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Concise review of the genus *Solieria* J. Agardh, 1842

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Abstract :

Solieria spp. (Solieriaceae, Gigartinales, Rhodophyta) can be found in various habitats ranging from the marine environment to low-salinity estuarine environments. Of the commercially exploited carrageenophytes, some of the most abundant belong to the Solieriaceae family as, Kappaphycus, Eucheuma and Solieria. The supply of these seaweeds is ensured by their mastered culture and by large quantities of stranded wild seaweeds which are harvested. Rich in carrageenans, i.e., in linear sulfated galactans, these red macroalgae are widely used for their gelling, thickening, and stabilizing properties in food, cosmetic, or pharmaceutical industries. In addition, Solieria spp. provide scientific potential as a model for the development of cultures in Integrated Multitrophic Aquaculture (IMTA), for innovation in extraction and purification processes and in biorefineries to access to bioactive compounds. The genus Solieria was described using the species Solieria chordalis as the type species in 1842. Today, this species is found in large quantities on the beaches of the western Atlantic just like Solieria filiformis found on the other side of the Ocean on some beaches in Mexico. Due to its abundance, several scientific teams from France and from Mexico study these algae with high potential in nutrition, health and for environmental applications. Eight other species of the genus Solieria have been inventoried, the last one in 2018. Nevertheless, their abundance is lower as well as the number of scientific studies mentioning them. Therefore, in this review, we focus on the biology, ecophysiology, biochemical composition, and applications of Solieria spp. based mainly on the two species widely studied, namely Solieria chordalis and Solieria filiformis.

Keywords : Rhodophyta, Taxonomy, Ecophysiology, Seaweed farming, Harvesting, Transformation bioprocess, Economical applications

Identity of the genus and taxonomy

The genus *Solieria* (Rhodophyta, Florideophyceae, Gigartinales, Solieriaceae) was created by the Swedish botanist Jakob Georg Agardh in 1842 based on the species *Solieria chordalis* collected in Cadiz in Spain. He is the son of Carl Adolph Agardh also a great Swedish botanist and politician. These scientists gave their name to the macroalga. At that time, the genus *Solieria* included four species (*S. chordalis, S. dura, S. robusta* and *S. tenera*). Today, there are ten accepted species of *Solieria: S. anastomosa*, *S. chordalis*, *S. dichotoma*, *S. dura*, *S. filiformis*, *S. incurvata*, *S. jaasundii*, *S. pacifica*, *S. robusta* and *S. tenuis* (Fredericq et al. 1999; Gabrielson and Hommersand 1982; Xia and Zhang 1984; Guiry and Guiry 2022). The classification of the family Solieriaceae was only accepted in 1993 thanks to Silva's revision according to the 1959 Montreal Code and the Sydney Code of 1981 (Silva 1993; Fredericq et al. 1999). *Solieria chordalis* was first found in England in April 1976 during the inventory by Farnham and Jephson (1977). According to these researchers, the algae originated in the north of France and were introduced to other coasts as a result of clinging to boats. The book Crouan Algal Herbarium published in 1852 (located at the University of Western Brittany, Brest city, France) mentions a sample of red alga *S. chordalis* locally called “Bizhin Ru” collected at Rade de Brest (Crouan and Crouan 1852). It is quite possible that *S. chordalis* has always been present on the eastern coasts of the Atlantic although there is a lack of data to validate this hypothesis (Farnham 1980)

Twenty years later, molecular tools have been widely developed and have made it possible to gather species according to homologies in their genetic heritage which is acquired and modified during the evolution of the living world. In 1999, the American Fredericq and her collaborators classified the species of the family Solieriaceae (Gigartinales, Rhodophyta) thanks to the analysis of their rbcL gene sequence (Fredericq et al. 1999). This has allowed deepening the knowledge of the systematics and biogeography of these species. The nucleotide sequence data were generated from 37 taxa of red algae in the family Solieriaceae. Two major groups have been identified. It has been shown that these two groups defined by their phylogenetic tree based on their rbcL gene sequence could also be classified according to their morphological characters and their biogeographical distribution. According to these results, nine species of *Solieria* have been studied. Thus, in 2018, *Solieria incurvata* from Puerto Escondido, Estado Falcon, Venezuela, was described as a new species based on morpho-anatomical and molecular data. Based on the rbcL and COI-5P (5′ portion of mitochondrial cytochrome c oxidase subunit I) sequences, the new species forms an independent lineage that clearly belongs to the *Solieria* clade of the Solieriaceae (Resendiz et al. 2018).

Distribution and ecology

The Solieriaceae can be distinguished in two groups: species with thalli having uniaxial filaments, and species with thalli having multiaxial filaments resulting from an indefinite number of apical cells (Gabrielson and Hommersand 1982; Fredericq et al. 1999). The species of the first group are particularly found in the South and in the West of Australia and some in South Africa. Species of the other group are found in tropical or temperate areas. They were found in the Indo-Pacific Oceans (*S. anastomosa*, *S. dichotoma*, *S. dura*, *S. jaasundii*, *S. pacifica*, *S. robusta* and *S. tenuis*) and in the Atlantic Ocean (*S. chordalis*, *S. filiformis* and *S. incurvata*). The morphological distinction between the Atlantic and the Indo-Pacific would be based only on differences in the apical growth of the thallus. Fredericq et al. (1999) highlighted that molecular and morphological data support the idea that the common ancestor of the members of the family Solieriaceae lived in the temperate waters of Australia and South Africa. Moreover, the more widely distributed tropical and subtropical entities originated and evolved in the Tethys, the Ocean 200 million years ago. Solieriaceae family was split into two groups by the collapse of the Tethyan seaway in the vicinity of the Mediterranean Sea, beginning around 100 Ma ago and ending 20 Ma ago. Then, seawater currents changed and may have caused the distributions of algae in the West of the current Ocean (**Fig.1**).

[**Fig.1** Here]

Since then, the ancestral taxa of all genera composing the family Solieriaceae have been preserved in the Atlantic and for those currently found in the Indo-Pacific Ocean, they would have derived from these ancestral taxa (Hommersand 1994; Fredericq et al. 1999).

Solieria chordalis (C. Agardh) J. Agardh is found in various habitats ranging from a fully marine environment to low-salinity estuarine environments. *S. chordalis* is a sciaphilous seaweed that can form a veritable submarine prairie at 7-8 m depth. It is also found between 0 and 5 m below the surface of the sea. To develop, it needs to be in a turbid marine environment, semi-sheltered and preferentially on a hard substrate. Comparing four places, where *S. chordalis* was collected and used for different research work, it is easy to notice the geomorphological similitudes (Rogers and Topliss 1983; Deslandes et al. 1985; Floc'h et al. 1987; Bondu et al. 2008; Burlot 2016). Indeed, all places present semi-sheltered sites, like bays or gulfs, close to the continent. The geomorphological structure characterized by the presence of islands or peninsulas forming semi-open bays, can hinder waves and currents. Moreover, nutrient-laden freshwater effluents, due to land leaching, are located nearby. These places can constitute therefore protected and rich in nutrients sites, favourable to the development of *S. chordalis.* Moreover, Floc'h et al. (1987) wrote that the hydrological characteristics of the Bay of Brest are similar to those of the Gulf of Morbihan, which could explain the presence of *S. chordalis* in both locations.

Phenology

An abundant biomass, mainly composed of *S. chordalis*, arrives, and ends up on the beaches every year in the Gulf of Morbihan, from the end of summer to autumn **(Fig. 2)**. At this time of the year, the environmental conditions are characterized by a rainy weather with frequently strong winds. Seaweeds break away from their substrates. Moreover, the morphology of the thallus, notably their mature size and their numerous filaments, facilitates their substrate detachment by mechanical force **(Fig. 3)**.

[**Fig. 2** Here]

[**Fig. 3** Here]

According to Cabioc'h et al. (2006), juvenile thalli (**Fig. 3**, January) do not have a lot of ramuli compared to adult thalli (**Fig.3**, April, August, October). During growth phase, adult thalli of *S. chordalis* are covered with small propagules that develop themselves to thorny ramuli reaching 1 to 4 cm long. Similar morphologies between *Solieria* species were found in Mexico, in France and in Australia (personal data from Burlot A.S). These ramuli have a primordial function for the development and growth of *S. chordalis*. A crucial step contributing to the survival and persistence of species over time is reproduction.

Reproduction

Solieria sp. is able to reproduce by using both strategies, sexual and asexual reproductions.

Sexual reproduction

In 1982, Gabrielson and Hommersand highlighted the presence of reproductive organs in cortical cells that represent evidence of sexual reproduction (Grabrielson and Hommersand 1982). Indeed, they have taken a microscopic photography of ramuli with carposporangia that showed trichogynes, that is to say hair like projections of the female reproductive organs of red algae which receive the male gametes before fertilization takes place.

Rhodophyta has some of the most complex life cycles known to living organisms. They have a triphasic (gametophyte, carposporophyte, and tetrasporophyte) sexual life cycle. It is karyologically trigenetic (i.e., one haploid and two diploid phases). The morphologies of male and female gametophytes and tetrasporophytes of *S. chordalis* are isomorph, while the carposporophytes have on the rigid filamentous thallus some small balls, the cystocarps (**Fig. 4)**.

[Fig. 4 Here]

Spermatia and oospheres are produced by male and female gametophytes, respectively. These haploid gametes fertilize within terminal parts of the female thalli (trichogyne) to form diploid carposporophyte, which subsequently produces diploid carpospores. Repeated mitotic divisions take place in the carpospores that grow to diploid tetrasporophytes. Meiotic divisions within tetrasporangia result in the haploid tetraspores production. Finally, released tetraspores develop to respective gametophytes to complete the life cycle (Bast 2014).

Asexual reproduction

In 1987, Floc'h et al. hypothesized that *S. chordalis* multiplies mainly vegetatively according to their observations of the thallus morphology over time. Moreover, they cultivated *S. chordalis* thanks to ramuli and to thallus fragmentation and later the French team of Eric Deslandes did the same in 1999 (Floc'h et al. 1987; Fournet et al. 1999).

