A Comprehensive and Comparative Analysis of the Fucoidan Compositional Data Across the Phaeophyceae

Nora M. A. Ponce* and Carlos A. Stortz*

Departamento de Química Orgánica, Ciudad Universitaria, Facultad de Ciencias Exactas y Naturales, Consejo Nacional de Investigaciones Científicas y Técnicas, Centro de Investigaciones en Hidratos de Carbono (CIHIDECAR/CONICET), Universidad de Buenos Aires, Buenos Aires, Argentina

In the current review, compositional data on fucoids extracted from more than hundred different species were surveyed through the available literature. The analysis of crude extracts, purified extracts or carefully isolated fractions is included in tabular form, discriminating the seaweed source by its taxonomical order (and sometimes the family). This survey was able to encounter some similarities between the different species, as well as some differences. Fractions which were obtained through anion-exchange chromatography or cationic detergent precipitation showed the best separation patterns: the fractions with low charge correspond mostly to highly heterogeneous fucoids, containing (besides fucose) other monosaccharides like xylose, galactose, mannose, rhamnose, and glucuronic acid, and contain low-sulfate/high uronic acid proportions, whereas those with higher total charge usually contain mainly fucose, accompanied with variable proportions of galactose, are highly sulfated and show almost no uronic acids. The latter fractions are usually the most biologically active. Fractions containing intermediate proportions of both polysaccharides appear at middle ionic strengths. This pattern is common for all the orders of brown seaweeds, and most differences appear from the seaweed source (habitat, season), and from the diverse extraction, purification, and analytical methods. The Dictyotales appear to be the most atypical order, as usually large proportions of mannose and uronic acids appear, and thus they obscure the differences between the fractions with different charge. Within the family Alariaceae (order Laminariales), the presence of sulfated galactofucans with high galactose content (almost equal to that of fucose) is especially noteworthy.

Keywords: fucoids, brown seaweeds, phaeophyceae, taxonomy, phylogeny

INTRODUCTION: AIM OF THE REVIEW

Fucoids are sulfated polysaccharides present in the cell walls of the Phaeophyceae (brown seaweeds) composed usually by fucose (Fuc) as the main monosaccharide, but accompanied by very variable amounts of other monosaccharides like galactose (Gal), xylose (Xyl), mannose (Man), rhamnose (Rha), and/or glucuronic acid (GlcA). The scientific literature on different aspects of
The taxonomy of brown algae (Heterokonta, Ochrophyta, Phaeophyceae) had many controversies throughout the history (Silberfeld et al., 2014). Order delineation in the Phaeophyceae has traditionally been based on the type of life cycle, reproductive aspects, mode of growth, and filamentous vs. parenchymatous construction of the thallus (Rousseau and de Reviers, 1999a,b). However, with the advent of molecular systematics, new insights were brought, thoroughly reshaping the evolutionary concepts of brown algae. Rousseau and de Reviers (1999b) and de Reviers et al. (2007) have provided a detailed evolution of classificatory concepts within the Phaeophyceae. Several changes in the classification at the ordinal level have been set between the Oltmanns (1922), comprising 8 orders to the present times classification, encompassing 18 orders (Silberfeld et al., 2014; Figure 1). Major changes were produced after the DNA sequencing of brown seaweeds started in 1993 (Draisma et al., 2001, 2003; de Reviers et al., 2007). Different molecular markers can be used, but phylogenetic studies of Phaeophyceae have mostly utilized the rDNA sequences, which include four subunits (18S, 5.8S, 26S, and 5S), containing regions which are highly conserved as well as others highly variable. Most information arose from studies on the 18S subunit of rDNA, although those studies had limited results for more recent Phaeophycean lineages (Tan and Druhl, 1996). In this way, Rousseau et al. (2001) utilized the 26S sequence, which altogether with a larger taxonomic sampling, solved some of the earlier divergences. Thus, a phylogenetic tree was constructed (Draisma et al., 2001, 2003). It has been concluded that morphological characters, many times useful to understand the ecology of brown seaweeds, have no value at all for phylogeny. Different degrees of organization, diffuse or apical growth, or life stages have appeared and disappeared repeatedly in the history of the different taxonomic groups.

Silberfeld et al. (2014) have introduced a thorough phylogenetic analysis based on a dataset generated previously (Silberfeld et al., 2011), including seven markers, for a total of 6804 nucleotides, determined for 91 Phaeophycean taxa, including minor orders for which there were very few studies. In this way, the shape of phylogenetic trees changed sharply the previous knowledge (Silberfeld et al., 2011; Charrrier et al., 2012). Figure 1 depicts the outcome of the tree for the 18 orders determined by Silberfeld et al. (2014), grouped in four subclasses (Discosporangiophycidae and Ishigeophycidae, including one order each, Dictyotophycidae, including four orders, and Fucophycidae, including the remaining 12 orders).

POLYSACCHARIDES FROM THE PHAEOPHYCEAE: THE FUCOIDANS

Most macroalgae exhibit polysaccharides as their most abundant constituents. Taking into account their function, they can be classified into two main groups: storage and structural polysaccharides. The formers are polymers such as starch/glycogen or laminaran considered as food reserve materials, whereas the latters are structural elements of the cell walls, intercellular tissues and mucilaginous matrix. Sulfated polysaccharides are a group of anionic structural polysaccharides, useful for the seaweed in the marine environment to avoid desiccation. Their gross composition is characteristic of each algal group (galactans in red seaweeds, fucoids in brown seaweeds, rhamnoglucuronans, and arabinogalactans in green seaweeds, van den Hock et al., 1996), whereas more or less subtle differences appear often depending on the order, family, genus and species, as well as sometimes on the season, geographic location, or reproductive stage (Mackie and Preston, 1974). Other roles of the polysaccharides might include participations in cell-cell communication (Deniaud-Bouët et al., 2014), and in cell division processes (Skripitsova, 2015).

In macroalgae, the cell walls comprise a fibrillar skeleton immersed in an amorphous matrix. In the case of the Phaeophyceae, the fibrillar skeleton is mainly made up of cellulose [a linear β-(1→4)-glucan], and the surrounding matrix is composed predominantly by alginic acid or its salts, together with a system of sulfated polysaccharides (the fucoids; Mackie and Preston, 1974). In this way, the cell wall is composed of two different layers: the inner layer consisting of a skeleton of microfibrils providing rigidity to the cell wall, and the outermost layer, which is usually observed as a poorly crystalline matrix
in which the set of microfibrils is embedded. There is also evidence that the matrix does not penetrate the fibers, but remains attached to this layer through hydrogen bonds (Davis et al., 2003). It has been suggested that fucoidans might play a key role in cell wall architecture, cross-linking cellulose and alginites (Kloareg et al., 1986). Besides this function, as occurs with other sulfated polysaccharides, the fucoidans help to protect the plant from desiccation. When the fronds are in contact with sea water the sulfate hemiester groups are strongly associated with magnesium ions, which are highly hydrated and thus retain water in the fronds (Percival, 1979). In a more modern model for the Fucales (Deniaud-Bouët et al., 2014, 2017; Torode et al., 2016), it has been proposed that two networks are assembled in the cell wall; the first one contains the fucoidans interlocking a cellulose (or other β-glucans) network, and the second one contains alginate crosslinked by polyphenols. The rigidity is controlled by the alginate structure and its calcium cross-linking capabilities, whereas the fucoidans participate mostly in adaptation to the osmotic stress.

More than one century ago, Kylin has isolated for the first time (from different seaweed species of the genera Fucus, Laminaria, and Ascophyllum) a group of sulfated polysaccharides with a high...
Fuc content and called them “fucoidin” (Kylin, 1913). Originally the name fucoidin (later changed to the more systematic fucoidan) was coined for the polysaccharides from those species, but this term was rapidly extended to any fucose-rich polysaccharides, including not only those becoming from brown seaweeds, but also to those present in echinoderms (Olatunji, 2020). As noted above, fucoidans are sulfated polysaccharides present mainly in the intercellular tissue of mucilaginous matrix of the cell walls of brown algae (Deniaud-Bouët et al., 2017).

Fucoidans comprise a family of diverse molecules containing, in addition to Fuc, varying proportions of Gal, Man, Xyl and GlcA (Figure 2). Acetate esters have also been found, especially in modern studies (see below). In the early studies extensive purification was carried out in an effort to isolate a “fucan” containing only Fuc residues, assuming that the remaining monosaccharides were originated in other, contaminating polysaccharides. Nevertheless, even in the allegedly pure samples, small proportions of Gal, Xyl, and/or uronic acid persisted (Percival, 1979). Later, only in a few species a pure fucan was isolated after purification (see below). Thus, most of the samples so far isolated are heterofucans (Deniaud-Bouët et al., 2014).

**FUCOIDANS FROM DIFFERENT SPECIES OF PHAEOPHYCEAE**

In this section, the main chemical characteristics of fucoidans extracted from different species of brown seaweeds reported so far to the best of our knowledge (with compositional data provided) will be described in tabular form. They will be shown separately for each of the different orders (Figure 1). When numerous species of an order were studied, separations in families or genera are also displayed. It is worth noting that depending on the way that the analyses were expressed in the original papers, the uronic acids in the following tables were indicated as a percentage of the total sample (in most cases) or as part of the molar ratio of all the monosaccharides. Thus, these molar ratios might or might not include the uronic acid components. The main monosaccharidic units appearing in fucoidans are shown in Figure 2. When the authors have isolated a large number of fractions, only those more abundant or representative are listed in the tables. The reported presence of acetyl groups is indicated qualitatively with the “Ac” acronym. It should be noted that the geographic location and season of harvest of the seaweed can also have significant effects on the composition of the extracted fucoidans (e.g., Zvyagintseva et al., 2003). The extraction and fractionation procedures are schematically displayed, neglecting defatting and depigmenting steps, as well as usual procedures like dialysis or single alcohol precipitations. The methods used for monosaccharide and sulfate quantitation are also shown.

**Fucales**

As expected, samples of fucoidans from this is order were the most studied. Samples from five different families of the Fucales have been studied. Two species from the Fucaceae, i.e., *Fucus vesiculosus* and *Asphodelinum nodosum* appear in the earlier studies by Kylin (1913). The polysaccharides from these species were studied extensively by different research groups (see below). However, the family with more species studied was the Sargassaceae. Considering only the genus *Sargassum*, studies on the fucoidans from 26 different species were found in the current survey.

