**Concise review of green algal genus *Ulva* Linnaeus**

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**Abstract**

The oldest green algal genus *Ulva* has wide spread distribution to all the continents. The distromatic and monostromatic thallus both now form single taxa based on ITS rDNA and *rbc*L gene sequencing. *Ulva* is known to occupy several ecological niches including fresh and marine (intertidal and subtidal) habitats, attributed to its tolerance to key determinants such as light, temperature, salinity etc. The genus is perceived as model system to study life-cycle, morphogenesis and development from simple to complex multicellularity. The life cycle is isomorphic and biphasic type, knowledge of which is important in developing viable cultivation techniques. The culture is being attempted by photo-bioreactor, land based and open sea farming which registered 1,500 tones dry annum-1 biomass production. The understanding of scientific basis for eutrophication-driven green tide events is of paramount importance for coastal ecosystem management. The studies related to cross – kingdom cross – talkbetween *Ulva* and surrounding microbe are recently undertaken through high-throughput techniques to understand their role in growth, development and morphogenesis. The several regional species are rich in vital nutrients thus qualify in functional food sector, but recent research is poised to develop bio-refinery model for complete utilization of feedstock.

**Key words**

Bio-refinery, green tide, life cycle, microbiome, photo-bioreactor, *Ulva*

**Initial Taxonomy**

The pre- Linnaean naturalists in all probability adopted term “*Ulva*” from Latin word for “a sedge” or “marsh plant” or Proto-Indo-European word for “to grow” (Guiry and Guiry 2020). In ‘Synopsis Methodica’ Ray (1724) described *Ulva* as a leafy moss. Carolus Linnaeus in his “Species Plantarum” first time reported the genus *Ulva* in class Cryptogams (Linnaeus 1753) and described binomials of 9 species under this genus. In 1764 Gleditsch listed genus *Ulva* in his list of 7 algal genera of class Algacea in Systema Plantarum. The genus *Ulva* described in these earlier works was also consisted of some unrelated algae. Consequently, most of these unrelated species were moved to other genera (Papenfuss 1960). In 19th century these thalloid ulvaceous algae were reorganized into several genera including *Ulva* Linn, *Enteromorpha* Link and *Monostroma* Thuret or *Ulvaria* Ruptecht. According to Papenfuss (1960), Linnaeus used *E. intestinalis* (Linnaeus) Nees to describe genus *Ulva* and argued that it should be typified by one of the hollow plants. However, Bliding (1968) compared the detail morphological, anatomical and reproductive characters of *U. lactuca* (only distromatic green algae in Linnaeus description) with Linnaean type specimen studied by Papenfuss (1960) and maintained it as type species of the genus *Ulva*.

**Diagnostic characters**

The study of morphological characters of the genus *Ulva* includes macroscopic and microscopic observations. Macroscopic diagnostic features are thallus colour, texture, shape, perforations, size of holdfast, presence of stipe and its size while microscopic features are cell size, shape and arrangement, arrangement of chloroplast, number and distribution of pyrenoids, thallus thickness (Woolcott and King 1993). Foliaceous thallus of *Ulva* is thin, distromatic (two layers of cells adhering throughout) or monostromatic (tubular), when flat consist of marginal canaliculi. The thalli may be branched or unbranched attached by a short stalk and basal branched rhizoids. Colour of blade varies from dark green to pale yellow. Multicellular thallus consists of irregularly shaped uninucleate cells. Thallus attached to solid surface with tough rhizoids which forms disc like structure known as holdfast. Plants begins as a single row of cells but soon becomes hollow and turn to distromatic or monostromatic form at maturity (Fig. 1). It can reach up to 1 m in length. Blades show microscopic dentation at margins and are perforated or unperforated.

**Traditional and recent classification**

In initial subdivision into classes and orders, Blackman and Tansley (1902) introduced order Ulvales in class Chlorophyceae Wille. This order consisted of a family Ulvaceae J.V. Lamouroux ex Dumortier and five genera: *Monostroma*, *Ulva*, *Enteromorpha, Letterstedtia* Areschoug*, and Ilea* J. Agardh. The classification was depending on the morphological concept. *Ulva* was characterized by foliaceous thallus with polygonal cells arranged in two definite layers. Whereas *Enteromorpha* was characterized by branched or unbranched tubular thallus with one layer of cells. The further studies have introduced more characters to define interspecific differences. For example, characters such as, reproductive structures, sexual compatibility, development of zygotes or zoospores in culture, number of pyrenoids (Bliding 1968; van den Hoek 1964).

In current classification scheme the genus *Ulva* belongs to the class Ulvophyceae K.R.Mattox & K.D.Stewart, order Ulvales and family Ulvaceae. A new classification scheme for green algae were proposed by Mattox and Stewart (1984) based on Ultrastructure characteristics. The five classes were formulated on the basis of ultrastructure of flagellar apparatus and the process of mitotic division of cells. Further it was refined by van den Hoek et al. (1995) who subdivided division Chlorophyta Reichenbach into eleven classes. The classification was depending on the characters such as flagellar architecture, process of mitosis and cytokinesis, structure of thallus, chloroplast and cell wall envelope, differences in photosynthetic pigments and storage products, difference in life history stages. *Ulva* and *Enteromorpha* were characterized by 11 o’clock – 5 o’clock orientation of the basal body of flagella, closed mitosis with strictly coupled cytokinesis, and isomorphic, diplohaplontic life cycle.

The delineation in ulvaceous algal genera and species was observed to be difficult on ground of morphological characters (Tanner 1980). The transition and overlapping of characters was reported in previous studies in early developmental stages of thallus ontogeny in *Enteromorpha* and *Ulva* (Bliding 1963; Bonneau, 1977). Even a single mutation or change in culture condition can affect the morphology (Lovlie 1968). Unravelling the evolutionary history using molecular phylogenetic analysis has played a crucial part in defining the recent classification of ulvaceous algae. The molecular phylogenetics using small subunit (SSU) rDNA (Zechman et al. 1990; Pröschold and Leliaert 2007) and large subunit of ribulose bisphosphate carboxylase/oxygenase (*rbc*L) gene (Zechman 2003) has supported the disintegration of Ulvophyceae Mattox and Stewart into five different classes proposed by van den Hoek (1995). Similarly the phylogenetic studies using internal transcribed spacer of nuclear ribosomal DNA (ITS rDNA) and *rbc*L gene abolishes the distinction between *Ulva* and *Enteromorpha* as two separate genera (Hayden et al. 2003; Shimada et al. 2003).

