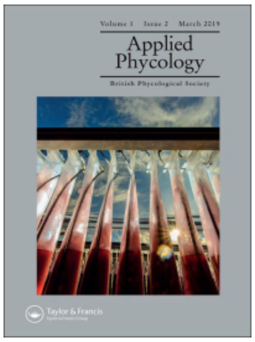

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REVIEW

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Seaweed resources of Argentina (S W Atlantic): production, bio-ecological, applied research and challenges for sustainable development

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ABSTRACT

Argentina comprises more than 5000 km of coastline with a considerable diversity of seaweeds, some of which have the potential to be transformed into fishery resources. However, when compared with other marine resources, the exploitation of the seaweed species in terms of the harvesting methods, their sustainability and available information on biological and ecological features, as well as their potential applications, is scarce or outdated. In this context, this review includes an integrated analysis of production statistics of selected seaweeds in Argentina. In addition, an extensive revision of taxonomic, bio-ecological, environmental and applied issues involving Argentinean seaweed resources is provided. Furthermore, we include novel information about the changes in resource availability which occurred during the last 20 years and their consequent impacts on the seaweed industry. The Argentinean seaweed industry developed raw materials biomass production in the 1960s and extraction of phycocolloids in the 1970s which dropped to very low levels to the present. Information here presented contributes directly to the UN SDG Goal 14: Life below water, providing a theoretical framework to understand how and which of the global change drivers affect sustainability of marine resources. Additionally, a detailed review is presented on phycocolloids from Argentinean seaweed resources. Actions are proposed that would contribute to the enhanced sustainable development in Argentina. The review suggests that reactivation of an Argentinean seaweed industry requires an update of legal frameworks, regarding exploitation of Argentinean seaweeds together with the necessary developments of science and industry.

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Introduction

Oceans have historically provided multiple ecosystem goods and services (Borja et al., 2020) but, in recent years, ocean health is rapidly deteriorating, driven by global factors such as climate change, pollution and over-exploitation of marine resources, especially due to increased human activities (Hall-Spencer & Firth, 2021). Oceans play crucial roles in the regulation of some of these factors. In particular, some seaweed species could provide ecosystem services such as environmental benefits and provision of food, having a strong impact on the achievement of the United Nations' (UN) Sustainable Development Goals (SDGs).

Some seaweed species represent collectively an important marine resource and constitute – by weight – more than 50% of the total production of marine aquaculture. Around 500 seaweed species have been used for different purposes and more than 200 species are reportedly farmed worldwide. However, only eight genera provided more than 96% of global seaweed farming. In contrast, harvesting of wild seaweeds represented only 2.9% of the total global reported seaweed production in 2018 (Chopin & Tacon, 2020). Applications of selected seaweeds are indeed numerous which target diverse markets. It is apparent that the traditional phycocolloids market is decreasing in importance, while the edible food market is increasing (Chopin & Tacon, 2020). Seaweeds also provide a wide range of ecosystem services and non-food products (Naylor et al., 2021), and promise emerging markets for seaweed products, like nutritional supplements, agrichemicals, animal feed, cosmetics and cosmeceuticals, biomaterials and bioplastics, and as an alternative to fossil fuel (Cottier-Cook et al., 2021). In 2018, 32.4 million tons of algae were

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produced and more than 99% of the biomass production, being China and Indonesia by far the largest seaweed producers (Buschmann et al., 2017). Of the total production, 97.1% of the total biomass was produced by aquaculture (Naylor et al., 2021). The income generated by the seaweed production was USD 13.3 billion, accounting for 5.4% of the USD 275 billion of world aquaculture (FAO, 2020). It is estimated that, by 2050, 0.1% of the ocean could be dedicated to seaweed production for food, nutraceutic and chemical uses (The Seaweed Manifesto, 2020).

On the Pacific coast of South America, Chile produces more than 400000 dry tons of seaweeds from at least 14 different species (i.e., *Lessonia* spp., *Macrocystis pyrifera, Mazzaella* spp., *Gracilaria chilensis, Gelidium rex, Porphyra* spp./*Pyropia* spp.) mainly from wild populations (Camus, Del Carmen Hernández-González, & Buschmann, 2019). In contrast, Argentina comprises a vast marine coast facing the southwestern Atlantic, with both warm and cold temperate waters and a wide continental shelf and an important commercial exploitation of wild seaweeds occurred between 1950–1970 (FAO, 2021). However, in the last two decades, commercial production of seaweed biomass decreased, showing a drastic fall in biomass availability of the main harvested species *Gracilaria gracilis* for agar production. The actual seaweed production of the country is very low (less than 50 tons in dry biomass, Robert & Raffo, 2021). Meanwhile, the invasive species *Undaria pinnatifida*, spread along the Argentine coast (see section 2) representing a threat to the native macroalgae and the nearshore community, and also being utilized as a harvestable resource (Casas & Piriz, 1996; Dellatorre, Amoroso, Saravia, & Orensanz, 2014).

Although the current scenario shows a low use of seaweed resources, based on its wide and productive continental shelf and seaweed resources diversity, Argentina would have the potential to increase its production as well as its industrialization. In this sense, an increase of seaweed biomass production along the Argentine coast would have positive impacts on several of the Sustainable Development Goals of the United Nations, providing biomass that can be consumed directly (UNDG Zero hunger) or beneficial to health through its bioactive compounds (UNDG Good health and well-being). Decent work and economic growth (seaweeds are clearly underutilized resources that could be sustainably used, generating jobs and value for local communities). To achieve these objectives, it is necessary to change the traditional way of using resources and move towards a more sustainable exploitation, either through the direct harvesting of wild beds, or gathering from the coastline. This change must be supported by an increase in scientific and technical studies accompanied by government policies that regulate its sustainable use and favour new activities for its use (UNDGLife below water)

Although seaweed resources of Argentina have been revised, changes both on its commercial exploitation and availability have not been addressed in the previous revisions of the last 20 years (Boraso de Zaixso, Ciancia, & Cerezo, 1998; Boraso de Zaixso & Zaixso, 2015). The marine macroalgae of Argentina have been studied for more than 60 years, starting with the first catalogues and descriptions of the flora (i.e., Pujals, 1963; Pappenfuss 1964; Kuhnemann, 1972; Pujals, 1977). Most of these studies were carried out between 1960–1980, promoted by research programmes on seaweeds of commercial interest and focused mainly on the Sub-Antarctic region because of its great diversity and algal biomass (Liuzzi, Gappa, & Piriz, 2011). The first programme was performed in 1963 through an agreement between the Argentine Government and the Technical Assistance Management of the United Nations, to promote the industrial use of algae (Kühnemann, 1970). The aim of this study was to assess the abundance and distribution of seaweeds of commercial interest, and the study of their chemical constituents and some of their properties. Further research analysed the challenges associated with the manufacture of products derived from Argentinean seaweeds (Asensi, 1981; Halperín, Asensi, & Boraso, 1973). As a result of these programs, a broad background was generated both in taxonomy, biology and distribution of marine algae along the Patagonia coast of Argentina; and also on their chemical composition, mainly focused on phycocolloids (see section 5). A large amount of this information was published as "grey literature" i.e., technical reports, PhD theses and local journals/popular press, remaining largely unknown to the international research community. This invaluable information has been summarized in the present review together with more recent publications describing the taxonomy, biology, ecology (see section 4) and applied studies (see section 5).

In this work we revised the seaweed resources of the Argentine coast from two different perspectives:

(1) A revision of the scientific knowledge about the presence, distribution, abundance, phenology and ecological features of species that can be considered as seaweed resources. In addition, the statistics of seaweed biomass production in Argentina were also evaluated

(see section 3), from two sources of information: FAO statistics for aquaculture and fisheries production (FAO fishstat) and statistics from the Chubut Province government (Estadísticas Chubut 2000 to 2016).

(2) A revision of the local scientific research in the main fields of application focused on seaweed hydrocolloids, considered as the main field of basic and applied phycological research developed in Argentina. We consider that this field of research makes an important contribution to the potential development of the local seaweed industry, and therefore it is extensively reviewed (see section 5).

Biology, taxonomy and ecology of the actual and potential commercial seaweeds species along the Argentine coast

Seaweed biodiversity of Argentina comprises more than 200 species belonging to almost 140 genera (Boraso, 2013) distributed along more than 18.5 degrees of latitude, from the Río de la Plata mouth (36.5°S) to the south of Tierra del Fuego (55°S, Figure 1). Excluding Islands (in particular the Malvinas/Falkland Islands), its length is approximately 5700 km (Lanfredi, Pousa, & D'Onofrio, 1998; Schnack, Pousa, Bértola, & Isla, 2010). Macroalgal assemblages vary along the coast from communities dominated by seasonal and small-sized algae (e.g., *Codium* spp., *Ulva* spp., *Ceramium* spp., *Corallina officinalis*), ranging between 10–30 cm in height (Boraso de Zaixso, 2013), to perennial giant kelp forests that can reach up to 20 m (Eyras & Boraso de Zaixso, 1994). Regarding the latitudinal diversity patterns, the macroalgal assemblages have a clear trend of decreasing macroalgae diversity towards the tropics as occurs for some algal genera (Kerswell, 2006; Liuzzi et al., 2011). However, it is acknowledged this trend could be partially biased due to the difference in the sampling effort, being greater in the southern region.

There is a 51% reduction in algal species richness between 42–41° S, consistent with the boundary between the Warm Temperate South West Atlantic and the Magellanic Ecoregion (Spalding et al., 2007). These ecoregions include three Biogeographic Provinces, i.e., the Uruguay–Buenos Aires Shelf Province (belonging to the Warm Temperate SWA ecoregion), the North Patagonian Gulfs and Patagonian Shelf (these last two belonging to the Magellanic Ecoregion). We exclude here the insular Province of the Malvinas/Falklands and Sub-Antarctic Islands (Spalding et al., 2007). The breaking point between both ecoregions is related to some environmental factors important for the establishments of macroalgae, presents major differences between both ecoregions. The part of the Argentine coast that belongs to the Warm Temperate SWA ecoregion is dominated by exposed sandy beaches, along with salt marshes, mud flats and some shallow bays (Dellatorre et al., 2014 and references therein). Substrata in these habitats are generally unsuitable for the establishment of most macroalgal species. Surface temperature varies between 20°C in summer and 10°C in winter (Dellatorre et al., 2014), and tidal regimes are micro and mesotidal (between 1 and 4 m; Isla, 2006; Schnack et al., 2010).

