypes were detected based on both the 774 and the 500 bp-long sequence alignments (Tables 2 and 3). Haplotype 1 was sampled at all sites. Haplotypes 2 and 4 were sampled in Brittany only (Concarneau and Roscoff), while haplotypes 3 and 5 were private to Concarneau, and sampled in small numbers (<10 thalli).

Concarneau therefore had the highest haplotypic richness (R=5) and diversity (H = 1.178), followed by Roscoff (R=3, H=1.095) and La Tranche (R=1), where only the most common haplotype (1) was found. The haplotype distribution was more even in Roscoff (J=.9968) than Concarneau (J=0.7318). Rarefaction suggests that little haplotype diversity was missed during sampling, as the rarefaction curve almost reaches an asymptote (Supplementary S3). Preston's Lognormal Model to Abundance Data suggests that 0.05 haplotypes were missed during sampling (5.0538 haplotypes were extrapolated with the method).

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Haplotypes were aligned with sequences of *Ulva* spp. and *Umbraulva japonica* from Genbank. To evaluate the number of nominal species, these haplotypes may correspond to p distances among haplotypes (Table 3). Haplotypes 1 and 2 differ by 1.2 % (6 mutations, half of them being synonymous) and with the three other~~s~~ haplotypes with distances up to 8.2%. Distances between these three haplotypes range from 6% to 10.4% (from 33 to 52 mutations).

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ML trees were inferred using 53 haplotypes representing 24 species of *Ulva* and one species of *Umbraulva* from GenBank (Figure 2). The alignment contains 135 variable sites and 99 parsimony-informative sites. No indel was detected (alignment provided as Supplemental FIle S7).

Four clades including our haplotypes can be distinguished. The first one contains 30 sequences of *U. laetevirens*, 14 sequences of *U. rigida*, one sequence from MNHN specimen of *U. rigida var. fimbriata* (MT078957), one sequence from MNHN specimen of *U. scandinavica* (MT078956), the sequence from the holotype of *U. armoricana* (MT078955) and our haplotypes 1 and 2 (MT078946-MT078950), supported with a 93% bootstrap value. Within this clade, uncorrected-p distances range from 0 to 1.2% and the number of substitutions is less than 7. The second clade contains 30 sequences of *U. lobata*, 9 sequences of *U. expansa* and our haplotype 3 (MT078951), supported with a 85% bootstrap value. Our haplotype presents 22 mutations, i.e. 4.4% p distance, with *U. lobata* and *U. expansa* sequences.

The third one contains 144 sequences of *U. australis*, divided into two subclades, distanced by 4 mutations, i.e. 0.2% p distance. The first subclade comprises 143 *U. australis*, 5 *U. pertusa* and our haplotype 4 (MT078952, MT078953), supported with a 100% bootstrap value. The second is composed of a single *U. australis* sequence.

The last clade contains 180 sequences of *U. lactuca*, divided into three subclades, distanced by 3 mutations, i.e. 0.6% p distance. The first subclade contains 107 *U. lactuca* and our haplotype 5 (MT078954), supported with a 100% bootstrap value. The second subclade contains one *U. fenestrata*, and the third 73 *U. lactuca*.

Discussion

Our *Ulva*-specific *tuf*A primers allowed the amplification of this barcoding gene for 94.2% of sampled specimens. Based on previously reported intra- and inter-specific genetic distances at *tuf*A for green macroalgae (Kirkendale, Saunders & Winberg, 2013), we identified five haplotypes, constituting four clades that we attribute here to nominal species, based on the General Lineage Concept of species (De Queiroz, 1998).

