



# Concise review of green algal genus *Monostroma* Thuret

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Received: 3 August 2022 / Revised and accepted: 9 October 2022 / Published online: 27 October 2022  
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## Abstract

*Monostroma* (Ulotrichales, Chlorophyta) is the most intensively cultivated genus among green seaweeds, accounting for over 90% of total green algal cultivation. It is commonly found in the eulittoral zones of marine and estuarine habitats, thus contributing significantly to the ecology of the coastal ecosystem. Morphologically, the frond of *Monostroma* is blade-like with eponymous one-cell thickness; therefore, it is also known as “Slender sea lettuce”. *Monostroma nitidum* is often used for salad ingredients, boiled tsukudani, soups, etc., due to its health benefits. *Monostroma kuroshiense* is commercially cultivated in East Asia and South America for the edible product “hitoegusa-nori” or “hirohano-hitoegusa nori”, popular sushi wraps. This genus remains one of the well-studied seaweed genera for ecophysiology, habitat-dependent seasonality of its growth pattern, gametangial ontogeny and phylogenetics. Moreover, rhamnan sulfate (RS), a sulfated polysaccharide, is the main component of the fiber extracted from *M. nitidum* and studied for various biological activities. This review presents the taxonomy, morphology, anatomy, life history, distribution, ecology, physiology, cultivation and harvesting, chemical composition, and biotechnological applications of this genus.

**Keywords** *Monostroma* · Chlorophyta · Estuarine · Rhamnan sulfate · Seedling culture

## Taxonomy

All single cell-layered green algae with blade-like thallus were traditionally grouped under the eponymous genus *Monostroma* (Thuret 1854). Kunieda (1934) erected the family Monostromaceae (later synonym for Monostromataceae Kunieda ex Suneson 1947) to include this genus. Overclassification and a lack of a clear-cut systematic placement of this ulvophycean group have emerged from several and often contradicting taxonomic revisions. In *Monostroma*, for example, there are two lectotypifications: one recognizes *Monostroma oxyspermum* (Papenfuss 1960), and the other recognizes *Monostroma bullosum* (Kornmann 1964). Codiolales (Kornmann 1964; Hoek et al. 1995), Ulotrichales (Gayral 1964; Chapman and Chapman 1973; Floyd and O’Kelly 1990; Graham and Wilcox 2000; Gabrielson et al. 2004) and Ulvales (Bliding 1968; Vinogradova 1974; Bold and Wynne 1985) were at least three ordinal placements of this family as well.

Due to shared ontogeny (Disc-Sac-Blade; DSB) and swarmer release (simultaneously through an irregular rent), Gayral (1964) grouped *Monostroma angicava*, *Monostroma grevillei*, and *M. bullosum* under *Ulvopsis*, and reserved the genus *Monostroma* only for asexual species with typical ontogeny (presence of a filament stage) and zoid release mechanism (en-masse without pore). In contrast, Kornmann (1964) and Bliding (1968) advocated that asexual *Monostroma* members be removed. To accommodate the asexual members such as *Monostroma undulatum* and *M. oxyspermum*, Vinogradova (1969) created two monotypic genera, *Protomonostroma* and *Gayralia*. Because of their isomorphic life cycle patterns, *Monostroma fuscum* and *Monostroma obscurum* have been reclassified with the resurrected genus *Ulvaria* in the order Ulvaceae (Gayral 1964). Due to shared life cycle and ontogenetic patterns, *Monostroma leptodermum* and *Monostroma zostericola* have been grouped under the new genus *Kornmannia*, and placed under Ulvales due to a typical flagellate release mechanism in which swarmers are released one by one through a gametangial exit pore (Bliding 1968). Due to similarities in habit (cylindrical gametophyte), thallus ontogeny (filament-tube), and swarmer release mechanism, *Monostroma groenlandicus* has

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been placed in the genus *Capsosiphon* (en-masse), enclosed within hyaline sheath (Vinogradova 1969).

Polyphyly in this group of algae has resulted in a lack of synapomorphic features, leading to taxonomic uncertainty. Many studies have found that Ulvophycean algae have a high degree of phenotypic plasticity, making diagnostic characters like "monostromatic blade" unreliable taxonomically. *Prasiola* green algae, for example, exhibit macroscopic monostromatic thalli that resemble *Kornmannia*, but they belong to another class (Trebouxiophyceae). A green-tide forming single cell-layered algae that looked like *Monostroma* isolated from the west coast of Finland turned out to be a tubular *Ulva* morphotype (Blomster et al. 2002). Abiotic factors such as nutrient supply (Valiela et al. 1997) and salinity (Reed and Russell 1978) are believed to induce morphological changes in green algae. For a long time, phenotypical polymorphism caused by biotic factors has been known in green algae. Specific bacterial strains isolated from *M. oxyspermum* have been shown to cause morphogenic alterations in axenic cultures of this alga and in *Ulva pertrusa* and *Ulva intestinalis* (Matsuo et al. 2003).