Salinity is quite stable along the Argentine coast (Esteves et al., 2000). Nutrients show a strong tendency to decrease from south. Nitrate concentration shows maximum values of 10–14 μmolkg-1 along the year in the southern region (most of Santa Cruz and Tierra del Fuego Provinces, decreasing to values lower 4 μmolkg^{-1} for Chubut, Río Negro and Buenos Aires region (Arhex & Esteves, 2009; Paparazzo & Esteves, 2018; Piola, 2008). Phosphate concentration ranges between 1.2–1.5 μmol kg^{-1} in the southern region and 0.4–0.8 μmolkg^{-1} in the northern region of the Argentine coast (op. cit). The part of the Argentine coast belonging to the magellanic ecoregion is dominated by cliffs and exposed beaches with coarse sand and gravel. Abrasion platforms of friable sedimentary rocks are frequent along the Patagonian coast between 40.5–55°S (Schnack et al., 2010). Surface temperature ranges between 10–18°C in summer and between 4–10°C in winter, and tidal regimes are mostly macro-tidal (> 4 m tidal range) and megatidal (> 8 m tidal range, Isla 2006) such as temperature (Mendoza, 1999). However, other environmental factors such as nutrient availability, substrate hardness, and wave action, are also important to determine the settlement of benthic algae. Therefore, the reduction of seaweed diversity between 38–37°S could be explained by the discontinuity of suitable hard substrata and the extension of exposed sandy beaches (Dellatorre et al., 2014), together with the variation in nutrient availability. In addition, in the north of the Magellanic ecoregion, ecological interactions such as herbivory, also seem to be weak in comparison to the physical stresses (e.g., high winds, low humidity) that largely determine structure in these systems (Bazterrica, Silliman, Hidalgo, Crain, & Bertness, 2007; Hidalgo, Silliman, Bazterrica, & Bertness, 2007). The impoverished algal assemblages inhabiting the northern coast of Argentina are mainly related to the reduction or disappearance of the Antarctic/Sub-

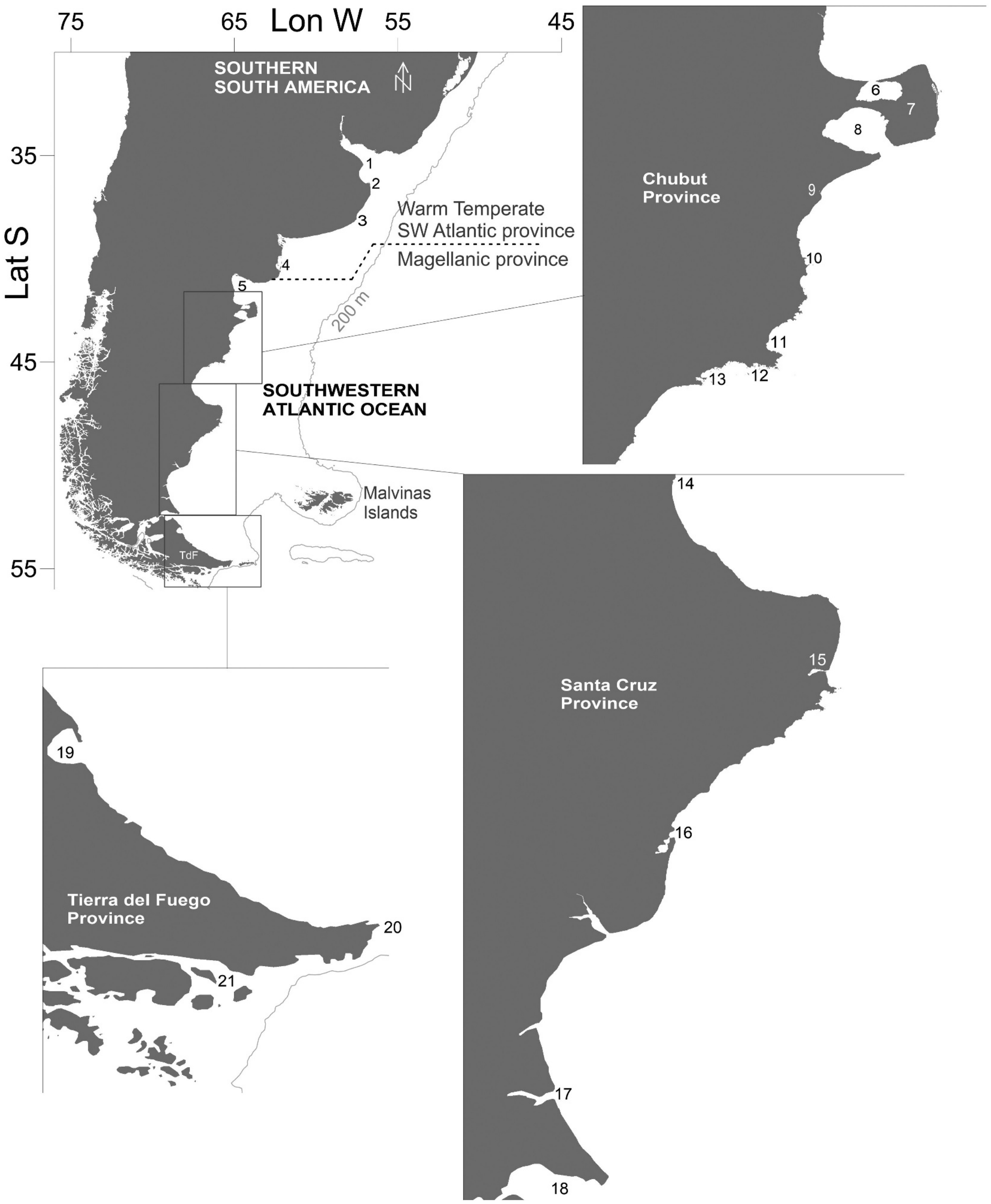

Figure 1. Study area. Minor arrows indicate political limits between provinces. Numbers indicate different coastal features named in the text. 1: Río de la Plata; 2: San Matías gulf; 3: San José gulf; 4: Nuevo gulf; 5: mouth of the Chubut river; 6: Bahía Bustamante; 7: mouth of the Deseado river; 8: San Julián bay; 9: mouth of the Gallegos river; 10: Magallanes strait; TdF: Tierra del Fuego Province. Dashed lines indicate the boundary between Ecoregions.

Antarctic assemblages, suggesting that variations in environmental factors are important drivers of algal diversity patterns.

Thus, most of the species of commercial interest included in this review inhabit coastal environments of Patagonia (Boraso de Zaixso et al., 1998; Boraso, 2013, 2015). In the following subsection, we present a detailed description of those species that were traditionally exploited in Argentina, as well as those that represent a potential resource, since they are reported in FAO statistics as taxa harvested or farmed in other countries. Of the total of 17 seaweed taxa here included (ten red, four brown, three green), only nine taxa (four red, three brown and two green) were or are harvested in Argentina.

Red algae (Phylum Rhodophyta)

Order Gracilariales

***Gracilaria gracilis* (Stackhouse) Steentoft, L.M. Irvine & Farnham.** Early studies in Argentina referred to this species as *Gracilaria verrucosa* Hudson (Papenfuss) (= *Gracilariopsis longissima* (S.G.Gmelin) Steentoft, Irvine and Farnham). In 1990 Rice and Bird analysed samples from Puerto Madryn (Chubut, Patagonia) and found a group with similar banding DNA patterns composed of strains from Wales, Norway, France, Argentina and Japan. This group was assigned to *G. verrucosa*. In 1995, Steentoff et al. studied the morphology and anatomy of different populations of gracilarioid species for the British Isles and compared them with samples from European populations. As a result, they described two new species, i.e., *Gracilaria gracilis* comb. nov. and *Gracilariopsis longissima* comb. nov. (*Gracilariopsis verrucosa* nom. rej. prop.). Those superficially similar species were long confused under the name *Gracilaria verrucosa* (Hudson) Papenfuss (= *G. confervoides* (Stackhouse) Greville). Further studies including samples of *G. gracilis* from Patagonia (Argentina) supported this relationship between European and Argentinean populations through a multi-locus barcode analysis, including independent markers (i.e., plastid, mitochondria, and nuclear) exploring the limits in the *G. gracilis* species complex (Destombe, Valero, & Guillemin, 2010). Thus, publications after this cumulative research refer to the valid name of this species, viz., *Gracilaria gracilis*.

Regarding the status of this *G. gracilis* as native, cryptogenic or introduced, Rice & Bird (1990) observed that the trans-oceanic disjunct distribution of *G. gracilis* could be explained as the Japanese and Argentinean populations might represent introductions from Europe via shipping. Whilst there is evidence from the comparative genome study confirming con-specificity with European *G. gracilis* (Levy, Beer, & Friedlander, 1990), further studies are needed to clarify the alga's status as a probable, introduced species in Argentina.

Gracilaria gracilis (Figure 4e) is one of the most important seaweed resources of Argentina in terms of its historical exploitation for agar production (Piriz & Casas, 1996). Notwithstanding its great economic importance, its distribution in Argentina is relatively narrow. This species is distributed along the coast of Chubut Province, from Golfo Nuevo (42° 46' S, 65° 02' W) to the North of San Jorge Gulf (45° 12' S, 66° 30' W, Figure 1). *Gracilaria gracilis* beds were historically harvested in wave protected bays in southern Chubut. While populations from the north of the Province (Golfo Nuevo, Figure 1) are not suitable for harvesting due to their low biomass (Casas & Piriz, 1998). Largest populations from the south were found at Bustamante Bay, Arredondo Bay and Caleta Malaspina (Boraso de Zaixso et al., 1998). First studies on distribution, biology and phenology of *G. gracilis* started in 1970–80 (Boraso de Zaixo, 1983, 1989, 1984, 1987; Halperín et al., 1973) responding to the need for information for the management of this economic resource.

Length of the thallus ranges between 15–80 cm and grows attached to hard substrata such as gravel and shells from intertidal tide pools to subtidal from 2–9 m depth. It can also be found buried in soft sandy bottoms. Different morphological types have been described by Boraso de Zaixso & Paternoster (1985) and Boraso de Zaixso (1995a, b), showing a variety of branching patterns. There is a relationship between seasonality and branching pattern (Boraso de Zaixso, 1987). The number of branches is positively correlated with a higher biomass and an increase of environmental parameters such as temperature, salinity and phosphate concentrations. There is also a negative correlation between branch proliferation and spore recruitment (Boraso de Zaixso & Zaixso, 1997).