The extraction of fucoidans from *Fucus vesiculosus* was originated in the early Kylin studies, when Fuc was characterized after hydrolysis as phenyl-L-fucosazone; pentoses in the hydrolyzate were also reported (Kylin, 1913). Different products from this species were extensively studied (Table 1). Originally, the presence of Xyl was ascribed to a contaminating xylan that accompanied the fucoidan (Percival and McDowell, 1967). As a matter of fact, they reported the isolation of a xylan, although uronic acid residues were found in the xylan fraction and, furthermore, the authors were not able to separate any fraction composed just by Fuc residues. The studies by Nishino et al. (1994a) on a commercial sample from this seaweed were highly comprehensive: they were able to separate 13 different fractions and analyze them thoroughly, showing structures ranging from typical fucans (containing mainly Fuc and sulfate, and free of uronic acids) to heteropolysaccharides with low sulfate content and high content of uronic acids. In a minor fraction, they were able to find an appreciable amount of glucosamine (11.5%). In an interesting study using microwave extraction of this seaweed, Rodriguez-Jasso et al. (2011) showed that depending on the pressure and extraction time, fucoidans with different ratios Fuc/Gal were obtained (ranging from 100% Fuc to a 1:1 ratio), plus variable proportions of Xyl and sulfation degrees. Another species from the same genus that has been studied is *Fucus evanescens*. Zvyagintseva et al. (1999) separated the polysaccharides using a chromatography system on a hydrophobic resin. It is interesting to note that in a subsequent work Zvyagintseva et al. (2003) analyzed specimens of three different seaweeds (*F. evanescens*, *Laminaria cichorioides*, and *Saccharina japonica*) collected at different places, at various stages of development and at different seasons, and found some
| Species          | Extraction          | Purification/ Acronym | Monosaccharide composition (moles %) | Sulfate | UA (%) | References            |
|------------------|---------------------|-----------------------|-------------------------------------|---------|--------|-----------------------|
|                  |                     |                       | Fuc | Xyl | Gal | Man | Glc | Rha | GlcA | Others | Method | Method | %       |
| **Fucus vesiculosus** |                    |                       |     |     |     |     |     |     |     |        |         |         |
| HCl pH 2         | Ethanol ppt         | F1                    | GC  | 50  | 15  | 4   | 17 | 14  |      | Pb 4   | 22      | Medicall and Larsen (1977a) |
| HCl 0.01M + CaCl₂ 1% | Ethanol ppt         | F2                    | GC  | 70  | 7   | 8   | 4  | 11  |      | Pb 25  | 6       | Mabeau and Kloareg (1987) |
| pH 7.5 + CaCl₂ 1% | EtOH + TCA 10%      | FF                    | GC  | 79  | 10  | 6   | 3  | 2   |      | Tit 31  | 14      | Mabeau et al. (1990)       |
| Trion 0.5%, pH 7.5 + CaCl₂ 1% | EtOH + TCA 10%      | TF                    | GC  | 84  | 2   | 13  | 1  |      |      | Tit 26  | 4       | Mabeau et al. (1990)       |
| HCl 0.01M + CaCl₂ 1% | HCl 0.01M ppt       | OHF                   | GC  | 78  | 11  | 5   | 3  | 3   |      | Tit 14  | 9       | Mabeau et al. (1990)       |
| Na₂CO₃ 3%        |                     |                       |     |     |     |     |     |     |     |        |         | Nishino et al. (1994a)     |
| SigmaTM          | SEC + AEC I1.8      | GC                    | 90  | 3   | 5   | 2   |     |     |     |        | DP 32  | 3       | *        |
| SigmaTM          | SEC + AEC I1.35     | GC                    | 94  | 1   | 5   | tr. |     |     |     |        | DP 33  | –       | *        |
| SigmaTM          | SEC + AEC I2        | GC                    | 94  | 1   | 5   |     |     |     |     |        | DP 36  | –       | *        |
| SigmaTM          | SEC + AEC III11.5   | GC                    | 93  | 2   | 5   |     |     |     |     |        | DP 34  | –       | *        |
| H₂O, r.t.        | F1                  | GC                    | 55  | 11  | 9   | 25  |     |     |     |        | DP 6   | 39      | Rupérez et al. (2002)      |
| HCl 0.1M         | F3                  | GC                    | 89  | 6   | 5   |     |     |     |     |        | DP 11  | 9       | *        |
| CaCl₂ 2% hot     | PQA                 | GC                    | 67  | 6   | 13  | 8   | 6   |     |     |        | DP 24  | 10      | Cumashi et al. (2007)      |
| CaCl₂ 2% hot     | PQA + AEC F₂        | GC                    | 84  | 10  | 3   | 2   | 1   |     |     |        | DP 24  | –       | *        |
| CaCl₂ 2% hot     | PQA + AEC F₂        | GC                    | 83  | 9   | 4   | 2   | 1   |     |     |        | DP 24  | –       | *        |
| CaCl₂ 2% hot     | PQA + AEC F₂        | GC                    | 96  | 2   | 2   | Ac  |     |     |     |        | DP 35  | –       | *        |
| H₂O₂, r.t.       | F1                  | HPLC                  | 90  | 3   | 1   | 6   |     |     |     |        | DP ~12 | ND      | Zvyagintseva et al. (1999) |
| HCl 0.4% r.t. + H₂O hot | F₂ | HPLC                  | 91  | 7   | 1   |     |     |     |     |        | DP ~25 | ND      | *        |
| CaCl₂ 2% hot     | PQA + AEC F₃        | GC                    | 67  | 16  | 9   | 7   |     |     |     |        | DP 29  | 11      | Bittkau et al. (2002)      |
| CaCl₂ 2% hot     | PQA + AEC F₄        | GC                    | 94  | 3   | 6   |     | Ac  | 43  |     |        | DP 46  | –       | *        |
| HCl pH 2-2.3 hot | AEC                 | HPLC                  | 87  | 2   | 2   | 4   | 1   |     |     |        | DP 28  | ND      | Anastyuk et al. (2012b)    |
| HCl 0.2M hot     | Sterile HPLC        | HPLC                  | 69  | 7   | 9   | 8   | 6   | 1   |     |        | ND    | ND      | Skripotsova et al. (2012)  |
| HCl 0.2M hot     | Reprod. HPLC        | HPLC                  | 77  | 5   | 5   | 3   | 10  |     |     |        | ND    | ND      | *        |
| HCl pH 2-2.3     | FeF                 | HPLC                  | 78  | 8   | 10  | 4   | Ac  |     |     |        | DP 23  | ND      | Prokofjeva et al. (2013)   |
| CaCl₂ 2% hot     | GC                  | 96                 | 4   |     |     |     |     |     |     |        | EA 27  | 4       | Bittkau et al. (2020)      |
| **Fucus ceranoides** |                    |                       |     |     |     |     |     |     |     |        |         |         |
| HCl 0.01M + CaCl₂ 1% | Ethanol ppt         | F1                    | GC  | 76  | 18  | 5   | 1   |     |     |        | DP 22  | 15      | Mabeau and Kloareg (1987)  |
| CaCl₂ 2% hot     | AEC                 | F₂                    | GC  | 86  | 6   | 4   | 2   | 1   | Ac   |        | DP 22  | –       | Bilan et al. (2006)        |
| CaCl₂ 2% hot     | AEC                 | F₄                    | GC  | 94  | 3   | 3   |     |     |     | Ac    | DP 32  | –       | *        |
| CaCl₂ 2% hot     | PQA + AEC F₂        | GC                    | 69  | 7   | 13  | 6   | 5   |     |     |        | DP 29  | 8       | Cumashi et al. (2007)      |
| CaCl₂ 2% hot     | GC                  | 41                 | 10  | 4   | 2   | 43  |     |     |     |        | EA 12  | 6       | Bittkau et al. (2020)      |

(Continued)
| Species                  | Extraction                  | Purification/ Acronym | Monosaccharide composition (moles %) | Sulfate | UA (%) | References               |
|-------------------------|-----------------------------|-----------------------|--------------------------------------|---------|--------|--------------------------|
| **Fucus spiralis**      | HCl 0.01M + CaCl₂ 1%        |                       | Fuc 90 | Xyl 7 | Gal 3 | Man 1 | Glc 3 | Rha 3 | Others 1 | Tit 36 | 10 | Mabeau and Kloareg (1987) |
|                         | CaCl₂ 2% hot                |                       | GC 80 | 7 | 7 | 3 | 3 |        |        |        | DP 26 | 8 | Cumashi et al. (2007)     |
| **Ascophyllum nodosum** | HCl 0.2M                    |                       | GC 49 | 51 | 1% | GC 90 | 7 | 3 | 3 |        |        |     | Larsen et al. (1966)      |
|                         | AP/R                        |                       | CC 49 | 51 | 1% | GC 86 | 14 | 16 |        |        |     | Larsen et al. (1966)      |
|                         | CaCl₂ 0.04M + CE            | F₂                    | GC 73 | 11 | 1% | 2 | 10 | 5 |        |        |     | Larsen et al. (1966)      |
|                         | H₂O + NaOH pH 2.8g          | CaCl₂ 2%              | GC 73 | 11 | 1% | 2 | 10 | 5 |        |        |     | Cumashi et al. (2007)     |
|                         | HCl pH 2                    | Ethanol ppt            | F₁     | GC 37 | 29 | 3 | 21 | 11 |        |        |     | Percival (1968)           |
|                         | HCl pH 2                    | Ethanol ppt            | F₂     | GC 73 | 11 | 1% | 2 | 10 | 5 |        |        |     | Percival (1968)           |
|                         | HCl pH 2                    | Ethanol ppt            | F₃     | GC 81 | 9 | 2 | 4 | 4 |        |        |     | Percival (1968)           |
|                         | HCl pH 2                    | Ethanol ppt            | F₄     | GC 34 | 14 | 27 | 15 | 10 |        |        |     | Percival (1968)           |
|                         | HCl pH 2                    | Ethanol ppt            | F₅     | GC 71 | 7 | 14 | 4 | 4 |        |        |     | Percival (1968)           |
| **Ascophyllum mackaii** | H₂O hot                     | CaCl₂ 1% + AP/R        | GC 67 | 11 | 12 | 7 | 3 |        |        |     | Medcalf et al. (1978)     |
|                         | CaCl₂ 2% hot                | PQA                   | GC 67 | 11 | 12 | 7 | 3 |        |        |     | Medcalf et al. (1978)     |
|                         | H₂O + HCl 0.2M              | AP/R                  | HPLC 47 | 40 | 2 | 10 | 1 |        |        |     | Medcalf et al. (1978)     |
|                         | CaCl₂ 1% + AP/R             | F₂                   | GC 82 | 8 | 7 | 2 | 1 |        |        |     | Medcalf et al. (1978)     |
| **Pelvetia canaliculata**| pH 7.5 + CaCl₂ 1%           | EtOH + TCA 10%        | GC 82 | 4 | 10 | 2 | 2 |        |        |     | Mabeau et al. (1990)      |
|                         | Trigon 0.5%, pH 7.5 + CaCl₂ 1%| EtOH + TCA 10%     | GC 65 | 13 | 11 | 6 | 5 |        |        |     | Mabeau et al. (1990)      |
|                         | Na₂CO₃ 3%                   | HCl 0.01M ppt         | GC 90 | 4 | 4 | 1 | 1 |        |        |     | Yuan and Macquarrie (2015) |
| **Silvetia babingtonii**| HCl pH 2-2.3 hot            | AEC                   | HPLC 77 | 5 | 12 | 6 |        |        |     | Ou et al. (2014)          |
|                         | HCl 0.2M hot                | Sterile               | HPLC 71 | 7 | 6 | 5 | 10 |        |        |     | Mabeau et al. (1990)      |
|                         | HCl 0.2M hot                | Reprod.               | HPLC 80 | 6 | 6 | 4 | 4 |        |        |     | Mabeau et al. (1990)      |

*a* Key: AEC, anion exchange chromatography; SEC, size-exclusion chromatography; HC, hydrophobic chromatography; CE, cation exchange; PQA, precipitation with quaternary ammonium salts; AP/R alcohol precipitation and redissolution.