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Haplotypes 1 & 2: Ulva rigida / Ulva laetevirens

~~On~~ Within the ML tree, haplotypes 1 & 2 cluster with sequences of *U. rigida*, *U. scandinavica*, *U. armoricana* (holotype) and *U. laetevirens* with a p distance ranging~~ed~~ from 0.2 to 1.2%. Kirkendale, Saunders & Winberg (2013) calculated interspecific distances between 19 *Ulva* taxa, ranging from 0.65 to 5.56%. ~~According~~ Based upon~~to~~ 774 bp sequences deposited by Kirkendale, Saunders & Winberg (2013) on Genbank, we also calculated a genetic distance based on 774 bp ~~on~~ for our sequences, to allow for a direct comparison of both studies. ~~compare their values to our distances~~. If we focus on *U. laetevirens*, as delimited by Kirkendale, Saunders & Winberg (2013), the minimum interspecific divergence of the *U. laetevirens* taxon and other~~s~~ studied taxa would be 1.16% based on 774 bp. Our delimited clade, comprising our tw~~ice~~o

haplotypes 1 & 2 is below this ~~range~~ divergence (0.9% on 774 bp) and clusters ~~would be~~with in~~to~~ the intraspecific range. Our two haplotypes could also be considered to represent ~~as~~ a unique species ~~into the clade comprising,~~ together with sequences of *U. rigida*, *U. scandinavica*, *U. armoricana* and *U. laetevirens.*

Ulva rigida has been morphologically described by Agardh (1823) based on samples collected at Cadiz, on the Atlantic coast of southern Spain in 1822. Although he did not assign type specimens ~~to~~ ~~a type series~~, a lectotype, placed in Lund Herbarium in Sweden, was designated by Papenfuss (1960). Through an investigation of southern Australian *Ulva* species, Phillips (1988) synonymized *U. rigida* sensu Bliding (1968) and *U. laetevirens* Areschoug (1854) based on similar morphologies. ~~It~~ This view was contradicted by Sfriso (2010), who ~~reported separately~~considered these two species in Venice lagoon as separate, based on cell conformation. According to Guiry & Guiry (2020) , the view~~s~~ of *Ulva laetevirens* as a valid species, and *Ulva rigida* as a temperate and boreal species not present in tropical and subtropical regions (O'Kelly *et al.*, 2010) are currently accepted.

As pointed out by Wolf *et al.* (2012), further analysis of ~~the nightmare of~~ synonyms within *U. rigida* sensu Bliding~~,~~ requires analysis of ~~M~~museum types. With the development of molecular

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studies, the *U. rigida* C. Agardh taxon ~~has known~~underwent many changes including incorporation of many synonyms. Hayden *et al.* (2003) and Hayden & Waaland (2004) proposed the synonymy of *U. armoricana* and *U. scandinavica* with *U. rigida* based on *rbc*L and ITS. This taxonomic rearrangement of the *U. rigida* taxon was then discussed by Loughnane *et al.* (2008), Kraft, Kraft & Waller (2010) and Wolf *et al*. (2012). According to Guiry & Guiry (2020), *U. rigida* C. Agardh currently comprises the five following different *Ulva* taxa : *Ulva thuretii* B. Föyn, *Ulva petiolata* (J. Agardh) Womersley, *Ulva spathulata* Papenfuss, *Ulva scandinavica* Bliding and *Ulva armoricana* Dion, de Reviers & Coat. Based on sequencing of the holotype of the latter species, our study supports the synonymy of *Ulva armoricana* with *U. rigida* as initially proposed by Hayden *et al*. (2003) and Hayden & Waaland (2004). However, considering our two haplotypes as the same species could be further discussed in terms of ecological conditions.

Unlike the other sites from Brittany, La Tranche sur Mer in Vendée harboured only haplotype 1. If haplotypes 1 and 2 would be a single species, the absence of haplotype 2 at this site suggests that these different mitotypes have different geographic distributions, either due to neutral (e.g. historical, biogeographic processes) or non-neutral (e.g. selection on different ecotypes) processes. We only sampled the upper intertidal zone in La Tranche sur Mer, unlike other sites in Brittany, due to sampling and tide time constraints. The haplotype 1 could be an ecotype, more adapted to the upper shore (in terms of temperature and light variation, wave impacts, nutriment fluxes, etc.) than the haplotype 2, which is more adapted to lower shore conditions. A case of ecotypic differences between attached and floating populations was reported for *Ulva prolifera* (Zhao *et al.*, 2015) in which the two ecotypes show genetical, morphological, physiological and ecological specificities. Further sampling in La Tranche sur Mer should integrate both upper and lower zones on the shore in order to clarify this hypothesis in respect of Sfriso's (2010) observations from the Venice lagoon, where the two taxa coexist in the same environments and substrata.