Studies conducted on natural populations of southern Chubut Province showed that *G. gracilis* sexual reproduction and vegetative propagation occur simultaneously during spring and summer (October to April; Boraso de Zaixso, 1995a). In Golfo Nuevo, reproductive thalli can reach up to 50% of the population and vary seasonally, with tetrasporophytes predominating in spring and gametophytes in autumn and winter, while in Bahía Arredondo, both phases predominate in summer. In Bahía Bustamante, mature thalli represents only the 30% of the population during spring (Boraso de Zaixso, 1995a; Boraso de Zaixso et al., 2015; Boraso de Zaixso & Zaixso, 1997). The standing crop in Arredondo Bay was estimated in 1979–1980, as ranging from 2–4 kg m^{-2} wet biomass (Boraso de Zaixso, 1995a), while in Bahía Melo, a lower standing crop was estimated, in 1986–1987 varying from 0.7–2.2 kg m^{-2}. This represents a total production of around 5000 tons wet biomass for a bay of approximately 350 ha (Romanello, Arnoldi, García, Taylor, & Medina, 1993). Since 1984 *G. gracilis* biomass available to be harvested from the shore line in Bustamante Bay decreased by 50%, in 1988 a new fishing area (Caleta Malaspina) was allowed, introducing direct harvesting with boats and fishing nets (G. Soriano pers. comm.). Since 1995, the beach-cast quantities of *G. gracilis* from these localities showed an even more drastic decline to virtually zero near 2000, and consequently the agar industry was also affected.

Different hypotheses were tested to evaluate the causes of the decrease of the *Gracilaria*'s populations and beach-cast biomass, but the origin of these dramatic declines could not be established (Piriz, 1996). After these events, the concessionaires who harvested the seaweed biomass from beach-cast began to import other species to replace *Gracilaria gracilis* (Hayashi, Bulboa, Kradolfer, Soriano, & Robledo, 2014). In order to evaluate the repopulation potential of the wild beds, some cultivation projects were carried out by Casas and Piriz (1998), but only on a pilot-scale. Later, complementary studies were performed in order to evaluate the biomass variation, reproductive phenology, carpospore release and epiphytism (Hughes, Michetti, & Leonardi, 2014; Martín, de Zaixso, & Leonardi, 2011; Michetti, Martín, & Leonardi, 2013). One of these studies showed a seasonal variation of the biomass of *G. gracilis* from Bahía Bustamante population (between March 2006 and February 2008) with a minimum in winter and a maximum in late spring and summer, and a coexistence of the three life-cycle phases, with dominance of tetrasporophytes (Martín et al., 2011). These results were similar to those previously found in Bahía Arredondo 15 years before (Boraso de Zaixso, 1995). Moreover, sporulation showed a total carpospore release of about 2000 carpospores cystocarp^{-1} day^{-1} during the first week of sporulation (Michetti et al., 2013). These findings suggested that reproductive capacity via sexual reproduction is still viable in these populations. Regarding *G. gracilis* populations from northern Chubut (Golfo Nuevo), no recent studies were found reporting population or ecological features and their changes in recent years.

Order Gigartinales

Within this Order, seven species belonging to six genera will be described: *Sarcopeltis skottsbergii, Asterofilopsis furcellata, Gymnogongrus torulosus, Callophyllis variegata, Iridaea cordata, Sarcothalia crispata* and *Sarcothalia dichotoma*. The last two species have been reported in early studies of the Argentine marine flora as belonging to the genus *Iridaea* (Pujals, 1963, Khüneman 1970, 1972). In previous work (particularly those referred to chemical properties (see section 5), the species *Iridaea undulosa* is mentioned in North and Central Patagonia. Although this name is currently accepted taxonomically (Guiry & Guiry, 2021), this species is not found in Argentina (excluding Antarctica and the Malvinas/Falkland Islands), and probably has been a misidentification of *Sarcothalia crispata* (Piriz, 1996; Scrosati, 1991b). Throughout the description of each species, synonyms and current status of each species will be mentioned. However, a thorough taxonomic review including both morphological and molecular studies of the species reported in Argentina within this Order is required to clarify the presence and distribution of each species with accuracy.

Sarcopeltis skottsbergii (Setchell and N.L.Gardner) Hommersand, Hughey, Leister & P.W.Gabrielson 2020

This species was described in the literature until 2020 as *Gigartina skottsbergii*. Some authors suggested it differed both in its morphological and phylogenetic characteristics from other *Gigartina* species, and therefore, should be considered as a new monotypic genus (Hommersand, Guiry, Fredericq, & Leister, 1993: p. 1999). Thus, it was recently assigned to the new genus *Sarcopeltis* by Hughey, Leister, Gabrielson, & Hommersand (2020).

Sarcopeltis skottsbergii (Figure 4h) is an endemic species from southern South America and Antarctica. Its distribution in Argentina is wide but discontinuous along the Patagonian coast from Punta Lobería (44° 16 ′S) to Tierra del Fuego Province (Figure 1, Piriz, 1996a). Subtidal beds are located from 3–12 m depth approximately, on rocky bottoms of wave exposed or moderately exposed areas (Piriz, 1996a; Boraso de Zaixso et al., 2015). These beds are composed of thalli with large fleshy fronds which can exceed half a metre in diameter (Boraso de Zaixso, 2013).

Most studies of *S. skottsbergii* (formerly *G. skottsbergii*) were focused on population features and their phenological variations. In recent years, studies also included their potential for sporulation and growth for aquaculture purposes (Hughes, 2018). Natural beds from Pta. Thompson (Chubut Province, North Patagonia, Figure 1) showed a clear contrast in their biological characteristics between spring and autumn. Density and biomass of cystocarpic thalli were higher in autumn, while vegetative thalli (probably including non-fertilized female thalli) predominated throughout the year showing the highest biomass in spring (Piriz, 1996). Tetrasporic plants were present in very low numbers and did not show a seasonal pattern. There was also a difference between the gametophytes and sporophytes, the latter being almost four times smaller (average wet weight per plant; cystocarpic: 113.3g and tetrasporophytic: 29.4g; Piriz, 1996). In contrast, *S. skottsbergii* population from the SE Pacific

(Chile) reported maximum values for biomass and growth rates in spring–summer and maximum growth of gametophytes and tetrasporophytes in warm seasons (Westermeier, Aguilar, Sigel, Quintanilla, & Morales, 1999).

There are no ecological studies on *S. skottsbergii* in Argentina but it was often recorded as part of the understory of *Macrocystis pyrifera* kelp forests (Barrales & Lobban, 1975; Mendoza, Boraso de Zaixso, Zaixso, Nizovoy, & Ramos, 2005). The average wet biomass *S. skottsbergii* in the Beagle Channel was around 2.19 kg m^{-2}, representing one of the main species that inhabits under the *M. pyrifera* canopy in terms of biomass (Boraso de Zaixso et al., 2015; Mendoza et al., 2005). This density is more than four times higher than the record for Punta Thompson, where the wet biomass did not exceed 500 g m^{-2} (Piriz, 1996). According to Boraso et al. (2015), this could be due to differences in the sampling area, since in Beagle Channel sampling was limited to depths with optimal conditions for this species, while in Punta Thompson were taken throughout its bathymetric distribution.

Recent studies analysed the seasonal availability of *S. skottsbergii* spores from Cabo Raso (Chubut Province) obtaining considerable amounts of carpospores (100, 000–200, 000 spores cm^{-2}) and tetraspores (600, 000–700, 000 spores cm^{-2}) only in the winter and spring months (Hughes, 2018). The density of cystocarps on female gametophytes was highest during summer and autumn (9 cm^2 and 7 cm^2 respectively), decreasing towards winter and being minimal in spring. In contrast, the size of cystocarps was higher during winter and spring. Thus, as spore release begins in early winter, the density of cystocarps on the female gametophyte would decrease (Hughes et al., 2018). Regarding the viability of *in vitro* sporoculture, the release of carpospores was slower and longer than the tetraspores. While 90% of the total carpospores were obtained between the fourth and sixth day of release, the tetraspores already reached this percentage on the second day (Hughes, 2018; Hughes, Michetti, & Leonardi, 2020). In addition, since spore release of both phases occurred at the same time of the year in natural populations, it would take at least two years to complete the life cycle of this species. This is particularly important for its applications in aquaculture, since it is necessary to maintain both phases to obtain the two types of carrageenan with different industrial uses (see section 5).

Sarcothalia crispata (Bory) Leister 1993

This species was previously reported in Argentina as *Iridaea crispata* (Scrosati, 1991). *I. crispata* was reassigned to the genus *Sarcothalia* according to Hommersand et al. (1993). Some ecological (Kühnemann, 1970, 1972) and chemical studies (see section 5) cite the presence of *Iridaea undulosa* in Argentina, but it was probably confused with *S. crispata* (Scrosati 1991). In addition, Scrosati (1991) pointed out that there is not available herbarium material from the ecological research that listed *I. undulosa* to verify the taxonomic identification of the species.

Sarcothalia crispata (Figure 4g) is the most abundant and widely distributed species of this genus in Argentina (Boraso de Zaixso, 2013). It was commercially exploited along the Patagonian coast together with *S. skottsbergii* for the production of carrageenan and carrageenophyte seaweed flour (Hayashi et al., 2014). However, statistics only report the harvesting of *S. skottsbergii* (see section 3), probably because this last species is of greater abundance and more frequent than *S. crispata* (Piriz & Casas, 1996). People dedicated to manually harvesting seaweed can easily differentiate *Sarcopeltis* from *Sarcothalia* and observed that their biomass from beach cast is scarce as compared to *S. skottsbergii* (Piriz & Casas, 1996). In addition, because both species were processed together, their biomass was probably stored mixed and classified as the most abundant one (i.e., *S. skottsbergii*).

Gametophytes and sporophytes thalli of *S. crispata* grow together reaching up to 40–50 cm long and 30–40 cm wide, although they are smaller at the northern limit of their distribution (Boraso de Zaixso et al., 2015), near Camarones Bay (Chubut Province). Moreover, the density of *S. crispata* in this area is too low to be considered as a suitable wild bed harvesting (Piriz & Casas, 1996). Larger plants were found in Santa Cruz Province inhabiting from intertidal to shallow subtidal rocky bottoms, and occasionally sharing the substratum with *Sarcothalia dichotoma* and *Sarcopeltis skottsbergii*, these two species with lower densities than *S. crispata* (Boraso de Zaixso et al., 2015; Piriz & Casas, 1996). Larger plants were found at the southern distribution in San Sebastián Bay (Tierra del Fuego), reaching up to 80 cm in length (Boraso de Zaixso et al., 1998).

A recent study evaluated methods for spore release (i.e., desiccation, osmotic shock, low temperature, and spontaneous discharge) and germling development of

S. crispata in different substrates (e.g., glass, ropes, shells and gravel). No differences were found amongst the induction methods, and shells and gravel seem to be better substrates than rope and glass (Hughes, Michetti, & Leonardi, 2019). Therefore, spontaneous sporulation (both for carpospores and tetraspores) seems to be enough to initiate cultures of *S. crispata*, using shells and gravel as suitable natural substrata for the settlement and growth of both types of spores in laboratory conditions (Hughes et al., 2019).