*b* Key for the less common abbreviations: PAD, HPAEC with pulse amperometric detector; GC, gas chromatography; CC, column chromatography on carbon-Celite.

*c* Key: DP, method of Dodgson and Price (1962) or equivalent; Pb, titration with lead nitrate (Medcalf et al., 1972); EA, elemental analysis; Tit, titration with cetylpyridinium chloride, pH 1.5 (Scott, 1960); BC, method of barium chloranilate (Lloyd, 1959).

*d* Analyzed as Fucus distichus subsp. evanescens.

*e* The information for the uronic acid is included in the molar ratio of monosaccharides.

*f* Oxalic acid/ammonium oxalate extraction of the residue.

*g* Microwave-aided extraction.
### TABLE 2 | Reported compositions of the fucoidans from the genus Sargassum (Sargassaceae, Fucales).

| Species              | Extraction                  | Purification/ Fractionation$^a$ | Acronym | Method$^b$ | Fuc | Xyl | Gal | Man | Glc | Rha | GlcA | Others | Sulfate | UA (%) | References                  |
|----------------------|-----------------------------|---------------------------------|---------|------------|-----|-----|-----|-----|-----|-----|------|-------|--------|---------|
| *Sargassum aquifolium* | $H_2O + HCl pH 1$           | AEC 0.5M                         | GC      |            | 14  | 15  | 37  | 13  | 21  |     |      |        |        | Bilan et al. (2017) |
|                      | $H_2O + HCl pH 1$           | AEC 1.0M                         | GC      |            | 15  | 9   | 25  | 10  | 6   |     |      |        |        | "                  |
|                      | $H_2O + HCl pH 1$           | AEC 1.0M                         | GC      |            | 21  | 17  | 10  | 14  | 6   |     |      |        |        | "                  |
| *Sargassum bindii*    | CaCl$_2$ 2% hot             | PQA Fisol                       | GC      |            | 60  | 5   | 19  | 7   | 3   |     |      |        |        | Lim et al. (2016)  |
| *Sargassum cinereum*  | $H_2O + CaCl_2$ 1%          | HPDC AEC 0.5M                    | PAD     |            | 66  | 7   | 24  | 3   |     |     |      |        |        | Somasundaram et al. (2016) |
| *Sargassum crassifolium* | $H_2O + CaCl_2$ 1%          | HPDC AEC 0.5M                    | PAD     |            | 60  | 5   | 19  | 7   | 3   |     |      |        |        | "                  |
|                      | $H_2O + CaCl_2$ 1%          | HPDC AEC 1.0M                    | PAD     |            | 60  | 5   | 19  | 7   | 3   |     |      |        |        | "                  |
| *Sargassum duplicatum* | HC$_2$O 1.0M hot            | AEC+HC SdF$_1$                  | GC      |            | 40  | 5   | 7   | 3   |     |     |      |        |        | Shevchenko et al. (2017) |
|                      | HC$_2$O 0.1M hot             | AEC+HC SdF$_2$                  | GC      |            | 59  | 2   | 8   | 3   |     |     |      |        |        | "                  |
|                      | HC$_2$O 0.1M hot             | AEC+HC SdF$_3$                  | GC      |            | 51  | 4   | 9   |     |     |     |      |        |        | "                  |
|                      | HC$_2$O 0.1M hot             | AEC+HC SdF$_4$                  | GC      |            | 51  | 4   | 9   |     |     |      |        |        | "                  |
| *Sargassum feldmannii* | Enzymes pH 8                 | Acetone ppt SH-0.7HPLC          | GC      |            | 22  | 16  | 27  | 16  | 16  |     |      |        |        | Costa et al. (2011) |
|                      | Enzymes pH 8                 | Acetone ppt SH-1.0HPLC          | GC      |            | 22  | 16  | 27  | 16  | 16  |     |      |        |        | "                  |
| *Sargassum fusiforme*  | $H_2O$, hot                  | AEC+SEC SFPs                    | GC      |            | 53  | 9   | 20  | 21  |     |     |      |        |        | Chen et al. (2012)  |
|                      | Enzymes                     | AEC+SEC 65A                     | GC      |            | 42  | 15  | 21  | 6   | 2   |     |      |        |        | "                  |
| *Sargassum hemiphyllum* | Enzymes pH 8                | Acetone ppt SH-0.7HPLC          | GC      |            | 22  | 16  | 27  | 16  | 16  |     |      |        |        | Huang et al. (2017) |
|                      | Enzymes pH 8                | Acetone ppt SH-0.7HPLC          | GC      |            | 22  | 16  | 27  | 16  | 16  |     |      |        |        | "                  |
| *Sargassum henslowianum* | $H_2O$, AP/R               | AEC+SEC SHAP-1                  | HPLC    |            | 76  | 24  |    |     |     |      |      |        |        | Sun et al. (2020)  |
|                      | $H_2O$, AP/R               | AEC+SEC SHAP-2                  | HPLC    |            | 75  | 25  |    |     |     |      |      |        |        | "                  |
| *Sargassum horneri*   | HC$_2$O 0.1M hot            | AEC Sh-F1                       | HPLC    |            | 81  | 3   | 8   | 7   |     |     |      |        |        | "                  |
|                      | HC$_2$O 0.1M hot            | AEC Sh-F2                       | HPLC    |            | 90  | 10  |    |     |     |      |      |        |        | "                  |
|                      | HC$_2$O 0.1M hot            | AEC Sh-F3                       | HPLC    |            | 69  | 31  |    |     |     |      |      |        |        | "                  |
|                      | CaCl$_2$ 2% hot             | AEC                             | GC      |            | 90  | 10  |    |     |     |      |      |        |        | "                  |
| *Sargassum isatofolium* | $H_2O$, hot                | AEC+SEC SP-I                    | HPLC    |            | 14  | 14  | 42  | 23  |     |     |      |        |        | Asker et al. (2007)  |
|                      | $H_2O$, hot                | AEC+SEC SP-II                   | HPLC    |            | 15  | 13  | 41  | 29  |     |     |      |        |        | "                  |
|                      | $H_2O$, hot                | AEC+SEC SP-III                  | HPLC    |            | 15  | 13  | 41  | 29  |     |     |      |        |        | "                  |
| *Sargassum mcclurei*  | HC$_2$O 2.5 hot             | AEC SmF1                        | HPLC    |            | 27  | 6   | 20  | 13  |     |     |      |        |        | Thinh et al. (2013) |
|                      | HC$_2$O 2.5 hot             | AEC SmF2                        | HPLC    |            | 45  | 5   | 34  | 5   | 10  |     |      |        |        | "                  |
|                      | HC$_2$O 2.5 hot             | AEC SmF3                        | HPLC    |            | 59  | 34  | 41  |    |     |      |        |        | "                  |
| *Sargassum muticum*   | pH 7.5+CaCl$_2$ 1%          | EtOH+TCA 10%                     | GC      |            | 44  | 5   | 46  | 3   | 3   |     |      |        |        | "                  |
|                      | pH 7.5+CaCl$_2$ 1%          | EtOH+TCA 10%                     | GC      |            | 44  | 5   | 46  | 3   | 3   |     |      |        |        | "                  |
|                      | pH 7.5+CaCl$_2$ 1%          | EtOH+TCA 10%                     | GC      |            | 44  | 5   | 46  | 3   | 3   |     |      |        |        | Usoltseva et al. (2017b) |
|                      | Triton 0.5%                 | EtOH+TCA 10%                     | GC      |            | 44  | 5   | 46  | 3   | 3   |     |      |        |        | "                  |

(Continued)
### TABLE 2 | Continued

| Species                  | Extraction                          | Purification/ Acronym | Monosaccharide composition (moles %) | Sulfate | UA (%) | References                      |
|--------------------------|-------------------------------------|-----------------------|--------------------------------------|---------|--------|----------------------------------|
|                          |                                     |                       |                                      |         |        |                                  |
|                          |                                     |                       |                                      | Method  | %      |                                  |
|                          |                                     |                       |                                      |         |        |                                  |
| Sargassum elongatum      | HCl 0.1M hot                         | AEC                   | 1SoF1 HPLC                           | DP      | 17     | ND                              |
|                          | HCl 0.1M hot                         | AEC                   | 1SoF2 HPLC                           | DP      | 24     | ND                              |
|                          | HCl 0.1M hot                         | AEC                   | 1SoF3 HPLC                           | DP      | 32     | ND                              |
| Sargassum pallidum       | HCl 0.2M hot                         | Sterile               | HPLC                                | ND      | ND     | Skriptsova et al. (2012)        |
|                          | Hi 0.1M hot                          | AEC                   | HPLC                                | DP      | 4      | 33                              |
|                          | Hi 0.1M hot                          | AEC                   | HPLC                                | DP      | 4      | 29                              |
|                          | Hi 0.1M hot                          | AEC                   | HPLC                                | DP      | 7      | 20                              |
| Sargassum polyestrum     | HCl pH 2-3 hot                       | HC+AE                | F1 GC                               | 76      | 23     | Bilan et al. (2013)             |
|                          | HCl pH 2-3 hot                       | HC+AE                | F2 GC                               | 20      | 11    |                                 |
|                          | HCl pH 2-3 hot                       | HC+AE                | F3 GC                               | 33      | 2     |                                 |
|                          | HCl pH 2-3 hot                       | HC+AE                | F4 GC                               | 34      | 2     |                                 |
|                          | Enzymes pH 4.5                       | CaCl 5M               | SPF PAD                             | 28      | 22    | Fernando et al. (2018)          |
| Sargassum ringgoldianum  | HCl 0.05M Ca(AcO) 2+ AEC             | Fr-B                  | GC                                   | 16      | 10    | Mori and Nisizawa (1982)        |
|                          | HCl 0.5M Ca(AcO) 2+ AEC              | Fr-C                  | GC                                   | 24      | 7     |                                 |
| Sargassum stenophyllum   | H2O + CaCl 2 4M                      | PQA                  | F2 GC                               | 19      | 11    | Duarte et al. (2001)            |
|                          | H2O + CaCl 2 4M                      | PQA                  | F3 GC                               | 21      | 10    |                                 |
|                          | H2O + CaCl 4 4M                      | PQA                  | F5 GC                               | 28      | 2     |                                 |
| Sargassum swartzi        | HCl 0.1M + CaCl 2 2%                 | PQA+AE               | F2 PAD                             | 15      | 13    | Ly et al. (2005)                |
|                          | HCl 0.1M + CaCl 2 2%                 | PQA+AE               | F3 PAD                             | 18      | 5     |                                 |
|                          | HCl 0.1M + CaCl 4 4%                 | PQA+AE               | F4 PAD                             | 28      | 8     |                                 |
|                          | HCl 0.05 M+ CaCl 2 4%                | AEC                  | FF1 HPLC                           | 19      | 18    | Dinesch et al. (2016)           |
|                          | HCl 0.05 M+ CaCl 4 4%                | AEC                  | FF2 HPLC                           | 24      | 13    |                                 |
| Sargassum tenerrimum     | HCl 0.1M - K2CO3 2%                  | CaCl 2% + HCl 0.1M   | C GC                                | 2      | 9     | Sinha et al. (2010)             |
| Sargassum tricharophyllum| H2O, hot                            | AEC+SEC              | STF GC                              | 23      | 1     | Lee et al. (2011)               |
|                          | H2O + NaOH 0.5M                      | AEC                  | STSP-I GC                           | 0       | ND    | Luo et al. (2019)               |
| Sargassum hentillanum    | H2O                                 | CaCl 2                | SPS HPLC                           | 12      | 1     | Jesumani et al. (2020)          |
| Sargassum vulgare        | Enz, pH 8                           | AEC                  | Flo 1.5 Col. 50                     | HexA 25 | 15 d | Dietrich et al. (1995)          |
|                          | Enz, pH 8                           | AEC                  | Flo 2.5 Col. 77                     | HexA 15 | 41 d |                                 |