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Haplotype 3: *Ulva pseudorotundata*

The third haplotype, containing 9 samples from Concarneau presents 22 substitutions (4.4% p distance) with the closest clade, composed of *U. expansa* and *U. lobata*. According to Hughey *et al*. (2019), these *U. lobata* sequences sampled in ~~to~~the northeast Pacific~~,~~ should be named *Ulva expansa*, because of the synonymy of the *U. expansa* holotype and *U. lobata* sequences from the Northeast Pacific, based on *tuf*A and *rbc*L analysis. Between the 32 Genbank samples of *U. expansa*, the maximum of intraspecific p distance is 0% ~~on~~ for the *tuf*A gene. Between these sequences and our haplotype, the 4.4% p distance is also too large to consider our haplotype to fall into the intraspecific range of this species. To extend our taxonomic interpretation of this haplotype, we sequenced a short part of the *rbc*L gene (MW013545) that was~~,~~ used in type analyses (Hanyuda & Kawai, 2018). The Blastn analysis (Zhang *et al*., 2000) of 230 bp sequences of two samples of our haplotype (truncated to have no ambiguities) reveals a 100% similarity with 5 sequences of *U. rotundata* and 1 sequence of *Ulva* sp. This suggests that this haplotype belongs to *U. rotundata* Bliding~~ taxon~~, actually renamed into *U. pseudorotundata* by Cormaci, Furnari & Alongi (2014). *U. pseudorotundata* has been reported in Roscoff with the name of *U. rotundata* (Hoeksema & van den Hoek, 1983), and has been described in a green tides context in Ireland (Wan *et al*., 2017; Fort, Guiry & Sulpice, 2018). Haplotype 3 would therefore represent *U. pseudorotundata* newly sequenced at *tuf*A in Brittany and this will help further comparisons with similar sequences from the Irish coast to be made (Fort *et al*., 2019). Ecological conditions could correspond to our context and reinforce our hypothesis. To find *U. pseudorotundata* in Concarneau would potentially add a new record of the species for southern Brittany (Dizerbo & Herpe, 2007 ; Burel, Le Duff & Ar Gall, 2019).

Haplotype 4: *Ulva australis*

In this study, haplotype 4 was reported from two sites along Brittany coasts, *i.e.* Concarneau and Roscoff. It ~~is~~ clustered with many sequences of *U. australis* and *U. pertusa* ~~on *tuf*A gene analysis~~, with a p distance below 0.2% on 500 bp. Similarly, Lee, Kang & Kim (2019)

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determined the intraspecific variation ~~at~~of *tuf*A (ca 800 bp) in the range 0-0.4% for *U. australis* from Jeju Island-Korea, within the native distribution area of the species. Kirkendale, Saunders & Winberg (2013) determined a minimum of interspecific divergence ~~equal to~~of 5.56% based on on 774bp, corresponding to 6.8% on our 500 bp for *U. australis*. Based on these values, haplotype 4 presents a p distance falling within the intraspecific range of *U. australis*. This taxon was described in 1851 from Port Adelaide, South Australia (Areschoug, 1854). Based on morphological and development characteristics, Phillips (1988), however, included *U. australis* within the *U. rigida* taxon. On the contrary, Kraft *et al.* (2010) excluded it from this taxon and considered *U. australis* as a species on its own.

Kjellman (1897) described *Ulva pertusa* from three localities in Japan independently from observations of Areschoug (1854). A more recent comparative study based on the analysis of *rbc*L and ITS1 sequences suggested that *U. australis* from southern Australia and *U. pertusa* from Japan are conspecific and actually ~~well~~ widely distributed, as an introduced species, along Iberian coasts (Couceiro, Cremades & Barreiro, 2011). *U. pertusa* Kjellman is today recognised as a synonym of *U. australis* Areschoug, the oldest name (Guiry & Guiry, 2020). Molecular analysis of the holotype of *U. australis* supported this synonymy, and further suggested that populations of *U. australis* are non-indigenous in Australia but introduced from northeastern Asia (not directly from Japan) by the middle of 19th century (Hanyuda & Kawai, 2018). *U. australis*, as *U. pertusa*, has been reported from various worldwide regions, including the Mediterranean Sea, since the early 1970's (Verlaque, Belsher & Deslous-Paoli, 2002; Hanyuda *et al.*, 2016). This species has already been reported in Brittany, more precisely at Roscoff from October 1994 to October 1995 by Coat *et al.* (1998) as *Ulva rotundata* (Couceiro, Cremades & Barreiro, 2011) and at Beg Meil, near Concarneau, in 2018 by Fort *et al.* (2020). These authors also reported the