Moreover, a molecular approach can relatively accurately identify the taxonomic positions of species and subspecies compared with traditional morphological methods (Blomster 2000). Therefore, species identification in recent taxonomic studies has been confirmed using molecular markers (such as chloroplast *rbcL* genes, ITS regions, or 5S rDNA regions) combined with morphological characteristics (Blomster 2000; Ding 2015; Cui et al. 2018; Yang et al. 2020; Tandel et al. 2021; VinceCruz-Abeledo et al. 2021). The compiled nrITS sequence homology of approximately 600 nucleotide base pairs by Cui et al. (2021) found that all *Monostroma* strains collected from Naozhou Island belonged to the same clade as *M. nitidum* (AF415170) in the ML (Maximum Likelihood) and NJ (Neighbor joining) phylogenetic trees. The same molecular method and referred sequences were also applied to confirm the identity of *Monostroma* strains from Guangdong and Zhejiang (Ding 2015).

*Monostroma* does not appear to be monophyletic based on the ITS sequence. Many entities included in *Ulva* have been shifted to *Monostroma* based on molecular analysis (Brodie et al. 2016; Sfriso 2010; Alongi et al. 2014). As a result, about 32 species of this genus are currently accepted worldwide (Guiry and Guiry 2021).

## Morphology and anatomy

*Monostroma* is macroscopic, initially sacklike, later splitting to form a single-layered membrane, parenchymatous or cells rounded and grouped in fours or separated by mucilage, commonly attached by rhizoidal protuberances. Cells are angular by compression or rounded, each with a single

parietal chloroplast encircling most of the cell and a single pyrenoid (Wehr et al. 2015). The morphology of monostromatic Ulvotrichales members varies little; nonetheless, the genera differ in the number of flagella on reproductive cells, ontogeny, and life history (Bast et al. 2009a).

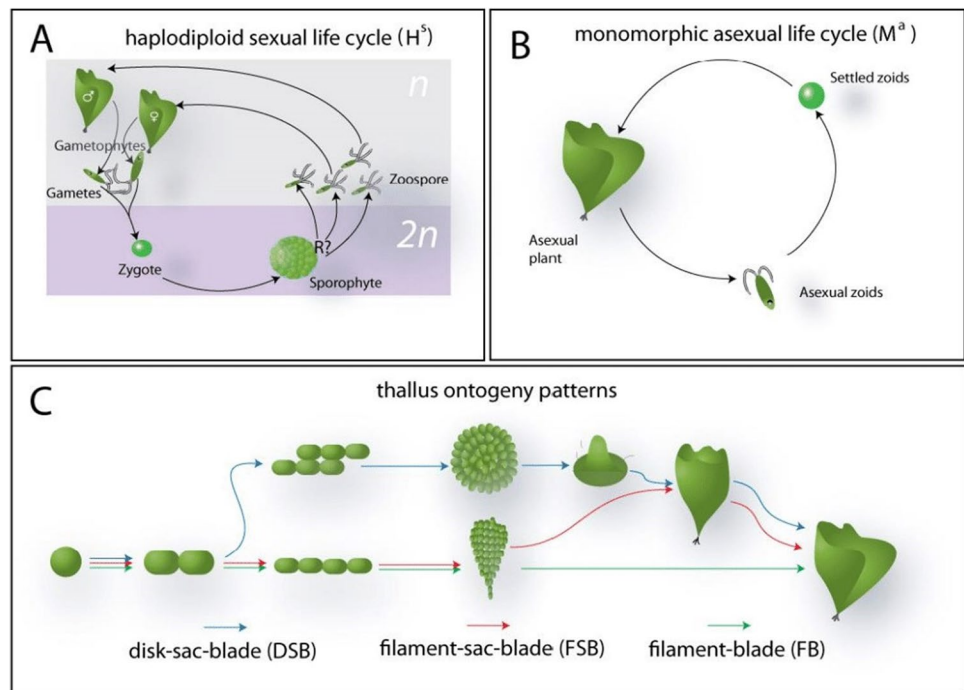
Cui et al. (2021) reported that the thalli of attached *Monostroma* strains (collected from Dalang, Naozhou Island, near the South China Sea Coast of Zhanjiang City) were yellowish or light green, flat, monostromatic and approximately  $11.60 \pm 6.23$  cm long and  $7.55 \pm 3.45$  cm wide. Cells in surface view were irregularly arranged and triangular or polygonal with three to five rounded corners. A single prominent chloroplast covered most of the outer cell in the surface view and contained mainly one (90%), and rarely two (6%) or three (4%), pyrenoids. Cells in transverse sections were circular or quadrangular with rounded corners and  $38.80 \pm 2.40$   $\mu\text{m}$  thick (Cui et al. 2021). Based on morphological and developmental characteristics combined with nuclear-encoded internal transcribed spacer sequences, Cui et al. (2021) identified these strains as *M. nitidum*. Similarly, Wang et al. (2015) described the frond of *M. nitidum* as monostromatic, yellowish-green or light green, 2–15 cm long, and shiny, with a frilly and mangled edge. In the cross section, the frond is composed of a single layer of cells enclosed within a gelatinous matrix 30–40  $\mu\text{m}$  thick. In the surface view, cells are unordered and polygonal with three to five rounded corners.