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*Key: AEC = anion exchange chromatography; SEC = size-exclusion chromatography; HC = hydrophobic chromatography; PQA = precipitation with quaternary ammonium salts; AP/R = alcohol precipitation and redissolution.*

*Key for the less common abbreviations: PAD = HPAEC with pulse amperometric detector; GC = gas chromatography; Col. = colorimetric methods.*

*Key: DP = method of Dodgson and Price (1962) or equivalent; IC = ion chromatography; EA = elemental analysis; IR = estimation by area of IR bands; TB = toluidine blue; Rho = rhodizonate; Tit = titration with cetylpyridinium chloride, pH 1.5 (Scott, 1960).*

*The information for the uronic acid is included in the molar ratio of monosaccharides.*

*PT = high pressure and temperature.*

*NI = sugar not identified.*

*Fuc, Xyl and uronic acid were the only monosaccharides which could be determined.*
| Species | Extraction | Purification/ Fractionation | Acronym | Monosaccharide composition (moles %) | Sulfate | UA (%) | References |
|---------|------------|---------------------------|---------|-------------------------------------|---------|--------|------------|
|         |            | Method | Fuc | Xyl | Gal | Man | Glc | Rha | GlcA | Others | Method | %     |
| **Species** | **Extraction** | | | | | | | | | | | | **References** |
| **Family Sargassaceae** | | | | | | | | | | | | |
| Bifurcaria bifurcata | CaCl₂, 2% + HCl pH2 | AEC | 0.3M | GC+PC | XX | X | | | | | | JL | 5 | 20 | Mian and Percival (1973) |
| Cystoseira compressa | HCl 0.1M hot | AEC | CI | GC | 62 | 4 | 24 | 8 | | | | | DP | 19 | 9 | Hentati et al. (2018) |
| Cystoseira indica | H₂O, r.t. | AEC | CIWE | GC | 75 | 14 | 11 | | | | | DP/IR | 8 | 4 | Mandal et al. (2007) |
| Hormophysa cuneiformis | H₂O, CaCl₂ 2M | AEC | F | GC | 52 | 38 | 4 | 18 | | | | | JI | 22 | 30 | Wang et al. (2012) |
| Nizamuddinia zanardinii | H₂O, CaCl₂ 1% | AEC | YF5 | GC | 44 | 21 | 18 | | | | | DP | 20 | 32 | |
| Turbinaria conoides | HCl 0.1M | AEC | AF3 | GC | 54 | 18 | 28 | | | | | DP/IR | 4 | ND | Chattopadhyay et al. (2010) |
| Turbinaria ornata | HCl 0.1M | AEC | ToF2 | GC | 83 | 17 | | | | | | DP | 32 | ND | Ermakova et al. (2016) |
| Turbinaria turbinata | Enzymes pH 4.5 | AEC | F2 | PAD | 46 | 22 | Ni' | 32 | | | | | DP | 10 | ND | Jayawardena et al. (2019) |
| **Family Durvillaeaceae** | | | | | | | | | | | | |
| Durvillaea antarctica | H₂O, MW³ | DAP | GC | 3 | 3 | 9 | 78 | Sorbose 8 | | | | ND | ND | He et al. (2016) |
| Durvillaea potatorum | HCl pH 1 hot | Acetone ppt | AFS | HPLC | 32 | 4 | 64 | | | | | DP | 13 | – | Lorbeer et al. (2017) |
| **Family Himanthalaceae** | | | | | | | | | | | | |
| Himanthalia elongata | H₂O + HCl 0.1M | F-HCl | GC | 17 | 1 | 29 | 3 | 50 | | | | | DP | 6 | 3 | Mateos-Aparicio et al. (2018) |
| Himanthalia lorea | CaCl₂, 2% + HCl pH2 | AEC | 0.3M | GC+PC | XX | X | | | | | | JI | 2 | 19 | Mian and Percival (1973) |
| **Family Seirococcaceae** | | | | | | | | | | | | |
| Marginariella boryana | H₂SO₄ 1% r.t. | Reprod. | GC | 72 | 2 | 17 | 1 | 7 | | | | | ND | 3 | Wozniak et al. (2015) |
| Seirococcus axillaris | HCl pH 1 hot | Acetone ppt | AFS | HPLC | 61 | 16 | 14 | 3 | 2 | 4 | | DP | 20 | 3 | Lorbeer et al. (2017) |

**Key:**
- AEC, anion exchange chromatography.
- SEC, size-exclusion chromatography.
- PC, paper chromatography.
- GC, gas chromatography.
- PAD, HPAEC with pulse amperometric detector.
- Ni, estimation by area of Ni bands.
- EA, elemental analysis by different methods.
- Tit, titration with cetylpyridinium chloride, pH 1.5 (Scott, 1960).
- ND, not detected.
- SD, standard deviation.
- MI, molar ratio.
- SU, sulfate unit.
- DA, data available.
- **a** Key: AEC, anion exchange chromatography; SEC, size-exclusion chromatography.
- **b** Key for the less common abbreviations: PC, paper chromatography; GC, gas chromatography; PAD, HPAEC with pulse amperometric detector.
- **c** Key DP, method of Dodgson and Price (1962) or equivalent; JL, method of Jones and Letham (1954); IR, estimation by area of IR bands; EA, elemental analysis by different methods; Tit, titration with cetylpyridinium chloride, pH 1.5 (Scott, 1960).
- **d** The information for the uronic acid is included in the molar ratio of monosaccharides.
- **e** As galactose could not be quantified, the data is semiquantitative.
- **f** ND = sugar not identified.
- **g** Microwave-aided extraction.
## Table 4: Reported compositions of the fucoids from the order Dictyotales.

| Species                  | Extraction Method | Purification/ Fractionation | Acronym | Monosaccharide composition (moles %) | Sulfate | References |
|-------------------------|-------------------|----------------------------|---------|--------------------------------------|---------|------------|
| *Canistrocarpus cervicornis* | Enz. pH 8         | Acetone ppt                | CC-0.7  | HPLC 33 17 50                       | DP 19   | Camara et al. (2011) |
|                         | Enz. pH 8         | Acetone ppt                | CC-2.0  | HPLC 20 10 40 20                    | DP 20   |                        |
| *Dictyopteris plagiogramma*  | CaCl<sub>2</sub> 2% + HCl pH 2 | C                        | GC 42 10 16 8 3 21                   | JL 4    | Percival et al. (1981) |
| *Dictyopteris polyiodoideae* | HCl 0.1M hot     | HC+AEC Dp-F2               | HPLC 48 19 5 14 5 9                 | DP 13   | Sokolova et al. (2011) |
|                         | HCl 0.1M hot     | HC+AEC Dp-F4               | HPLC 38 8 31 4 8 12                 | DP 13   |                        |
| *Dictyota dichotoma*      | HCl pH 1 hot      | Ethanol ppt                | R      | PC 25 16 25 10 24                   | BC 16   | Abdel-Fattah et al. (1978) |
|                         | HCl pH 2 rt.      | PQA EAR-0.5                | GC 40 30 6 16 4                     | DP 13   | Rabanal et al. (2014) |
|                         | HCl pH 2 hot      | PQA EA1-1.5                | GC 41 26 5 25 1 2                   | DP 19   |                        |
|                         | HCl pH 2 hot      | PQA EA2-0.5                | GC 26 36 4 33 1                     | DP 10   |                        |
|                         | HCl pH 2 hot      | PQA EAH4-0.5               | GC 10 30 5 51 3                     | DP 5    |                        |
|                         | HCl 0.1M hot      | AEC+HC DiF                 | GC 52 12 10 9 17                    | Ac      | Shevchenko et al. (2017) |
|                         | HCl 0.1M hot      | AEC (x 2) DiF              | HPLC 43 5 44 4                      | Ac      | Shevchenko et al. (2017) |
| *Dictyota divaricata*     | HCl 0.1M hot      | AEC+HC DiF1                | GC 61 31 4 4                        | Ac      | Shevchenko et al. (2017) |
|                         | HCl 0.1M hot      | AEC+HC DiF2                | GC 43 5 44 4                        | Ac      | Shevchenko et al. (2017) |
| *Dictyota menstrualis*    | Enz. pH 8         | Acetone ppt                | F1.0v PC 30 24 24                   | HexA 21 | Albuquerque et al. (2004) |
|                         | Enz. pH 8         | Acetone ppt                | F1.5v PC 31 9 47                    | HexA 13 |                        |
| *Dictyota mertensii*      | Enz. pH 8         | AEC 1M Col. 26 11          | Col. 56 11                         | HexA 33 | Dietrich et al. (1995) |
|                         | Enz. pH 8         | AEC 2.5-2.5M               | Col. 56 11                         | Ac      |                        |
| *Dictyota mertensii*      | Enz. pH 8         | AEC 0.1M AEC Dm            | 33 20                              | Ac      |                        |
| *Lobophora variegata*     | Enz. pH 8         | Acet + SEC Lj              | GC 25 75                           | Ac      | Medeiros et al. (2006) |
| *Padina australis*        | CaCl<sub>2</sub> 2% hot | PQA                       | Fpa 60 8 29 3                       | DP 22   | Yuguichi et al. (2016) |
| *Padina boryana*          | HCl 0.1M hot      | AEC+HC PbF                 | GC 61 31 4 3                       | Ac      | Shevchenko et al. (2017) |
|                         | HCl 0.1M hot      | AEC (x 2) PbF              | GC 40 37 17 6                      | Ac      | Shevchenko et al. (2017) |
| *Padina gymnospora*       | Enz. pH 8         | Acet + SEC PF1             | PC+GC 36 11 7                      | 46      | Silva et al. (2005)    |
|                         | Enz. pH 8         | Acet + SEC PF2             | PC+GC 39 8 6                       | 47      |                        |
| *Padina pavorica*         | CaCl<sub>2</sub> 2% + HCl pH 2 | AEC 0.3M PC+GC X X tr. | PC+GC 31 9 47                      | HexA 13 | Man and Percival (1973) |
|                         | CaCl<sub>2</sub> 2% + HCl pH 2 | AEC 1M PC+GC X X tr. | PC+GC 31 9 47                      | HexA 13 |                        |
|                         | HCl pH 2.5 hot    | AEC Purified               | PC 16 11 11 13 30                  | BC 19   | Hussein et al. (1980)  |
|                         | HCl 0.1M hot      | AEC 4PpF1                 | HPLC 43 13 9 17 17                 | DP 4    | Men'shova et al. (2012) |
|                         | HCl 0.1M hot      | AEC 4PpF2                 | HPLC 53 16 16 10 5                 | DP 14   |                        |
| *Padina tetrasomatica*    | H<sub>2</sub>O    | CaCl<sub>2</sub> 2% ppt   | PW1E 59 23 10 3 5                 | ND 9    | Karmakar et al. (2009) |
|                         | H<sub>2</sub>O    | AEC+SEC F3                 | GC 72 25 3                         | DP/R    | 8 4                   |
|                         | HCl 0.1M rt.      | Ext. A GC 68 16 9 5 2     | DP/R 3 5                           | Karmakar et al. (2010) |
|                         | HCl 0.1M + K<sub>2</sub>CO<sub>3</sub> 2% | CaCl<sub>2</sub> 2% ppt | PW1E 73 16 11                      | DP/R    | 6 5                   |
| **Spatoglossum asperum**  | H<sub>2</sub>O    | CaCl<sub>2</sub> 1%        | AP/R HPLC 61 6 25 4 3              | DP 21   | Paliarsamy et al. (2017) |
| **Spatoglossum schroederi** | Enz. pH 8        | Acetone ppt                | Fuc. A GC 53 18 4 29               | DP 28   | Queiruz et al. (2008)  |
|                         | Enz. pH 8        | Acetone ppt                | Fuc. A GC 27 14 55 4 2             | DP 37   |                        |
|                         | Enz. pH 8        | Acet. + AEC Fuc. B GC 28 14 56 2 | TB 19 | Menezes et al. (2018) |
| **Stereocladus marginatum** | H<sub>2</sub>O  | AEC (x 2) F3               | GC 96 2 2                          | IR/PR 13 | Adhikari et al. (2006) |