On *S. chordalis* filaments, can expand ramuli from multicellular propagules that germinate as a unit to form propagule-forming plants. This structure can spontaneously come off the filaments and grow to a new thallus. Multicellular propagules offer numerous benefits for the perpetuity of the species. Indeed, they can efficiently multiply the number of individuals, reach new habitats, spread the species over long distances and can be a competitive feature for the species evolution. Fragmentation is a common technique used to increase the number of macroalgal individuals in aquaculture and in laboratory (Andersen 2005).

Growth rate and season

To highlight the influence of the environment, especially of the abiotic factors on *S. chordalis*, a phenological study was led at the same intertidal site in Saint Gildas de Rhuys (South Brittany, France) for two years, from October 2013 to October 2015 (Burlot 2016). Results and notes are given in this part of this review.

Seasonal variations in macro- and microscopic morphologies

To differentiate *Solieria* species from other species, microscopic cross sections of thalli are necessary. Indeed, according to the macroscopic morphologies of *Solieria* sp. and *Gracilaria* sp., confusions are possible. *Solieria chordalis* is a perennial species that is found all the year on the Rhuys Peninsula, France. The morphology changes with the seasons. Three types of morphology can be distinguished (**Fig 3**).

In winter, the thallus size can range from 5 cm to more than 10 cm in high. It does not have many filaments and has few ramuli **(Fig. 3 January)**. The microscopic cross sections show a thick belt of pigmented cortical cells (> 100 µm) and the presence of floridean starch granules (Burlot 2016).

In spring, *Solieria chordalis* has a size greater than 10 cm and presents many ramuli attached to the filaments **(Fig. 3 April)**. The microscopic sections highlight the light in the medulla that means that there are less compounds inside the cells. The section of the filament still shows many pigmented cortical cells (Burlot 2016).

In summer, the thallus is small, between 5 and 10 cm. It has many filaments and ramuli, which combine (ramuli from 2 to 5 cm) **(Fig. 3 August)**.

Thalli collected in autumn look like them, while they are larger (> 10 cm). In addition, many ramuli are gradually detached **(Fig. 3 October**).

Microscopic observations do not show big differences between species collected in summer and in autumn, although during this last season, the belt of pigmented cortical cells is much thicker (> 100 µm). Moreover, there are more floridean starch granules in autumn resulting from the intense photosynthetic activity of the summer season (Burlot 2016). In summer, phycoerythrin is deteriorated due to heat and solar radiation, that is why the thallus appears green (Hurd et al. 2014; Yong et al. 2014).

During the monthly collections, it was noticed that all types of *S. chordalis* morphology could be found at the same time. Nevertheless, morphological dominances such as those presented previously have been noted as well as in a study of Floc'h et al. (1987) and in a study of benthic *S. chordalis* in the Rhuys Peninsula led by CEVA in May, July, and September 2013 (Floc'h et al. 1987; CEVA 2013).

Seasonal variations in the dry weight

The dry weight content of *S. chordalis* from Saint Gildas de Rhuys varies over the seasons and over the years (Burlot 2016). From October 2013 to October 2015, it ranged from 11.4±1.1% (in autumn) to 15.6±1.6% (in winter) for an annual average of 13.0±1.4% of the fresh weight. These results are conformed with those measured on *Solieria tenera*, i.e., 6-16% (Prasad 1986). A positive correlation was found between the dry matter content of *S. chordalis* and the mineral matter suspended in seawater, especially with the nitrate concentration (Burlot 2016). The intensity of cortical cell coloration observed on microscopic sections indicates the assimilation of nitrogen and its incorporation into the production of the red pigment phycoerythrin in winter (Burlot 2016). Dry weight profiles of *S. chordalis* over years are similar (Burlot 2016). Three phases stand out. From February to May / June, the dry weight decreases gradually, which means that seaweeds grow. This is the phase of "fast growth" (Prasad 1986). The cells stretch and fill with water. Nevertheless, the dry weight remains important because ramuli are formed (**Fig. 3 April)**. From June to September, the dry weight increases sharply. Then, it decreases very fast. During summer, photosynthesis is intense. The produced floridean starch granules accumulate in the cells. Moreover, seawater salinity increases and *S. chordalis* synthetizes osmoregulators like the floridoside to counter the osmotic pressure. The decrease in the dry weight can be explained by the loss of ramuli and/or by the growth of filament and ramuli which fill with water. Finally, the last phase takes place from September / October to February. The dry weight of *S. chordalis* is relatively low compared to the rest of the year. It increases little by little. This is the phase of "slow growth" (Prasad 1986). The ramuli fall off and attach themselves to the substrate to develop into new filaments. Thus, seaweeds grow and synthesize new compounds notably from nitrogen in seawater.

Although asexual reproduction is dominant in *S. chordalis* (Floc'h et al. 1987), the three phases of the dry weight evolution over year, previously mentioned, may be in relation with the triphasic life cycle, which has been demonstrated in some species of Solieraceae (Bast 2014).

In this study, no macroscopic morphology and no microscopic section have shown reproductive structures, except a *Solieria* species collected in June 2016 in Saint-Malo, in North Brittany, France **(Fig. 4)**. Nevertheless, a carposporophyte specimen of *Solieria* sp. was observed by scuba diving in Brittany at the beginning of September 2018 (personal data from Burlot A.S.). In fact, it could be assumed that a juvenile tetrasporophyte develops from the end of summer to February. A release of tetraspores, triggered by a strong nitrogen supply and by a temperature increase, would be carried out little by little from February to May / June, which give birth to haploidic gametophytes. The fertilization between female and male gametes could take place during the summer. Carposporophytes could appear from June / July to September. Finally, a release of carpospores would occur during the last sunny month, in September, before the temperature drops (>15 °C). The carpospores attached to the substrate would form new tetrasporophytes. This hypothesis remains to be verified by making microscopic sections on a larger number of individuals. More studies must be conducted to understand the release of gametes and spores, depending on environmental factors.

Seasonal variations in the biochemical composition of Solieria chordalis

According to **Table I**, no important annual changes in the biochemical composition of *S. chordalis* were observed.

[Table I Here]

As mentioned previously, the dry weight content of *S. chordalis* varies from 11.4 ± 1.1% (in autumn) to 15.6 ± 1.6% (in winter). Thus, *S. chordalis* is essentially composed of water, nearly 90% of the seaweed fresh weight (Burlot 2016). The dried matter is rich in minerals (28.7%) and in total sugars (28.6%). Sulfated polysaccharides, represented overall by the neutral sugars, uronic acids and sulfate groups, match almost 50% of the seaweed dry weight. Proteins constitute one-fifth of the dry weight (14.8 to 18.4%), which is a little less than the content measured in *Solieria robusta* collected in Pakistan (between 25 and 32% of the dry weight) (Khanzada et al. 2007). To complete the whole characterization of the dried matter, other compounds like the 3,6-anhydro-galactose should be measured. Nevertheless, **Table I** already illustrates a good estimation on *S. chordalis* composition. Standard deviations of the first two rows in **Table I** (October 2013 – October 2014 and October 2014 – October 2015) give information about the intra-annual variation of the different biochemical compounds in *S. chordalis*. Inter-annual variations are shown with the standard deviations indicated in the last row in **Table I**. The biochemical composition of *S. chordalis* collected on the Rhuys Peninsula shows many variations over the seasons, in particular for the mineral content (8.9% dispersion in the content during the year), neutral sugars (between 5 and 5.5% dispersion around the average) and in sulfate groups (between 5.1 and 6.4%). Nevertheless, even if this annual content does not change from year to year, it changes with the seasons **(Table I)**. *S. chordalis* contains more minerals in autumn (34.4±3.9%) than in winter (20.0±3.7%). The mineral content is positively correlated with the seawater salinity. In summer, salinity increases due to the evaporation of seawater that takes place during the longer summer photoperiod.

Neutral sugar content varies from 27.8±2.2% (in winter) to 31.2±1.7% (in summer). Positive correlations were observed between sugar content, water temperature, salinity, and sun exposure time (Burlot 2016).

Protein content ranges from 14.5±2.0% (in summer) to 18.5±3.2% (in autumn) of the seaweed dry weight. Differences can be observed from year to year **(Table I)**. An annual average difference of 4% is obtained. The samples of *S. chordalis* collected from October 2013 to October 2014 are richer in protein than the samples collected from October 2014 to October 2015. This result is explained by the heavy rains that marked the beginning of 2014. The characterization of the amino acids content reveals small variations between the different samples, which indicates that protein quality remains stable over the season and the year (Burlot 2016). Furthermore, the protein content is negatively correlated with the total sugar content (Burlot 2016).

In autumn and in winter, precipitation is more intense, and the rain leaches the land. Large volumes of freshwater from rivers, rich with nutrients such as nitrate, ammonium, and phosphate, reach coastal waters. Seaweeds assimilate the abundant nitrogen and phosphorus during this period to produce notably proteins such as phycobiliproteins, necessary to capture light energy, which is reduced at this time of year. The previously mentioned "slow growth" of seaweeds characterizes this period with a low dry weight which increases progressively. In addition, the seawater salinity decreased at this season because of the arrival of freshwater. The osmolarity of seawater changes (hypo-osmotic medium). To respond to this osmotic stress and avoid the phenomenon of turgid cells, seaweeds would synthesize small solutes. In a medium rich in inorganic matter, it could be nitrogen derivatives such as mycosporine-like amino acids (Bedoux et al. 2014), amino acid derivatives like betaine and taurine (Niwa et al. 2007) or halogenated compounds (Bondu et al. 2008). Furthermore, Bondu et al. (2007) showed by NMR that carbon metabolism was inhibited by nitrogen metabolism under osmotic stress conditions.

Reserve carbohydrates, such as floridean starch, accumulated during the summer are mobilized (Burlot 2016). On the one hand, they provide energy for the synthesis of compounds, and on the other hand they provide structural constituent units. The action of the enzyme UDP-galactose epimerase forms parietal carbohydrates for new cells, mainly carrageenans that are sulfated polysaccharides rich in galactose (Goulard et al. 1999; Freile-Pelegrin and Robledo 2006). A study using the Carbon-14 method showed this conversion of floridean starch to carrageenans (Fournet et al. 1999), and confirmed by the monosaccharide profiles (Burlot 2016). Indeed, two monosaccharides represent more than 80% of the total sugars after acid hydrolysis in *S. chordalis*: the glucose and the galactose. Variation and alternation of proportions between these two monosaccharides are remarkable. Glucose, which is a component of floridean starch, cellulose and hemicellulose (parietal constituents) represents the majority of *S. chordalis* monosaccharides in summer (59.9±7.0% of total monosaccharides detected by anion exchange chromatography) and in autumn (56.3±3.9%). While galactose, the main unit of carrageenans and floridoside, is found mainly during winter (46.5±6.7%) and spring (51.7±2.5%) (Burlot 2016). Seasonal variation of uronic acids, which are involved in the synaptic plugs of cell wells, has shown higher concentrations in autumn (3.3±0.1% of dry weight) and in spring (2.8±0.5%) (de Reviers 2003; Burlot 2016). Consequently, the high proportions of galactose and uronic acids from the end of autumn to spring support the parietal synthesis during these seasons.