Titlyanov et al. (2016) described the thallus of *Monostroma latissimum* as being membranous, flaccid, soft, thin, ruffled surface, and perforated with many holes of various sizes, light green, 10–20 cm across. Margins are smooth or undulating. Cell from surface view rectangular to polygonal with rounded corners, disordered, often in groups of 2–3(–4), 15–17  $\mu\text{m}$  across. In the transverse section, blade one cell thick, 30(–35)  $\mu\text{m}$  at the basal portion and 20–25  $\mu\text{m}$  above; cells vertically oval 12.5–117.5(–20)  $\mu\text{m}$  high. Chloroplast single, central with one pyrenoid. Attachment by a small holdfast. They grow on rocks and dead corals in the upper intertidal zone.

## Life history

The lifecycle is haplodiploid alternation, with the dominant, macroscopic phase being the haploid dioecious gametophyte (Fig. 1A). Upon maturity, apical parts of the fronds mature and phototactic biflagellate gametes are released. Fertilization is anisogamous and settled zygotes mature into microscopic, spherical diploid codium-sporophytes. After 3–4 months of growth sporophytes are matured and quadriflagellate zoospores are produced. Settled zoospores germinate and develop into respective gametophytes, thus completing the life cycle. Various life stages are known;

**Fig. 1** Life cycle and thallus ontogeny patterns of *Monostroma*. An “R?” indicates presumable sporic meiosis (Bast 2015)



sexual forms (dioecious/monoecious, isogamous/anisogamous) and asexual forms without a codium/cyst stage or with a codium/cyst phase (produced via parthenogenetic female pseudo-gametes). A monomorphic asexual lifecycle in this genus has also been reported from a population in Japan (Bast et al. 2009b). In this lifecycle, there is no sexual fusion and the swarmer germinates directly without passing through the sporophyte stage (Fig. 1B). Ontogenetic patterns of *Monostroma* can be broadly divided into two categories: one with disc-phase intermediate and second with filamentous intermediate. The former pattern always results in a sac stage that bursts out to produce a leafy monostromatic blade (Disc-Sac-Blade, DSB), whereas the latter pattern develops into expanded blade with (Filament-Sac-Blade, FSB) or without (Filament-Blade, FB) the sac stage intermediate (Bast 2015).

## Ecology and distribution

The benthic green alga, *Monostroma*, grows abundantly on high-to-mid intertidal rocks. This genus is distributed in marine, brackish water, and estuarine habitats of South America, North-Western Europe, East Asia, Australia and New Zealand (Guiry and Guiry 2021). Only one or two species are known exclusively from freshwater habitats. *Monostroma* often grows on rocks or lodged driftwood in swift-flowing streams and rivers (Taft 1964); it is also reported from standing water in Arctic Canada. It is a spring ephemeral and has a characteristic growth pattern distinctive

to the habitats where it grows and recurs annually. Three distinct thallus types (inner-bay type, estuary type, and open-sea type) of *Monostroma* have been characterized based on the habitat (Kida 1990). Physico-chemical characteristics such as temperature, irradiance, salinity, nutrient level and biological (presence or absence of grazers) characteristics of the habitat or a combination of these factors could cause these habitat-dependent differences (Bast et al. 2009b). Wave action might be a limiting factor as it is shorter in wave-swept habitats than in sheltered ones. In high saline habitats, both the arrival and deterioration of thalli are found earlier, suggesting that salinity positively influences either the maturation of sporophytes or the senescence of gametophyte plants. Overall sex ratio in nature is about 1:1 and there are no remarkable fluctuations in the secondary sex ratio either temporally or spatially.

## Physiology

According to several studies, seaweed growth, reproduction, and distribution are constrained by salinity, temperature, light intensity, and photoperiod (Wilson et al. 2015; Mosquera-Murillo and Peña-Salamanca 2016). Being an estuarine alga, *Monostroma* species experience wide fluctuations in temperature, salinity, and light which may cause a reduction in species number and a shift in perennial taxa (Wilkinson 1980; Mathieson and Penniman 1986, 1991). The light, temperature, and salinity conditions affect the net photosynthesis of *Monostroma*. For instance, the light compensation

point for *M. grevillei* is approximately  $8 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , beyond which photosynthesis increases rapidly up to around  $120 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (Guo and Mathieson 1992). The temperature optima range from  $10\text{--}15 \text{ }^\circ\text{C}$ , with the optima being more circumscribed in 10% (i.e.,  $10 \text{ }^\circ\text{C}$ ) than 30% salinity (i.e.,  $10\text{--}15 \text{ }^\circ\text{C}$ ). The salinity optimum is approximately 10%, although relatively high rates of photosynthesis also occurred between 0 and 40% salinity (Guo and Mathieson 1992).