**Key:** AEC, anion exchange chromatography; SEC, size-exclusion chromatography; HC, hydrophobic chromatography; PQA, precipitation with quaternary ammonium salts; Acet, fractional precipitation with acetone; AP/R alcohol precipitation and redissolution.

**Key for the less common abbreviations:** PC, paper chromatography; GC, gas chromatography; Col., colorimetric methods.

**Key DP, method of Dodgson and Price (1962) or equivalent; JL, method of Jones and Letham (1954); BC, method of barium chloranilate (Lloyd, 1959); TB, method of toluidine blue; IR, estimation by area of IR bands.

**The information for the uronic acid is included in the molar ratio of monosaccharides.

**Fuc, Xyl and uronic acid were the only monosaccharides which could be determined.

**As galactose could not be quantified, the data is semiquantitative.
### TABLE 5 | Reported compositions of the fucoidans from the family Laminariaceae (order Laminariales).

| Species | Extraction | Purification/ Method | Acronym | Monosaccharide composition (moles %) | Sulfate | UA (%) | References |
|---------|------------|----------------------|---------|------------------------------------|---------|--------|------------|
| *Kjellmania crassifolia* | pH 6.5 hot | HCl pH 2 ppt | HPLC | Fuc 84 | Xyl 5 | Gal 10 | ND | 7 | Sakai et al. (2002) |
| Enz. pH 4.5 | AEC | F1 | HPLC | 30 3 | 49 6 | 4 | 9 | Ac | DP 23 | a | Song et al. (2018) |
| Enz. pH 4.5 | AEC | F2 | HPLC | 47 8 | 15 12 | 1 | 16 | Ac | DP 16 | a | |
| Enz. pH 4.5 | AEC | F3 | HPLC | 67 2 | 23 3 | 1 | 4 | | DP 32 | a | |
| *Laminaria angustata* | H2O | PQA+AE | F4 | GC | 90 | 10 | | | |
| HCl pH 2+PQA | AEC+SEC | LA-5 | GC | 2 | 98 | | | |
| *Laminaria bongardiana* | CaCl2 2% hot | PQA+AE | F-2 | GC | 53 8 | 20 15 | 3 | Ac | DP 20 | 12 | Bilan et al. (2016) |
| CaCl2 2% hot | PQA+AE | F-3 | GC | 39 4 | 54 2 | 1 | 4 | Ac | DP 26 | 3 | |
| *Laminaria chilensis* | See *Saccharina cichorioides* |
| *Laminaria digitata* | pH 0.01M+CaCl2 1% | ETOH+TCA 10% | FF | GC | 62 21 | 9 4 | 4 | | |
| Triton 0.5%, pH 7.5+CaCl2 1% | ETOH+TCA 10% | TF | GC | 47 15 | 20 11 | 7 | | |
| *Laminaria japonica* | See *Saccharina japonica* |
| *Laminaria longipes* | HCl 0.1M r.t. | AEC | LlF | GC | 100 | | | | |
| *Laminaria religiosa* | HCl pH 2 hot | PQA | Fr 0.5 | GC | 34 12 | 14 21 | 19 | | |
| HCl pH 2 hot | PQA | Fr. 3 | GC | 61 28 | 17 7 | 3 | | |
| *Macrocytis pyriforma* | Exudation | UF | pFuc | GC | 98 2 | | tr. | | |
| HCl pH 1 hot | Acetone ppt | AFS | HPLC | 79 3 | 12 3 | 3 | | |
| *Saccharina cichorioides* | HCl 0.4%+H2O | Lc-0.5F-2 | HPLC | 81 2 | 4 2 | 3 | 8 | | |
| HCl pH 2-2.3 hot | AEC | Lc-F2 | HPLC | 98 2 | | | | |
| HCl 0.4% r.t. | HC | Lc2-F1 | HPLC | 72 7 | 8 8 | 5 | | |
| HCl 0.4% +H2O | HC | Lc2-F2 | HPLC | 100 | | | | |
| HCl 0.1M r.t. | AEC | Sc-F1 | HPLC | 95 | | | | |
| HCl 0.1M r.t. | AEC | Sc-F2 | HPLC | 100 | | | | |
| HCl pH 2-2.3 | AEC | ScF | HPLC | 89 2 | 6 | 3 | | |
| HCl pH 2-2.3 | AEC | ScF | GC | 98 2 | | | | |
| *Saccharina gujarinovae* | HCl pH 2-2.3 | AEC | SgQF | HPLC | 84 21 | 15 | | Ac | |
| CaCl2 2% hot | AEC | SgF | GC | 76 24 | | | Ac | |
| *Saccharina japonica* | HCl 0.4%+H2O | Lj-1.2F-2 | HPLC | 94 2 | 3 | 1 | | |
| HCl 0.4% r.t. | HC | Lj1-F1 | HPLC | 55 7 | 26 6 | 3 | 3 | | |
| HCl 0.4%+H2O | HC | Lj1-F2 | HPLC | 84 1 | 12 | 1 | 2 | | |
| HCl pH 3 r.t. | AEC | L | HPLC | 61 5 | 14 16 | 4 | | |
| HCl pH 3 r.t. | AEC | GA | HPLC | 90 | 10 | | | |
| HCl 0.1M hot | AEC | Si-F1 | HPLC | 53 1 | 29 15 | 2 | | |
| HCl 0.1M hot | AEC | Si-F2 | HPLC | 61 2 | 33 1 | 3 | | Ac | |
| HCl 0.2M hot | Sterile | HPLC | 41 8 | 14 12 | 14 | 11 | | |
| HCl 0.2M hot | Reprod. | HPLC | 25 3 | 13 4 | 48 7 | | | |
| HCl 0.1M hot | AEC | Si-sF2 | HPLC | 62 6 | 21 | 9 | 2 | | |

(Continued)
TABLE 5 | Continued

| Species | Monosaccharide composition (moles %) | Sulfate | Acronym | Method | Purification/ Fractionation | References |
|---------|-------------------------------------|---------|---------|--------|-----------------------------|------------|
| Fucus serratus | Fuc Xyl Gal Man Glc Rha GlcA Others | Meth. | HCl 0.1M hot | AEC | Sj-fF2 HPLC | 58 37 5 DP 23 ND | Prokofjeva et al. (2013) |
| | | | HCl pH 2-2.3 | AEC | SjGF HPLC | 50 1 44 5 Ac DP 23 ND | Prokofjeva et al. (2013) |
| Saccharina latissima | Fuc Xyl Gal Man Glc Rha GlcA Others | Meth. | HCl pH 2.5 hot | B | CZE | 54 3 29 3 1 10 ND | Qu et al. (2014) |
| | | | H2O hot | CaCl2 | AP/R LJF HPLC | 34 2 37 23 1 3 DP 14 3 | Qu et al. (2014) |
| | | | CaCl2 | HCO2H 0.1%, PT 21% | HPLC | 57 17 21 5 DP 24 10 | Saravana et al. (2016) |
| | | | CaCl2 | 2% hot | PQA GC | 80 3 10 2 5 DP 30 5 | Cumashi et al. (2007) |
| | | | | CaCl2 | AEC F-1.0 GC | 46 5 32 14 3 DP 16 23 | Bilan et al. (2010) |
| | | | | CaCl2 | 2% hot | PQA GC | 78 2 18 2 DP 37 2 | Bittkau et al. (2020) |
| | | | | | Enz.pH6 | CaCl2 | 2% hot | PQA GC | 84 7 7 2 EA 29 6 | Bittkau et al. (2020) |
| | | | | | Enz.pH6 | CaCl2 | 2% hot | PQA GC | 63 3 27 2 | Nguyen et al. (2020) |

Key: AEC, anion exchange chromatography; SEC, size-exclusion chromatography; HC, hydrophobic chromatography; PQA, precipitation with quaternary ammonium salts; AP/R alcohol precipitation and redissolution; UF, ultrafiltration.

b Key for the less common abbreviations: PAD, HPAEC with pulse amperometric detector; PC, paper chromatography; GC, gas chromatography; CC, column chromatography on cellulose; CZE, capillary zone electrophoresis.

c The information for the uronic acid is included in the molar ratio of monosaccharides.

d High pressure and temperature have been applied.
### TABLE 6 | Reported compositions of the fucoids from the order Laminariales (families other than the Laminariaceae).