*Ulva* comprises of 130 taxonomically accepted species worldwide (Guiry and Guiry 2020). As mentioned above the delineation of species of the genus *Ulva* is a difficult task and hence in last two decades many researchers have tried the DNA taxonomy to deal with it. The recent surveys of diversity of *Ulva* have extensively utilized molecular markers for classification studies (Hayden et al. 2004; Shimada et al. 2008; Heesch et al. 2009; Loughnane et al. 2009; Kraft et al. 2010; O’Kelly et al. 2010; Wolf et al. 2012; Kazi et al. 2016; Kang et al. 2019). It also contributed for identification of new species (Hiraoka et al. 2004; Ichihara et al. 2009; Kraft et al. 2010; Masakiyo and Shimada 2014; Chen et al. 2015; Kazi et al. 2016; Spalding et al. 2016; Krupnik et al. 2018;), cryptic diversity (López et al. 2007; Hofmann et al. 2010; [Wolf](https://www.ncbi.nlm.nih.gov/pubmed/?term=Wolf%20MA%5BAuthor%5D&cauthor=true&cauthor_uid=27010000) et al. 2012), introduced species and green tide forming free floating species of *Ulva* (Malta et al. 1999; Shimada et al. 2003**;** Leliaert et al. 2009; Liu et al. 2010; Wan et al. 2017; Krupnik et al. 2018). The examination of holotype specimen of *U. lactuca* with DNA sequence data has hypothesized its origin from Indo-pacific region and also supports the synonymization with *U. fasciata* Delile (O’Kelly et al. 2010; Hughey et al. 2019).

**Ecology and distribution**

*Ulva* is probably one of the few genera in green lineage which has fresh as well as marine species. Although primarily marine its presence was recorded from supralittoral zone up to 40 m subtidal habitats (Chapman 1956). A record of freshwater *U. flexuosa* was dated back to 19th and 20th Century in Central Europe (c.f. Rybak 2015) and recently *U. limnetica* was reported from Ryukyu Islands, Japan (Ichihara 2009). Hofmann et al. (2010) reported *U. lactuca, U. rigida, U. compressa,* and *U. pertusa* from Great Bay estuaries system, USA. The species were recorded in salinity ranged from <0.5 to 49 PSU, the tubular species were more tolerant to low salinity while leafy thallus typically found in marine environment (Rybak, 2018). The species are distributed in all the seven continents including in Antarctica. The highest number of species were distributed in Asia (56), followed by Australia (40), Europe (38), North America (34), Africa (31), South America (20), Antarctica (12) [Fig. 2, Supplementary table 1]. Of which 18 are endemic to Asia 11 to Australia, 9 to Europe, 6 to Africa, 2 to North America, 1 to South America [Supplementary table 2] (Guiry and Guiry 2020).

The widespread distribution is attributed to its tolerance and adaptation to key environmental factors such as light, temperature, salinity etc. The seasonality in the growth with abundance in winter (Yoshida et al. 2015); swarmer induction in summer (Uchimura et al. 2004) are recorded. The other factors such as light and nutrients also affect the growth (Yamasaki 1996). *Ulva* shows linear relationship between growth rate and light intensity up to 30 µM m-2 s-1 photon, while growth becomes saturated above 70 µM m-2 s-1 photon flux (Fortes et al. 1980). Further, it may be noted that, ultraviolet (UV) radiation has negative effect on the growth (Grobe and Murphy 1998). The mitigation to UV exposure was achieved by accumulation of UV absorbing compounds like carotenoids, coumarins, phenolic compounds, and mycosporine‐like amino acids (MAAs) (Shick and Dunlap 2002; Schoenwaeler et al. 2003). The successful colonization of *Ulva* spp. over the wide range of environmental conditions relates to physiological, biochemical and molecular adaptation. These responses ranged from accumulation of sucrose, proline and free amino acids, elevated antioxidant response (catalase, peroxidase and superoxide dismutase), induction of molecular chaperone (UfHsp90A) and protease (UfPbf1, UfClpC) (Edwards et al. 1987; Lee and Chen 1998; Sung et al. 2011).

**Life cycle**

The reproduction in *Ulva* is governed by complex process and complete life cycle has been successfully established under laboratory conditions in *U. lactuca* and *Ulva compressa* (formerly *U. mutabilis*)(Wichard et al. 2015). Nevertheless, type of life cycle pattern was deciphered in 14 different species till date (Balar and Mantri, 2020). The reproduction can occur sexually as well as asexually. The life cycle is isomorphic and biphasic type where both the multicellular adult sporophytic and gametophytic phases are morphologically similar but genetically different (Fig. 3). Sexual reproduction involved development and production of haploid biflagellate gametes which copulate to produce diploid zygote. The zygote germinates to produce diploid multicellular adult sporophytic thallus. The normal vegetative cells upon maturity transformed into zoospore mother cell and undergo meiosis to produce haploid quadri-flagellate zoospores. They germinate and form haploid male and female isomorphic multicellular adult gametophytic thalli via mitosis. These thalli at maturity again produce respective gametes through mitosis. It is thus termed as “haplodiplontic” life cycle (Hoxmark 1975). Alternation of generation take place on regular basis from sporophytes to gametophytes or vice versa (Hoxmark 1975; Fjeld and Løvlie 1976). This is a normal mode of development and happens routinely in nature. Nevertheless, parthenocarpy and asexual reproduction via biflagellate zoospores is also not un-common (Mantri et al. 2019).

**Factors for inducing the reproduction**

The reproductive processes in *Ulva* are influenced by abiotic factors namely, light, temperature, and desiccation but the mode of action for each factor is different and always works in combination than alone (reviewed in Balar and Mantri 2020). Besides, biological factors such as algal microbial interaction, age of the thallus, concentrations of growth regulators (hormonal second messenger) and sporulation as well as swarming inhibitors also play critical role in maturation (Singh et al., 2011; Vesty et al. 2015; Wichard et al., 2015). Semilunar rhythm of gamete release was reported in *Enteromorpha* spp*., U. labota* (Brawley and Johnson 1992), *U. pseudocurvata* (Luning et al. 2008). This type of reproduction induction is due to combination of day length, desiccation and exposure to threshold light intensity. The optimal range of temperature effective in induction of reproduction was found to be in a range of 15 ºC – 20 ºC in several *Ulva* spp, however, difference of 5 ºC is essential for effective induction of gametes or spores (Balar and Mantri 2020). Thallus fragmentation is one of the most tested mechanism for induction of reproduction in *Ulva* (Hiraoka et al. 1998). The sporulation inhibitors viz. inhibitor-1a (SI-1a) and inhibitor-2 (SI-2), whereas, additional compound known as swarming inhibitor (SWI) was also identified which prevents release of reproductive cells. These compounds work in tandem in the process of induction of reproduction and gamete or zoospore release. It was further found that these SIs use analogous signals to regulate reproduction induction in different species. But recent study revealed that life cycle regulators are not species but clade specific in *Ulva* (Alsufyani et al. 2014). It is also interesting to note that, cells are no longer susceptible to the action of sporulation inhibitors after 23-26 h [when cells entered into determination phase] (Kessler et al. 2018). Metabolite profiling of *U. prolifera* revealed significant changes in 63 metabolites out of total 156 metabolites studied during fragmentation-induced proliferation. Further, malic acid, glutamic acid, γ-Aminobutyric acid (GABA) and gallic acid were found to be accountable for reproductive induction (He et al. 2019). DMSP and 55 specific molecular biomarkers were found to be related to dynamic changes in surface-associated compounds in *U. mutabilis*. Information on molecular mechanism underpinning the induction of reproduction in *Ulva* is still in its infancy and therefore needs to be persuaded.