In spring (April to June), *S. chordalis* continues to grow, its size increases ("fast growth") and cells fill with water. In addition, ramuli begin to appear on filaments. The dry weight remains high. The time of sun exposure increases as well as the salinity of seawater. The synthesis of the cell walls is still active. The high content of total sugars rich in galactose would explain the synthesis of carrageenans and osmoregulators such as floridoside that possess a water retention property (Goulard et al. 2001; Deslandes and Bodeau 2006). This period is also marked by the presence of chlorophyll organisms (potential competitors for light and aggressors) (Burlot 2016). Small nitrogenous compounds with a role in the capture of light radiation, in the defence and in the repair strategies of the seaweed (mycosporine-like amino acids, halogenated compounds) could also be synthesized by *S. chordalis* (Bondu et al. 2008; Bedoux et al. 2014; Bedoux and Bourgougnon 2015).

In summer, the photoperiod remains long. Thus, the photosynthetic activity of the seaweed continues to be intense. Floridean starch composed of glucosidic units is then produced in large quantities and accumulates progressively in the cytoplasm of the cells. Because of the high salinity, the production of osmoregulators should stay active too. At the end of summer and in autumn, algae are large, mature, and more fragile. They contain a lot of floridean starch granules and ramuli start to be released. Filaments break away from their substrate and arrive on beaches where they die by desiccation and fermentation.

Importance of ecophysiology and life cycle control of seaweeds for an industrial exploitation.

With these results from Burlot (2016), it is possible to estimate the available biomass and to have an idea about the quality of *S. chordalis* in term of its biochemical composition over the year. By observing the geomorphology of a site and accessing to environmental conditions (precipitation, temperature, salinity, time of sun exposure, nutrients), it is possible to predict the presence and possible strandings of *S. chordalis*. This anticipation allows a better management of the littoral.

For industrials, who want to exploit *S. chordalis* from Saint Gildas de Rhuys, a rich-mineral biomass is available abundantly in autumn for a possible exploitation as agricultural supplies (feed or fertilizers and biostimulants). For added-value compounds like floridoside for its moisturizing property, seaweeds collected from autumn to spring would be adequate. Active compounds such as photoprotective agents, antioxidants, antibacterial, antivirals may be isolated from *S. chordalis* collected in winter and in spring. In summer, seaweeds rich in neutral sugars, in particular in glucans, can provide the basis for research into the production of biofuels (Kawai and Murata 2016). Recently, Torres et al. (2019) provides the potential for emerging technologies to produce valuable oligomers and the sequential extraction of the constituent fractions for cosmeceuticals. Finally, this seasonality study provides a lot of information from the perspective of culture and upgrading of *S. chordalis* biomass.

Red tide events

Because of its abundance, notably in France, *S. chordalis* is studied to understand its proliferation on beaches and to look for add-valued compounds. Indeed, *S. chordalis* is able to proliferate locally. It also seems to be extending its range, particularly in the Normandy-Breton Gulf (West Cotentin coast), South Brittany, Brest Bay, Saint Malo Bay, and Vendée (France). Considering the environmental factors, strandings are explained for two reasons. First, rains and especially wind (autumn storms) help remove algae from the substrate. They come then, according to the tides and currents, run aground on the beaches. Secondly, the alga must reach a certain phase of its life cycle during which is of mature size and detaches itself because of mechanical forces from currents and large swells. In summer / autumn, the morphology of the seaweed promotes its proliferation on beaches. The large size of the fragile thallus facilitates its stall. These weather conditions promote the detachment of weakened seaweeds from their substrate, that float depending on currents and accumulate finally on beaches.

S. chordalis is adapted to the environment where the geomorphology and hydrological properties offer turbid seawater, hard substrates at 0 to 8 m deep and a semi-sheltered area. Moreover, all the environmental parameters (temperature, salinity, sun exposure time) are gathered for the good development of *S. chordalis*, especially high concentrations in nutrients (nitrate, phosphate, and ammonium) boosting its growth. This last parameter is one of the most determinant for the *Solieria* abundance.

On average by year, 7 000 m^3 or about 5 600 T of *Solieria* sp. are stranded in Rhuys Peninsula. Average annual cost of collecting proliferating red seaweeds in Morbihan is 100,000 €/ year during 2002-2015. This cost corresponds approximately to 4,000 €/year in harvesting costs by each coastal town (Neveu 2016). This biomass is harvested to avoid sanitary problems and to satisfy the residents and tourists who enjoy the beaches and seascapes. Some of these red seaweeds are used directly as fertilizers on the crops of the Rhuys Peninsula and others are washed and processed in order to obtain extracts used in animal and plant care by a local company.

Proliferation of Solieriaceae species has also been observed in southwestern Florida, since 2009 (*Solieria filiformis*) and in south-eastern Australia (*Solieria robusta*) in April 2014 (CEVA 2014). However, few explanations are given to clarify these massive arrivals on the beaches. Only American researchers have advanced the cause of high concentrations of nitrogen and phosphorus in the marine environment. In addition, they describe *S. filiformis* as an opportunistic alga that can attach to other algae and grows rapidly in the presence of nitrogen in the environment (CEVA 2014).

Culture and cultivation

Advances in the development of seaweed cultivation mean that the use of this resource is not only dependent on natural source. Although harvesting of seaweed is economically and environmentally sustainable, new applications for algae in developing markets add value to this biomass. In addition, the expansion of the seaweed industry depends on reliable access to raw materials, the development of high value-added products, and on the transfer of expertise between developed and less developed regions. There are several ways to access the biomass of *Solieria* sp. First, as previously mentioned, companies can harvest the wild biomass stranded on beaches in agreement with the institutional authorities and by respecting at best the environment. Moreover, it is possible to produce *Solieria* sp. by protoplast production, by fragmentation and in Integrated Multitrophic Aquaculture (Peñuela et al. 2018).

Protoplast production

To overcome environmental, technical, and economic potential issues, different strategies can be considered for the development of seaweed regeneration systems or *in vitro* growth production systems. Production and regeneration of protoplasts can particularly offer a better alternative to increase production, improve productivity and quality of the resource. It can also allow a continuous and adequate supply for the operation of secondary metabolites of interest. Most of the protoplasts appeared to be viable, photosynthetically active, or produced new cell walls complete regeneration has been described in *Solieria filiformis* (Kützing) Gabrielson. Pinchetti et al. (1993) reported a reproducible method to isolate large amounts of viable cells and protoplasts from *Solieria filiformis* using a commercial cellulase and various enzymatic extracts prepared from abalone *Haliotis coccinea canariensis* fed on a diet containing this alga. The influence of age, pH of the culture medium, pre-treatment of tissues, enzyme sources and enzymatic adaptability of phytophages fed with a monospecific diet, on the yielding of *Solieria filiformis* protoplasts was analyzed. New apices from fast growing plants showed the highest protoplast yields. The protoplast yield decreased when the pH of the culture medium increased from 6.0 to 9.0. Crude extracts from the abalone *Haliotis coccinea canariensis*, fed with *Solieria filiformis* thalli for three months in combination with cellulysin, released the highest number of viable cells. Yields ranged from 1 to 8.5 million of protoplasts per gram of fresh weight species (Pinchetti et al. 1993).

Fragmentation and cultivation

Cultivated Solieriaceae are predominantly grown from fragments tied to ropes, although they are cultures using mesh bags and tubes. *Solieria robusta* (Greville) Kylin showed the greatest aquaculture potential. This species performed well in laboratory experiments and showed promising, although highly variable, growth in field trials (Wiltshire et al. 2015). A study by Wiltshire et al. (2015) reported the responses of *S. robusta* to temperature, light and nutrients to determine the appropriate seasons for culture and growth for this species. *Solieria* grew faster at temperatures greater than 14°C and had a greater maximum growth rate and higher tolerance. Summer temperatures would have been within the range tolerated by *Solieria* but higher than its optimal temperature for growth. *Solieria*'s responses to light and nutrients showed that low ammonia enrichment did not increase growth or nitrogen storage in this species, but growth, photosynthesis efficiency and nitrogen content increased with higher ammonia supplement levels. *Solieria* was able to grow over a range of PAR levels, indicating that this species is able to photo-acclimate (Wiltshire et al. 2015).

Solieria chordalis has been cultivated by Deslandes's research group to study the metabolism of the seaweed under different environmental conditions (**Fig. 5**) (Fournet et al. 1999; Goulard et al. 2001a, b; Bondu et al. 2008). In Bondu et al. (2008), fragments of *S. chordalis* were harvested on beaches and then incubated in open Plexiglass cylinders (50 cm length=20 cm diameter) filled with 10 L of seawater made up to different salinities. Continual aeration was supplied to provide mixing. Only volatile halogenated organic compounds yield in ng per g dry weight^{-1} day^{-1} were given according to different salinity conditions. Indeed, these compounds derive from secondary metabolism. Chlorinated and brominated volatile halocarbons are thought to be physiologically essential, whereas iodinated compounds are thought to play a role in chemical defence mechanisms against organisms, such as fungi, bacteria, grazers, and epiphytes, in inter-algal allelopathic communication, and in the removal of toxic, surplus hydrogen peroxide generated under oxidative stress (Bondu et al. 2008). Under controlled conditions, physiology of *S. chordalis* can be studied as well as the production of enriched extracts in compounds of interest.

[**Fig. 5** Here]

Solieria sp. *biomass production under IMTA system*

More sustainable seaweed production using new aquaculture technologies could help commercial growth of seaweed while improving the environment (Wiltshire et al. 2015). Notably the concept of Integrated Multitrophic Aquaculture was developed at the beginning of this century (Chopin et al. 1999) and was inspired by traditional, mixed fish, crustacean and some seaweed farming, as practiced in Asia.