| Species                  | Extraction                  | Purification/Method | Acronym | Monosaccharide composition (moles %) | Sulfate | UA (%) | References                  |
|-------------------------|-----------------------------|---------------------|---------|------------------------------------|---------|--------|------------------------------|
| **Family Agaraceae**    |                             |                     |         |                                    |         |        |                              |
| *Costaria costata*      | HCl pH 2-2.3 hot            | FLM7                | HPLC    | Fuc Xyl Gal Man Glc Rha GlcA Others | DP 12   | ND     | Imbs et al. (2009)           |
|                         | HCl 0.1M hot AEC            | CcF                 | HPLC    | 62 4 18 5 7 4                     | DP 19   | ND     | Ermakova et al. (2011)       |
|                         | HCl pH 2-2.3 r.t.           | F1.5                | HPLC    | 70 20 7 6 3                       | DP 24   | a      | Imbs et al. (2011)           |
|                         | HCl pH 2-2.3 hot AEC        | 5F2                 | GC      | 30 16 8 15 15                     | DP 15   | a      | Anastyuk et al. (2012a)      |
|                         | HCl pH 2-2.3 hot AEC        | 5F3                 | GC      | 40 12 21 12 6 7                   | DP 15   | a      |                              |
|                         | HCl pH 2-2.3                 | CcGF                | HPLC    | 63 30 3 2 Ac                      | DP 23   | ND     | Prokofjeva et al. (2013)     |
|                         | Enz. pH 4.5                 | AP/R+AEC            | F2      | 17 7 8 61 8                       | Grav 1  | ND     | Wang et al. (2014)           |
|                         | Enz. pH 4.5                 | AP/R+AEC            | F4      | 47 17 17 12 8                     | Grav 23 | ND     |                              |
|                         | Enz. pH 4.5                 | AEC                  | 6F1     | 21 11 20 30 7 10                  | DP 9    | 4      | Liu et al. (2018)            |
|                         | Enz. pH 4.5                 | AEC                  | 6F2     | 31 15 9 26 11 8                   | DP 10   | 6      |                              |
| **Family Alariaceae**   |                             |                     |         |                                    |         |        |                              |
| *Alaria angusta*        | HCl 0.1M hot                | HC+AEC              | AaF2    | HPLC 75 7 18                      | DP 14   | ND     | Menshova et al. (2015)       |
|                         | HCl 0.1M hot                | HC+AEC              | AaF3    | HPLC 53 47                       | DP 24   | ND     |                              |
|                         | Alaria marginata            | HC+AEC              | AmF2    | HPLC 81 9 11                      | DP 21   | ND     | Usoltseva et al. (2016)      |
|                         | Alaria ochotensis           | HC+AEC              | AmF3    | HPLC 48 5 47                      | DP 28   | ND     |                              |
|                         | Alaria ochotensis           | Sterile             | HPLC    | 18 4 10 4 5 9 6                   | ND ND   |        | Skripkova et al. (2012)      |
|                         | Alaria ochotensis           | Reprod.             | HPLC    | 25 3 23 5 40 4                   | ND ND   |        |                              |
|                         | Undaria pinnatifida         | AEC                  | AaGF    | HPLC 54 38 8                      | DP 24   | ND     | Prokofjeva et al. (2013)     |
|                         | Undaria pinnatifida         | AEC                  | CF-4B   | GC 48 52                          | EA 32   | 2      | Lee et al. (2004)            |
|                         | Undaria pinnatifida         | H$_2$SO$_4$ 1% r.t. | AEC     | F2M GC 54 45 1                    | EA ~ 28 | 1      | Hemmingson et al. (2006)     |
|                         | Undaria pinnatifida         | H$_2$O+CaCl$_2$ 2%  | UF      | F > 30K HPLC 64 32 4              | DP 32   | ND     | You et al. (2010)            |
|                         | Undaria pinnatifida         | H$_2$O+CaCl$_2$ 2%  | AP/R    | F > 30K HPLC 64 32 4              | DP 32   | ND     | Sytysya et al. (2010)        |
|                         | Undaria pinnatifida         | H$_2$O+CaCl$_2$ 2%  | Up-F1   | HPLC 59 2 30 8 1                  | DP 14   | ND     | Vishchuk et al. (2011)       |
|                         | Undaria pinnatifida         | H$_2$O+CaCl$_2$ 2%  | Up-F2   | HPLC 51 48 1                      | DP 29   | ND     |                              |
|                         | Undaria pinnatifida         | CaCl$_2$ 2% hot     | PQA+AEC | F1 GC 49 4 38 7 3                 | DP 7    | 4      | Mak et al. (2013)            |
|                         | Undaria pinnatifida         | CaCl$_2$ 2% hot     | PQA+AEC | F3 GC 60 2 29 7 3                 | DP 25   | 1      |                              |
|                         | Undaria pinnatifida         | H$_2$O+CaCl$_2$ 2%  | Sigmap  | PAD 55 45                         | DP 26   | 2      | Lu et al. (2018)             |
| **Family Chordaceae**   |                             |                     |         |                                    |         |        |                              |
| *Chorda filum*          | CaCl$_2$ 2% hot             | AEC                  | A-2     | GC 95 1 1 1 2                     | Ac DP 26 | –      | Chizhov et al. (1999)        |
|                         | Na$_2$CO$_3$ 3%             | AEC                  | C-1     | GC 83 3 1 8 4                     | DP 13   | 3      |                              |
|                         | Na$_2$CO$_3$ 3%             | AEC                  | C-2     | GC 72 11 5 7 4                    | DP 13   | 3      |                              |
| **Family Lessoniaceae** |                             |                     |         |                                    |         |        |                              |
| *Ecklonia cava*         | HCl pH 2.0 hot              | AEC                  | Ec-F1   | HPLC 70 15 4 11                   | DP 19   | ND     | Ermakova et al. (2011)       |
|                         | HCl pH 2.0 hot              | AEC                  | Ec-F2   | HPLC 57 16 23 4                   | DP 22   | ND     |                              |
|                         | Enz.+CaCl$_2$ 4M            | PQA+AEC              | F1      | PAD 53 8 33 2 4                   | DP 20   | 16     | Lee et al. (2012)            |
|                         | Enz.+CaCl$_2$ 4M            | PQA+AEC              | F2      | PAD 60 4 31 1 4                   | DP 16   | 14     |                              |
|                         | Enz.+CaCl$_2$ 4M            | PQA+AEC              | F3      | PAD 78 8 10 2 2                   | DP 39   | 9      |                              |

(Continued)
### TABLE 6 | Continued

| Species                     | Monosaccharide composition (moles %) | Sulfate | Purification/Fractionation | Method | References          |
|-----------------------------|-------------------------------------|---------|---------------------------|--------|---------------------|
| Ecklonia kurome             |                                     |         |                           |        |                     |
|                            | FUc Xyl Gal Man Glc Rha GlcA Others |         |                           |        |                     |
|                            |                                    |         | HCl pH 2 hot CaCl₂       |        |                     |
|                            |                                    |         | +                           |        |                     |
|                            |                                    |         | PQA AEC                  |        |                     |
|                            |                                    |         | SEC B-I GC               |        |                     |
|                            |                                    |         | 34 34 13 18 DP 19 20 4 4 |        |                     |
|                            |                                    |         |                            |        |                     |
|                            |                                    |         | HCl pH 2 hot CaCl₂       |        |                     |
|                            |                                    |         | +                           |        |                     |
|                            |                                    |         | PQA AEC                  |        |                     |
|                            |                                    |         | SEC C-I GC               |        |                     |
|                            |                                    |         | 97 3 DP 47 2              |        |                     |
|                            |                                    |         |                            |        |                     |
|                            |                                    |         | HCl pH 2 hot CaCl₂       |        |                     |
|                            |                                    |         | +                           |        |                     |
|                            |                                    |         | PQA AEC                  |        |                     |
|                            |                                    |         | SEC C-II GC              |        |                     |
|                            |                                    |         | 83 17 DP 43 4             |        |                     |
|                            |                                    |         |                            |        |                     |
|                            |                                    |         | HCl pH 2 hot CaCl₂       |        |                     |
|                            |                                    |         | +                           |        |                     |
|                            |                                    |         | PQA AEC                  |        |                     |
|                            |                                    |         | SEC C-II GC              |        |                     |
|                            |                                    |         | 83 17 DP 43 4             |        |                     |
|                            |                                    |         |                            |        |                     |
|                            |                                    |         | HCl pH 2 hot CaCl₂       |        |                     |
|                            |                                    |         | +                           |        |                     |
|                            |                                    |         | PQA AEC                  |        |                     |
|                            |                                    |         | SEC C-II GC              |        |                     |
|                            |                                    |         | 83 17 DP 43 4             |        |                     |
|                            |                                    |         |                            |        |                     |
|                            |                                    |         | HCl pH 2 hot CaCl₂       |        |                     |
|                            |                                    |         | +                           |        |                     |
|                            |                                    |         | PQA AEC                  |        |                     |
|                            |                                    |         | SEC C-II GC              |        |                     |
|                            |                                    |         | 83 17 DP 43 4             |        |                     |

**Key:** AEC, anion exchange chromatography; SEC, size-exclusion chromatography; HC, hydrophobic chromatography; PQA, precipitation with quaternary ammonium salts; AP/R, alcohol precipitation and redissolution; UF, ultrafiltration.

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The family Sargassaceae comprises much more species than the Fucales (512 against 18, Guiry and Guiry, 2020). This family has the largest number of species studied from the point of view of its polysaccharides. The fucoidans from at least 26 different species of the genus *Sargassum* alone were analyzed. Table 2 shows the results for the different fucoidans isolated from this genus. For *S. horneri*, Ermakova et al. (2011) postulated the presence of *Rha* in substantial amounts within the polysaccharides (Table 2). However, their NMR spectra did not show the presence of this sugar, and in a further work by the same group (Silchenko et al., 2017) the fucoidans were purified without any trace of *Rha*. In *S. latifolium*, Asher et al. (2007) isolated three fractions where *Glc* and *GlcA* are the major components and *Fuc* is a minor one, not responding to the classical fucoidan composition. Other atypical polysaccharides were reported in *S. pallidum* (Liu et al., 2016) carrying high-mannose fucoidans, rich in uronic acids and scarcely sulfated, and in *S. thunbergii* (Luo et al., 2019), where a fucoidan completely devoid of sulfate groups was reported (Table 2).

Dietrich et al. (1995) studied the polysaccharides from *Sargassum vulgare*, differentiating whole plants and floaters. The fucoidan fractions corresponded to sulfated xylofucans containing important proportions of uronic acids. The proportion of sulfate is clearly higher in floaters. The ratio *Fuc/Xyl/HexA* varied between 1.0:5.0:0.5 and 1.0:1.0:0.2. However, only *Fuc*, *Xyl* and *uronic acid* have been determined in this investigation, missing other sugars possibly present.

For *Sargassum fusiforme*, the presence of galacturonic acid was detected (Hu et al., 2014). However, it has been shown later that this monosaccharide was part of a contaminating polysaccharide which could be separated by careful fractionation (Cong et al., 2016; Hu et al., 2016).

For the remaining members of the Fucales, the data is shown in Table 3. Mian and Percival (1973) carried out studies on *Bifurcaria bifurcata* and *Himanthalia lorea*. The data is shown only partially in Table 3, as *Gal* could not be quantified. Fractionation by ion exchange chromatography showed fractions with high uronic acid/low sulfate content using lower ionic strengths, and high sulfate, high *Fuc*, low uronic acid content in the later elutions. This behavior was observed for many further studies, regardless of the taxonomy of the seaweed. In some cases, like for *Nizamuddinia zanardinii*, the authors have devoted a lot of work in order to search for different extraction methods (Alboofetileh et al., 2019a,b,c). In Table 3 we have included the analysis of one extraction method, as the characteristics of the polysaccharides appear to be quite similar.