**Ultrastructure and development**

Genus *Ulva* has been a model candidate for understanding the multicellularity, and, integrated and coordinated developmental studies. The ultrastructure investigations are crucial in classification, reproduction, cell division and morphogenesis. *Ulva* contains multilayer and complex structure of cell wall with highly irregular electron dense fibrillar network (Messyasz et al. 2013). In ultrastructure of vegetative cells studied by McArthur and Moss (1978) in *U. intestinalis*, chloroplast was found as the most conspicuous organelle with a single pyrenoid. It may be noted that usually only one cup shaped parietal chloroplast is present in every cell. Inter-thylakoidal spaces were observed to be filled with chloroplast stroma. Single centrally placed nucleus bounded by double nuclear membranes having nuclear pores. Golgi complex consisted of 15-18 individual dictyosomes. Tonoplast (a single membrane) acts as a barrier between vacuolar contents and organelles and cytoplasm. Ultrastructural studies also showed the presence of microbodies (cytoplasmic organelle containing catalase and other oxidative enzymes) in *Ulva* (Silverberg 1975). The duplication of pyrenoid is seen as an indication of onset of cell division which is further followed by mitosis, cytokinesis and cell wall deposition (McArthur and Moss 1978). Mitosis in *Ulva* followed the classical pathway except the nuclear envelop disappears only at polar fenestrae during interphase (Lovlie and Braten 1970). Cytokinesis in *Ulva* occurred by division furrow and invagination of plasmodesmata into the cytoplasm (Lovlie and Braten 1970; McArthur and Moss 1978).

Recent outcome of genome sequence for *Ulva* has disclosed interesting insights about the evolution of multicellularity (De Clerck et al. 2018). Significant difference in *Ulva* genome with unicellular life forms highlighted its independent evolution. *Ulva* genome revealed smaller numbers of transcriptional regulators than other green algal lineages. Further, the development of multicellularity in *Ulva* presumably follows an alternative route as it lost the known key multicellularity gene retinoblastoma (RB)/E2F pathway and associated D-type cyclins. Along with these family of genes, homologs of Cln 2/3, SBF, and Whi5, which mediate G1-S transition in yeast were not determined in the sequenced genome. This clearly indicated an alternative orchestral suit of regulation for development of multicellularity. Beside, loss of gene families, expansion for some gene families were also noted. For instance, *Ulva* showed five genes for CONSTANS-like (CO-like) transcription factors which otherwise ranged from 0-2 in other sequenced algae. These families of proteins have notable functions in angiosperms including multicellularity, and in developmental processes such as photoperiodic flowering (Putterill et al. 1995), regulation of circadian rhythms (Strayer et al. 2000), and abiotic stress responses (Liu et al. 2016). To further get insights about the hormonal role in development, the genome shed light on the existence of genes responsible for biosynthesis of abscisic acid (ABA), ethylene, salicylic acid and auxin (IAA). Though culture studies showed the synthesis of GA3 in both exenic and axenic *Ulva*, no GA3 precursor ent-kaurene (CPP synthase, ent-kaurene synthase) was found from the genome. Interestingly, no homolog of angiospermic hormone sensing and signalling genes were found in *Ulva* genome which presumably implies a different and independent hormonal signalling mechanism in *Ulva* like diatoms. The development of genetic-toolkits and genome editing techniques for *Ulva* is needed to experimentally validate the sequenced gene functions and to get better insights about its independent and/or diverged evolution.

**Green tide event**

*Ulva* spp. are well known for developing un-controlled, rapid and colossal mass production termed as ‘green tide’. The free floating fragments act as nucleus to form green tide in newer location by posing significant ecological and economic hazards. Brittany, France a popular tourist destination reported 100,000 tons of *Ulva* through green tide event with estimated cost of US$ 10–150 tonne-1 to the local economy for cleaning and disposal (Charlier et al. 2008). In another example, 30 km long green tide bloom of *Ulva* was reported at Qingdao coast during 2008 at the time of Beijing Olympics. An estimated expenditure of US$ 30 million was incurred to dispose over million tons of biomass by employing 10,000 people (Ye et al. 2011). The wide-spread ubiquity, potential longevity of culturable free living microscopic stages culminated into green tide outbreak. Eutrophication, especially enhanced supply of nitrate and phosphate coupled availability of more surface-area-to-volume ratios in this alga were found to be responsible for exceptionally high growth rates [10 – 50 % per day] in *U. prolifera* (Alstyne et al. 2015). Nevertheless, low salinities (10‰ and 20‰) and low pH values (pH around 7.0) registered considerable biomass increase (Lin et al. 2011). Thus enhanced inflows of freshwater before, and during, 2007 flood might have played important role in bloom formation. Further, it may be noted that, sporulation triggered by fragmentation(as small as 1 – 2 mm diameter)triggered mass production leading to unprecedented growth. ITS nrDNA and *rbc*L phylogenetic analyses revealed single strain of the *U*. *linza‐procera‐prolifera* clade responsible for bloom in the Yellow Sea of China (Liu et al. 2010). The hybridization experiments confirmed presence of two types of sexual strains in *U. prolifera* distinguishable by crossing affinity to *U. linza* (Hiraoka et al. 2011). The presence of a single genetic entity (floating *U. prolifera* strain) was further augmented with SCAR (sequence characterized amplified region) marker studies endorsing unique ecotype responsible for recurrence of bloom during 2007 to 2013 (Zhao et al. 2015). Nevertheless, transcriptome sequencing revealed that both C3 and C4 photosynthesis genes are present, wherein the further functional analysis of key C4 enzymes confirmed operation of C4- carbon pathway in *U. prolifera* (Xu et al. 2012).

**Culture and cultivation**

The initial culture experiments were carried out to aid genetic, growth, physiological, biochemical and electron-microscopical studies with *U. mutabilis* as model organism. Soil extract was used to supplement essential nutrients from which doubling time of 24 h (mutant) and 72 h (wile type) was recorded (Lovlie 1969). Nevertheless, soil extract was replaced with defined supplements (Provasoli 1968). The subsequent studies evaluated effect of various culture media namely plain filtered pasteurized seawater, Schreiber media, Erd-Schreiber media, Iwasak’s enriched seawater, Provasoli's enriched seawater, von Stosch media and SWM-3 media on growth of *U. fasciata* with an aim to understand the requirement for field cultivation (Oza and Rao 1977).