Solieria filiformis has been reported for the Gulf of Mexico and Caribbean Sea as an abundant carrageenophyte with aquaculture potential. *S. filiformis* is commonly found as beach cast material during north wind season due to the strong seasonality of the natural populations. Because of the need to maintain biomass availability over the years, *S. filiformis* is currently cultivated by Robledo's research group (CINVESTAV, Mexico) under an environmentally friendly IMTA system. *Solieria filiformis*, described as a promising source of valuable compounds with bioactive capacity (see part on biological activities and applications), has also been successfully integrated into sustainable aquaculture systems (Peñuela et al. 2018; Felaco et al. 2020). The growth performance of this species was recently evaluated in experimental IMTA designs integrated in a trophic cascade by economic important marine species such as snooks (*Centropomus undecimalis*) (Peñuela et al. 2018), red drum (*Sciaenops ocellatus*) (Felaco et al. 2020) and sea cucumbers (*Isostichopus badionotus*), with fishes at the first level, sea cucumber in the second level and *S. filiformis* in the last level being cultivated with the effluents of the previous organisms. Under these systems, Peñuela et al. (2018) reported high growth and productivity (12.2±2.1% day^{-1} and 26.2±11.4 g dry weight $m^{2}\cdot day^{-1}$, respectively), two times and 2.6 times higher respectively, when compared to the control unit (receiving only a continuous flow of plain seawater). In addition, *S. filiformis* from the IMTA showed higher values of dry weight and carbohydrates than the control biomass, corroborating the higher growth rate obtained under the IMTA system. No significant differences were observed in algal tissue C:N ratios from *S. filiformis* cultured under IMTA and under the control unit, thereby, the authors suggest that this species has a high nitrogen storage capacity under different nutrient conditions that allow it to grow and use it for its metabolic maintenance. This was corroborated by the observed high ammonium removal efficiency which was similar (~40%) for algae grown in both systems, despite the different ammonium input (31.8±16.0 in the IMTA system versus 25.8±14.9 M NH_4^+ in the control unit). An especially higher sulfate content was also found in polysaccharides extracted from IMTA algae. The authors related this to the increase in polysaccharide sulfation associated with a defence response against pathogens, since *S. filiformis* in the IMTA system was fed with discharge waters from both snooks and sea cucumbers, probably with a higher load of microorganisms. This fact is important since many biological effects of sulfated polysaccharides in algae have been attributed to the degree of sulfation (Jiao et al. 2011). From this study it was also interesting to note that the content of epiphytes (filamentous algae and invertebrates) was significantly lower in *S. filiformis* grown in the IMTA system compared to those grown only with seawater, showing also a deeper red color and a healthier appearance than those in the control unit.

In the study carried out by Felaco et al. (2020), the authors evaluated the potential successful development of *S. filiformis* in the IMTA system considering the interaction and potential synergies with fishes and sea cucumbers. Thereby, *S. filiformis* was integrated with red drums and sea cucumbers in the trophic cascade above described. The integration of *S. filiformis* with sea cucumbers alone, and with fish alone was also evaluated. Further, *S. filiformis* receiving only a continuous flow of plain seawater served as control. This design resulted in four treatments based on an integrated trophic cascade (C: control with no integrated organisms; H:

holothurids; F: fish; and FH: fish and holothurids). The C had a significantly lower growth rate (10.6±0.9% day^{-1}), while the others did not differ significantly among them, presenting a maximum of 16.7±0.9% day^{-1} for F, followed by FH with 16.1±1.1% day^{-1} and H with 14.6± 1.84% day^{-1}. The chlorophyll *a* increased from 0.11±0.01 up to 0.88±0.13 mg g^{-1} dry weight for the FH treatment after 15 days. The phycoerythrin content (red pigment) remained constant throughout the experimentation period as well as the C:N ratio, coinciding with that previously reported by Peñuela et al. (2018) and confirming that suggested by these authors in relation to the high nitrogen storage capacity of *S. filiformis*. Regarding the morphological differences, seaweeds without integration (C) showed less branching, and were brittle in texture. Flexibility improved with the integration of H, meanwhile, with F, branches were thinner and more abundant. Authors highlighted that when integrated with FH, seaweeds showed most abundant, flexible, and deeper coloured branches.

On the other hand, a bottleneck in the aquaculture of any commercial animal species is the availability of efficient feed to achieve optimum growth rates, and in this regard, seaweed-based feeds have been described as promising raw materials for aquafeed development (Jusadi et al. 2021). Having this is mind, *S. filiformis* obtained from an IMTA system was recently evaluated as a potential ingredient in the diets of juveniles of sea cucumber (*Isostichopus badionotus*) (Martínez-Millán and Olvera-Novoa 2016). In this study, *S. filiformis* was included both as dry-meal powder and as well as a pre-digested meal since sea cucumbers are detritivores. For comparison, the commercial meal BajaKelp® containing *Macrocystis pyrifera* (brown seaweed) was also included. This study included two phases. The first one was directed at determining which algal species, *S. filiformis* or *M. pyrifera*, resulted in better specific growth rate (SGR) and survival of *I. badionotus*, and in the second phase, the feeding efficiency was analysed in terms of ingestion rate (IR) and feed conversion rate (FCR). The growth experiment lasted 54 days. Results showed that 1) survival exceeded 90% in all treatments; 2) after the first 28 days, differences in weight gain between the feeding treatments were found, with *S. filiformis* demonstrating significantly better performance both as dry-meal or pre-digested meal. Authors mention that during the feeding efficiency trial, all diets were well accepted, and no significant differences were found in IR between algae; 3) however they noted that both SGR and FCR were significantly higher in *S. filiformis*-fed juveniles probably related to its protein content (10% higher than in commercial meal). The protein of *S. filiformis* was richer in arginine and histidine (both amino acids playing an important role in the nutrition of detritivores), and also rich in proline, a precursor of collagen, which is the most significant constituent in the sea cucumber's body wall. Therefore, *S. filiformis* produced under Integrated

Multitrophic Aquaculture could provide a suitable feed complement, saving part of the cost that could be economically significant in an intensive aquaculture system (Peñuela et al. 2018; Felaco et al. 2020).

Bio-refinery and the potential of *Solieria* sp. in a context of "blue economy"

The importance of seaweeds in maintaining the ecological balance, as well as their potential for sustainable cultivation, makes them a relevant resource for the "blue economy" strategy (Katari et al. 2022). In this context, the conversion of dissolved nutrients into valuable algal biomass through IMTA systems, for example, added to cascading extraction processes using environmentally friendly techniques, are novel approaches that focus on blue biotechnology. Some recently published *Solieria filiformis* data on the above aspects have shown the importance and potential of this species for the blue economy.

In the light of the above promising results presented previously and its potential development under a blue economy scheme, *S. filiformis* biomass obtained from IMTA was valorised. *S. filiformis* successfully obtained by Peñuela et al. (2018) was used in the same study as a feedstock to develop a valorisation strategy of the species to obtain valuable products. A biorefinery approach of three sequential extractions with the assistance of green technologies such as Enzyme-Assisted Extraction (EAE) and Microwave-Assisted Extraction (MAE) was carried out. The first step of the sequential extractions used EAE with protease enzyme (Protamex®) resulted in a water-soluble extract rich in proteins and in sulfated polysaccharides, suitable as a food supplement. The insoluble residue was used as raw material for an organic extraction, and a lipid fraction rich in polyunsaturated fatty acids (PUFAs), suitable for the use in the nutraceutical industry was obtained as the second product. From the solid residue and using MAE, a pure ι-carrageenan with a powerful antiviral activity against Herpes simplex virus (EC_{50} = 6.3 μg mL^{-1}) comparable to the commercial antiviral acyclovir (EC_{50} = 3.2–5.4 μg mL^{-1}) was obtained as third product. For comparison, the authors also performed direct extractions and noted the advantages of using the biorefinery approach over direct extractions when comparing yields and waste. From these results, they inferred that, by biorefinery approach, one ton of dry *S. filiformis* biomass could produce approximately 700 kg of an enriched extract, 700 g of PUFAs, and around 300 kg of ι-carrageenan with antiviral activity. This process generated 6.3–10.4% of residues from the initial biomass, while the residues obtained from a direct extraction were 15 times higher (Peñuela et al. 2018).

In an attempt to improve the antiviral and antioxidant capacity of extracts obtained from the same *S. filiformis* biomass, the same authors proposed a modification on the EAE conditions in a subsequent study (Peñuela et al. 2021). Due to the heterogeneity of red algal cell walls, enzyme selection has been described as a crucial step to successfully recover compounds of interest. In this sense, the authors proposed to use five combinations of commercial enzymes Protamex® (PRO) and AMG 300L® (AMG) (1:0, 0:1, 2:1, 1:1, 1:2 PRO:AMG) to achieve bioactive crude extracts. The hydrolysates obtained were chemically and structurally characterized and were mainly composed by ι-carrageenan and phenols. These extracts were analysed for their antioxidant capacity (DPPH, ABTS and FRAP assays), and *in vitro* HSV-1 (Herpes simplex virus type 1) activity. Results showed that the combination of 2:1 PRO:AMG was the most effective method to obtain the best yield and the highest antiviral activity. This condition resulted in an extract with a very improved antiherpetic activity (EC_{50} 4.5 μg mL^{-1}) with the highest selectivity index (SI 88.9) compared to that obtained in the previous study (Peñuela et al. 2018) using Protamex® alone (EC_{50} 93 μg mL^{-1}; SI 4) and was even higher than that obtained in that study specifically for the ι-carrageenan fraction (EC_{50} 6.3 μg mL^{-1}; SI 63). Higher phenolic content and antioxidant capacity, and also a lower molecular weight was obtained at this combination, probably playing a synergistic role associated with the strong antiviral activity obtained. Therefore, this combination of enzymes used for *S. filiformis* hydrolysis may exert a greater advantage rather than the use of a single one (Peñuela et al. 2021).