For *Marginariella boryana*, Wozniak et al. (2015) analyzed the polysaccharides extracted from vegetative structures (blades and vesicles) and receptacles (reproductive structures) separately. The proportions of *Xyl*, *Man*, and uronic acid increase significantly in the vegetative structures (Table 3). Within the family Durvillaeaaceae two species were studied. Both in *Durvillaea antarctica* (He et al., 2016) and *D. potatorum* (Lorbeer et al., 2017), the proportion of *Glc* was so large that it obscured the analysis of the fucoidan constituents, even when purification procedures (successful with other seaweeds)
## TABLE 7 | Reported compositions of the fucoidans from the orders Ascoseirales, Desmarestiales, Ectocarpales, Ralfsiales, and Scytosphaeriales.

| Species                  | Extraction | Purification/ Fractionationa | Acronym | Monosaccharide composition (moles %) | Sulfate | UA (%) | References                |
|--------------------------|------------|-------------------------------|---------|--------------------------------------|---------|--------|---------------------------|
| **Ascoseirales**         |            |                               |         |                                      |         |        |                           |
| Ascoseira mirabilis      | CaCl₂ 2% hot | AEC+SEC 1AF                | GC      | PC 29 9 19 9 10 25                 | JL 12   |        | Finch et al. (1986)       |
| Na₂CO₃ 3% hot            | AEC+SEC 3AF | PC+GC 17 9 31 14 9 17        |         |                                      | JL 8    |        |                           |
| **Desmarestiales**       |            |                               |         |                                      |         |        |                           |
| Desmarestia aculeata     | Na₂CO₃ 3% hot | GC+PC 21 3 41 35            |         |                                      | JL Low  | d      | Percival and Young (1974) |
| Desmarestia firma        | H₂O        | AEC F0.3M GC                |         | PC X X X ~50' X ManA X             | JL 1    | 17     | Carberg et al. (1978)     |
| Desmarestia ligulata     | H₂O        | AEC F0.2M GC                |         | GC 52 3 5 1 38                     | JL 3    |        |                           |
| Desmarestia viridis      | HCl 0.1M hot | AEC+HC DvF                 | GC      | 63 13 17 7                         | Ac      | DP 12  | Shevchenko et al. (2017)  |
| **Ectocarpales**         |            |                               |         |                                      |         |        |                           |
| **Family Adenocystaceae**|            |                               |         |                                      |         |        |                           |
| Adenocystis utricularis  | HCl pH 2 r.t | PQA EA1-5                  | GC      | 47 4 9 26 6 8                     | DP 5    | 42     | Ponce et al. (2003)       |
| HCl pH 2 r.t.            | PQA EA1-20 | GC 83 15 1                 | DP 23   | 4                                    |         |        |                           |
| HCl pH 2 hot             | PQA EA2-5  | GC 58 3 6 29 1 3           | DP 6    | 31                                   |         |        |                           |
| HCl pH 2 hot             | PQA EA2-20 | GC 75 1 21 1 11 1          | DP 21   | 6                                    |         |        |                           |
| **Family Chordariaceae** |            |                               |         |                                      |         |        |                           |
| Cladosiphon okamuratus   | HCl pH3    | CaCl₂ 0.5M+Caf             | PD 99   | 1                                    | Ac      | DP 15  | Cumashi et al. (2007)     |
| ND                       | CaCl₂ 0.1M | CAF G 95 3 1               | Ac      | DP 15 9                              |         |        |                           |
| Chordaria flagelliformis | H₂O        | AEC F2 GC                  | Ac      | DP 18 16                             |         |        |                           |
| Chordaria flagelliformis | H₂O        | AEC F3 GC                  | Ac      | DP 27 13                             |         |        |                           |
| Chordaria flagelliformis | H₂O        | AEC F4 GC                  | Ac      | DP 27 10                             |         |        |                           |
| **Family Scytosiphonaceae** | HCl pH 2 r.t | Nmcl 6 6 4                 | DP 6    | 3                                    |         |        |                           |
| Nmcl Pressure            | H₂O        | CaCl₂ 3M+AEC               | HPLC 74 | 3 5 2 15                             | DP 4    | d      | Cui et al. (2018)         |
| H₂O                     | CaCl₂ 3M+AEC | NP1 HPLC 76 2 2 20 Ac    |         | DP 19 d                              |         |        |                           |
| Papenfussiella lutea     | H₂SO₄ 1% r.t | GC 55 4 9 1 31            | ND 5    |                                    |         |        | Wozniak et al. (2015)     |
| Punctaria plantaginaria  | CaCl₂ 2% hot | PQA GC 69 27 4            |         |                                      |         |        | Bilan et al. (2014)       |
| **Family Sctiosiphonaceae** | Enzymes ph 4.5 and B | CaCl₂+AEC F2,1 PAD 19 38 7 |         | Nfr 31, Ara 3                       | DP 5    | ND     | Fernando et al. (2017)    |
| Enzymes ph 4.5 and B     | CaCl₂+AEC  F2,4 PAD 79 3 |                     |         | Nfr 18                              | DP 34   | ND     |                           |

(Continued)
TABLE 7

| Species                          | Extraction  | Monosaccharide composition (moles %) | Sulfate | Acronym | Ura (%) |
|----------------------------------|-------------|-------------------------------------|---------|---------|--------|
|                                  |             | Fuc Xyl Gal Man Glc Rha GlcA Others |         |         |        |
|                                  |             | Method                              |         |         |        |
|                                  |             | Fractionation                       |         |         |        |
|                                  |             | Purification/                        |         |         |        |
|                                  |             | Acronym                             |         |         |        |
|                                  |             | Reference                           |         |         |        |
| **Fucus</i>**                    |             |                                     |         |         |        |
| Laminaria *digitata*             |             |                                     |         |         |        |
|                                  |             | Enzymes pH 4.5                       |         |         |        |
|                                  |             | CaCl<sub>2</sub>                     |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | FAD                                 |         |         |        |
|                                  |             | HPAGE                               |         |         |        |
|                                  |             | GC                                   |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Man                                 |         |         |        |
|                                  |             | Gal                                 |         |         |        |
|                                  |             | Xyl                                 |         |         |        |
|                                  |             | Rha                                 |         |         |        |
|                                  |             | Glc                                 |         |         |        |
|                                  |             | GlcA                                |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | Fractionation                       |         |         |        |
|                                  |             | Purification/                        |         |         |        |
|                                  |             | Acronym                             |         |         |        |
|                                  |             | Reference                           |         |         |        |
|                                  |             |                                     |         |         |        |
| **Ralfsiales**                   |             |                                     |         |         |        |
| Analipus *japonicus*             |             |                                     |         |         |        |
|                                  |             | Enzymes pH 2.0                       |         |         |        |
|                                  |             | CaCl<sub>2</sub>                     |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | FAD                                 |         |         |        |
|                                  |             | HPAGE                               |         |         |        |
|                                  |             | GC                                   |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Man                                 |         |         |        |
|                                  |             | Gal                                 |         |         |        |
|                                  |             | Xyl                                 |         |         |        |
|                                  |             | Rha                                 |         |         |        |
|                                  |             | Glc                                 |         |         |        |
|                                  |             | GlcA                                |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | Fractionation                       |         |         |        |
|                                  |             | Purification/                        |         |         |        |
|                                  |             | Acronym                             |         |         |        |
|                                  |             | Reference                           |         |         |        |
|                                  |             |                                     |         |         |        |
| **Scytothamnus australis**       |             |                                     |         |         |        |
|                                  |             | Enzymes pH 1.0                       |         |         |        |
|                                  |             | CaCl<sub>2</sub>                     |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | FAD                                 |         |         |        |
|                                  |             | HPAGE                               |         |         |        |
|                                  |             | GC                                   |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Man                                 |         |         |        |
|                                  |             | Gal                                 |         |         |        |
|                                  |             | Xyl                                 |         |         |        |
|                                  |             | Rha                                 |         |         |        |
|                                  |             | Glc                                 |         |         |        |
|                                  |             | GlcA                                |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | Fractionation                       |         |         |        |
|                                  |             | Purification/                        |         |         |        |
|                                  |             | Acronym                             |         |         |        |
|                                  |             | Reference                           |         |         |        |
|                                  |             |                                     |         |         |        |
| **Saccharina lattissima**        |             |                                     |         |         |        |
|                                  |             | Enzymes pH 2.0                       |         |         |        |
|                                  |             | CaCl<sub>2</sub>                     |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | FAD                                 |         |         |        |
|                                  |             | HPAGE                               |         |         |        |
|                                  |             | GC                                   |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Man                                 |         |         |        |
|                                  |             | Gal                                 |         |         |        |
|                                  |             | Xyl                                 |         |         |        |
|                                  |             | Rha                                 |         |         |        |
|                                  |             | Glc                                 |         |         |        |
|                                  |             | GlcA                                |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | Fractionation                       |         |         |        |
|                                  |             | Purification/                        |         |         |        |
|                                  |             | Acronym                             |         |         |        |
|                                  |             | Reference                           |         |         |        |
|                                  |             |                                     |         |         |        |
| **Stoechospermum marginatum**    |             |                                     |         |         |        |
|                                  |             | Enzymes pH 2.0                       |         |         |        |
|                                  |             | CaCl<sub>2</sub>                     |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | FAD                                 |         |         |        |
|                                  |             | HPAGE                               |         |         |        |
|                                  |             | GC                                   |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Man                                 |         |         |        |
|                                  |             | Gal                                 |         |         |        |
|                                  |             | Xyl                                 |         |         |        |
|                                  |             | Rha                                 |         |         |        |
|                                  |             | Glc                                 |         |         |        |
|                                  |             | GlcA                                |         |         |        |
|                                  |             | Others                               |         |         |        |
|                                  |             | Method                               |         |         |        |
|                                  |             | Fractionation                       |         |         |        |
|                                  |             | Purification/                        |         |         |        |
|                                  |             | Acronym                             |         |         |        |
|                                  |             | Reference                           |         |         |        |
|                                  |             |                                     |         |         |        |

**Key:** AEC, anion exchange chromatography; SEC, size-exclusion chromatography; HPLC, high-performance liquid chromatography; POA, precipitation with quaternary ammonium salts; CE, cation exchange.

**Key for the less common abbreviations:** PAD, HPAEC with pulsed amperometric detector; GC, gas chromatography.

**Key:** JL, method of Jones and Letham (1954); DP, method of Dodgson and Price (1962) or equivalent; IC, ion chromatography; EA, elemental analysis.

**Key:** The information for the uronic acid is included in the molar ratio of monosaccharides.

**Key:** Even after purification, these samples contain 10–12% of alginic acid.

**Key:** NI = sugar not identified.

**Key:** Only the proportion of Glc is indicated. The remaining monosaccharides were not quantified.
Figure 3 | Difference in selected reported compositions of fucoidans submitted to charge-based separation methods. Fractions on the left side were eluted or redissolved at low ionic strengths, whereas those on the right side were eluted or redissolved at higher ionic strengths. Upper panel, neutral monosaccharide composition (mol/100 mols); lower panel, sulfate and uronic acid content. The data were reported by Koo et al. (2001), Bilan et al. (2002, 2008, 2010, 2013, 2018), and Ponce et al. (2003, 2019).
early-eluting fractions of anion exchange chromatography, whereas highly sulfated fucans or galactofucans appear in the late-eluting fractions.

Seasonal differences were also observed: for Costaria costata, Imbs et al. (2009) determined that the proportion of Fuc, Gal, Glc, and sulfate increased from spring to summer, whereas those of Man, Rha, and Xyl decreased. This trend is similar to that observed by Men’shova et al. (2012) for Padina pavonica (see above). In another study, carried out for Saccharina pavonica (as Laminaria cichorioides), it has been shown that after the summer, and through fall, the proportion of Fuc decreases again, whereas that of Man increases clearly (Anastyuk et al., 2010).