The field cultivation is achieved by employing either artificial or natural seeding, while former is more scientific or results into consistent growth and yield (Ohno 2006). Nevertheless, common environmental parameters namely salinity and temperature were standardized for effective zoospore induction, regeneration and daily growth in *U. fasciata* (Mantri et al. 2011). Clonal tissue (Polne-Fuller and Gibor 1986), asexual thallus (de Góes and Reis 2011) and spores (Oza et al. 1985) were used for cultivation of different *Ulva* species either in out-door tank facilities or in the open sea. *Ulva* has been successfully tested in abalone co-farming, in South Africa (Steyn 2000). A daily growth rate (DGR) reported as 21.6 - 26.5 % day-1 for *U. flexuosa* in pond culture (Mairh et al. 1986); 27.9 ± 4.4% day-1 in tank and 20.1 ± 1.8% day-1 in open sea for *U. flexuosa* (Castelar et al. 2014). Besides these conventional farming methodologies considerable progress has been made in photobioreactor culture where average growth of 2.89 and 3.65% day*-1* for *U. compressa* was recorded (Chemodanov et al. 2017). Nevertheless, off-shore farming of *Ulva* sp. reported 838 ± 201 g C m-2 year-1 net annual primary productivity which was considerably higher than terrestrial plants (Chemodanov et al. 2017). It may be noted that targets of future development of scale up *Ulva* farming required feasible techniques for offshore cultivation. The farming protocol requires considerable mechanization. The pilot-scale net and rope systems (either vertical, horizontal or circular modules) were tested only in Germany, the United States and Japan (Van den Burg et al. 2013). These designs are inexpensive and low in maintenance, thus became significant for techno-economic validation. The new designs for flexible submersible aquaculture structures such as “SUBFLEX” can also be useful when taken the advantage of offshore wind farms, which provide cost-effective anchoring. Further, two stage approach where seeding and initial rearing of seedlings can be accomplished in land-based tanks (Gupta et al. 2018) and then transplanting the seeded ropes and nets in the offshore farm. This ensures reduced mortality of germlings due to diseases, pests and adverse environmental fluctuations. The integration of deep water pumping with Ocean thermal energy conversion (OTEC) technology and Integrated Multitrophic Aquaculture (IMTA) were two viable options considered to supply nutrients to the offshore farms (Zollmann et al. 2019). It may be noted that, these technologies are in nascent stage and required specialized infrastructure and expertise. The considerable R & D developments are necessary in these fields to successfully deploying offshore farming for commercial gains.

*Ulva* farming has recently attracted attention due to its potential role and scope in fixing CO2. The green algal genus *Ulva* has considerable potential and reported great efficiency for carbon sequestration. *U. lactuca* reported to utilize 100% CO2 for carbon fixation up to 15 mg/l (Kaladharan et al. 2009). Agarwal et al. (2016) studied CO2 sequestration capacity of *U. intestinalis* and *U. lactuca*. These species can accumulate carbon in large proportion with minimum time and thus could play catalytic role as natural sink for carbon cycle.

**Epiphytes, grazers and competitors in *Ulva***

Although, there is evidence of *Ulva* that act as competitor for nutrients (Xu et al. 2012), cause epiphytic infestation (Muñoz and Fotedar 2010; Ganesan et al. 2015), exhibit allopathic effect on other seaweeds (Friedlander et al. 1996; Xu et al. 2012); likewise, epiphytes, grazers and competitors in its culture and farming system are inevitable. It may be noted that several bacterial epiphytes and endophytes were found to be associated with *Ulva* and positively influence morphogenesis, growth and other developmental processes (Wichard 2015; Wichard et al. 2015). The annual cycle of members of epiphytic Dinophyceae (Miozoa), Chlorophyceae (Chlorophyta) and Cyanophyceae (Cyanobacteria) on *Ulva* in relation to intertidal elevation, season and position on host along northern Patagonia in Argentina, revealed clear seasonality pattern. Seawater temperature, exposure to longer day length and high irradiation favoured high frequency of *Lyngbya* sp., (Cyanobacteria), *Cocconeis* sp., *Navicula* spp., *Rhabdonema arcuatum* (Bacillariophyta), *Stylonema alsidii* (Rhodophyta) and *Myrionema strangulans* (Ochrophyta, Phaeophyceae); with hold fast being the preferred location (Gauna et al. 2016). Microalgae are not known to harm seaweeds, but in exceptionally high densities they may tend to compete for nutrient or cause shading effect. The brown alga *Myrionema strangulans* is known to cause exclusive epiphytic infection in *Ulva* spp in aquaculture as well as wild populations world-wide. The symptoms exhibited includes perforations, massive depigmentation, cellular disorganization, and cuticle rupture. The prevalence of infection was found to be 100% under controlled laboratory studies (Siniscalchi et al. 2012). The low density of inoculums (minimum 11.5 g) under closed indoor plastic photobioreactor culture collapsed due to proliferation of epiphytes (other seaweeds, nematodes, copepods and bacterial proliferation), but in high density of inoculums (minimum 179–264 g), yielded 15 % day-1 DGR (Ingle et al. 2018). Nevertheless, epiphytes attract grazers which intern feed on them or on host tissue. *Gammarus locusta* (amphipod) and *Idotea chelipes*, *Sphaeroma hookeri* (isopod) were identified as grazers on *Ulva*, but it was found that only *I. chelipes* graze on algal tissue and other two feed on epiphytic diatoms (Kamermans et al. 2002). The cage culture of *Ulva* with addition of double protecting net resulted in appreciable growth (DGR) of 8.1 % day-1 in open sea farming at Israel in one month of growth cycle, which in absence of protective net reduced to – 2.5 % day-1 (Ingle et al. 2018). The framework for epiphyte and pest management is essential for mitigation strategies for improved culture and cultivation practices.

**Microbial interaction**

*Ulva* has been in focus for algal-microbe interaction studies and conceived as a model system for studies of algal growth, development and morphogenesis (Wichard et al. 2015). Analysis of 16S rRNA gene libraries of epiphytic bacterial communities of *Ulva* revealed their dissimilarity with libraries of the surrounding seawater (Burke et al. 2011, Ismail et al. 2018). The functional redundancy (i.e. more than one species is capable of performing a specific role) within communities was observed in different samples of *U. australis* (Burke et al. 2011). Similarly, Ghaderiardakani et al. (2017) showed the existence of a ‘competitive lottery’ theory, wherein, a different set of microbial communities with similar functional characteristics induce the development of *Ulva* species. Alpha-, Gamma-, and Delta -Proteobacteria, Bacteriodetes, and Planctomycetes forms the major communities on the surface of *U. australis* (Tujula 2006). The host specificity of bacterial communities was not observed by Roth-Schulze et al. (2016) in *Ulva* however a stable core set of functional genes was observed in bacterial communities associated with closely related *Ulva* species. Nevertheless, host specificity was observed by other researcher wherein they reported similar bacterial assemblage in a species from different habitat (Goecke et al. 2010). The morphological variability within this genus is not only dependent on physical and chemical parameters of habitat, but associated bacteria as well play an important role in defining morphology (Provasoli and Pintner 1980). It was confirmed beyond doubt that the species of *Ulva* lose its morphological features when grown in axenic culture; however, the incubation with its associated bacterial isolates or their cell free extract restores the normal morphology (Provasoli 1965; Provasoli and Pintner 1980; Nakanishi et al. 1996; Marshall et al. 2006). Synergistic effect of bacterial communities was also considered as important factor in development of normal morphology (Wichard 2015). Spoerner et al. (2012) showed that normal growth and morphogenesis of thallus in *U. mutabilis* is governed by regulatory factors secreted by Cytophaga MS6 (auxin-like activity) and Roseobacter MS2 (cytokinin-like activity).