All the above findings show that *S. filiformis* cultured in an IMTA system exhibits good growth performance with the potential to mitigate the environmental impacts of aquaculture by improving water quality. Clean and healthy biomass can be obtained from this system for marketable uses. The combination of green and conventional protocols through a cascade approach is a promising way to develop efficient extraction technologies to obtain products with pharmacological and nutraceutical potential. This knowledge can serve as a basis for future research aimed at promoting this species within the blue economy.

Biological activities and applications in food, in feed, in plant biostimulation and in bioremediation

Many biological activities have been demonstrated from aqueous or alcoholic extracts or from purified molecules of *Solieria* sp. A bibliographical synthesis is presented in **Table II**. Some examples are detailed in this part of this review.

[**Table II** Here]

Active and nutritional components

Sulfated polysaccharides represent a high proportion of the dry and organic weights of *Solieria* sp., 42 to 49.5% of the dry weight (Burlot et al. 2016; Peñuela et al. 2018). Proteins constituted over one-fifth of the dry matter; 22 to 32% of dry weight from *S. chordalis and S. robusta* respectively (Khanzada et al. 2007; Burlot et al. 2016). The rest of the dry matter composition corresponds mainly to the ash.

Carrageenans

Carrageenan is a generic name for a family of water-soluble sulfated galactans that are isolated from Rhodophyta and exploited on commercial scale. Carrageenans are high molecular weight galactans composed of repeating disaccharide units with alternating 3-linked β-D-galactopyranose (G-units) and 4-linked α-galactopyranose (D-units) or 3,6-anhydro-α-galactopyranose (AnGal-units). They are classified in at least 15 families according to their structural characteristics, including their sulfatation patterns and the presence or absence of AnGal-units, uronic acid, methoxyl groups or pyruvic acid acetal constituents on D-units (Knutsen et al. 1994). These phycocolloids exhibit high viscosity, and stabilizing, emulsifying and unique gelling properties used in the pharmaceutical, chemical and food industries with a global value of 1,4 billion of dollars in 2018 (Chopin and Tacon 2020).

Carrageenans from *S. chordalis* contain a higher number of different structural elements. The main structural component of carrageenans is a 3,6-anhydrogalactose 2-sulfate-galactose 4-sulfate (AnGal 2S-G4S)- type structure, which is characteristic of gelling carrageenans with a dominant ι-carrageenan repeating structure. Additionally, α-carrageenan in C6 and C4 and γ-carrageenan could be detected in *S. chordalis*, although with a very low intensity (Burlot 2016; Boulho et al. 2017).

Some studies on the carrageenan from *S. filiformis* have reported this species as a source of relatively pure ι-type although a high number of different structural elements, including both ι- and κ-carrageenans and their precursors υ and μ have been also identified (Murano et al. 1997). These structural differences, linked to the number and position of sulfated ester groups, are related to differences in the precursor content, which can derive from seaweed growth and environmental variations.

The cell-wall galactans of the most common Australian *Solieria* species, like *S. robusta*, are shown to be composed predominantly of carrabiose 2,4'-disulfate units (the repeating unit of -

carrageenan) and a significant proportion of 4',6'-pyruvated carrabiose 2-sulfate units (Chiovitti et al. 1999).

Fibrillar polysaccharides

Cellulose is clearly the most intensively studied polysaccharide. At the molecular level, the polymer consists solely of β-(1 → 4)-linked glucopyranosyl units in a ribbon-like structure. These chains are arranged in sheets and further stabilized by hydrogen bonds in two directions along the chain and by intermolecular forces to form a highly rigid structure. There are no free hydroxyl groups in crystalline cellulose, and the polymer is insoluble in physiological fluids. D-xylose is observed as a common and possibly universal acid hydrolysis product of red algal cell walls. Both β-(1 → 3) and β-(1 → 4) glycosidic linkages could be reported. Fibrillar polysaccharides constitute insoluble dietary fibers. They are thought to be an important food component resistant to hydrolysis by the enzymes of the human digestive tract. From a nutritional viewpoint, dietary fiber's resistance to digestion provides bulk to faeces, holds water, acts as a site for ion exchange, and binds organic molecules (Suzuki et al. 1996).

Storage and low molecular carbohydrates (floridean starch and floridoside)

The term “storage” is often used rather loosely to encompass any accumulation of metabolites with no obvious immediate role. It is assumed that these metabolite pools will be used later in some event.

The characteristic reserve carbon storage material found in red algae is floridean starch, first described by Kutzing in 1843 (Greenwood and Thompson 1961). Floridean starch is probably universal as polymeric storage compound for organic carbon and for energy, its storage role is attested by its accumulation in the light phase (Fournet et al. 1999). Floridean starch from *S. chordalis* occurs (Fournet 1996) in birefringent granules, often of small size (0.5- 25 µm in diameter). Granules appear to lie free in the cytoplasm although they may be formed in proximity to the chloroplast. They are never formed within the latter according to Martin and Smith (1995). On treatment with iodine solution (specific of α 1,4 glucan), the granules of floridean starch from *S. chordalis* are stained yellow although a blue coloration may appear with prolonged exposure. Floridean starch polymer is an α 1,4 glucan that has many α 1,6 branch points and the basic chain has an average of 15 glucose residue (Deslandes and Maume 1987; Fournet et al. 1999). Based on research on the red alga *S. chordalis* used as a laboratory model, the synthesis of floridean starch occurs, starting from glucose-1-phosphate, using adenosine diphosphate glucose (ADPG), or uridine diphosphate glycose (UDPG), pyrophosphates; ADPG or UDPG glucosyl transferase; branching enzymes and the ADPG glucosyl transferase resulting in floridean starch granules (Fournet et al. 1999; Goulard et al. 2001a; b).

The use of soluble and low molecular carbohydrates like floridoside and related compounds in an osmotic role (e.g., as a compatible solute) means that is cannot (unless replaced by a solute of equal utility) simultaneously act as carbon and energy source at constant, or decreasing, external water potential. The soluble organic compounds are diverse; floridoside (and related compounds) is by no means universal in the Rhodophyta.

As a laboratory model, the red alga *S. chordalis* has been extensively examined by Deslandes's research group to understand the enigmatic function of osmoprotectants and stress protection in macroalgae (Fournet 1996; Goulard 2001; Bondu 2008). Previously the osmolytes from red algae have been first purified using chromatographic methods and then characterized by spectroscopic methods (Simon et al. 2002; Simon et al. 2003; Bondu et al. 2007). In *Solieria* sp., floridoside (and related compounds) is a low-molecular weight, highly hydrophilic organic compound without net charge and, contrary to ions, could be accumulated in high concentrations without interfering with cellular metabolism. Due to the increase in the number of dissolved molecules, the internal osmolality is raised, forcing water to re-enter the cell and restore turgor and volume. This is the inherent osmolytic function of any compatible solute. It is also assumed that the osmolytes exert a direct protective effect on biomolecules against the damage of low water activity and/or high concentrations of inorganics ions (Bisson and Kirst 1995). The protective effect has been investigated by *in vitro* and *in vivo* studies. *In vitro* studies probed the mitigating effect of a compatible solute on the stress-dependent activity of an enzyme in the presence of different salt concentrations. The intracellular distribution of water-soluble reserves is not well understood and need to be more investigated. If organic solute can function as compatible solute, it would be expected that they are found in osmotically useful concentrations in such enzyme rich areas as cytoplasm, stroma, and matrix. The demonstration that the compatible solute act in protectively useful concentration in any no vacuolar compartment (stroma) need to investigate in red algae for the future.

Radiocarbon tracer studies on *Solieria chordalis* showed that exogenous inorganic Carbone-14 is rapidly assimilated into floridoside, acting as a major photo-assimilatory product. In contrast, isofloridoside is generally rather weakly ^{14}C-labelled and pulsed-chase experiments suggest that the ^{14}C is transferred very slowly from floridoside to isofloridoside under light and dark conditions, it could be considered that the isofloridoside result of isomerization reaction from floridoside rather than as a direct product of photosynthesis (Bondu et al. 2008). Floridoside is a molecule with potential in cosmetics and in biomedicine, for its antiviral and antitumoral properties both using cells cultures and mammals' models (Stiger-Pouvreau and Guerard 2018).

Human care

Every day, we use seaweeds compounds in our life (e.g., phycocolloids in toothpaste, in cream; whole seaweed as "sea vegetable" in Asia). In this section, we focused on the use of *Solieria* sp. in nutrition and in human health.

Solieria sp. is not a common seaweed used as "sea vegetable" in the world, but it can be mentioned in some studies. For example, *Solieria robusta* has a long history of utilization in Philippines (Tito and Liao 2000) and Pacific islands (Novaczek 2001). In Philippines, *S. robusta* species are among the Samal and Tausug ethnic groups who call it "tajuk bau'no." This is harvested almost year-round, with variable seasonal supply which the natives attribute to rainfall variations. They are sold to retail vendors by volume, rather than by weight, in rectangular rattan baskets of approximately 15 kg per basket at Php120 (US$1=Php38). Seaweeds are prepared as salads; these are washed in tap water and garnished with sliced tomatoes, onions, vinegar, and green mango slivers. The harvesting of *S. robusta* from wild populations in the waters around Zamboanga is mainly carried out by Tausug and Samal fisherfolk who are mostly marginal earners with practically no resource conservation knowledge. Fisheries authorities lack statistical data for the harvested *S. robusta*. Indeed, these seaweeds are mixed with others carrageenophytes and agarophytes which are similar in appearance. Many of the natural seaweed beds containing *S. robusta* face the threat of habitat degradation owing to intensive *Kappaphycus* seaweed cultivation and pollution discharges from coastal villages. Unless conservation measures are implemented, the combined effects of these ecological and anthropogenic factors on *S. robusta* may result in its local extinction even before it can formally be documented, a scenario that is prevalent in other critical ecosystems such as tropical rain forests and coral reefs (Tito and Liao 2000). *Solieria* sp. collected from Fiji and New Caledonia is transformed into pickles or is used in salads, or cooked in coconut milk, prepared as a vegetable, like *Gracilaria*, *Hypnea* or *Acanthophora*. The seaweed can be also chopped into 0.5-1 cm bits and mixed with salted raw fish (Novaczek 2001).