Similarly, Choi et al. (2010) reported that *Monostroma* sp. is highly tolerant to a wide range of salinities ranging from 15 to 45 psu, which showed euryhaline nature. This euryhaline response is due to the adaptation of this species to the fluctuating salinities in coastal water or estuarine, because of rainwater influx, evaporation, and precipitation (Yu et al. 2013). Moreover, Kavale et al. (2020) assessed the effect of photoperiod (8:16–16:8 L/D), salinity (15–45 psu), temperature ( $15\text{--}35 \text{ }^\circ\text{C}$ ), and light intensity ( $2\text{--}60 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) on the growth of *Monostroma* sp. The highest growth rate was observed in the range of  $5.73$  to  $14.41\% \text{ day}^{-1}$ , achieved at  $25 \text{ }^\circ\text{C}$  temperature, 35 psu salinity,  $60 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  light intensity, 14:10 (L/D) photoperiod, and 1/4 MP1 medium. It was discovered that the modified 1/4MP1 medium was suitable for promoting *Monostroma* sp. growth. The maximum daily growth rate was seen in an outdoor tank culture using 1/4 MP1 medium ( $14.38 \pm 0.32\% \text{ day}^{-1}$ ).

Saco et al. (2018) studied the photosynthesis and growth in *M. nitidum* in the laboratory from a naturally occurring intertidal population. Photosynthesis did not differ significantly under various temperatures that might reflect the growing season of the species from autumn to mid-spring. In parallel, the growth rate (cultured for 5 and 10 days) was the same under various temperatures but decreased at  $25 \text{ }^\circ\text{C}$  (cultured for 15 days), suggesting that prolonged exposure to higher temperatures might have an adverse effect. Similarly, the maximum quantum yield of photosystem II ( $F_v/F_m$ ) decreases as temperature increases suggesting some physiological stress on photosystem II (PSII) at a higher temperature. Contrarily, the light compensation point, saturating irradiance, initial slope, and efficiency of light absorption by PSII ( $\Phi_{\text{PSII}}$ ) increases as temperature increases. This suggests that the species optimized the photosynthesis to low and high light conditions that might reflect the growing season of the species characterized by irradiance limitation in winter and higher irradiance in spring. No photoinhibitory responses occurred indicating tolerance to higher irradiance. In parallel, the growth rate increases significantly as irradiance increases, indicating a higher growth rate response at higher irradiance. Overall, the photosynthetic responses were parallel to the growth rate response of *M. nitidum*. Thus the fundamental information on the photosynthetic characteristics can be used to improve its cultivation techniques.

## Cultivation and harvesting

*Monostroma* is the most intensely cultivated genus of green algae, constituting about 90% of the total green algal cultivation (Nisizawa et al. 1987), almost exclusively for the Japanese food product, hitoegusa. As a non-clonal type of seaweed, appropriate seedling culture is needed before each farming season. The seeding method used in the cultivation can be artificial (e.g., Shimanto Estuary, Kochi prefecture) or natural (e.g., Ise Bay). Seedlings obtained from the naturally deposited zoospores on the culture nets are harvested in the natural seeding method. However, in the artificial seeding method, many zygotes obtained from in vitro fertilization of isolated gametes by the end of the growth period are grown throughout the summer. The resulting Codiolum-sporophytes are then treated with a high-intensity light to induce zoospore release. Culture nets are immersed in the concentrated zoospore solution under dark conditions to facilitate the successful attachment of released zoospores to the nets. These “seeded” nets are subsequently installed in the attached fabrication of wooden sticks in the coastal waters, and the height of nets is adjusted to provide adequate immersion and drying-out effects with each tidal range. Thalli are harvested and processed upon reaching the largest size, approximately 20–25 cm (Bast 2014).

## Nutritional value and biochemical composition

*Monostroma* and *Ulva* species are well known for their nutritional values and both have distinctive biochemical composition (Gupta et al. 2015). One of the important commercially utilized seaweed foods in Japan, “Green laver” or “aonori,” is a mixture of *Ulva* and *Monostroma* which contains high amounts of protein (20–26%), calcium (0.69–1.12%), vitamins (A = 590–13,000 IU, B<sub>1</sub> = 0.8–6.0 ppm, B<sub>2</sub> = 5.7–20.5 ppm, Niacin = 35–118 ppm, C = 120–540 ppm) and iron (25–62 ppm) and low content of fat and sodium (Nisizawa et al. 1987; McHugh 2003). Of these green algae, *Monostroma latissimum* amounts to 90% of the total products (Nisizawa et al. 1987). McDermid and Stuercke (2003) analyzed the nutritional composition of *M. oxyspermum* collected from Hawaiian Islands. They observed the water content relative to total fresh weight was  $92.9 \pm 0.6$ , and the ash, protein, carbohydrate, lipid and energy contents relative to total dry weight were  $22.4 \pm 0.5\%$ ,  $9.6 \pm 0.2$ ,  $31.8 \pm 0.8\%$ ,  $3.8 \pm 0.1\%$ , and  $3033 \pm 113.3 \text{ cal g}^{-1}$  (Mean  $\pm$  SE) respectively. In addition, they reported it