Sarcothalia dichotoma (J.D.Hooker & Harvey) Leister 1993

This species was previously reported in Argentina as *Iridaea dichotoma* (Boraso de Zaixso, 2013). Then it was reassigned to the genus *Sarcothalia* according to Hommersand et al. (1993). *S. dichotoma* is distributed along the Patagonian coast from the south of Chubut Province to Tierra del Fuego (Figure 1, Stortz, Bacon, Cherniak, & Cerezo, 1994; Boraso, 2013). This species can be found in tide pools from lower intertidal levels and more frequently in the subtidal with *G. skottsbergii* (Stortz et al., 1994). The thallus of *S. dichotoma* is laminar and typically V-shaped. In contrast to *S. crispata*, this species has no denticulation on the edges of the thalli (Giulietti & Boraso de Zaixso, 2006; Boraso de Zaixso 2013). Despite the potential economic importance of this species as a carragentophyte, we did not find any population or ecological studies in the literature.

Callophyllis variegata (Bory) Kützing 1843

There are currently two species belonging to the genus *Callophyllis* reported for Argentina (excluding Antarctica and the Malvinas/Falkland Islands): *C. atrosanguinea* and *C. variegata* (Boraso de Zaixso, 2013), both are currently accepted names (Guiry & Guiry, 2021). Despite there being no records of its harvesting in Argentina, we considered *C. variegata* as part of the Argentinean algal resources due to its commercial exploitation in Chile (FAO, 2021).

Callophyllis variegata (Figure 4f) is a subtidal species distributed along the Patagonian coast, from Chubut to Tierra del Fuego Province (Figure 1). It is a subtidal species, frequently found as part of the *Macrocystis pyrifera* kelp forest understory community (Boraso & Zaixso, 2008; Callebaut Cardu & Borzone, 1979; Mendoza et al., 2005; Raffo, Eyras, & Iribarne, 2009). We could not find any population or ecological studies on *C. variegata*, except for the Beagle Channel (Tierra del Fuego) where an average wet biomass of around 50 gm^2 was recorded (Boraso de Zaixso et al., 2015; Mendoza et al., 2005).

Although there are no records of its harvesting in Argentina, in Chile this edible species is exploited for commercial purposes and exported semi-processed to Japan (Ávila, Piel, & Alcapan, 2014). It is used in salads and soups in Asian countries and also consumed in Chile known as its common name "*carola*" (Astorga-España & Mansilla, 2014). In this country there are some studies on its population, ecological and cultivation aspects (i.e. Ávila et al., 2014; Hernández-González et al., 2010; Mansilla, Ávila, & Yokoya, 2012).

Iridaea cordata (Turner) Bory de Saint-Vincent 1826

This is the type species of the genus *Iridaea* (Guiry & Guiry, 2021). Although the location cited by Turner is in North America, there is evidence that the specimen was probably collected from Isla de los Estados (Tierra del Fuego, Argentina) (Guiry & Guiry, 2021; Hughey, Silva, & Hommersand, 2001). *Iridaea cordata* was previously reported in Argentina as *I. micans* Bory de Saint-Vincent 1825 (Papenfuss, 1964; Pujals, 1963). This last species is currently regarded as a synonym of *I. cordata* (Guiry & Guiry, 2021; Hughey et al., 2001).

I. cordata is a carragenophyte (see section 5) that can reach up to 35 cm in length, with a narrow latitudinal distribution along the Argentinean coast, inhabiting intertidal and subtidal rocky shores in Tierra del Fuego (Boraso de Zaixso, 2013). This species also has the potential application as a biofilter to remove contaminants as crystal violet and methylene blue dyes that are introduced into the environment mainly as waste from textile industries (Escudero, Smichowski, & Dotto, 2017). Despite these potential uses, there are no records in Argentina of its commercial exploitation or culture experiences. Most of the studies on this species were carried out on Antarctic populations (i.e., Quartino, Kloeser, Wiencke, & Schloss, 2001; Quartino et al. 2008a, b). A basic knowledge on biological, genetic and ecological information is required in order to evaluate its potential for being commercially harvested or indeed farmed.

Asterfilopsis furcellata (C.Agardh) M.S.Calderon & S.M.Boo 2016

This species was previously reported in Argentina as *Gymnogongrus furcellatus* (Pujals, 1963) and was synonymized as *Ahnfeltiopsis furcellata* (C.Agardh) P.C.Silva and DeCew 1992 (Boraso de Zaixso, 2008, 2013).Calderon & Boo (2016) transferred this species to a new genus *Asterofilopsis* based on morphological and molecular analyses. According to this study the currently accepted taxonomically name is *Asterfilopsis furcellata* (C.Agardh) M.S.Calderon and S.M.Boo (Calderon et al., 2016).

A. furcellata was reported in Argentina as part of intertidal and shallow subtidal rocky shores communities from Tierra del Fuego, and probably extends its distribution reaching the northern Patagonian coast, up to Nuevo gulf (Raffo pers. obs.). Gametophytes could attain 5–12 cm length (Boraso & Zaixso, 2008). As this species was previously reported in Argentina belonging to the genus *Gymnogongrus*, and later to the genus *Ahnfeltiopsis*, part of the literature on these genera probably also includes *Asterfilopsis furcellata*. However, information about both genera in Argentina is scarce. There is a population study carried out between 1985–1987 on *Gymnogongrus* sp., which probably corresponds to the current species *A. furcellata* (Krehibom, Romanello, & Espindola, 1995). This study reported a population from northern Chubut inhabiting rocky bottoms of the middle to lower intertidal attached to gravel in the shallow subtidal. Thalli can reach up to 25 cm in length with the highest density in winter, reaching up to 106 ind m^{-2}. Wet biomass values increased in summer and were higher in autumn, varying between 0.88–1.15 g ind^{-1}. Carpospore culture from an apomictic population were also carried out obtaining basal discs with fronds from 1–2 mm, 10 days after germination (Krehibom et al., 1995; Romanello, Kreibohm, & Escobar, 1983). Despite its value as a carrageenophyte, there are no records of the harvest of this species in Argentina. However, it was included in this work since there are records of its harvesting in Chile, where it is still reported as *Gymnogongrus furcellatus* (FAO, 2021).

Gymnogongrus torulosus (J.D. Hooker and Harvey) F. Schmitz 1897

This name is currently accepted taxonomically (Guiry & Guiry, 2021). In Argentina this species is only reported for Buenos Aires Province. Cystocarpic thalli are up to 8 cm long. Estevez & Cáceres (2003) analysed several characteristics such as cellular structure of the thallus, pit plug and cell wall ultrastructure, as well as morphology of some organelles of this species from populations sampled at Mar del Plata (Buenos Aires, Figure 1). These populations showed inner carposporphytes and no tetrasporophytes were found (Estevez, 2003).

Due to the potential commercial interest in *Gymnogongrus torulosus* (J.D.Hooker and Harvey) F. Schmitz 1897 as an iota- and kappa/iota-carrageenan producer (see section 5), future studies on the abundance, phenology, ecology and genetic diversity of its natural populations, as well as its potential for cultivation should be carried out.

Order Gelidiales

Genus Gelidium

This genus has been reported in Argentina as *Gelidium* sp. (Pujals, 1977). Here we included the only species we found in the literature from Argentina as currently accepted taxonomically, i.e., *G. crinale*. Furthermore, Croce & Parodi (2012) reported the presence of *G. magssiae* in Anegada Bay (Buenos Aires Province, Figure 1). In a later study, these authors analysed new specimens from the same population and revealed that the species was misidentified and corresponded to *G. crinale* (Croce & Parodi, 2013). Although there are no reports of the exploitation of this genus in Argentina, it was included here since FAO (2021) reported *Gelidium* spp. as harvested both from wild populations and produced by aquaculture due to the commercial importance of its phycocolloids.

Gelidium crinale (Hare ex Turner) Gaillon 1828

Gelidium crinale was reported along the Argentinean coast from Buenos Aires to Tierra del Fuego (Croce & Parodi, 2013; Pujals, 1963; Sar, Pascual, & Parma, 1984). In Anegada Bay (40° 25′ S, Buenos Aires) intertidal populations of *G. crinale* forms dense assemblages or "turfs" frequently attached to the shells of the mussel *Brachidontes rodriguezii* and the exotic oyster *Crassostrea gigas* (Croce & Parodi, 2013). Individuals are small, ranging from 1–3 cm (Croce & Parodi, 2013). This population showed a marked seasonality, present in spring and summer. In this last season thalli were more developed than in spring, with longer erect axis and more branching at the apices (Croce & Parodi, 2013). These authors also carried out *in vitro* cultures of apical sections to analyse relative growth rate. They found that explants rapidly duplicated their initial size, producing numerous proliferations and achieving structural complexity. The relative growth of explants, primary proliferations, and secondary proliferations were considerable and consistent, suggesting they should be observed at further for cultivation (Croce, Villar, & Parodi, 2015).

Order Bangiales

Pyropia columbina (Montagne) W.A.Nelson 2011.

This species was previously reported in Argentina as *Porphyra columbina* Montagne 1842. Then, it was transferred to the Genus *Pyropia* and the currently accepted name is *Pyropia columbina* (Sutherland et al., 2011). This species (Figure 4a–d) is a frequent species of the rocky intertidal communities of the Patagonian coast. Thalli are around 15 cm length and could reach up to

40 cm, varying from yellowish (Figure 4d to a) dark, reddish colour (Figure 4c). Thickness of the thallus ranges according to the environmental conditions (i.e., desiccation during low tide, wave exposure) and the reproductive stage (Boraso de Zaixso, 2013).

Among the *Porphyra/Pyropia* species reported for Argentina, *P. columbina* is the most studied both for its economic importance and its wide distribution and abundance along the Patagonian coast, from Rio Negro to Tierra del Fuego (Figure 1). Largest populations inhabit the central coast of Chubut and Santa Cruz Province (Boraso de Zaixso et al., 2015). Populations from Punta Maqueda (Santa Cruz) were well studied by Boraso de Zaixso & Zaixso (1997) as part of a thorough study to assess the sustainability of commercial harvesting (Boraso de Zaixso & Zaixso, 1997). In this study, morphological and ontogenic features were evaluated. Punta Maqueda coast is a wide rocky intertidal, with moderate wave exposure and well-defined intertidal level. *P. columbina* inhabits the middle intertidal forming a dense belt together with mussel beds and barnacles; it is also found in the low intertidal level where fronds are wider and thicker (Boraso de Zaixso & Zaixso, 1997). Populations from Maqueda Point were reported to produce a dominance of young thalli in late summer and autumn, that were gradually replaced by mature thalli in winter and early spring, and finally by senescent fronds towards the summer. Regarding its yield, 80–100 kg dry biomass per 0.1 km of coastline was calculated in this locality. However, it must be considered that, since the recruitment and survival of thalli fluctuates inter-annually, their productivity may also vary (Boraso de Zaixso & Zaixso, 1997).