In addition, a study was conducted to develop a diet to significantly reduce low-density. Ethanol extracts of *Solieria robusta* at 10 mg/200 g body weight were tested for their hypolipidemic activity. Ethanol extracts significantly decreased the serum total cholesterol, triglyceride, and low-density lipoprotein cholesterol levels in normal, in triton-induced and diet-induced hyperlipidaemic rats. *Solieria robusta* was found to be the most effective in reducing the lipid profile, particularly in diet-induced hyperlipidaemic rats (Ara et al. 2002).

Several studies on *Solieria chordalis* from France and on *Solieria filiformis* from Mexico have shown considerable potential for biotechnological development. Indeed, some of their polymers have already given positive results after evaluating their antioxidant, antitumoral, immunological, antiviral, antiprotozoal activities and, nociceptive and inflammatory effects (Li et al. 2009; Bondu et al. 2010; de Araújo et al. 2011; Morán-Santibañez et al. 2016; Burlot et al. 2016; Caamal-Fuentes et al. 2017; Terme et al. 2017; Boulho et al. 2017; Pliego-Cortés et al. 2022).

Oxidative stress can induce many kinds of human diseases such as stroke, neurodegeneration, cancer etc. Searching for effective antioxidants is an intense and continuous process. Considerable laboratory evidence indicates that antioxidants may slow or possibly prevent the development of cancers. Floridoside, a 2-O-D-glycerol-D-galactoside, is not only the main photosynthetic product of *Solieria* sp., but also plays a role in cell protection under many stressful conditions, such as hyperosmolality or high temperature. Ochsenkühn et al. (2017) have indicated that floridoside has an ability to prevent salinity- and heat stress-induced reactive oxygen species (ROS) production. Moreover, the biological activities of floridoside have been studied such as immune regulatory (Courtois et al. 2008), antiinflammatory (Kim et al. 2013), antibacterial (Liu et al. 2008) and antioxidant properties (Li et al. 2009). The antioxidant activity of floridoside helps red algae to fight, in particular, by inhibiting the production of ROS in these stressful environments and by increasing gene expressions of glutathione and superoxide dismutase (SOD). However, the molecular mechanism underlying its antioxidant activity remains largely unexplored (Simon et al. 2002, 2003).

Cytotoxicity and pro-apoptotic activities of extract from *Solieria chordalis* were evaluated by a bioactivity guided approach. Marine algae represent an exceptionally rich source of bioactive compounds with various biological activities. Halogenated terpenoids from red algae represent the most promising macroalgae secondary metabolites in anticancer research. The study of Bondu et al. (2010) has focused on the abundant *Solieria chordalis* harvested on Brittany coast (France). Primary metabolism is well investigated in *S. chordalis* contrary to its secondary metabolism and related bioactivity. The cytotoxic and pro-apoptotic effects of non-polar crude extracts from *S. chordalis* have been examined on several human cell lines: Jurkat (leukaemia T cell), Daudi (Burkitt lymphoma, B cell) and A549 (non-small cell lung cancer). Two crude extracts (CH_2Cl_2 and $CHCl_3$ extracts) have demonstrated a rapid cell death in all these cell lines, revealed by Annexin staining in flow cytometry (Bondu et al. 2010). Moreover, apoptosis induced by 100 µg of these extracts was accompanied by exposure of membrane phosphatidylserines and caspases activation in all cell lines. Intracellular ROS have increased about up 20 to 60% in Jurkat and Daudi cells, and the mitochondrial potential has decreased 24 to 48h after treatment. Purification protocols of the CH_2Cl_2 crude extracts obtained from *S. chordalis* were performed and several compounds (**Table III**) were analysed and suggested that probably polyunsaturated fatty acid, terpenes and pigments compounds in *S. chordalis* induced cytotoxic effects and apoptosis in human cancer cell lines.

[Table III Here]

The antiproliferative effect of *S. chordalis* extracts was also evaluated *in vitro* on human bronchopulmonary carcinoma cell line with an IC_{50} of 23 µg mL^{-1} for monogalactosyldiacylglycerols obtained thanks to a supercritical carbon dioxide extraction, which can be considered as a green extraction method of lipids and non-polar compounds from seaweeds (Terme et al. 2017).

Carrageenans have been shown to exhibit antiviral activity against a wide spectrum of viruses including important human pathogenic agents such as human immunodeficiency virus (HIV), Herpes simplex virus (HSV), Vesicular stomatitis virus (VSV), and Cytomegalovirus (CMV) (Necas and Bartosikova 2013). Recently, Pliego-Cortés et al. (2022) have added evidence of the potential antiviral activity *in vitro* of the carrageenan extracted from stranding biomass of *S. chordalis* against Herpes simplex virus type 1 (HSV-1). The carrageenan obtained by Enzyme-Assisted Extraction (EAE) or by Hot Water (HWE) was isolated by ethanol and dialysis (named semi-refined sulfated polysaccharides sr-SPs), and further purified by ion-exchange resin (named fractions F1, F2 and F3). A significant increase in the antiviral activity was observed in the EAE compared to HWE extracts (EC_{50} 60 vs 73 µg mL^{-1}). Whilst the purification process increased by 3-fold the activity in F2 compared to sr-SPs with an EC_{50} 18 µg mL^{-1}, and a MOI 0.01 ID_{50} mL^{-1} after 72 h of infection. Furthermore, none of the carrageenan fractions with concentrations up to 1000 µg mL^{-1} showed cytotoxicity on Vero Cells (Pliego-Cortés et al. 2022). Moreover, Burlot et al. (2016) and Boulho et al. (2017) showed similar results after evaluating the antiviral activity against Herpes simplex virus of the native and alkali-treated carrageenans from *S. chordalis* obtained by EAE and Microwave-Assisted Extraction (MAE) under different extractions conditions. Their results have shown an EC_{50} of the iota carrageenans fractions in the range of 3.2 to 54.4 µg mL^{-1} without cytotoxicity in that range of concentrations. Furthermore, sulfated polysaccharides extracted from *Solieria* *filiformis* obtained from an aquaculture facility at the Telchac Marine station-CINVESTAV, Yucatan (Mexico), where it was periodically cultivated in bimonthly cycles in semi open tanks as part of an Integrated Multitrophic Aquaculture system, were tested in order to evaluate their effect on Measles virus (MeV) *in vitro.* Measles virus, non-segmented negative strand RNA virus, causes a highly contagious disease. Although preventable by vaccination, measles still remains one of the causes of death among young children worldwide. Sulfated polysaccharides showed antiviral activity (as measured by the reduction of syncytia formation) and low cytotoxicity (MTT assay) at inhibitory concentrations. Sulfated polysaccharide from *Solieria filiformis* showed the highest antiviral activities (96% syncytia reduction with a concentration of 0.011 μg mL^{-1} of *S. filiformis*). Time of addition experiments and viral penetration assays suggest that the best activities of sulfated polysaccharides occur at different stages of infection. Sulfated polysaccharides of the *Solieria* species appear as promising candidates for the development of natural antiviral agents (Morán-Santibañez et al. 2016).

To this is added the study by Caamal-Fuentes et al. (2017) demonstrating that crude carrageenan from *S. filiformis* exhibits antiprotozoal activity against *Giardia intestinalis*. Enteric protozoan infection produced by *Giardia lamblia* is a significant cause of morbidity and mortality in developing countries. Other antiprotozoal activity (i.e., against *Leishmania amazonensis*) has been recently reported for sulfated polysaccharides received from *S. filiformis* (Lehnhardt Pires et al. 2013).

Finally, another study on sulfated polysaccharides from *Solieria filiformis* may be mentioned, which showed nociceptive and inflammatory effects. Fernandes de Araújo et al. (2011) demonstrated that the antinociceptive effects of polysaccharides occur via a peripheral mechanism in Male Swiss mice. However, the edematogenic effects of polysaccharide suggest the involvement of prostaglandins, NO and primary cytokines (IL-1 and TNF). Their data suggest that sulfated polysaccharides from *S. filiformis* may be a key tool to study the inflammatory processes associated with nociception.

Plant care

Today, in Morbihan (France), to cope with abundant quantities of *Solieria* sp. on the beaches, communities have to harvest this biomass in order to avoid any sanitary risk and also to satisfy local populations and tourists. Thus, stranded algae are harvested and directly spread on farmer's fields without prior treatment of the biomass. Farmers accepted to receive these algae to have a free and fresh contribution to organic matter. This kind of use of seaweeds comes also from a traditional practice by farmer's families living near the seacoast. Moreover, farmers accepting to receive algae must own many fields and/or must be numerous. Indeed, fields can receive seaweeds only every 3-5 years, because of the salt from seaweeds which lowers the crop yield. To spread the algae on fields, a spreading agreement is signed between the community of communes and the farmers. Analyses on the agronomic values (total nitrogen, phosphorus, potassium, etc.) are performed in order to determine the quantity of seaweeds to be spread on the fields. The recommended rate is 20 to 40 m^3 ha^{-1}, or 10 to 20 T ha^{-1}, depending on the type of crop plants. Furthermore, green waste can be mixed with other organic materials such as seaweed to produce compost. However, there are few details about composting techniques. Most often, the algae are stored on land owned by the farmer who will then process them by adding manure and leaves (Neveu 2016). Furthermore, a local company, working in cooperation with communities and farmers from Morbihan (France), adds value to this *Solieria* biomass for plant care. Wheat and barley are among the more important staple foods for human and animal nutrition in the world. Nevertheless, these crops constantly suffer from the Fusarium Heat Blight disease, responsible for a decrease in yields and the bioaccumulation of the trichothecene deoxynivalenol in kernels. It is estimated that around 25% of all the harvested crops around the world are contaminated by mycotoxins and, besides being a threat to human and animal health and life, they are the cause of losses of billions of dollars around the world every year (Duccati et al. 2020). Searching for alternatives to overcome these problems, the French company developed a carrageenan-rich product (Algomel Push®) produced from the red alga *Solieria chordalis*. The use of carrageenan decreased mycotoxins contamination up to 34.6 and 35.7% when 1.0 and 2.0 L ha^{-1} of carrageenan-rich product was applied in wheat and barley, respectively. The study of Duccati et al. (2020) suggests that the bioactive carrageenan-rich product, has the ability of eliciting the plant's mechanisms of defence and growth. They mentioned that this algae-based product can be considered as a potential option/tool for farmers and industries to cope with the problem of food quality in their mycotoxicological and bromatological aspects (Duccati et al. 2020).