contains 70 IU g<sup>-1</sup> β-carotene, 0.70 mg g<sup>-1</sup> niacinamide, and 1.3 mg g<sup>-1</sup> Vitamin C. Based on dry weight, the essential mineral element content in algae was: 2.58 N, 0.35 P, 3.14 K, 1.36 Mg, 0.58 Ca, 6.23 S, 52 μg g<sup>-1</sup> B, 32 μg g<sup>-1</sup> Zn, 10 μg g<sup>-1</sup> Mn, 142 μg g<sup>-1</sup> Fe, 28 μg g<sup>-1</sup> Cu.

Risso et al. (2003) studied the chemical composition of green seaweed, *M. undulatum* Wittrock, growing on the Southern Argentina coast. The ranges expressed per 100 g dry algae were: protein (N × 6.25): 12.89–21.85; ashe (g): 33.92–40.05; lipid (g): 0.32–1.47; total fiber (g): 14.36–19.6; digestible carbohydrates (calculated by difference) (g): 20.86–32.48; sodium (g): 7.39–13.11; potassium (g): 1.38–3.18; calcium (mg): 149–226; phosphorus (mg): 190–447; Vitamin C (mg): 159–455. Their results indicate that this green seaweed is an important source of protein, fibre, macronutrients, minerals and vitamin C during the macroscopic period.

## Utilization and potential biotechnological applications

The potential biotechnological applications of the *Monostroma* are shown in Fig. 2.

### Wastewater treatment

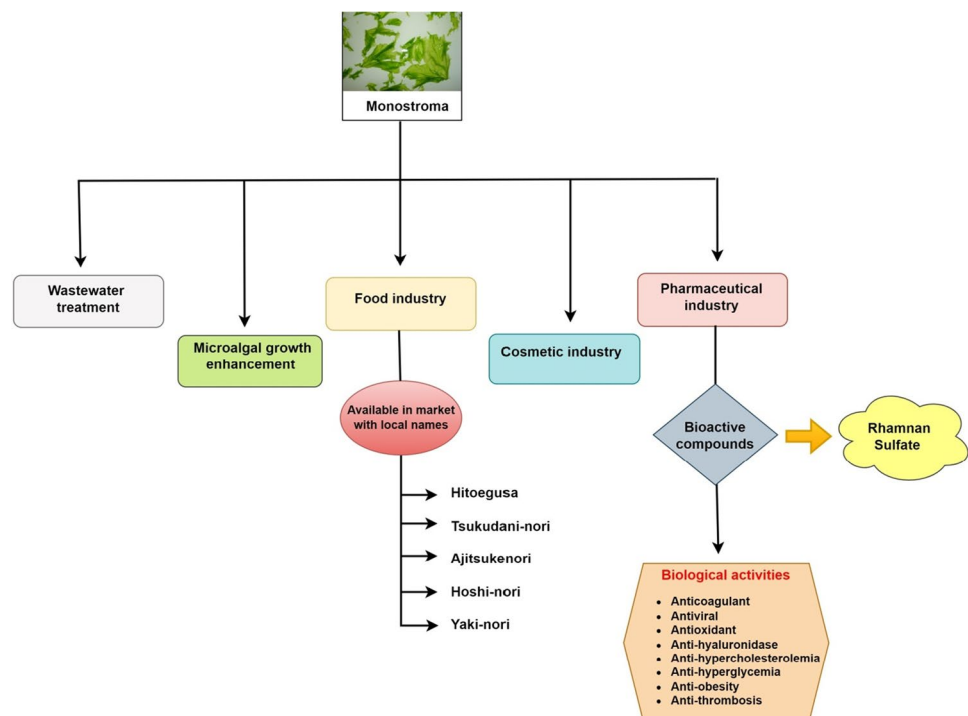
Seaweeds are used to treat agricultural wastes and sewage to reduce nitrogen and phosphorus-containing compounds before releasing them into oceans or rivers. Enrichment

or excessive deposition of nutrients such as nitrogen and phosphorus-containing materials into water bodies is called eutrophication. The process of eutrophication is natural. However, it can be increased by allowing water rich in dissolved fertilizers to seep into nearby streams and lakes or by introducing effluent of sewage into rivers and coastal waters. This will cause unwanted and excessive growth of aquatic or marine plants. Another essential feature of many types of seaweed is their ability to take up more phosphorus than required for maximum growth. Estuarine and intertidal species are the most tolerant, especially green seaweeds such as *Ulva* and *Monostroma* (Pati et al. 2016).