Epibiotic bacteria of *Ulva* played an important role in antifouling mechanism. The antifouling mechanism exhibited by *U. reticulata* by secreting bioactive substances is also complimented by compound secreted by associated bacteria (Dobretsov and Qian 2002; Harder 2004). Egan et al. (2000) showed that bacteria from the surface of *U. lactuca* were capable of inhibiting bacteria, fungi, settlement of invertebrate larvae and germination of algal spores. Rao et al. (2007) found that low densities of bacteria like *Pseudoalteromonas tunicata* and *Phaeobacter* sp. strain 2.10 on the surface of *U. australis* inhibits settlement of fouling organisms. Ismail et al. (2018) found antibacterial activity in 36 % of bacterial isolates from surface of *U. rigida*. Bacterial biofilm from surface of *Ulva* is known to secret signalling molecule N-acylhomoserine lactones that involves in settlement of zoospores (Joint et al. 2007).

Besides the role discussed above associated bacteria also increases the bioavailability of metals by providing organic ligands for metal acquisition. Bacteria associated with *U. mutabilis* found to release organic ligands which form a complex with iron and become part of the organic matter in the chemosphere and as a source of iron (Wichard 2016). Phylogenomic analysis of *U. mutabilis* showed the presence of 13 horizontally transferred genes from prokaryotes (De Clerck et al. 2018).

**Phytochemistry, pharmacological activities and food value**

The species of *Ulva* have been extensively analysed for their chemical constituents useful as food, fertilizer and medicine. The variation in protein content is very high and ranged from 4-29% (w/w) dry weight (DW) basis. The highest protein content recorded was 29% DW in *U. lactuca* (Marsham et al. 2007). The major amino acids in *Ulva* are cysteinolic acid, cysteic acid, praline, glutamic acid and chondrine (Holdt and Kraan 2011). *Ulva* is also a good source of essential amino acids and accounts up to 39 % of total protein DW (Wong and Cheung 2001). Apart from protein *Ulva* is also a rich source of carbohydrate and presents up to 61.5 ± 2.3 % DW (Ortiz et al. 2006). However, the greater portion of this polysaccharides are not digested by humans and termed as dietary fibers. The amount of dietary fibers in *Ulva* ranged from 24.8 ± 0.2 - 60.5 ± 1.5 % DW (Ortiz et al. 2006; Peña-Rodríguez et al. 2011). One of the major cell wall polysaccharides in *Ulva* is a water soluble Ulvan and constituted about 8 – 29 % DW (Lahaye and Robic 2007). The lipid content is low in *Ulva* and ranged between 0.3–3.5 % DW (Ortiz et al. 2006; Fleurence 2016). Nevertheless, in some studies higher amount of lipid ca. 7.87 % DW was also reported (Yaich et al. 2011). The polyunsaturated fatty acids are the significant part of this lipids and constituted up to 35.3 % of total fatty acid (Taboada et al. 2010). The amount of ash content in *Ulva* is generally high and found up to 52 % DW (Foster and Hodgson 1998). *Ulva* is also considered as an important source of minerals such as calcium and magnesium. The amount of calcium can reach up to 325 mg/100 g wet weight (Brown et al. 2014). Whereas magnesium was found up to 465 mg/100 g wet weight (MacArtain et al. 2007). Moreover, *Ulva* is also known for containing both water- and fat-soluble vitamins A, B, C, and E (MacArtain et al. 2007; Taboada et al. 2010). The various bioactive secondary metabolites such as terpenes, polyphenolic compounds and steroids were also reported from *Ulva* (Fujimura et al. 1990; Flodin and Whitfield 1999; Awad 2000; Chakraborty et al. 2010a; 2010b; Yildiz et al. 2012).

The various phytochemicals extracted from *Ulva* are known to exhibit antimicrobial, antiviral, antioxidant, anticoagulant, anti-inflammatory, and anticancer activities. A mitogenic hexapeptide reported from *Ulva* had shown to modulate the production of proteoglycans and glycosaminoglycans in extracellular matrix of human foreskin fibroblast (Ennamany et al. 1998). Ethanolic extract of *U. fasciata* showed antigenotoxic effects against damage induced by benzo[a]pyrene. The water-soluble fraction of methanolic extract from *U. lactuca* showed the antitumor activity and also boost immune system by stimulating the growth of splenocytes and production of nitric oxide by macrophages (Lee et al. 2004). The anticancer activity of desulphated, reduced and desulphated-reduced polysaccharides fractions of Ulvan was reported by Kaeffer et al. (1999). Ulvan also reported to show hypocholesterolemic and hypolipidemic effect by reducing absorption of cholesterol in gut (Smit 2004). The sulphated polysaccharides from *U. lactuca* also showed their neuroprotective potentials by exhibiting the antioxidant and cholinesterase inhibitory activity (Olasehinde et al. 2019). Sulphated polysaccharides from *U. conglobata* inhibits the thrombin and potentiates the heparin cofactor II which leads to anticoagulation activity (Mao et al. 2006). Ismail et al. (2018) reported the antimicrobial activity of fatty acids extracted from *U. rigida*. Extracts of *U. intestinalis* and *U. lactuca* were also reported to show antiprotozoal and antimycobacterial activity (Spavieri et al. 2010). Taurine an amino acid from *Ulva* (Ito and Hari 1989, Peña-Rodríguez 2011) is a broad-spectrum cytoprotective agent which involved in cell volume regulation and formation of bile salts (Ripps and Shen 2012). Labdane diterpenoids from *U. fasciata* was showed as promising agent against multi-resistant Gram-negative fish pathogenic bacteria (Chakraborty 2010b).