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species from several Brittany localities (Lannion Bay and Brest), suggesting that *U. australis* ~~would~~ might be a common inhabitant of West Brittany coasts and a major contributor to local green tides (Fort *et al.*, 2020).

Haplotype 5: *Ulva fenestrata*

Haplotype 5 was detected ~~from~~ only tw~~o samples~~ice at ~~from~~ Concarneau. It ~~is~~ clustered with many sequences of *U. lactuca* and *U. fenestrata*, including a sequence from the holotype of *U. fenestrata* MK456404 (Hughey *et al.*, 2019). Uncorrected-p distances range from 0 to 0.6% (3 substitutions). Taking into account its p distance of 3% with all *U. arasakii* M. Chihara sequences, we ~~could~~ hypothesize that haplotype 5 belongs to the *U. fenestrata* group. *Ulva lactuca* has been described in 1753 by Linnaeus who did not designate a type specimen. A specimen of the Linnaean herbarium has been designated as the type of *U. lactuca* by Papenfuss (1960), based on the analysis of the Species Plantarum (Linnaeus, 1753). However, when he examined it, he found a difference with the modern taxonomic hypothesis for *U. lactuca*. This specimen had marginal teeth on thallus margin, unlike the description of the current *U. lactuca*. He also decided to typify it as *U. rigida* C. Agardh. Bliding (1968) identified this type as a sample collected in the Swedish west coast. The *U. lactuca* holotype have been molecularly analyzed by Hughey *et al.* (2019) revealing that the *U. lactuca* described by Linnaeus is currently called *U. fasciata* Delile in the subtropics and *U. lobata* in the eastern Pacific Ocean. The lectotype of *U. lobata* (Kützing) Harvey is then renamed as *U. lactuca* (Hughey *et al.*, 2019). These authors also found that European *U. lactuca rbc*L sequences clustered with the *U. fenestrata* Postels & Ruprecht holotype sampled in eastern Russia, in Avacha bay. This suggests that all the *U. lactuca tuf*A sequences within the group of the *U. fenestrata* holotype (MK456404) should be *U. fenestrata*. Many authors ~~had~~ already ~~hypothesized~~ suggested a conspecificity between *U. lactuca* and *U. fenestrata* (Hayden *et al.*, 2003; Hayden & Waaland, 2004; Loughnane *et al.*, 2008). *U. fenestrata* has been reported on some northwestern Atlantic coasts,

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like Washington ~~coasts~~ (Nelson, Nelson & Tjoelker, 2003), in the Pacific Ocean as *U. fenestrata* and more generally in Europe (Hughey *et al.*, 2019). It has already been reported in Beg Meil near Concarneau as *U. lactuca* (Fort *et al.*, 2020) ~~since~~ as the *rbc*L sequence AB097622 of *U. lactuca* used by these authors was identified as *U. fenestrata* by Hughey *et al.* (2019).