### Microalgal growth enhancement

According to several studies, adding extracts from *Monostroma* species promotes the growth of microalgae. For instance, Cho et al. (1998) found that the aqueous extract of *M. nitidum* stimulates the growth of several microalgae. Seaweed extracts were added to the culture medium of the marine microalga *Tetraselmis suecica* to regulate the proliferation of its cells (Cho et al. 2005). Among them, the water extract *M. nitidum* was the most efficient, increasing cell density by up to twofold when 1 mg mL<sup>-1</sup> of extract was added to the culture medium. There were slight differences in cell size, gross biochemical content, fatty acids, and digesting efficiency between *T. suecica* cultures cultivated with and without the *M. nitidum* extract. Luyen et al. (2007) isolated the compound levoglucosan from *M. nitidum* that enhances the growth of various microalgal species.

**Fig. 2** Utilization and potential biotechnological applications of *Monostroma*



## Food industry

*Monostroma* is popularly consumed in various forms and it is an important ingredient in salads, soups, jams and spices. It is highly consumed in countries such as Japan, China, Brazil, and the Pacific Coast of America (Kumar et al. 2021), and it is available with local names like hitoegusa, tsukudani-nori, ajitsukenori, hoshi-nori and yaki-nori (Braga et al. 1997; Pellizzari et al. 2007). This seaweed has significant nutritional value with a substantial amount of carbohydrate, protein, vitamins, minerals and dietary fibre (Risso et al. 2003; FAO 2018). Many food products are made from *Monostroma* and are available in the market place in these regions. Perhaps hitoegusa (*M. latissimum*), is the most important of all edible green sea plants in Japan in terms of economy and production quantity. The market value of this sea plant is the highest among all the cultivated edible green seaweeds, with 1 kg costing about US\$ 30 (Lindsey Zemke-White and Ohno 1999). Harvested hitoegusa is boiled down in soy sauce to make a jam-like product (tsukudani-nori), while dried sheets (Hoshi-nori) are used as sushi wraps. In their study, Chang and Wu (2008) incorporated green seaweed (*M. nitidum*) powder in different proportions with or without eggs to develop noodles. They found that by adding seaweed powder, the fibre content increased, leading to an increase in water absorption by the fibres during cooking. Higher water absorption by the seaweed led to softer and spongier textural intensities in the noodles. They also reported that breaking energy, springiness, and extensibility of freshly cooked noodles reduced, and cooking yield increased significantly with increased concentrations of seaweed. In conclusion, the results showed that additional seaweed powder can significantly affect the quality of fresh Chinese noodles either with or without the addition of eggs.

## Cosmetic industry

The world market for *Monostroma* is increasing due to demand from the cosmetics industry. *Monostroma* uses in cosmetics are broad and include skin hydration or the tension and lifting effect of the aqueous mucilage extract (Pellizzari and Reis 2011). Chen and Chen (2003) studied the replacing of the humectant and half of the thickening agent of moisture masks with *M. nitidum* water-soluble mucilage on the rheological parameters of colour, storage stability, water-holding capacity, and film forming time. The moisture masks containing water-soluble mucilage were pseudoplastic fluids (shear thinning fluids), and their apparent viscosity decreased with increasing shear rate and the film formation time of the moisture masks decreased (saving consumer time) with increasing concentration of the aqueous extract. Furthermore, the Draize score test that measures the extent and potential of skin allergy revealed

no erythema (superficial reddening of the skin, usually in patches). Chen and Chen (2003) also reported a potential for stimulating collagen synthesis, antioxidant and photoprotector bioactivities.