Other studies highlighted the biostimulant and antifungal activities of *Solieria* sp. extracts. Indeed, Spain et al. (2022), after following an eco-friendly approach, i.e., an Enzyme-Assisted-Extraction (EAE), produced a water-soluble extract, which was tested as a potential biostimulant for plant growth. This extract, rich in sulfated polysaccharides and proteins, was obtained from *S. chordalis* using Protamex® and Neutrase® and tested on radish seeds. Radish plants, treated with enzyme extracts, demonstrated higher chlorophyll content and were higher and heavier than plants in the control group. EAE also produces a post-extraction residue, which has not been used on a large scale so far. Considering the same idea of bio-based economy and sustainable development, this residue, depending on the chemical composition, can be valorised into many added-value products such as biosorbents of metal ions. Moreover, various fractions of ethanolic extract of *Solieria robusta* were screened for antifungal activity against five fruit spoiling fungi isolated from fruits. All fractions were able to inhibit fungal growth. Aqueous fraction showed maximum inhibition ratios followed by methanol, ethyl acetate, chloroform and ethanol fractions (Khanzada et al. 2007).

Animal care

To ensure a more sustainable food production, and to meet the increasing demand for animal-derived foods, novel feed ingredients for animal diets, especially protein sources, are receiving significant attention. Stokvis et al. (2022) investigated whether *Solieria chordalis* co-products can improve performance, *in vivo* digestibility, and health of broilers. They have proved that inclusion of seaweed in the broiler diet, containing 5 and 10% (w/w) seaweed product in starter and grower diet respectively, increased body weight gain (+14%), and feed intake (+12%) in the third week of the experiment (Stokvis et al. 2022).

In the aquaculture sector, contagious diseases are one of the major problems causing production and profit losses (Tharaka et al. 2020; Gunathilaka et al. 2021). Therefore, dietary supplementation of antibiotics, probiotics or immunostimulants has been practiced in aquaculture as a prophylactic method to prevent infectious diseases. Two kinds of extracts containing *Solieria* sp. were studied on olive flounder (*Paralichthys olivaceus*) diet. Metallic ion-rich polysaccharides have the ability to form a stable structure with montmorillonite layers in clay during its exfoliation. The specific structures could create a conducive environment by activating and stabilizing endogenous enzymes in gut to increase the host animal's digestive performance when an algae-clay powder (ACP) is ingested. Tharaka et al. (2020) evaluated the benefits of mixing algae (*Solieria chordalis* and *Ulva lactuca*) with clay and of supplementing the mixture into a fish meal-reduced diet for olive flounder diet. The ACP was added into a light fish meal (LFM) diet by 0.2%. The ACP inclusion in the LFM diet had positive effects on growth, feed utilization and diet digestibility of fish after 12 weeks of the feeding trials showing similar or higher growth than the high fish meal diet (Tharaka et al. 2020). Similar results were observed by Gunathilaka et al. (2021). Indeed, according to their results the supplementation of algae extracts (*Ulva* spp./*Solieria* spp. mixture) in the diet for olive flounders can enhance innate immunity, feed utilization, digestion, enzyme activity, nutrient digestibility, and intestinal morphology. The dietary supplementation of algae extracts seems to possess immunemodulating and gut barrier strengthening effects which resulted in the improved survival of fish exposed to *Edwardsiella tarda* (Enterobacterales) infection (Gunathilaka et al. 2021).

Bioremediation and Environmental tools

Solieria sp. can also be used as a biosorbent to remove pollutants from the wastewater as well as a tool in environmental engineering. Spain et al. (2022) showed that post-extraction residue obtained after an Enzyme-Assisted Extraction exhibited good biosorption properties towards Cr(III) ions and can be used in the production of novel components of fertilizers or as a biosorbent for wastewater treatment (Spain et al. 2022).

In 2018, scientists from a geology and oceanology laboratory from de South Brittany University in France created the first Algobox®, an environmental tool for the coast protection from erosion. The experiment was carried out on two beaches in Morbihan (France) with the following objectives: creation of an embryonic sand dune and sand dune protection by maintaining algae on the beach (nutrient). This Algobox project consisted of monitoring the dynamics of macroalgae strandings and their enhancement for the protection of the Morbihan coastline. The degradation of the algae and their accumulation bring organic matter to the system and, the sediment by wind capture is trapped in the ganivelles of the Algobox® allowing to protect and reconstitute the dune. At present, Penvins beach has gained in landscape aspect, a foredune has been created, i.e. sedimentary stock protecting the mobile dune, and the number of plant species has multiplied by four. The plant species that colonize the Algobox are generally annual species, common at the top of the beach (halophytic nitrophils such as the sea rocket *Cakile maritima*). In addition, there are perennial species such as the large grasses of the genus *Elytrigia* which are found the following year (**Fig. 6)** (Sedrati 2018).

[Fig. 6 Here]

Conclusion

In conclusion, *Solieria* spp. represents a natural and available source with nutritional and functional properties. Indeed, these seaweeds can be used due to their biochemical composition. Their extracts are rich in mineral matter, proteins and carbohydrates. Moreover, they have shown antiviral, antimicrobial, antioxidant and anti-tumoral activities. Thus, the nutritional and functional complementation provided by their extracts can be used in prevention of infectious diseases in plants and animals as well as in humans. Based on molecular biology, ten species of *Solieria* spp. were identified, and are found in Atlantic, Pacific and Indian Oceans under tropical and temperate climate. The availability of huge quantities in some regions, the eco-physiology, and the quality of the raw material of *Solieria* sp. are important and fundamental elements to consider in the many applications of this biomass. Similarly, the impact of production, extraction and purification methods that may have an environmental impact must be examined in the biorefinery concept to access active compounds from seaweed that play a key role in the blue economy.

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Data availability statement

The datasets analysed during the current study are available from the corresponding author on reasonable request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contribution Statement

All authors have contributed to research works on *Solieria* sp. notably on *S. filiformis* from Mexico (Freile Y., Pliego Cortes H. Penuela A., Robledo D.) and on *S. chordalis* from France (Bedoux G., Bondu S., Boulho R., Bourgougnon N., Burlot AS., Deslandes E., Latire T., Michalak I., Spain O., Terme N)

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Fig.1 Distribution of species of the genus *Solieria* in the world with both groups splitted by the collapse of the Tethyan seaway in the vicinity of the Mediterranean Sea, beginning around 100 Ma ago and ending 20 Ma ago (inspired by Fredericq et al. 1999). The arrows show the migration of species over time because of a robust current flowed westward through the continental configuration of that time.

Fig. 2 *Solieria chordalis* biomass on Kerfago beach, in Saint Gildas de Rhuys (South Brittany, France) from October 2013 to August 2016. Photographs of Burlot AS. (Month/Year).

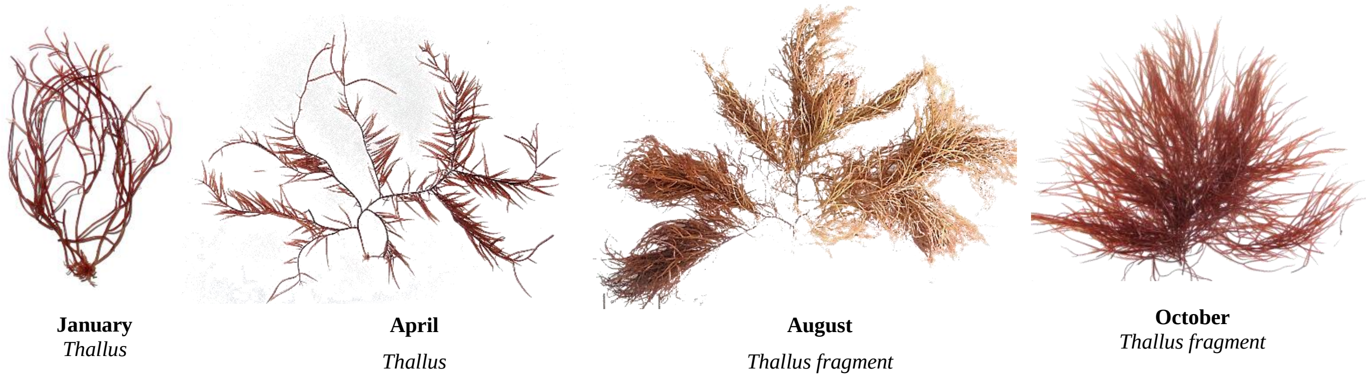
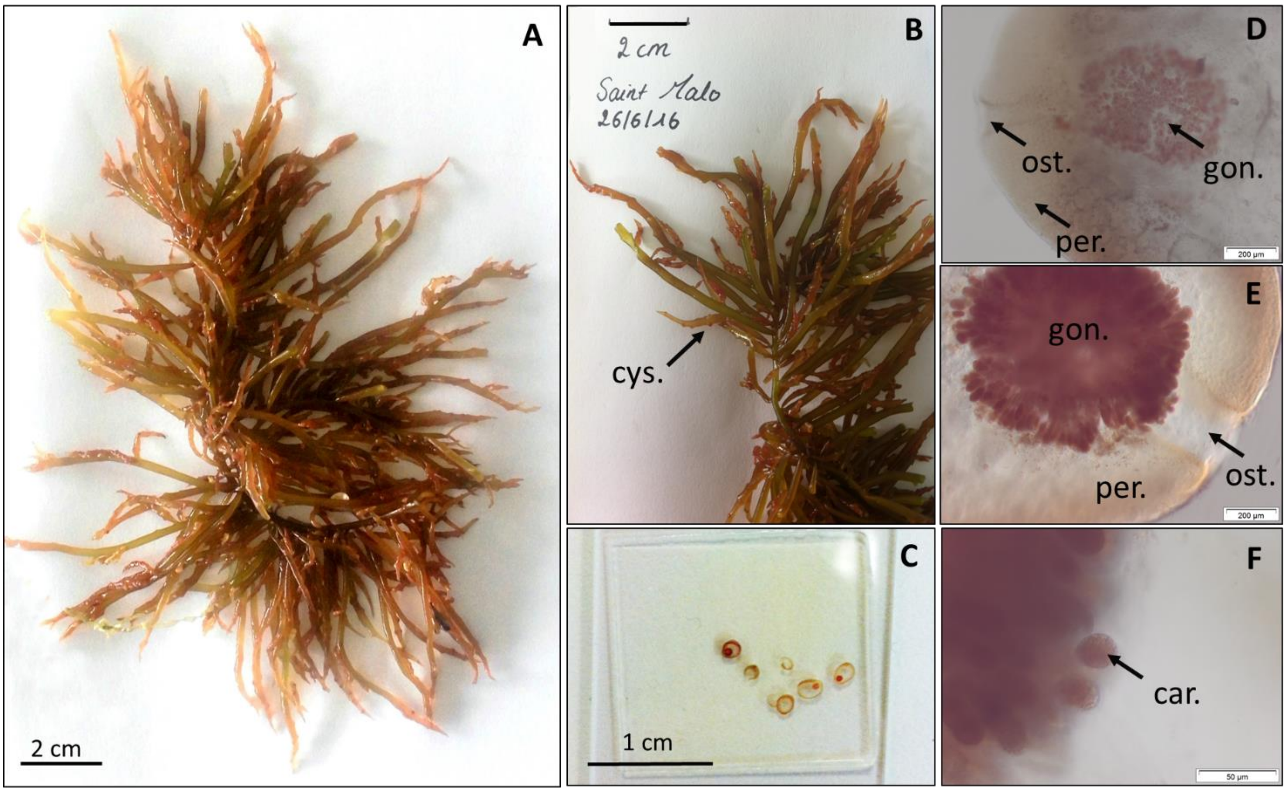