Potential issues with type specimens

As previously demonstrated for many species, *U. armoricana, U. scandinavica, U. rigida, U. laetevirens, U. lobata, U. expansa, U. pertusa, U. fasciata, U. lactuca* and *U. fenestrata* species names assigned to Genbank sequences, based on morphological identification, must be carefully considered. Assuming that the *tuf*A gene trees represent species trees within the genus, our study revealed some potential issues with the identification of some *Ulva* sequences on Genbank. For instance, *U. laetevirens* LT969813 and *U. rigida* KC661447 are not included in our haplotypes 1 & 2 *Ulva rigida* / *U. laetevirens* (Figure 2). Similarly, we identified 5 different clades of *U. fasciata* sequences, but only one clade could be interpreted based on the recent analysis of the holotype of *U. lactuca* at *rbc*L (Hughey *et al.*, 2019). Given the 0% p distances between *U. lactuca* MH730972 and 24 *U. fasciata* sequences identical to JN029299, 2 sequences of *U. reticulata* identical to MG963806 together with the sequence KC661468, each sequence of *U. reticulata* and *U. fasciata* of this clade should be renamed into *U. lactuca*. Including museum types into taxonomic analysis thus allows to clarify the taxonomy of the *Ulva* genus and to clarify taxonomic issues (e.g. Hughey *et al.*, 2019). These issues could be explained by incorrect morphological descriptions because of the high phenotypic plasticity of the *Ulva* genus, ~~who~~ that allows species to invade many biotopes (Hofmann *et al.*, 2010; Steinhagen, Karez & Weinberger, 2019). In addition to taxonomic issues, and as hinted above, these issues could also be due to the lack of resolution of chloroplastic and nuclear-ribosomal molecular markers used to date. Indeed, what we (and other authors) identified as intra- and inter-specific variation at *tuf*A may not reflect true evolutionary history. As for many other taxonomic groups, there is a strong

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need to integrate data from morphology, physiology, ecology and different types of molecular markers in order to delineate species. In *Ulva*, the sequencing of restriction-site associated DNA (RAD-seq) has proven feasible and produced data that is partly incongruent with *rbcL* barcoding (Fort, Guiry & Sulpice, 2018). Other type of molecular markers, such as *trn*A-N or *atp*I-H regions, for *U. australis* could bring genetic diversity and biogeography of a species (Hanyuda *et al.*, 2016; Sauriau *et al.*, submitted)

Many *Ulva* species have been reported as responsible of green tides around the world e.g. *U. australis*, *U. expansa*, *U. fenestrata*, *U. lactuca*, *U. ohnoi*, *U. prolifera* and *U. rigida* (de Casabianca *et al.*, 2002; Nelson, Nelson & Tjoelker, 2003; Baamonde López *et al.*, 2007; Sfriso, 2010; Kirkendale, Saunders & Winberg, 2013; Kang *et al.*, 2014; Melton, Garcia-Soto & Lopez Bautista, 2016). At the end of the 1990's, Coat *et al.* (1998) determined *Ulva* species composing Brittany's green tides on the basis of rDNA internal transcribed spacer (ITS) compared to morphological characters. They identified two species *U. armoricana* and *U. rotundata* but both species went through major taxonomic revisions motivated by molecular data. *U. armoricana* is now considered as synonym of *U. rigida* (Shimada *et al.*, 2003; Hayden & Waaland, 2004) and Brittany samples of *U. rotundata* have been renamed as *U. australis* (see the reviews by Couceiro, Cremades & Barreiro, 2011 and Sauriau *et al.*, submitted). These statements are confirmed by Fort *et al.* (2020), who reported the contribution of six *Ulva* species to green tides in Brittany: *U. rigida* and *U. australis* are the dominant species in around 50% and 32% of Brittany *Ulva* green tides sites, respectively. Similar proportions arise from our study. Unlike *Ulva rigida*, *Ulva australis* is an introduced species reported in many countries as an introduced and invasive species (Couceiro, Cremades & Barreiro, 2011 ; Kirkendale, Saunders & Winberg, 2013 ; Hanyuda *et al.*, 2016). Introductions of marine species are increased by the globalization

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of ship transport systems, fisheries and aquaculture activities, by the way of ballast waters and exchanges of attached organisms for fisheries (Carlton & Geller, 1993). At the end of the 20th century, Concarneau's port was the third biggest port involved in tuna fisheries in France (Couliou & Piriou, 1989). The large number of ships involved in mondial fisheries made Concarneau marine algae communities vulnerable to the introduction of non-native species such as *U. australis* (Couceiro, Cremades & Barreiro, 2011), *U. laetevirens* (Mao *et al.*, 2014) or *U. fasciata* Delile today, which is known as a synonym of the warm temperate-tropical *Ulva lactuca* Linnaeus (Hughey *et al.*, 2019).