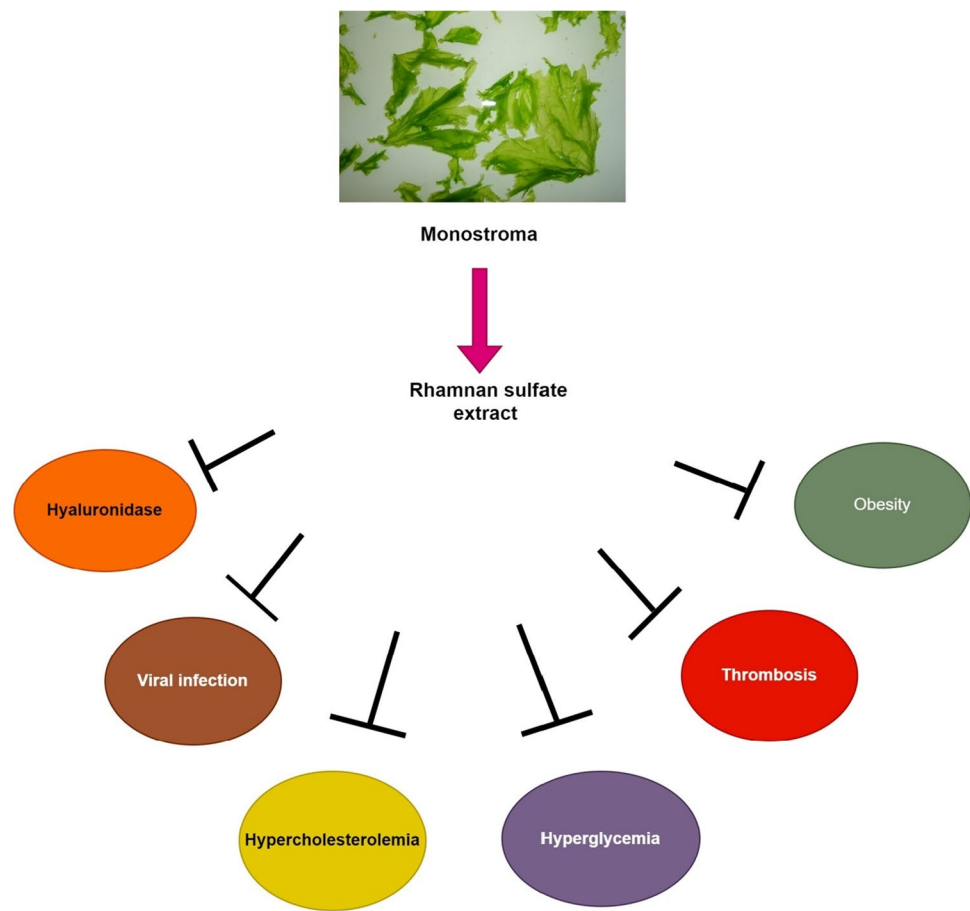
## Pharmaceutical industry

*Monostroma* is a rich source of biologically active compounds, including a sulfated polysaccharide called “rhamnan” which exhibits antioxidant, antiviral, and anticoagulant activity (Zhang et al. 2008; Li et al. 2011). Rhamnan sulphates (RS) from *Monostroma* have a wide range of health promoting activities and demonstrate preventative effects from viral infection, hyperglycemia, hypercholesterolemia, thrombotic disease and so on (Fig. 3). The main repeating unit of RS consist of rhamnose with a sulfate-group substituent that forms long linear chains with branched side chains. In vitro, Lee et al. (1999) found that RS, derived from *M. latissimum* inhibited the replication of herpes simplex virus type 1 (HSV-1), human cytomegalovirus (HCMV), and human immunodeficiency virus type 1 (HIV-1) viruses in cell cultures of Vero (African green monkey kidney) and HEL (Human Embryonic Lung) MT-4 cells.

Wang et al. (2020) isolated a homogeneous polysaccharide (MWS) from *M. nitidum*, which had broad-spectrum antiviral effects against influenza virus, HSV and enterovirus (EV71). MWS inhibited EV71 infection by targeting PI3K/Akt pathway or virus particle. MWS could be a potential antiviral agent. Terasawa et al. (2020) studied the antiviral activity of RS derived from *M. nitidum* against influenza A virus (IFV) infection in vitro and in vivo. The findings revealed that RS reduces influenza virus infection while promoting antibody synthesis, implying that RS could be used to treat influenza virus infections. Lee et al. (2010) also reported that RS from *Monostroma* showed potent antiviral activity against the herpes simplex virus type 2 virus, whereas it had no influence on the replication of the influenza A virus. Moreover, the anticoagulant activity of heparinoid-active sulfated polysaccharides obtained from *M. nitidum* was reported by Maeda et al. (1991).

Zang et al. (2015) investigated the effects of RS on metabolic disorders using zebrafish with diet-induced obesity (DIO). They found that oral administration of RS ( $250 \mu\text{g g}^{-1} \text{BW day}^{-1}$ ) attenuated body weight gain, dyslipidemia (plasma triacylglycerol and low-density lipoprotein cholesterol) and hepatic steatosis in DIO. As a result, consuming RS as a functional meal may be beneficial in preventing obesity and lowering the prevalence of obesity-related disorders. Tako et al. (2017) reported that RS from *M. nitidum* has unique gelling characteristics and suggests that RS can be used in foods, cosmetics and some other industries as gelling, thickening, stabilizing and water-holding agents. RS from *M. nitidum* also was evaluated for

**Fig. 3** Health promotion activities of rhamnan sulfate extracted from *Monostroma*



binding to the S-protein from severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) and inhibition of viral infectivity in vitro by Song et al. (2021). Firstly, surface plasmon resonance (SPR) was used to confirm that heparin has an affinity for the S-protein receptor binding domain (RBD) of the wild type SARS-CoV-2 and other variations. In a competition SPR assay, the  $IC_{50}$  of RS against the S-protein (RBD) binding to immobilized heparin was  $1.6 \text{ ng mL}^{-1}$ , which was significantly lower than the  $IC_{50}$  for heparin ( $750 \text{ ng mL}^{-1}$ ). In comparison to heparin at the same dose ( $5 \text{ ng mL}^{-1}$ ), RS also demonstrated a greater ability to bind the S-protein RBD from a variety of variants, and the pseudovirus particles of the wild type and delta variant. Thus, they found that the RS from *M. nitidum* is effective against the variant S-proteins of SARS-CoV-2 mutants, suggesting that it may be a potential candidate for COVID-19 treatment or prevention.