P. columbina is picked manually from rocks and mussel beds in the intertidal zone. It is one of the few species that is allowed to be harvested directly from natural beds, removing up to 70% of the cover in the concession areas per year, according to Chubut Province legislation (Chubut D-XVII-1981-N ° 759). However, this regulation is based on research carried out more than three decades ago. It should be considered a priority to carry out updated studies to provide a modern assessment on which to base a sustainable management plan for these populations. In the past, this species was air dried and finely milled to produce a coarse flour called "*Algarina*", which was commercialized by Soriano S.A. (Piriz, 1990, Piriz & Casas 1995). Despite this product being used by a limited number of consumers, some laboratory tests were carried out in order to assess this alga's potential for cultivation under different light and temperature conditions (Piriz & Casas 1995). Development of the conchocelis-phase and production of conchosporangia were obtained in high number after a month, under different treatments, but no conchospore release was observed. The authors finally concluded that, given the low commercial demands for the species which was supplied by the available wild biomass, the commercial cultivation of *P. columbina* was not viable under these conditions (Piriz & Casas 1995). However, given the current global climate change scenario, and considering that this species is harvested in a transition zone of Ecoregions, where climate change could affect resource availability, it is increasingly necessary to survey this species and its variations over time, for proper sustainable management.

Brown algae (Phylum Ochrophyta)

Order Laminariales

***Macrocystis pyrifera* (Linnaeus) C.Agardh 1820.** This species is currently accepted taxonomically. In addition, previous species belonging to this genus are now considered synonyms of *M. pyrifera* (Guiry & Guiry, 2021). Nevertheless, this species was only cited in Argentina as *Macrocystis pyrifera* in the literature, with no other synonyms reported. It is locally known as "*cachiyuyo*". *Macrocystis pyrifera* (Figure 5d) is distributed along the Patagonian coast increasing its abundance towards the south, from the northern limit of Chubut Province (Puerto Lobos, 42°00′S 65°04′W), where some isolated plants and annual kelp forests are found (Barrales, 1975; Eyras & Boraso de Zaixso, 1994; Raffo et al., 2009), to the southern limit at Tierra del Fuego Province, characterized by dense perennial forests (Friedlander et al., 2020). *Macrocystis pyrifera* populations settle mainly on rocky substrata, from the lower intertidal tide pools to around 15 m depth.

M. pyrifera kelp forests have been extensively studied in Argentina in the 1970s and 1980s, due to its commercial interest for the phycocolloid industry (alginic acid) and also because of its key role as an ecosystem engineer. These studies included ecological aspects (Kühnemann, 1963, 1970a, b, Kreibohm de Paternoster & Elías 1980; López Gappa, Romanello, & Hernandez, 1982; Adami & Gordillo, 1999); canopy cutting experiences for commercial harvesting (Boraso de Zaixso, Zaixso, & Taylor, 1982), and environmental and reproductive parameters (Eyras & Boraso de Zaixso, 1994; Hall & Molina, 1980) among others. These studies also were carried out at different scales, from local scale to evaluate population parameters of total length, number of stripes near the base, density and biomass estimated by destructive sampling "*in situ*" (Boraso de Zaixso & Elías, 1980), to remote sensing and aerial photographic surveys, to assess the total area covered by kelp forest (Hall, 1980; Pertini, Taylor, Boraso de

Zaixso, & Domínguez, 1980). The information carried out during that period is well summarized in Boraso de Zaixso et al. (1998).

Despite the significant economic and ecological importance of Argentinean *M. pyrifera* kelp forest, there are very few studies carried out on this species in recent decades. The aim of recent research is mainly focused on the study of this species as an ecosystem engineer (i.e., Adami & Gordillo, 1999; Martin & Bastida, 2008; Raffo et al., 2009; Vanella, Fernández, Romero, & Calvo, 2007). Population studies are also scarce and there is not enough information to be definitive regarding the evolution and current status of *M. pyrifera* kelp forests along the Patagonian coast and their responses/changes to global change. Despite this lack of information, the pre-existing historical data shows large seasonal and year-to-year variations of the *M. pyrifera* forests in northern Patagonia (Barrales & Lobban, 1975). This pattern is also consistent with a recent study conducted at the southernmost limit of distribution (i.e., Península Mitre and Isla de los Estados and Tierra del Fuego, Friedlander et al., 2020) showing a strong seasonal pattern and interannual variations in maximum canopy density at the regional scale (mean proportional kelp density ranged from 0 to 0.6 between 1998–2018), but no clear trend over the time-scale analysed. These studies analysed variation of *M. pyrifera* communities using a time-series of satellite images from 1998–2018 and showed no long-term trends in kelp canopy cover over the past 20 years. However, they also found approximate 4-year oscillations in canopy fraction, probably correlated with the NOAA Multivariate ENSO index and sea surface temperature (SST). Similar results were found by Torrusio (2009) where *M. pyrifera* distribution did not change greatly over time, using both satellite imagery and aerial photographs over the period of 1939–2007.

As we observed in *Pyropia columbina*, the biases for the commercial exploitation of *M. pyrifera* have been established more than four decades ago (Chubut D-XVII-1981-N °759). Based on these data, the law currently allows the cutting of *M. pyrifera* up to 1 m in depth from the surface with a rotary system. However, scientific information considered for the regulation of their harvest (on canopy cutting experiences, Boraso de Zaixso et al., 1982) is clearly outdated.

***Undaria pinnatifida* (Harvey) Suringar 1873.** This species is currently accepted taxonomically (Guiry & Guiry, 2021). It was first reported in Argentina in 1992 as an introduced species (Casas & Piriz, 1996).

The first reported specimens of *Undaria pinnatifida* were sporophytes (Figure 5c), found at the end of 1992, settled on piles of the merchant dock “Almirante Storni”, Puerto Madryn City (Golfo Nuevo, Chubut Province, Figure 1). Casas and Piriz (1996) proposed that this species may have been unintentionally introduced by shipping through ballast water. Since then, *U. pinnatifida* has spread along the coast at a rate of approximately 1–5 km yr-1 (Piriz & Casas, 2001). Currently, this species has expanded its distribution range more than 1200 km to the north (i.e., Mar del Plata, Buenos Aires; Meretta, Matula, & Casas, 2012) and approximately 700 km to the south (Puerto Deseado, Santa CruzMartin & Bastida, 2008). It could potentially spread to the coasts of Uruguay and Southern Brazil (Bunicontro, Marcomini, & Casas, 2019; Dellatorre et al., 2014). This species is usually associated with sheltered or semi-enclosed environments, attached to rocky bottoms, gravels or artificial structures and therefore, its distribution is scattered along the coast. *U. pinnatifida* has an annual life cycle, with microscopic gametophytes and a large macroscopic sporophyte. Macroscopic thalli start their recruitment in autumn and reach a maximum length and biomass in winter–early spring, with an average length of 88.5 cm (Casas, Piriz, & Parodi, 2008). At the end of the spring and beginning of summer, sporophytes start to senescence (Casas et al., 2008). *U. pinnatifida* sporophytes are composed of a blade, midrib, and when individuals are mature, the sporophyll looks like an undulated structure growing around the stipe, between the holdfast and the blade (Figure 5c; Casas & Piriz, 1996). Casas et al. (2008) analysed the relationship between the midrib width and the length of plants and also the variation of sporophyll diameter, which was found to be associated with environmental conditions, reaching around 18 cm in summer. Recent studies performed on morphological and anatomical aspects of *U. pinnatifida* from San Jorge Gulf (Alvarez & Boraso, 2020) found similar results as those described by Casas (2005) for *U. pinnatifida* f. *typical* and *U. pinnatifida* f. *distant* (Alvarez & Boraso, 2020).

Since its introduction, *U. pinnatifida* has dramatically changed the benthic community (Piriz & Casas, 2001). Among its multiple impacts on the invaded ecosystems is the reduction of local seaweed assemblages (Casas, Scrosati, & Piriz, 2004). A manipulative experiment involving *U. pinnatifida* removal showed that its presence was associated with a dramatic decrease in species richness and diversity of native seaweeds in Nuevo gulf (Casas et al., 2004). This experiment was repeated in 2008, 15 years after the beginning of the

U. pinnatifida invasion, and also showed a negative impact on native macroalgal assemblages (Raffo, Faleschini, Casas, & Schwindt, 2015). In both experiments, species richness and biomass decreased significantly in the presence of *U. pinnatifida*. The natural composition of species in the absence of *U. pinnatifida* varied in both periods (2001 and 2008). Eighteen species recorded in 2001 were no longer registered in 2008. Furthermore, the presence of *U. pinnatifida* generated an increase in total biomass by 550% in 2001 and 800% in 2008, compared to the treatment without *U. pinnatifida* (Raffo et al., 2015). These results suggested that the presence of *U. pinnatifida* over the time has an important effect on the reduction of the benthic macroalgal communities. In addition, the significant increase in biomass of *U. pinnatifida* could imply greater availability of food by modifying local trophic webs (Raffo, Irigoyen, Schwindt, & Casas, 2012). This large biomass input into the ecosystem can also affect seawater physicochemical properties and microbial communities through its exudates (Lozada et al., 2021). Another ecological effect of the presence of *U. pinnatifida* is the increase on the diversity and abundance of benthic macrofauna in Golfo Nuevo and the possible bottom-up effect on local food chains by increasing abundance of prey for a wide variety of predators, from invertebrates to marine mammals (Irigoyen, Trobbiani, Sgarlatta, & Raffo, 2011a). On the other side, the presence of detached *U. pinnatifida* off the coast results in transitory habitat loss for reef fishes inhabiting low-relief reefs during late spring and early summer (Irigoyen, Eyras, & Parma, 2011b).

Despite the multiple ecological and economic impacts of this species, there are still several aspects to be investigated. Considering that this invasive species currently represents one of the main seaweed resources of Argentina, there is still no information about the impact of its sustained harvest on the ecosystem or an assessment of its use as a resource in the local economy.