The use of *Ulva* as food in Asian countries is well known. The presence of high quantity of essential vitamins and trace elements and minerals compared to its terrestrial counterparts makes it a promising food source. One of the important commercially utilized seaweed food in japan “Green laver” or “aonori” is a mixture of *Ulva* and *Monostroma* which contain high amounts of protein, calcium, Vitamins and iron and low content of fat and sodium (Nisizawa et al. 1987; McHugh 2003). Recently *Ulva* is also authorized as a human food in Western countries like France (Marfaing and Lerat 2007). *Ulva* was also reported to be used as one of the ingredients in a snack “Pakoda” traditionally prepared in India (Mamatha et al. 2007). *Ulva intestinalis* was utilized in fortification of surimi-based product which improved the gel strength, water-holding capacity of gels and emulsifying stability of surimi pastes (Jannat-Alipour et al. 2019). *Ulva* biomass has gaining attention in several food applications for protein and starch in East Mediterranean (Israel et al. 2019). *Ulva lactuca* is also utilized as a diet source for abalone and trial with high levels of ammonia in integrated system showed improved growth in abalone (Shpigel et al. 1999). Abudabos et al. (2013) supported the partial incorporation of *U. lactuca* (up to 3 %) in poultry diets which resulted in higher dressing percentage and breast muscle yield in birds. The nutritive evaluation of *U. lactuca* for goats supported its inclusion as medium quality forage (Ventura and Castanňón 1998). Pariera (2016) had listed different edible *Ulva* species by geographic regions as follows: *U. intestinalis*, *U. lactuca* and *U. rotundata* in North Atlantic and Mediterranean region, *U. clathrata*, *U. linza* and *U. rigida* in South Atlantic and Caribbean Sea, *U. compressa* in East Asia (China, Japan, Korea), *U. australis*, *U. conglobata*, *U. reticulata* and *U. stenophylla* in Indo-Pacific (India, Indochina, the Philippines, Indonesia, Australia, New Zealand), *U. flexuosa*, *U. flexuosa* subsp. *paradoxa*, *U. lactuca* and *U. prolifera* in Pacific Islands (Micronesia, Polynesia, Melanesia, and Hawaiian Is), *U. lactuca* in East Pacific (Alaska to California, Mexico, Peru, Chile, Argentina).

***Ulva* as a potential candidate for bioremediation**

The rate of accumulation of metals is high in macroalgae which makes them efficient system of biosorbents in bioremediation process. The biomass can be utilized in living or non-living form (Hlihor et al. 2017). The characters such as wide distribution, availability of high surface area and fast growth make *Ulva* suitable candidate for bioremediation processes (Ho 1990, Nielsen et al. 2012). *U. intestinalis* was found useful in accumulating highest amount of metal such as copper (Cu), chromium (Cr), Zinc (Zn), cadmium (Cd) and lead (Pb) in comparison to other marine algae employed (Baumann et al. 2009). Similarly, the use of KOH-activated carbon of *U. lactuca* was also found as a potent remedy to removal metal ions (Ibrahim et al. 2016). Karthikeyan et al. (2007) reported the use of *U. fasciata* as efficient biosorbent material for uptake of Cu ions and its possible regeneration by the process of desorption. In *U. fasciata* the rate of adsorption of Cu ions was fast (80% in 5 min.) with the maximum capacity found up to 26.88 mg g-1 (Prasanna Kumar et al. 2006). Similarly, the rate of adsorption for Ni(II), Cd(II), and Pb(II) ions by *U. linza* was found as high as 90% of initial concentration within 10 min. (Yalςın 2014). The high uronic content in *Ulva* may be the reason for its capacity to uptake high amount of ions (Wang and Chen 2009). The uptake rate was also found to be influenced by pH and the maximum rate for Ni(II), Cd(II), and Pb(II) ions was observed at pH of 5-5.5 in *U. linza* (Yalςın 2014). Kinetic studies of metal uptake in *U. lactuca* showed that decrease in salinity (from 28 to 10‰) increased the uptake of metals such as Cd, Cr, Se and Zn by 1.9-, 3.0-, 3.6-, and 1.9-fold, respectively (Wang and Dei 1999). The study also suggested the use of *U. lactuca* as a biomonitor of Cr and Zn contamination. Statistical optimization using Plackett–Burman and face centered central composite designs for removal of cadmium ions from aqueous solutions yielded reduction of 99.96% at pH 5, 25 ºC for 60 min using dry biomass of *U. fasciata* (El-Naggar et al. 2018)*.* Bădescu et al. (2017) showed the utilization of Zn(II) ions loaded *Ulva* material as fertilizers to improve the soil quality. Even though biosorption by *Ulva* have many advantages, the disposal or reuse of heavy metal loaded material is still a bigger challenge. It is therefore necessary to ascertain viability of the large-scale applications considering its environmental impacts.

**Bio-refinery**

A comprehensive listing of potential bio-refinery approaches applied so far for *Ulva* spp. is presented in the Table 1. Carbohydrates remain the major product of interest as in addition to dietary fibers (Yaich et al. 2015) and bioactive sulphated polysaccharides (Glasson et al. 2017), it provides further extensions for obtaining precursor molecules for biofuel (van der Wal et al. 2013). The abundancy and remarkable productivity of *Ulva* spp. adds to its enriched protein contents and thus have made it a viable source of dietary proteins. The essential and non-essential amino acid contents have been found comparable to those traditional sources of proteins utilized so far, particularly rich in glutamic acid, aspartic acid, arginine, alanine and leucine. There are various processes for effective protein extraction from *Ulva* biomass in which alkali-based processing methods reported highest extraction efficiencies (Gajaria et al. 2017; Fleurence et al. 1995; Shuuluka et al. 2013). The observed changes may be the result of extensive cell wall disruption due to the alkali incubation which accelerated the liberation of crude proteins from the biomass. However, the use of pulsed electric field is also an emerging chemically benign technology that minimize the usage of chemicals for the extraction and thermal denaturation of proteins (Polikovsky et al. 2016). However, number of single product oriented studies are found in literature targeting the sulphated polysaccharide ulvan (Paradossi et al. 1999; Lahaye and Robic 2007; Robic et al. 2009a; 2009b; Alves et al. 2010), celluloses (Siddhanta et al. 2001; Choi et al. 2013), starch (Choi et al. 2013; Prabhu et al. 2019), biofuel (Trivedi et al. 2013; Korzen et al. 2015; Hamouda et al. 2016), bio-oil (Suganya and Renganathan 2012; Zhuang et al. 2012; Liu et al. 2013; Singh et al. 2015) and minerals (Peña-Rodríguez et al. 2011; Yaich et al. 2011; Tabarsa et al. 2012; Magnusson et al. 2016), the recent studies by Trivedi et al. (2016), Gajaria et al. (2017), Glasson et al. (2017) and Mhatre et al. (2019) demonstrated successive densification of biomass with the progressing chemical extraction which significantly contributed towards the maximum biomass utilization, waste minimization and successive refined product extraction. The challenges about the scale-up and environmental impact of a bio-refinery process are still under evaluation. The products extracted are of various biochemical nature which demands diverse nature of chemicals and hence makes the process challenging rather than benefit from the view of techno-economic feasibility. However, indulging the usage of renewable energy sources and development of recyclable chemical regimes are the upcoming milestones for the marine algae-based bio-refinery processes.

**Conclusions**

The wide spread distribution, with about 130 taxonomically accepted species, short life cycle, fast growth, unique chemical composition and polysaccharide has made green algal genus *Ulva* a preferred model for numerous studies including morphogenesis, food and edible applications, bio-filtering and bio-remediation, offshore farming, green technologies, bio-refinery, genome and evolutionary investigations. The knowledge of control over reproduction has facilitated to overcome impediment over conventional farming technologies. The addition of multiple steps especially nursery/ hatchery, intensive out-door tank system and then out-planting has enabled to obtain continuous crop cycles, reduced mortality, disease, pest infestation, and improved yield. The technological and engineering improvements have also envisaged great deal of attention in offshore farming. The high uptake rate of adsorption and accumulation of heavy metals by living as well as non-living biomass has opened up avenues for developing bioremediation in eutrophic waters but ascertaining viability of the large-scale applications and environmental implication needs further consideration. The genetic transformation was successful and 98.5 Mbp haploid genome (12,924 protein coding genes) of *U. mutabilis* reported. The genome study offered plethora avenues to decipher coastal and marine ecosystems processes and fundamental evolution of the green lineage.