Seaweeds contain a number of bioactive compounds which may have potential as a product in the nutraceutical, functional food, and pharmaceutical industries. Some of the pharmaceutical applications of compounds derived from *Monostroma* are summarised below (Table 1). In recent years, there has been an rise in patent activity in this field, and several unique macroalgal-based products have entered

the market (Kraan 2012). In the case of carbohydrates, the Kabushiki Kaisha Yakult Honsha Company in Japan has patented rhamnan or RS polysaccharides isolated from maritime brown macroalgae and the green alga *M. nitidum*. The goal of this substance is to use it as a preventative agent and treatment for stomach ulcers (Nagaoka et al. 2000).

## Conclusions and future directions

There is a substantial volume of data available on its morphology, life history, and ecology of *Monostroma*. As for its morphology, it differs considerably according to the environment within which it grows. It is the most intensively cultivated genus among the green seaweeds, accounting for over 90% of total green algal cultivation. More recent studies have led to the development of new methods of cultivation that have since been applied widely. *Monostroma* is a rich source of biologically active compounds, including a sulfated polysaccharide called “rhamnan” which exhibits antioxidant, antiviral, and anticoagulant activity. In addition, it is consumed in various forms and is an important ingredient in salads, soups, jams and spices. However, more research is required in the field of

**Table 1** Pharmaceutical applications of bioactive compounds derived from *Monostroma*

Species	Product	Biological activity	References
<i>Monostroma latissimum</i>	RS	Inhibit HCMV, HSV-1, and Human immunodeficiency virus type 1 (HIV-1)	(Lee et al. 1999)
<i>M. latissimum</i>	Sulfated polysaccharide	Anticoagulant activity	(Zhang et al. 2008)
<i>M. latissimum</i>	Sulfated rhamnan	Antiviral activity	(Wang et al. 2018)
<i>M. latissimum</i>	Sulfated polysaccharide	Anticoagulant activity	(Mao et al. 2009)
<i>M. latissimum</i>	Sulfated polysaccharide	Anticoagulant activity	(Li et al. 2011)
<i>M. latissimum</i>	RS	Antiviral activity	(Lee et al. 1999)
<i>Monostroma nitidum</i>	RS	Antioxidant, Antiviral, Anticoagulant activity	(Zhang et al. 2008; Li et al. 2011)
<i>M. nitidum</i>	Homogeneous polysaccharide (MWS)	Inhibit HSV and EV71 infection	(Wang et al. 2020)
<i>M. nitidum</i>	RS	Inhibit Influenza A virus (IFV) infection	(Terasawa et al. 2020)
<i>M. nitidum</i>	RS	Antiviral activity against herpes simplex virus type 2 virus	(Lee et al. 2010)
<i>M. nitidum</i>	RS	Inhibition of SARS-CoV-2 viral infection	(Song et al. 2021)
<i>M. nitidum</i>	RS	Anti-hyaluronidase	(Yamamoto et al. 2016)
<i>M. nitidum</i>	RS	Anti-hypercholesterolemia	(Zang et al. 2015)
<i>M. nitidum</i>	RS	Anti-hyperglycemia	(Kamimura et al. 2010)
<i>M. nitidum</i>	RS	Anti-obesity	(Zang et al. 2015)
<i>M. nitidum</i>	RS	Anti-thrombosis	(Li et al. 2017; Liu et al. 2017, 2018a, b; Okamoto et al. 2019)
<i>M. nitidum</i>	RS	Antivirus	(Wang et al. 2018, 2020)
<i>M. nitidum</i>	RS	Anticoagulant and antithrombotic activity	(Cao et al. 2019)

manufacturing technology for food products using *Monostroma* to help increase demand for this seaweed.

Furthermore, *Monostroma* harbours specific bacterial strains necessary for its morphological induction. Many studies showed that seaweed-associated microbes provide unique and novel metabolites of unprecedented structures, with antibacterial, antiviral, antifungal, anti-inflammatory, antiplasmodial, anticancer, antiangiogenic and nematocidal activities. These bioactive compounds may provide high-quality drug candidates for pharmaceutical, agricultural and industrial applications. Extensive randomized control clinical trials will be required to determine the in vivo fate of these bacterial extracts on cohorts. In addition, the exploration of *Monostroma*-associated microbes using new tools and techniques, such as those of high-throughput genomic and metagenomic approaches, might lead to the development of new bioactive natural products in the future and will help in utilizing their biotechnological potential.

**Acknowledgements** All authors acknowledge the Central University of Punjab for providing support, necessary resources and infrastructure during the study.

**Authors contribution** FB conceptualized the study. MK contributed to data acquisition, writing, reviewing, editing and preparing Figs. 2 and 3 of the manuscript. SK contributed to data acquisition and writing of the manuscript. AP contributed to writing and editing of the manuscript.

FB secured the funding for the study from DST-SERB, GOI. The final manuscript was read and approved by all authors.

**Funding** The study is supported by DST-SERB Core Research Grant (CRG/2019/005499). MK like to thank the University Grants Commission (UGC), New Delhi, India, for the financial support for Ph.D.

## Declarations

**Conflicts of interest** The authors declare no conflict of interest.

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