Lessonia flavicans Bory 1825. This species is currently accepted taxonomically (Guiry & Guiry, 2021). In Argentina it was previously reported as two different species: *Lessonia flavicans* and *Lessonia vadosa* Searles (1978). On the basis of anatomical and morphological studies carried out by Asensi & de Reviers (2009) the species *L. vadosa* becomes a taxonomic synonym of *L. flavicans*. Furthermore, these authors also proposed *L. flavicans* sensu Searles (1978) as the new species, and *L. searlesiana* as a holotype among Searles' original material (Asensi & de Riviers, 2009). Based on this research and considering that the most common species along the Argentinean coast is *L. flavicans* Bory 1825 (Boraso de Zaixso, 2013) we only describe this last species as an important algal resource.

Lessonia flavicans (Figure 5b, e) is a kelp species distributed along the Patagonian coast from 44o–54oS. This kelp species inhabits cold temperate waters, mainly in subtidal environments but could be also found in the lowest intertidal levels (Scrosati, 1991a). It is attached to rocky bottoms by a strong holdfast. Thalli from shallower habitats have shorter and stronger stipes than those growing deeper in subtidal environments. Its total length is around 60–80 cm but it is variable and, depending on the environment, could reach up to 4 m in total length (Boraso de Zaixso, 2013). Unilocular sporangia are present especially in summer over non-morphologically differentiated blades (Asensi, 1981; Asensi & Küpper, 2012). Despite *L. flavicans* being a very common species, and it is frequently mentioned as an important component of the understory of the *M. pyrifera* forest (Friedlander et al., 2020; Halperín et al., 1973; Kühnemann, 1969), there is little information on its biology or ecology. Due to its economic and ecological importance, this species should be studied in more detail in Argentina.

Order Fucales

Durvillaea antarctica (Chamisso) Hariot 1892

This species is currently accepted taxonomically (Guiry & Guiry, 2021). *Durvillaea antarctica* (Figure 5a) could also be found in the literature of Argentina as (Mendoza & Nizovoy, 2000). However, the latter is currently considered as a heterotypic synonym of *D. antarctica* (Guiry & Guiry, 2021) and therefore there is a single species belonging to the genus *Durvillaea* in this country. Recent studies analysed several non-buoyant and buoyant *Durvillaea* species (Fraser, Velásquez, Nelson, Macaya, & Hay, 2020). They described two new species and biogeographic analyses to determine the evolutionary history of buoyancy in the genus. In view of these new classifications, it is necessary to perform genetic analysis to assess the taxonomy of this species. *D. antarctica* is locally known both in Chilean and Argentinian Patagonia region as "*cochayuyo*" (Velásquez, Fraser, Nelson, Tala, & Macaya, 2020).

D. antartica has a narrow distribution in Argentina, reported only in the south of Tierra del Fuego inhabiting the low intertidal and shallow subtidal levels on wave-exposed areas like Bahía Thetis (54°38′41″S 65° 15′03″O). Thalli are perennial, reaching up to 10 m length (Mendoza & Nizovoy, 2000). The chemical composition of *D. antarctica* has been studied by Duville (1977) and by Duville, Duville, and Y Nadin (1976). However complementary information about the population biology, phenology, biomass or ecology of this species along the Argentine coast has not been found in the local literature.

This species was included in this review following the FAO statistics (2021). In Chile it is an important resource for food-gatherers and has multiple uses in the food industry (Ortiz et al., 2006). However, due to the narrow distribution of this species in the southwest Atlantic coast, together with its geographical location not being very accessible to urban settlements near the area, there are no current records documenting its use in Argentina.

Green algae (Phylum Chlorophyta)

Order: Ulotrichales

Monostroma hariotii Gain 1911

This species is currently accepted taxonomically (Guiry & Guiry, 2021). Its etymology indicates that it has a single layer, a distinctive characteristic of this genus. The species *Monostroma undulatum*, which currently belongs to the genus *Protomonostroma*, has been reported for Argentina (Boraso, 2013).

There is no precise information about the distribution of this species along the Argentine coast, but it has been cited in southern Patagonia at Tierra del Fuego Province (Mendoza & Nizovoy, 2000). Thalli ranging between 8–10 cm long and 4–10 cm wide. This species is relatively abundant and inhabits from the upper level to the lower limit of the low intertidal zone on rocky shores (Mendoza & Nizovoy, 2000).

Although no records of the exploitation of this species have been found in Argentina, it has been considered within the species of potential commercial interest, since according to the FAO (2021) reported that *M. nitidum* has been used, mainly through cultivation in Asia. This species is used in the food industry because of its great amount of bioactive-sulphated polysaccharides. The mucilage of *Monostroma nitidum* could also perform certain emulsifying and thickening properties (Chang & Wu, 2008).

Order: Ulvales

Genus *Ulva*. This genus includes two morphological types, i.e., blade (Figure 6a, b) and tubular (Figure 6d). This last morphological type was previously named as *Enteromorpha* and is currently considered synonymous with *Ulva* (Guiry & Guiry, 2021). There are eight species reported in Argentina as *Enteromorpha* and currently known as *Ulva*, i.e., *Ulva hookeriana* (Kützing) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope and Waaland 2003, *U. clathrata* (Roth) C. Agardh 1811, *U. compressa* Linnaeus 1753, *U. flexuosa* Wulfen 1803, *U. intestinalis* Linnaeus 1753, *Ulva linza* Linnaeus 1753, *Ulva prolifera* O.F.Müller and *Ulva torta* (Mertens) Trevisan. These species are well described by Boraso de Zaixso (2013). The other morphological group, corresponding to those species blade shaped (Figure 6a, b) are *Ulva lactuca* Linnaeus 1753 and *Ulva rigida* C. Agardh (Boraso, 1978; Boraso de Zaixso, 2013).

Commercial exploitation of members of this genus in Argentina has been at a very low scale and it is not specified in the statistics at species level (see section 3). Likewise, there are ecological studies that only identify the presence of the genus *Ulva*. Some species remain to be taxonomically studied to complement morphological studies together with genetic analysis, such as the widely distributed species *U. lactuca*. Based on this evidence, we only include in this review the genus *Ulva*, considered as a species complex along the Argentine coast.

Ulva is a widely distributed genus along the Argentinean coast, both the tubular and blade-shaped forms. The group of species previously known as *Enteromorpha* is distributed mainly in rocky intertidal environments. This genus is found characterizing the high intertidal levels of northern PatagoniaIn Gulfs (Chubut province) during the cold season (Raffo, Russo, & Schwindt, 2014). The laminar forms of *Ulva* spp. (i.e., *U. lactuca* and *U. rigida*) are abundant both in the subtidal and on the seaweed beach cast (Casas et al., 2004; Eyras & Sar, 2003; Piriz, Eyras, & Rostagno, 2003).

This genus has also been identified as an important biomonitor for eutrophication, given its ability to absorb nutrients and its facility to colonize environments impacted by human activities (Figure 6b ; Diaz, Gappa, & Piriz, 2002; Rico, Lanas, & López-Gappa, 2005). Eutrophication is frequently associated with hypoxia/anoxia events and a consequent decrease of marine diversity. In contrast, a study made in San Antonio Oeste Bay found that the high abundance of opportunistic *Ulva* species and other algae, increased the abundance of small infaunal and epifaunal invertebrates associated with high nutrient concentrations, as well as higher abundance and diversity of birds (Martinetto et al., 2010). The land-derived nitrogen was assimilated by macroalgae, as was evident by the high stable isotopic signature of *U. lactuca* fronds (Martinetto et al., 2010). A recent study concluded that recurrent blooms of *Ulva* spp. reported in the eutrophic channel in San Antonio Bay, was not associated hypoxia. Moreover, instead of being a driver of coastal acidification, *Ulva* blooms under certain conditions, seems to contribute to its prevention (Beccerruchi et al., 2021). Despite that *Ulva* spp. can be very abundant species along the Argentinean coast, molecular and morphological studies are still needed to clarify the taxonomy of some of the species, as well as studies on their potential for harvesting or aquaculture for commercial purposes.

Order: Brypsidales

Codium Stackhouse, 1797

This genus is currently accepted taxonomically (Guiry & Guiry, 2021). Four species belonging to this genus were reported for Argentina (Boraso & PIriz, 1975; Miravalles, 2009) but only *C. fragile* (Suringar) Hariot has been reported by FAO statistics (2021) as a species harvested in other countries. However, harvesting records of *Codium* in Argentina are not specified at any species level (see section 3). Considering that the harvested wild *Codium* beds are located in north Patagonia (Chubut and Santa Cruz Provinces), where *Codium subanctarticum* PC Silva is not present, biomass collected could be mostly a mix of *C. fragile* and *C. vermilara* (Olivi) Delle Chiaje, with smaller amounts of *C. decorticatum* (Woodward) M.Howe 1911. Following the criteria mentioned in section 1 we only included here *C. fragile* as a resource.

Codium fragile (Suringar) Hariot 1889

This species is distributed along the Argentinean coast from Buenos Aires to Tierra del Fuego (Boraso de Zaixso, 2013). Thalli are erect and dichotomously branched, fixed to the substratum by a basal disk (Figure 6c). The main morphological character to distinguish *C. fragile* from *C. vermilara*, together with the thallus length and utricles size, is the presence of mucrons (notably absent in *C. vermilara*). In specimens studied in Argentina, mucron size of *C. fragile* corresponded to the subspecies *novae-zelandiae* (Boraso & PIriz, 1975; Miravalles, 2009), but we will refer here only to the species level, naming it as *C. fragile*. Rico & Pérez (1993) found only female parthenogenetic reproduction in populations of *C. fragile* (as *C. fragile* subsp. *novae-zelandiae*) from Chubut. Miravalles (2009) found similar results, but also reported the fusion of male and female gametes, when male thalli are present. Parthenogenesis in *Codium fragile* subsp. *novae-zelandiae* would be the most common form of reproduction in this species. Another aspect to take into account about this species as a food resource, in addition to the complexity of its cultivation in the laboratory, is the high degree of epiphytism, with *Polysiphonia* spp., *Ceramium* spp., *Callithamnion montagnei* Hooker F., being the most common and the invasive *Anotrichium furcellatum* (J.Agardh) Baldock being reported (Miravalles, 2009).

In Patagonia *C. fragile* is frequently found together with *C. vermilara* forming dense belts between the lower intertidal and the shallow subtidal levels of rocky shores. In the last decade, this species association was probably displaced by the invasive species *Undaria pinnatifida* (Raffo pers. obs.). Piriz et al. (2003) also reported a shift in the abundance of the *Codium* spp. as part of the beach cast, indicating a succession in the dominance from *Codium* spp. to *Ulva* spp. during the 1990s and from *Ulva* spp. to *U. pinnatifida* particularly since 1998. Updated studies on the abundance and ecology of this species along with its genetic diversity must be carried out to consider its use as a species of sustained commercial interest.