Conclusions

Analyzing the diversity of *Ulva* species at Brittany sites known to suffer from large green tides compared to Vendée, we confirmed previous results by Fort *et al.* (2020) that Brittany's green tides are composed at least of~~from~~ *Ulva rigida*, as a temperate and boreal species, and *Ulva australis*, as an introduced species from northeastern Asia (Hanyuda *et al.*, 2016). The former result was substantiated with the sequence of the holotype specimen of *Ulva armoricana* on *tuf*A gene found to be identical to *U. rigida*, although the latter is in line with some earlier intriguing results made by Coat *et al.* (1998), wh~~en~~o compared~~ing~~ Brittany *U. rotundata* with Australian *U. australis*. Finally, our results suggest that the taxonomic ~~status~~ relationship of *U. laetevirens* and U. rigida remains questionable~~ compared to *U. rigida*~~.

Acknowledgements

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Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 482 + Ausrichtung: Links + Ausgerichtet an: 2,84 cm + Einzug bei: 2,84 cm

Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 489 + Ausrichtung: Links + Ausgerichtet an: 2,84 cm + Einzug bei: 2,84 cm

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Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 497 + Ausrichtung: Links + Ausgerichtet an: 1,99 cm + Einzug bei: 1,99 cm

Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 502 + Ausrichtung: Links + Ausgerichtet an: 1,99 cm + Einzug bei: 1,99 cm

Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 511 + Ausrichtung: Links + Ausgerichtet an: 1,99 cm + Einzug bei: 1,99 cm

Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 516 + Ausrichtung: Links + Ausgerichtet an: 2,84 cm + Einzug bei: 2,84 cm

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Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 552 + Ausrichtung: Links + Ausgerichtet an: 2,84 cm + Einzug bei: 2,84 cm

Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 557 + Ausrichtung: Links + Ausgerichtet an: 2,84 cm + Einzug bei: 2,84 cm

Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 566 + Ausrichtung: Links + Ausgerichtet an: 2,84 cm + Einzug bei: 2,84 cm

Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 570 + Ausrichtung: Links + Ausgerichtet an: 2,84 cm + Einzug bei: 2,84 cm

Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 574 + Ausrichtung: Links + Ausgerichtet an: 1,99 cm + Einzug bei: 1,99 cm

Formatiert: Nummerierte Liste + Ebene: 1 + Nummerierungsformatvorlage: 1, 2, 3, … + Beginnen bei: 578 + Ausrichtung: Links + Ausgerichtet an: 1,99 cm + Einzug bei: 1,99 cm, Tabstopps: Nicht an 1,27 cm

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Table 1

Parameters and sequences of *tuf*A primers, based on Saunders & Kucera (2010).

Tm: Melting temperature, bp: base-pair.

(on next page)

Primers name	Tm	Sequence (5’-3’)	Expected amplicon length (bp)
*tuf*GF4_MD (Forward)	58.5°C	GGTGCAGCYCAAATGGATGG	800
*tuf*AR_MD (Reverse)	63.3°C	CCTTCACGAATTGCAAAACGC	

1

Table 2

Number of samples per haplotypes on each site.

(on next page)

	La Tranche s/ Mer	Concarneau	Roscoff
Haplotype 1	118	36	38
Haplotype 2	0	61	34
Haplotype 3	0	9	0

Haplotype 4	0	10	31
Haplotype 5	0	2	0

1

Table 3

Percent p distances for each pair of *tuf*A haplotype, for the 500 bp (left value) and 774 bp (right value, in parentheses) alignment lengths.

(on next page)

	Haplotype 2	Haplotype 3	Haplotype 4	Haplotype 5
Haplotype 1	1.2 (0.9)	8.2 (7.6)	10.2 (9.3)	9.6 (8.4)
Haplotype 2		8.4 (7.9)	10.4 (9.6)	9.8 (8.6)
Haplotype 3			6.8 (6.5)	6.6 (5.2)

Haplotype 4				7.0 (5.7)

Figure 1

Map of sampling sites along the French Atlantic coast (Roscoff and Concarneau in Brittany, and La Tranche sur Mer in Vendée).