Fig. 3 Different morphologies of *S. chordalis* over the seasons. Photographs of Burlot AS. (Size scale is not considered on this Figure. See the text for more details).



A *Carposporophyte of* *<u>Solieria</u>* <u>sp.</u>

B *and* ***C*** *Filaments and cross sections. Cystocarps (fertilization receptacles) are visible to the eye (cys.).*

D, E *and* ***F*** *Cross section of a cystocarp (****D*** *and* ***E****) with a 4X zoom on the gonimoblast (****F****). After the fertilization, the zygote burgeons to a gonimoblast (gon.) surrounded by a pericarp (per.). The gonimoblast bearing terminal carposporangia that release carpospore each (car.) to the outside environment through an opening, the ostiole (ost.)*

Fig. 4 Macro- and microscopic photographs of reproductive organs in *Solieria sp.* from Saint-Malo, North Brittany, France (Burlot 2016).

Fig. 5 Culture of *Solieria chordalis* under controlled condition by Eric Deslandes's research group (E. Deslandes)

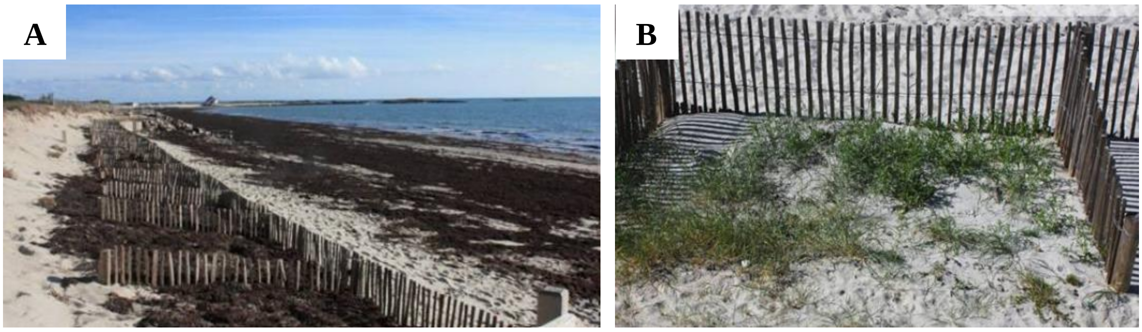


Fig. 6 Massive stranding of red algae and filling of AlgoBox® with *S. chordalis* in October 2014 (**A**) and colonization of AlgoBox® by vegetation (**B**) in April 2015 (Sedrati 2018)

Table I Biochemical composition of *S. chordalis* collected in Saint Gildas de Rhuys (South Brittany, France) from October 2013 to October 2015.

	Dry weight *(% fresh weight)*	Neutral sugars *(% dry weight)*	Proteins *(% dry weight)*	Uronic acids *(% dry weight)*	Sulfate groups *(% dry weight)*	Ash content *(% dry weight)*
October 201 3- October 2014	14.0 ± 2.9	30.7 ± 5.5	18.4 ± 5.2	2.9 ± 0.7	10,0 ± 6.4	28.6 ± 8.9
October 2014 - October 2015	12.1 ± 2.3	26.6 ± 5.0	14.8 ± 3.3	3.1 ± 0.6	14.5 ± 5.1	28.8 ± 8.9
Mean October 2013 - October 2015	13.0 ± 1.4	28.6 ± 2.9	16.6 ± 2.6	3.0 ± 0.1	12.6 ± 2.6	28.7 ± 0.2

Table II Biological activities from *Solieria sp.*

Solieria chordalis				
	seaweed co-products	**Bird health**	improves performance, in vivo digestibility and health in broilers	Stokvis et al. 2022
			increased body weight gain and feed intake	
	proteolytic enzyme treatment to seaweed co-products		reduction of digestibility of most nutrients, and increased crypt depth in birds fed	
			not improve performance nor health-related parameters, and reduced digestibility of the diets.	
	0.2 % algae-clay powder	**Feed**	Supplemental effect of algal-clay based biocatalyst in a low-fish meal diet was tested for olive flounder	Tharaka et al. 2020
			Dietary algal-clay supplementation improved the disease resistance of olive flounder against Edwardsiella tarda.	
		Food		
	non-thermal high hydrostatic pressure (HHP) technology in combination with polysaccharidases		improve the extraction of specific molecules such as proteins, polyphenols and polysaccharides	Suwal et al. 2019
			Increase antioxydant activity	
	enrichied extracts	**Human health**	3 fractions with DPPH radical scavenging activity. 4 compounds exhibited UV-B absorbing capacity regarding their absorption at 310 nm.	Boulho et al. 2017
			immunological, haemagglutinic activities	Bondu et al. 2020
	oligo- and polysaccharides		antiherpetic activities	Pliego-Cortés et al. 2021
	monogalactosyldiacylglycerols		antiproliferative activity	Kendel et al. 2015
Solieria robusta	whole seaweeds	**Food**	pickles, salads	Novaczek 2001
		Human health		
	Methanolic extracts		inhibition proliferation of oral cancer Ca9-22 cells via apoptosis and oxidative stress	Yen et al. 2014
	polyphenolic extracts		anti-inflammatory effects against multiple genera of fungi	Ejaz et al. 2020
	ethanol extracts		Hypolipidaemic activity	Ara et al. 2002
	methanolic extracts		anti-inflammatory activity	Yasmeen et al. 2020
	ethanol extracts		inhibition of mosquito larvicidal activity against 4th instar larvae of *Aedes aegyptii*.	Ira et al. 2017
Solieria filiformis	carrageenan-rich enzymatic extracts	**Human health**	antiviral activity against Herpes simplex virus (HSV-Type 1) , antioxidant capacity (radical scavenging activity and Ferric Reducing Antioxidant Power)	Peñuela et al. 2020
	water-soluble extract rich in proteins and sulfated polysaccharides suitable as a food supplement		food supplement	Peñuela et al. 2018
	lipid fraction rich in polyunsaturated fatty acids (PUFAs)		food supplement	Peñuela et al. 2018
	pure ι-carrageenan		antiviral activity against Herpes simplex virus (HSV-Type 1)	Peñuela et al. 2018
	lectines		antinociceptive and anti-inflammatory effects	Abreu et al. 2016
	Sulfated polysaccharides		gastroprotective and antioxidant effects	Sousa et al. 2016
	Isolectines		anticancer effect on MCF-7 breast cancer cells	Chaves et al. 2018
	Lectines		human pathogenic bacteria	Holanda et al. 2005
	Sulfated polysaccharides		antinociceptive effect in induced temporomandibular joint pain	Araujo et al. 2017
	Sulfated polysaccharides		antiviral activityagainst measles virus and low cytotoxicity at inhibitory concentrations	Morán-Santibañez et al. 2016, 2018
	Sulfated polysaccharides		Anticoagulant and antithrombotic properties	Assreuy et al. 2010
	Sulfated polysaccharides		modulate the growth rate and cell survival of Leishmania (L.) amazonensis promastigotes in in vitro assays	Lehnhardt Pires et al. 2013
	lectines		control inflammatory processes: promoted increased in cell viability and induced Th2 immune responses in mouse splenocytes, indicating that they have anti-inflammatory effects	Monteiro Abreu et al. 2012
	lectines		antiviral activities	Gondim et al. 2019
	carrageenan		antiprotozoal activity against Giardia intestinalis.	Caamla-Fuentes et al. 2017
	Sulfated polysaccharides		antiviral activity against Herpes simplex virus (HSV-Type 1)	Bedoux et al. 2017
	Sulfated polysaccharides		antiviral activity against measles virus	Morán-Santibañez et al. 2016
	Polyphenol-rich extracts plus Sulfated polysaccharides		antiviral activity against measles virus	Morán-Santibañez et al. 2018
	Pigments		antioxidant capacity (radical scavenging activity and Ferric Reducing Antioxidant Power)	Zepeda et al. 2020
	Lectins		antidepressant-like effect	Abreu et a. 2018
	Lectins		anticancer effect on MCF-7 breast cancer cells	Chaves et al. 2018
	Lectins		Antinociceptive and anti-inflammatory activities	Abreu et al. 2016
	Lectins		Human pathogenic bacteria	Holanda et al. 2005
	whole seaweeds	**Feed**	Dietary algal supplementation improved palatability and growth rates in the sea cucumber Isostichopus badionotus juveniles	Martínez-Millán and Olvera-Novoa 2016
Solieria sp.	carrageenan-rich enzymatic extracts	**Human health**	Antibacterial activity of the compound Solieritide A	Liu et al., 2020

Table III Cytotoxicity of compounds purified from *S. chordalis* Ch_2Cl_2 extracts

Compounds	EC_{50}
Eicosapentanoic acid	240.5µM
Arachidonic acid	283.3µM
Cholesterol	-
Pheophytin a (886Da)	64.18µM
Pheophytin a (871Da)	116.9µM