On the basis of chemical degradation and NMR spectroscopy, Bilan et al. (2010) arrived to many structural features of the fucoidans from Saccharina lattisima. Ehrig and Alban (2015) have shown the large effect of the marine habitat and season on the characteristics of the isolated fucoidans of this seaweed. Samples picked up in the Baltic Sea showed more laminaran contamination and lower fucoidan yields, fucose, and sulfate content than those collected around the Faroe Islands (regardless of the season), although the uronic acid content was similar. Regarding the season effects, the proportion of sulfate was higher in fucoidans from seaweeds collected in September than in May. Anion-exchange chromatography separation showed that only from the September-collected seaweed it was possible to obtain high yields of a high-fucose fraction with the highest biological activity. However, in a further work from the same group (Bittkau et al., 2020), the authors have isolated such a fraction with high fucose and sulfate content from the same North Atlantic location, in July without the need of any purification, suggesting that the year of collection has a major effect on the composition of the isolated fucoidans.

A study carried out with an unidentified species of Alaria (Alaria sp., Vishchuk et al., 2012) was later ascertained as being A. ochotensis (Prokofjeva et al., 2013). In the Alaria species studied so far, it is noteworthy to mention the presence of fucogalactans with approximately equal proportions of Fuc and Gal (Table 6).

For Costaria costata, high proportions of Man have been encountered in the polymers, especially in the less charged fractions isolated in some studies (Wang et al., 2014). In any case, Man appears conspicuously in most of the studies carried out on fucoidans of any origin.

The polysaccharides from Undaria pinnatifida were studied by many research groups, probably due to the fact that this seaweed, native from northeastern Asia, is very invasive and now is widespread all around the world (Casas et al., 2004; Thornber et al., 2004). It is worth noting that most of the studies have shown the presence of a galactofucan with high proportions of Gal, sometimes leveling out with Fuc. The proportion of other sugars (Man, Xyl and uronic acids) is usually low, whereas the proportion of sulfate is considerable, but lower than those of other species (Table 6).

Other Orders
The analysis of the fucoidans of different species of the order Ectocarpales appears in Table 7. In this survey, only reports for ten different species (belonging to three families) of the order have been found. Highly sulfated galactofucans or homofucans coexist with polysaccharides containing significant proportions of Man, GlcA and/or Xyl.

The analysis of the fucoidans from four species from the Desmarestiales is also shown in Table 7. It should be taken into account that these seaweeds contain free sulfuric acid in their vacuoles (Carlberg et al., 1978), making them very labile when taken out from the marine environment. This requires special techniques in order to obtain neutral extracts unaffected by the strong acid.

To the best of our knowledge, the fucoidans from only one species from the Ascoseirales and Ralfsiales, and two of the Scytoscleramiales have been studied (Table 7). The fucoidans from the three samples from the Ralfsiales and Scytoscleramiales appear to be particularly rich in Fuc and poor in uronic acids, whereas the Ascoseira sample was quite heterogeneous (Finch et al., 1986, Table 7).

CONCLUDING REMARKS
The current review has surveyed most of the compositional data on fucoidans extracted from different species, in many cases after purification; more than 100 species were screened through the literature. Besides the obvious purpose of providing a reliable source of compositional data gathered in a set of tables, this review attempted to foresee if there is any correlation of these compositional data with their taxonomy, or if other factors are more important than the taxonomic origin.

These general considerations can be deduced from the analysis of the compositional data:

1. Separation by charge is the most efficient method to obtain “pure” fucoidan fractions. Either using anion-exchange chromatography with increasing concentrations of salt as eluant, or by precipitating with cationic detergents and redissolving at increasing ionic strengths, two main type of polymers can be separated: (a) those appearing at low ionic strengths, usually highly heterogeneous in their monosaccharidic composition (containing Fuc, Xyl, Gal, Man, Rha, GlcA), with low-sulfate content, and high uronic acid content, and b) those appearing at high ionic strengths, containing mainly Fuc, accompanied with variable proportions of Gal, highly sulfated and containing little (or none) uronic acids. Fractions containing intermediate proportions of both polysaccharides appear at medium ionic strengths. Figure 3 depicts the composition of fractions belonging to each of the first groups from selected seaweeds, showing clearly the marked differences between both groups. This behavior is observed for samples from the orders Fucales, Laminariales, Ascosereales, Desmarestiales, Ectocarpales, and Ralfsiales (Mian and Percival, 1973; Carlberg et al., 1978; Bilan et al., 2002, 2013, 2016, 2018; Ponce et al., 2003, 2019; Ozawa et al., 2006; Mak et al., 2013); however, for the Dictyoales, the trend is obscured due to the abundance of Man and/or uronic acids in the products separated at
each ionic strength (Table 4). It has been postulated that the biological activity is concentrated on the galactofucan components (Ponce et al., 2003, 2019; Croci et al., 2011).

2. Acetate esters of the fucoidans are very common. As a matter of fact, this constituent has been found in almost every sample where it was searched. Determinations of acetyl groups are not very common, as they are only encountered through NMR spectra or specific colorimetric techniques. They are labile enough in mild alkaline or acid media as to get undetected when using some extraction procedures (Bernhard and Hammett, 1953; Wuts and Greene, 2006). Anyway, almost all of the seven tables report acetyl groups on some species. It is highly probable that searching in other species would have resulted in many more positive results.

3. In some cases, Man and Rha appear together, usually in fractions with lower sulfate contents. For Man, structural explanations have already been reported in terms of fucomannoglucuronans (Bilan et al., 2010), but for Rha no structural function has been found so far. Rha seems to appear in higher proportions within the order Dictyotales and the family Sargassaceae (Fucales).

4. The Dictyotales appear to be the most “atypical” order, as usually large proportions of Man and uronic acids appear. In one species which was highly fractionated, Man becomes the most important monosaccharide in the low-charged fractions, and it is still important in the fractions with more sulfate groups (Table 4: Rabanal et al., 2014). However, fractions with high proportions of monosaccharides different than Fuc were found in most of the taxa studied so far (see Tables).

5. The uronic acid content should be considered with due care. Sometimes it corresponds to GlcA actually comprising the fucoidan structure, but sometimes it corresponds to contamination with alginic acid (e.g., Finch et al., 1986; Lorbeer et al., 2017), a polysaccharide present in all of the brown seaweeds studied so far. By the same token, the Glc present in the samples should almost certainly correspond to contaminating laminarans (Lorbeer et al., 2017; Mateos-Aparicio et al., 2018). Only in a few cases, Glc has been shown to be part of the fucoidan structure (e.g., Duarte et al., 2001).

6. There are several factors to consider when comparing the compositional data of fucoidans from different seaweeds and research groups. The taxon is just one of them. Others like geographical location, year and season of harvest of the seaweed, extraction and purification methods, analytical methods, different parts or reproductive stages of the seaweeds are also of paramount importance in defining the final characteristics.

7. The geographic site of harvesting appears to be very important: Zvyagintseva et al. (2003) found marked differences between the fucoidans of Fucus evanescens collected in different spots of the southern Okhotsk Sea. Ehrig and Alban (2015) also found a significant difference between the composition and yields of fucoidans of Saccharina lattissima samples collected in the North Atlantic and in the Baltic Sea. This factor, together with the year of collection might explain the large differences in composition found for species studied by different groups (or at different times) even with similar extraction and purification procedures.

8. The season of harvesting has also influence over the composition of the fucoidans: a trend with increasing yields, and proportions of sulfate, Fuc, Gal and Glc (together with a decrease in the Man and Rha content) is observed as the collection month progressed from March to October, in the Northern Hemisphere (Imbs et al., 2009; Anastyuk et al., 2010; Menšíhova et al., 2012; Ehrig and Alban, 2015).

9. The effect of the extraction conditions is more controversial: Ponce et al. (2003) and Wozniak et al. (2015) found very little differences when switching the extraction solvent from water to CaCl₂ to diluted HCl. Alboofetileh et al. (2019b) found differences in yield and in sulfate content but a very similar monosaccharide composition using enzymes, ultrasound, or both combined. Rodriguez-Jasso et al. (2011) found a significant difference in composition and yields when changing the time and the pressure of a microwave-assisted water extraction. Nguyen et al. (2020) have shown a sharply different composition of the chemically and enzymatically-extracted crude products, being the latters richer in alginic acid and sulfate/Fuc ratios. After purification, the compositions might level off. However, the enzyme-aided extraction, also used by other groups (Dietrich et al., 1995; Albuquerque et al., 2004; Silva et al., 2005; Medeiros et al., 2008; Queiroz et al., 2008; Costa et al., 2011; Camara et al., 2011; Lee et al., 2012; Wang et al., 2014; Hu et al., 2016; Monsur et al., 2017; Fernando et al., 2017, 2018; Liu et al., 2018; Menezes et al., 2018; Song et al., 2018; Jayawardena et al., 2019; Alboofetileh et al., 2019a,b) appears to be an interesting prospect, considering cleaner chemical issues and the possibility of finding enhanced biological activities in comparison with chemically extracted products (Nguyen et al., 2020).

Some differences were found between the fucoidans isolated from reproductive and sterile tissue of five different seaweeds (Skripotsova et al., 2012, see Tables 1, 2, 5, 6). Usually the reproductive tissue is less heterogeneous, and carries more Fuc and less Glc than the sterile tissue. Regarding the extraction of fucoidans from different parts of the seaweeds, Percival et al. (1983) extracted separately the polysaccharides from fronds and stipes from Lessonia nigrescens, whereas Wozniak et al. (2015) compared the fucoidans isolated from reproductive structures and from vegetative structures in Marginariella boryana. The fucoidans from stipes and the vegetative structures, respectively, appear to be more heterogeneous (less Fuc and more uronic acids).

In order to obtain fucoidan samples devoid of contaminants, the best results were obtained by carrying out the extractions with dilute HCl or CaCl₂, or using these agents after the extraction (for instance enzymatic) in order to precipitate the
alginate in the first place, followed by a careful separation by charge (anion exchange chromatography eluting with increasing ionic strength, or precipitation with quaternary ammonium salts followed by redissolution with increasing ionic strengths). Further purification of each fraction by size-exclusion chromatography usually yield fucoidans devoid of alginic acid or laminaran contaminants.

The conclusion is that with so many variables determining the composition of the fucoidans, the subtle differences that might appear among the different higher taxa (order, family) surveyed in this review are overridden. Probably, comparisons carried out in the same labs with the same methods might help, or more profound structural studies might throw light on chemotaxonomical issues in the future.

**AUTHOR CONTRIBUTIONS**

NP was involved in the conceptualization, formal analysis, investigation, writing, and visualization of this work. CS was involved in the conceptualization, formal analysis, writing, visualization, and funding of this work. Both authors contributed to the article and approved the submitted version.

**FUNDING**

This work was supported by grants from the University of Buenos Aires (20020170100255BA), National Research Council of Argentina-CONICET (PIP 298/14 and P-UE 22920160100068CO), and ANPCyT-Argentina (PICT 2017-1675).

**ACKNOWLEDGMENTS**

We are indebted to Dr. María C. Rodríguez for her help on botanical/psychological issues, and to Dr. Marina Ciancia for her kind invitation to participate in this issue.
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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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