A brief history of seaweed production in Argentina

The output of Argentine marine fisheries increased almost steadily until 1997, when the country produced more than a combined total of 1.3 million tons of marine fishing products (i.e., fishes, molluscs, crustaceans and macroalgae) (FAO, 2020). In the last decade these values stabilized at around 0.8 million tons. The Argentine coast has been a source of seaweed biomass for commercial purposes since 1950, according to historical harvesting records (FAO, 2021). Between 1960 and 1978, the biomass of a few seaweed species represented more than 4% of total landed fishing products, peaking more than 10% between 1965 and 1970 (FAO, 2021). From 1950 (first available data in FAO Fishstat database) until the present, there hasn't been a single ton of seaweed biomass farmed in Argentina (FAO, 2021). Only 3 tons of seaweeds obtained by aquaculture were cited by Rebours et al. (2014), but the species is not mentioned. Since there are no FAO or local fishery reports on seaweed aquaculture for Argentina, it was probably produced from pilot-scale experiences. Seaweed aquaculture was performed only in some laboratory studies (Ferrario & Sar, 1990; Hughes et al., 2018; Poza, Fernández, Gauna, & Parodi, 2018) and a few, scarcely documented, pilot-scale attempts mainly for *Gracilaria gracilis* production (Casas & Piriz, 1993, 1998; Hayashi et al., 2014, Matías & Gonzalo Soriano pers. comm.).

Chubut (Figure 1) is the only one, out of the five provinces that border the Argentine coast with their own official records of seaweed harvesting. Seaweed harvesting also occurred in the northern coast of Santa Cruz province, at least between 1985 and 1995. But harvested biomass (mainly *Lessonia* spp., *Macrocystis* *pyrifera* and *Sarcopeltis skottsbergii*) was transported and processed in Chubut (Boraso de Zaixso et al., 1998; Rebours et al., 2014, G. Soriano pers. comm.) and recorded as part of Chubut statistics. Low amounts of seaweed (mainly *Macrocystis pyrifera* and *Lessonia* spp.) have also been harvested in Tierra del Fuego Province (Figure 1) between 1985 and 1995 (Boraso de Zaixso et al., 1998). We did not find any statistics or evidence on commercial seaweed harvesting in the northern argentine Provinces (Río Negro and Buenos Aires).

Seaweed harvesting is regulated by local (provincial) governments. The most important provinces in terms of historical biomass production are Chubut and Santa Cruz. A regulatory framework of both Provinces is composed by the Law XVII N° 6 (formerly Law N° 939) and Regulatory Decree N° XVII–N ° 759/81 for Chubut, and the Law N° 3273 for Santa Cruz. In both cases, seaweed harvesting is allowed from beach-cast seaweed biomass. Only for some species, direct harvesting of attached specimens is allowed. In Chubut, this is the case for the intertidal

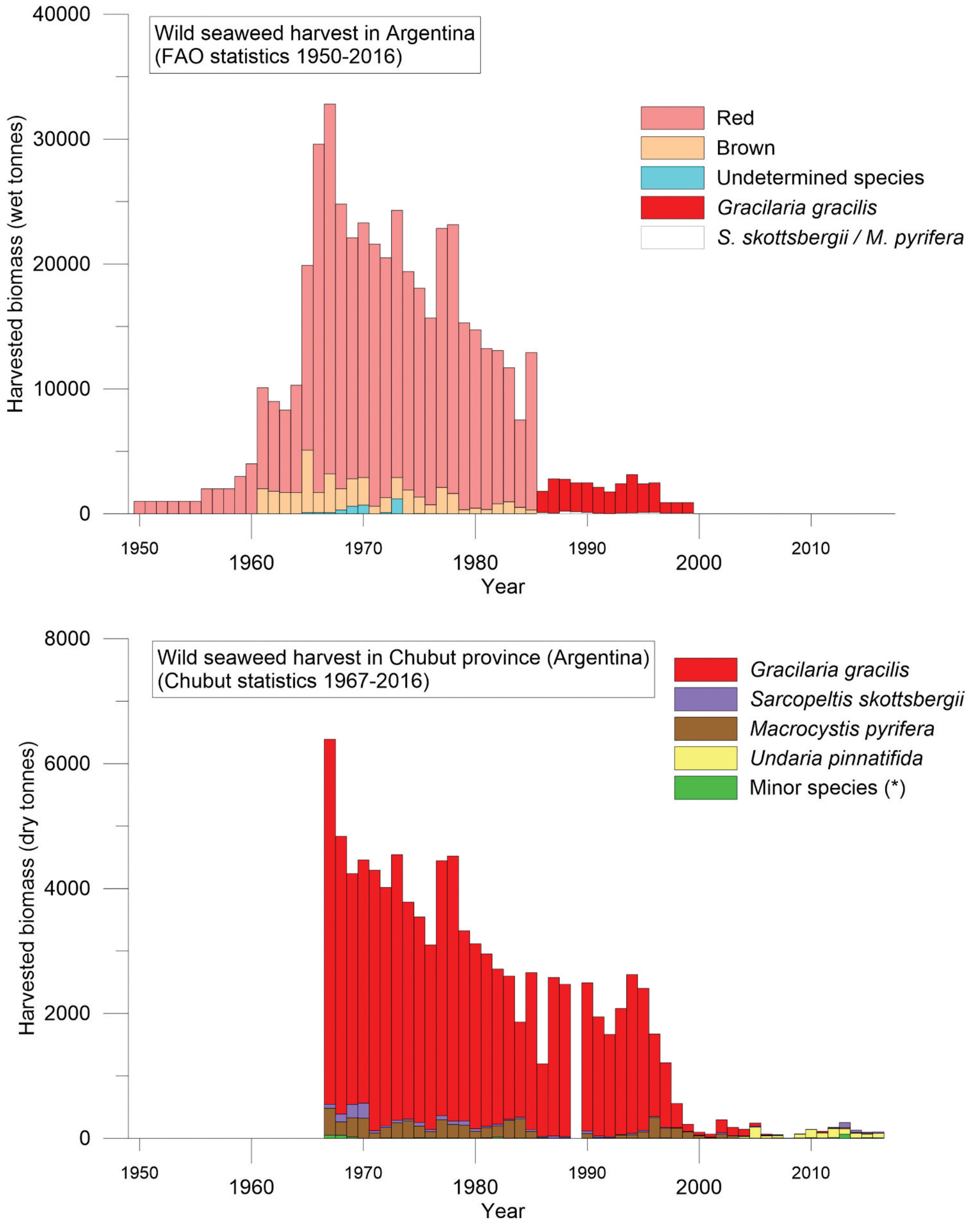

Figure 2. Seaweed production in Argentina for the period 1950–2016. Comparison of harvested seaweeds reported by FAO Statistics for Argentina, and by the Chubut Government (only for this province). Harvested biomass is expressed in wet tons by FAO and in dry tons by the Chubut Government. (*) The following minor species are included in this group: *Pyropia columbina, Corallina officinalis, Lessonia* spp., *Ulva* spp. (both laminar and tubular shapes) and *Codium* spp.

red seaweed *Pyropia columbina* (locally known as "Luche"), *Ulva* spp. (locally known as "Lechuga de mar") and of *Macrocystis pyrifera* (locally known as "Cachiyuyo"). Chubut law also limits the number of species allowed to be harvested to a fixed list including the genera *Macrocystis, Gracilaria, Gigartina, Ulva* and *Porphyra* (also *Pyropia columbina*). Chubut law is outdated (Law N° 1891, Promulgated in March 1981) and requires complementary regulations suitable to the actual global change scenarios, where natural resources can be strongly affected, as well as the appearance of new (introduced/invasive) species. This is the case of the invasive alga *Undaria pinnatifida* which represent both a threat to native species as well as a potentially important economic resource.

According to FAO statistics (2021), seaweed production in Argentina increased from 1000 to 2000 wet tons between 1950 and 1958. The main seaweed company (i.e., Soriano SA) in Patagonia began its operations in 1958 and three years later, the production increased to more than 10 000 wet tons (Figure 2). During the first years, seaweed production was entirely due to only one species, the red seaweed *Gracilaria gracilis*, used for agar production. In 1961, the production of 2000 wet tons of brown seaweed (mainly *Macrocystis pyrifera*) was reported for the first time. Overall production steadily increased up to 32 800 wet tons in 1967 (Figure 2). However after 1967 seaweed production in Argentina began to decline. Between 1965 and 1967, the harvest of green seaweeds and other aquatic plants was reported for the first time, but in low amounts compared to other red and brown seaweed species (Figure 2). Except *G. gracilis* and minor amounts of dry seaweed used in the local market for fertilizers and animal feed production and other uses (Halperín et al., 1973), most of the harvested biomass was exported as dried raw material.

Statistics of seaweed biomass production in Chubut Province are available from 1967 to 2016 expressed in dry weight and at the species/genera taxonomic level. Between 1967 and 1985, FAO reported the seaweed biomass production of Argentina expressed in wet weight units and at class taxonomic level, including *Gracilaria gracilis, Sarcopeltis skottsbergii* and *Porphyra* spp./*Pyropia columbina* in the Class Florideophyceae (Phylum Rhodophyta) and *Macrocystis pyrifera* and *Lessonia* spp. in the Class Phaeophyceae (Phylum Ochrophyta). The reported quantities in FAO statistics for red and brown seaweeds equalled approximately 5 and 7 times the sum of dry biomass production of red and brown seaweeds respectively reported in the Chubut statistics (Figure 2). This suggests that Argentine authorities converted the dry biomass recorded in Chubut´s statistics (assuming 80% and 86% of water content in the wet biomass of red and brown seaweeds respectively), to inform FAO the wet seaweed biomass production of the country.