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**Table 1: Specialty chemicals and value added products derived from *Ulva* biomass**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Species | Location | Product | Yield | Reference |
| *U. lactuca* | Mandapam, Tamil Nadu, India | Volatile solids | 82.93±2.58 % | (Mhatre et al., 2019) |
| Carbohydrates | 53.18 ± 2.61 % |
| Proteins | 16.65 ± 0.68 % |
| Ash | 17.06±2.94 % |
| Bio-gas | 489.86±28.38-614.28 ± 16.15\* |
| Methane | 210.08±6.15-408.81 ± 20.02\* |
| *U. pertusa* | Jeju Island, Korea | Lipids | 0.1% | (Lee et al., 2014) |
| Carbohydrates | 52.3% |
| Proteins | 25.2% |
| Ash | 22.5% |
| *U. lactuca* | Kuvehei, Qheshm island,  Iran | Lipids | 0.99 ± 0.00 | (Tabarsa et al., 2012a) |
| Crude fibers | 5.6 ± 1.69 |
| Proteins | 10.69 ± 0.67a |
| Ash | 18.03 ± 2.37 |
| [*U.*](https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/sea-lettuce)*ohnoi* | Queensland, Australia | Ulvan | 8.2 ± 1.1% | (Glasson et al., 2017) |
| Crude fibres | 29.0 ± 0.7% |
| Proteins | 18.5 ± 1.5% |
| Ash | 28.8 ± 1.6% |
| *U. lactuca* | Veraval, Gujarat, India | Sap | 14% | (Gajaria et al., 2017) |
| Lipids | 1.5% |
| Ulvan | 19.90% |
| Crude Proteins | 11 ± 2.12% |
| Cellulose | 10.35 ± 1.07% |
| *U. fasciata* | Veraval, Gujarat, India | Sap | 1.7-2.0 gm | (Trivedi et al., 2016) |
| Lipids | 2.7% |
| Ulvan | 25% |
| Cellulose | 10% |
| Ethanol | 450# |

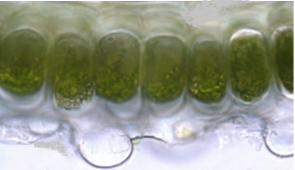
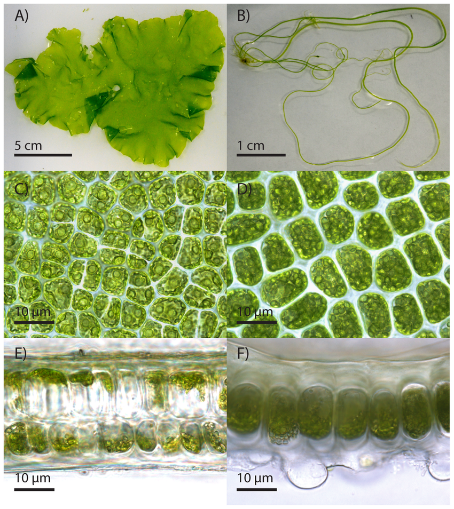
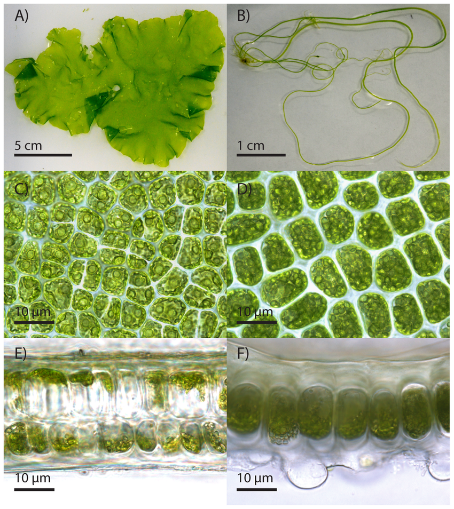
\*ml per g VS

\*\* (expressed as % rhamnose content in the raw seaweed dried at 50 C

\*\*\* L per dry tones

# mg ethanol per g reducing sugar

**Fig. 1 Thallus organisation in *Ulva***



a

b

c

d

(a: *Ulva* thallus, b: Cell organisation in surface view, c: Transverse section of thallus, d:

Transverse section of rhizoidal cell)

Source: Lawton et al. (2013)

**Fig. 2: World map showing continent wise distribution of number of distinct species of *Ulva***

****

Source:Guiry and Guiry (2020)

**Fig. 3: Typical life cycle in *Ulva***



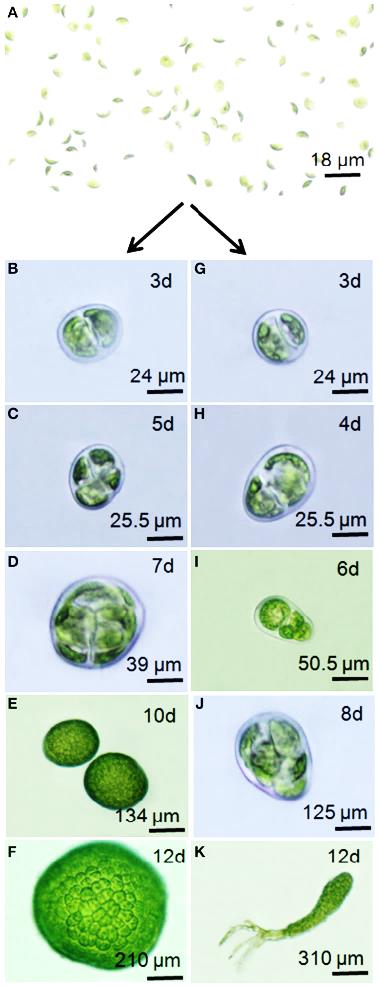
**Male plant (N)**

**Zygote (2N**)



Gametophyte (N)

**Fertilization**



**Sporophyte(2N)**



**Male**

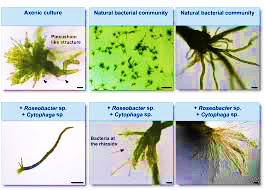
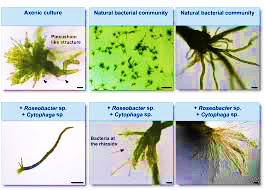
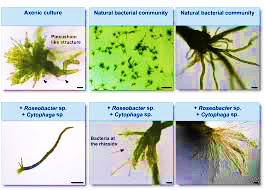
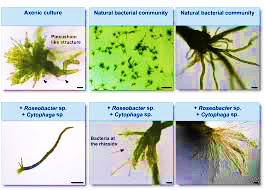
**Plant**

**(N)**

**female**

**Plant**

**(N)**



Zygote (2N)