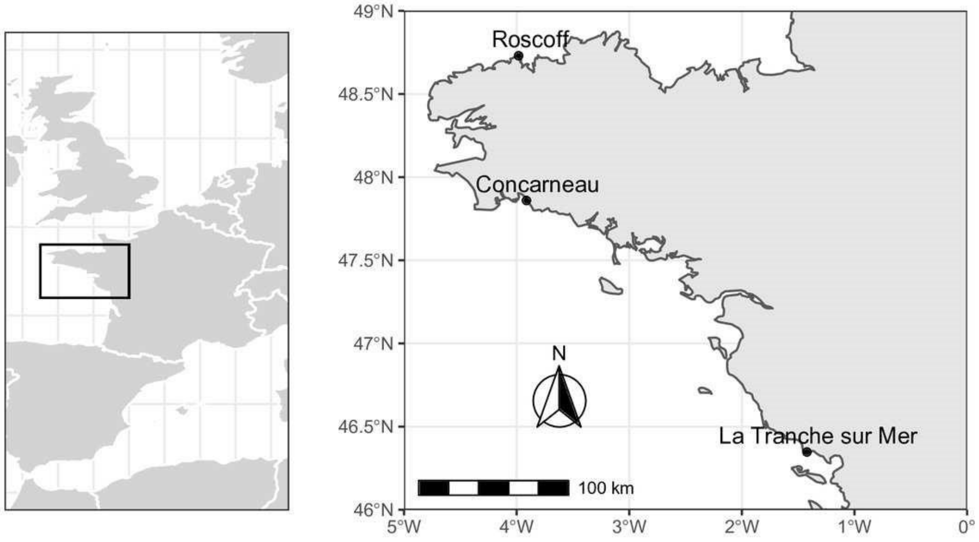
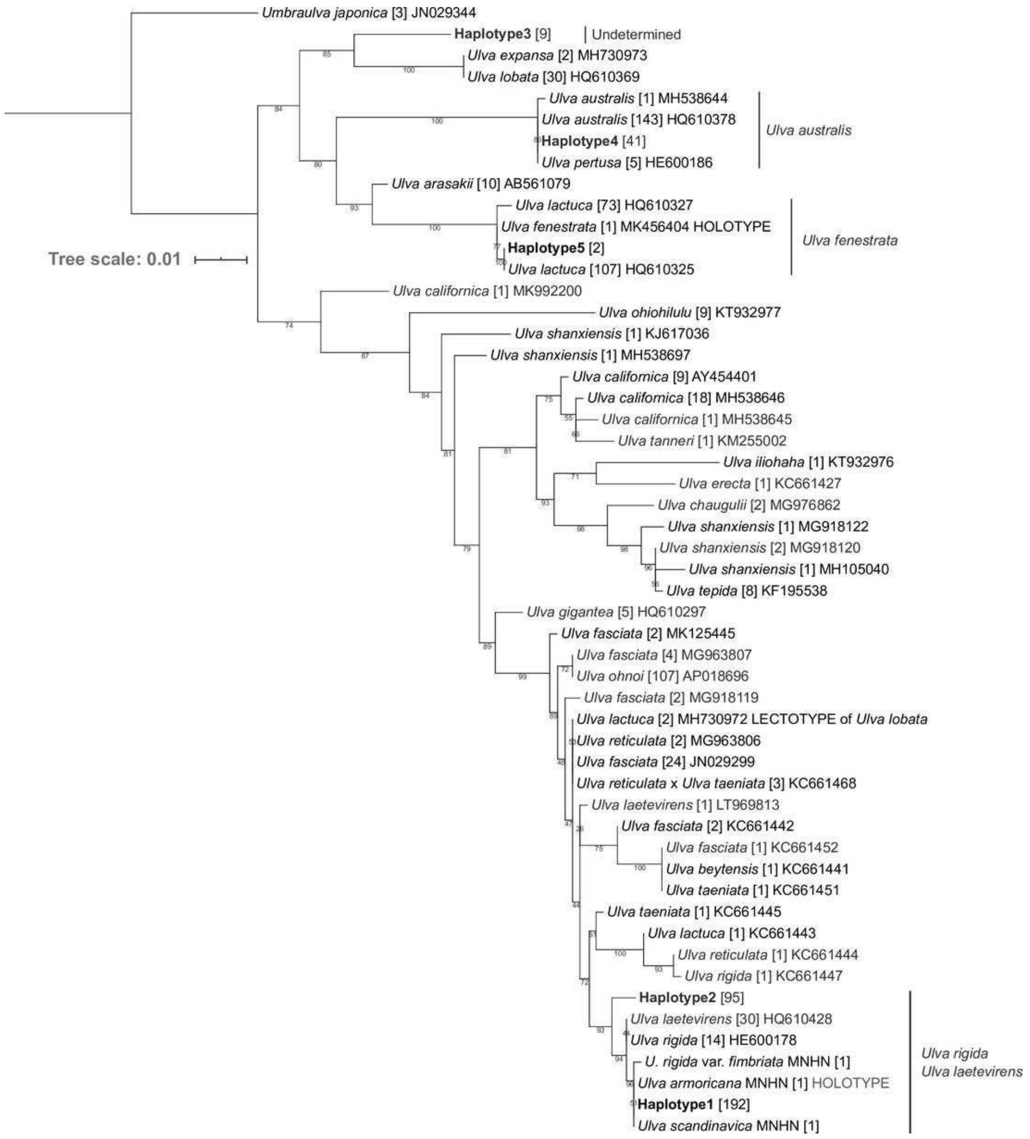