Asexual

reproduction

Asexual

reproduction

Asexual

reproduction



Germlings

Germlings

Germlings

Germlings

Gametes

Zoospores

**Supplementary Table 1: World distribution of *Ulva* spp.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Asia**  **(56)** | **Africa**  **(31 )** | **North America (34)** | **South America**  **(20)** | **Antarctica**  **(12)** | **Europe**  **(38)** | **Australia**  **(40)** |
| *Ulva adhaerens* | *Ulva aragoënsis* | *Ulva acanthophora* | *Ulva californica* | *Ulva chaetomorphoides* | *Ulva aragoënsis* | *Ulva australis* |
| *Ulva anandii* | *Ulva ardreana* | *Ulva australis* | *Ulva australis* | *Ulva clathrata* | *Ulva ardreana* | *Ulva brevistipita* |
| *Ulva aragoënsis* | *Ulva atroviridis* | *Ulva californica* | *Ulva chaetomorphoides* | *Ulva compressa* | *Ulva australis* | *Ulva brisbanensis* |
| *Ulva arasakii* | *Ulva californica* | *Ulva chaetomorphoides* | *Ulva clathrata* | *Ulva flexuosa* | *Ulva blidingii* | *Ulva californica* |
| *Ulva ardreana* | *Ulva clathrata* | *Ulva clathrata* | *Ulva compressa* | *Ulva geminoidea* | *Ulva californica* | *Ulva clathrata* |
| *Ulva australis* | *Ulva compressa* | *Ulva compressa* | *Ulva fenestrata* | *Ulva hookeriana* | *Ulva chaetomorphoides* | *Ulva clathratioides* |
| *Ulva beytensis* | *Ulva cuneata* | *Ulva cruciata* | *Ulva gigantea* | *Ulva hookeriana* | *Ulva clathrata* | *Ulva compressa* |
| *Ulva burmanica* | *Ulva curvata* | *Ulva curvata* | *Ulva hookeriana* | *Ulva intestinalis* | *Ulva compressa* | *Ulva crassa* |
| *Ulva californica* | *Ulva denticulata* | *Ulva expansa* | *Ulva intestinalis* | *Ulva lactuca* | *Ulva croatica* | *Ulva crassimembrana* |
| *Ulva chaugulii* | *Ulva elegans* | *Ulva fenestrata* | *Ulva lactuca* | *Ulva reticulata* | *Ulva curvata* |  |
| *Ulva clathrata* | *Ulva flexuosa* | *Ulva flexuosa* | *Ulva lobata* | *Ulva rigida* | *Ulva fenestrata* | *Ulva flexuosa* |
| *Ulva clathratioides* | *Ulva hookeriana* | *Ulva gigantea* | *Ulva nematoidea* | *Ulva sorensenii* | *Ulva flexuosa* | *Ulva geminoidea* |
| *Ulva compressa* | *Ulva intestinalis* | *Ulva intestinalis* | *Ulva ohnoi* | *Ulva gigantea* | *Ulva hookeriana* |
| *Ulva compressa* | *Ulva kylinii* | *Ulva kylinii* | *Ulva papenfussii* | *Ulva intestinalis* | *Ulva howensis* |
| *Ulva conglobata* | *Ulva lactuca* | *Ulva lactuca* | *Ulva plicata* | *Ulva intestinaloides* | *Ulva intestinalis* |
| *Ulva curvata* | *Ulva laetevirens* | *Ulva laetevirens* | *Ulva prolifera* | *Ulva kylinii* | *Ulva kraftiorum* |
| *Ulva covelongensis* | *Ulva linza* | *Ulva linza* | *Ulva ralfsii* | *Ulva lactuca* | *Ulva kylinii* |
| *Ulva expansa* | *Ulva nematoidea* | *Ulva lobata* | *Ulva reticulata* | *Ulva linza* | *Ulva lactuca* |
| *Ulva fenestrata* | *Ulva ohnoi* | *Ulva nematoidea* | *Ulva rigida* | *Ulva linzoides* | *Ulva laetevirens* |
| *Ulva flexuosa* | *Ulva polyclada* | *Ulva ohnoi* | *Ulva taeniata* | *Ulva maeotica* | *Ulva laingii* |
| *Ulva grandis* | *Ulva popenguinensis* | *Ulva paradoxa* | *Ulva ohnoi* | *Ulva linza* |
| *Ulva indica* | *Ulva profunda* | *Ulva profunda* | *Ulva paradoxa* | *Ulva lobata* |
| *Ulva intestinalis* | *Ulva prolifera* | *Ulva prolifera* | *Ulva pilifera* | *Ulva meridionalis* |
| *Ulva javanica* | *Ulva pulchra* | *Ulva pseudocurvata* | *Ulva polyclada* | *Ulva ohnoi* |
| *Ulva kylinii* | *Ulva ralfsii* | *Ulva pseudorotundata* | *Ulva prolifera* | *Ulva parva* |
| *Ulva lactuca* | *Ulva reticulata* | *Ulva radiata* | *Ulva pseudocurvata* | *Ulva phyllosa* |
| *Ulva laetevirens* | *Ulva rhacodes* | *Ulva rigida* | *Ulva pseudolinza* | *Ulva polyclada* |
| *Ulva limnetica* | *Ulva rigida* | *Ulva spinulosa* | *Ulva pseudorotundata* | *Ulva prolifera* |
| *Ulva linza* | *Ulva tanneri* | *Ulva stenophylla* | *Ulva radiata* | *Ulva ralfsii* |
| *Ulva lobata* | *Ulva torta* | *Ulva taeniata* | *Ulva ralfsii* | *Ulva ranunculata* |
| *Ulva meridionalis* | *Ulva uncialis* | *Ulva tanneri* | *Ulva repens* | *Ulva reticulata* |
| *Ulva ohnoi* | *Ulva tepida* | *Ulva rhacodes* | *Ulva rigida* |
| *Ulva pacifica* | *Ulva torta* | *Ulva rigida* | *Ulva sorensenii* |
| *Ulva papenfussii* | *Ulva schousboei* | *Ulva stenophylla* |
| *Ulva partita* | *Ulva splitiana* | *Ulva stenophylloides* |
| *Ulva patengensis* | *Ulva taeniata* | *Ulva taeniata* |
| *Ulva pilifera* | *Ulva torta* | *Ulva tanneri* |
| *Ulva profunda* | *Ulva tepida* |
| *Ulva prolifera* | *Ulva torta* |
| *Ulva pseudorotundata* |
| *Ulva quilonensis* |
| *Ulva radiata* |
| *Ulva ralfsii* |
| *Ulva reticulata* |
| *Ulva rigida* |
| *Ulva saifullahii* |
| *Ulva sorensenii* |
| *Ulva spinulosa* |
| *Ulva stenophylla* |
| *Ulva sublittoralis* |
| *Ulva taeniata* |
| *Ulva tanneri* |
| *Ulva tepida* |
| *Ulva torta* |
| *Ulva uncialis* |

Source: Guiry and Guiry (2020)