Figure 2

Maximum Likelihood (ML) phylogeny based on 500 bp of the tufA gene chloroplastic gene.

Haplotypes detected in this study are in bold. Bootstrap support values from the ML analysis are indicated under each node. Sample size, for each haplotype, is presented in brackets. Unit of scale bar: substitution/site. MNHN : Muséum National d’Histoire Naturelle, Paris.


Umbraulva japonica [3] JN029344
Haplotype3 [9]
Undetermined
Ulva expansa [2] MH730973
Ulva lobata [30] HQ610369
Ulva australis [1] MH538644
Ulva australis [143] HQ610378
Haplotype4 [41]
Ulva pertusa [5] HE600186
Ulva australis
Ulva arasakii [10] AB561079
Ulva lactuca [73] HQ610327
Ulva fenestrata [1] MK456404 HOLOTYPE
Haplotype5 [2]
Ulva lactuca [107] HQ610325
Ulva fenestrata
Tree scale: 0.01
Ulva californica [1] MK992200
Ulva ohiohilulu [9] KT932977
Ulva shanxiensis [1] KJ617036
Ulva shanxiensis [1] MH538697
Ulva californica [9] AY454401
Ulva californica [18] MH538646
Ulva californica [1] MH538645
Ulva tanneri [1] KM255002
Ulva iliohaha [1] KT932976
Ulva erecta [1] KC661427
Ulva chaugulii [2] MG976862
Ulva shanxiensis [1] MG918122
Ulva shanxiensis [2] MG918120
Ulva shanxiensis [1] MH105040
Ulva tepida [8] KF195538
Ulva gigantea [5] HQ610297
Ulva fasciata [2] MK125445
Ulva fasciata [4] MG963807
Ulva ohnoi [107] AP018696
Ulva fasciata [2] MG918119
Ulva lactuca [2] MH730972 LECTOTYPE of Ulva lobata
Ulva reticulata [2] MG963806
Ulva fasciata [24] JN029299
Ulva reticulata x Ulva taeniata [3] KC661468
Ulva laetevirens [1] LT969813
Ulva fasciata [2] KC661442
Ulva fasciata [1] KC661452
Ulva beytensis [1] KC661441
Ulva taeniata [1] KC661451
Ulva taeniata [1] KC661445
Ulva lactuca [1] KC661443
Ulva reticulata [1] KC661444
Ulva rigida [1] KC661447
Haplotype2 [95]
Ulva laetevirens [30] HQ610428
Ulva rigida [14] HE600178
U. rigida var. fimbriata MNHN [1]
Ulva armoricana MNHN [1] HOLOTYPE
Haplotype1 [192]
Ulva scandinavica MNHN [1]
Ulva rigida
Ulva laetevirens