Since 1986 FAO reports included lower taxonomic levels as order or species, which showed a drastic fall in the overall reported production, e.g., decreasing from approximately 10,000 tons to 2000 tons

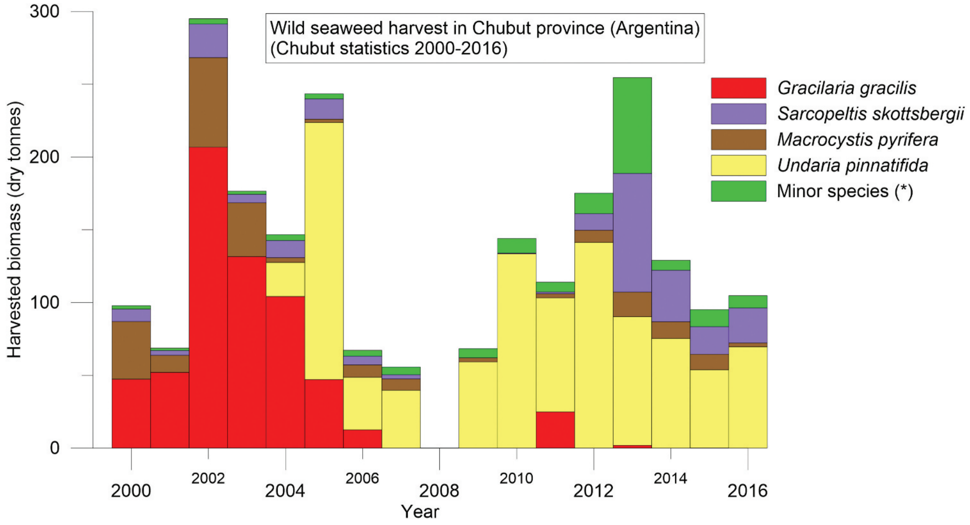

Figure 3. Detailed statistics of seaweed production in Chubut for the period 2000–2016. Seaweed biomass is expressed in dry tons. (*) The following minor species are included in this group: *Pyropia columbina, Corallina officinalis, Lessonia* spp., *Ulva* spp. (both laminar and tubular shapes) and *Codium* spp.

Figure 4. Red seaweeds (Phylum Rhodophyta). A: *Pyropia columbina* on rocky intertidal shore. B: *P. columbina*, detail of a thallus, C: *P. columbina* dark redish colour, D: *P. columbina* yellowish colour, E: *Gracilaria gracilis*, F: *Callophyllis variegata*, G: *Sarcothalia crispata* (Ph: M. Hughes), H: *Sarcopeltis skottsbergii* (M. Hughes).

(Figure 2). It seems that the conversion between dry and wet biomass was not further used. Consequently, the FAO statistics reflect a sharp decrease that was not observed in Chubut´s statistics (Figures 2 and 3). Between 1995 and 2000, the production decreased to virtually zero. Since 2000, FAO statistics reported no biomass production in Argentina, but the official statistics of the Chubut government have still reported a small level of production of around a few hundred tons of dry weight (Figure 3). One point that must be highlighted is the presence of the exotic algae *U. pinnatifida* in production statistics in the last 20 years. This species has been harvested since 2003 in Bahía Bustamante, and since 2012 in Nuevo gulf, both by diving in subtidal attached populations by cutting off the blade and sporophyll and also collected by hand from beach-cast material (G. Soriano pers. comm., Figures 1 and 2). Since 2005 this was the main harvested species in Argentina, and biomass is mainly destined for food use (blade and sporophyll) and exported for fucoidan production (sporophyll). A list of species, harvested in minor amounts, including *Sarcopeltis skottsbergii* (as *Gigartina skottsbergii*), *Gracilaria gracilis*, *Macrocystis pyrifera*, *Lessonia* spp., *Porphyra* spp./*Pyropia columbina*, *Ulva* spp. including both laminar and tubular shapes (previously known as *Enteromorpha*), *Corallina officinalis* and *Codium* spp. (only the genus is noted), were also reported (Figure 3).

In 2018 the main company dedicated to the commercialization of seaweed was closed (Soriano SA) and consequently, seaweed harvesting ceased for almost a year. At the end of 2019, with the creation of a cooperative dedicated to the seaweed harvesting (Coperativa de Recoleccion Acopio y Procesamiento de Productos del Mar- C.R.A.P.P.MAR ltda, M. Robert pers comm.), the activity resumed. In the last two years (2020–2021) the main harvested species were *U. pinnatifida* (sporophylls: 30 tons, blades: 1.5 tons), *P. columbina* (10 tons), *M. pyrifera* (3.2 tons), *S. skottsbergii* (3 tons) and *Ulva* spp. (90 kg), in dry biomass. Seaweed harvesting activities take place throughout the year, with different seasonalities according to the species availability, e.g.: *U. pinnatifida* (October-February), *M. pyrifera* (all year, maximum between January-March), *P. columbina* (all year, peaks in May and September), *S. skottsbergii* (April-November) and *Ulva*. spp. (September December; Robert & Raffo, 2021).

Figure 5. Brown seaweeds (Class Phaeophyceae) A: *Durvillaea Antarctica* (Ph: M. Brogger), B: *Lessonia flavicans* adult thallus, C: *Undaria pinnatifida*, D: *Macrocystis pyrifera* kelp forest, E: *L. flavicans* thalli (Ph: M. Hughes), F: *M. pyrifera* aerocyst and blade detail (Ph: B, C, D, F: G. Bravo).

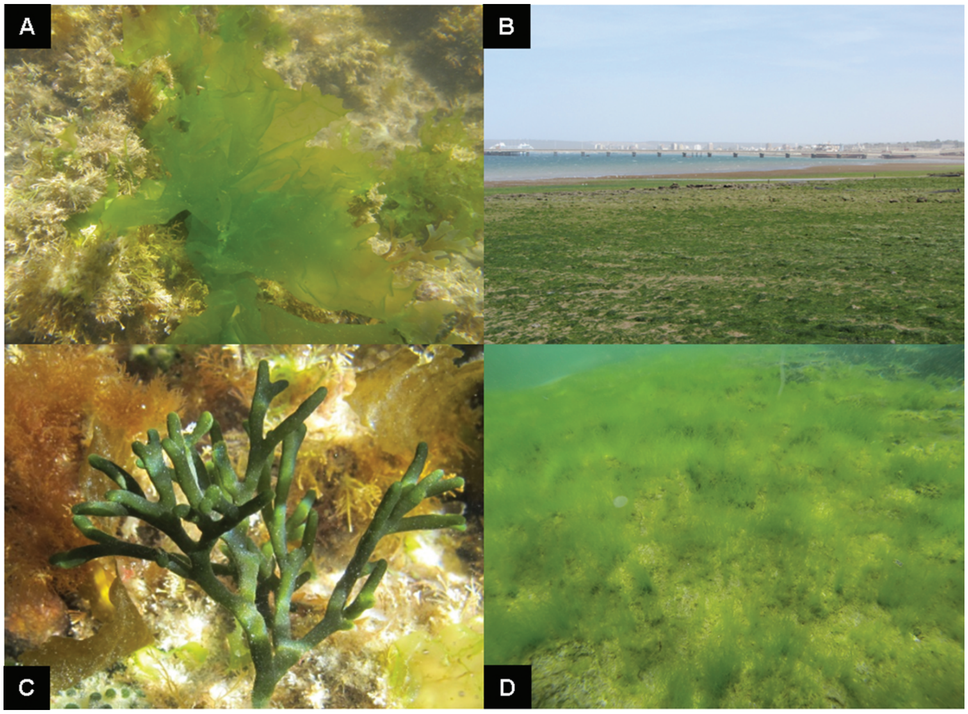

Figure 6. Green seaweeds (Phylum Chlorophyta). A: *Ulva* sp. (blade shape), B: Intertidal *Ulva* spp. (both tubular and blade shapes), C: *Codium* sp., D: *Ulva* sp. (tubular shape).

Local scientific research in the main fields of seaweeds application

Some lines of applied phycology and seaweed chemistry and derived compounds were developed in Argentina simultaneously with basic research (i.e., taxonomy and ecology of seaweed resources) that intended to promote the seaweed industry. Pioneering research in phycochemicals, their extraction and veterinary/agricultural applications were published before the mid-1970 (Halperín & Boraso, 1974). According to industry development, some of those pioneering chemical studies focused on phycocolloids (Halperín & Boraso, 1974). This specific line of research strengthened over time, generating an important number of publications and Argentinean research groups (Ferrario & Sar, 1990).

The potential applications of Argentine seaweeds were recently reviewed by Camurati, Hocsman & Salomone (2019). In this work, seaweed uses were divided into five categories of application, i.e., food and feed; pharmaceutical (including nutraceuticals and cosmeceutical); environmental (mainly bioremediation), energy production (biofuels), and agricultural. The synthesis of this information together with additional publications (not included in this review), showed some recent advances in research on food and feed applications of seaweed biomass. Biomass of different seaweed resources (mainly *Pyropia columbina* but also *Undaria pinnatifida, Macrocystis pyrifera* and other species of minor importance) were evaluated on their chemical composition and nutritional properties (Cian et al., 2014a; Cian, Drago, Sánchez de Medina, & Martinez, 2015; Cian, Garzón, Betancur, Guerrero, & Drago, 2016; Pérez Recalde, Carlucci, Noseda, & Matulewicz, 2012; Gil et al., 2014; Dellatorre, Avaro, Commendatore, Arce, & Díaz de Vivar, 2020), their content of toxic elements (Muse et al., 1989, Perez et al. 2007, 2011, Salomone et al. 2017, Gil et al. 2014, Salomone & Riera 2019, Camurati & Salomone 2019), as an ingredient in the development of different foods (Cian, Caballero, Sabbag, González, & Drago, 2014b, c; Varela et al., 2019) and as a feed supplement in aquaculture (Cian, Bacchetta, Rossi, Cazenave, & Drago, 2018). Also, many studies were published on bioactivity of seaweed compounds like the anticancer and antiviral effect of fucoidans (Cumashi et al., 2007, Trinchero et al. 2009; Croci et al., 2011), alginate cytotoxicity as natural matrix for tissue engineering (Torres, Fernandez, Dellatorre, Cortizo, & Oberti, 2019), antitumor effect of carrageenan-derived disaccharides (Calvo et al., 2019), and bioactivity of secondary metabolites: the antileishmanial activity of fucosterol from *Lessonia vadosa* (Becerra et al., 2015), and antioxidant and antibacterial activity of extracts from *Ulva* spp. (Uhrich, Córdoba, & Flores, 2016). It is remarkable that, to our knowledge, cosmetic applications of neither seaweed nor their extracts have been studied so far in Argentina. Bioremediation of polluted water using seaweed biomass has also been intensively studied during the last decade (i.e., Bertoni, Medeot, González, Sala, & Bellú, 2015; Camurati, Londonio, Smichowski, & Salomone, 2021; Carnevale, Blanes, Sala, & Bellú, 2017; Cazón, Viera, Sala, & Donati, 2014; Plaza Cazón, Benítez, Donati, & Viera, 2012; Plaza Cazón, Viera, & Donati, 2013; Trinelli, Areco, & Dos Santos Afonso, 2013). Although agriculture is one of the main industries in Argentina, the widely beneficial agricultural applications of seaweeds known globally, have been seemingly scarcely studied through the composting of beach cast biomass (Eyras, Defossé, & Dellatorre, 2008; Eyras, Rostagno, & Defossé, 1998). New local research groups have recently begun the search for *U. pinnatifida* agricultural applications of direct biomass as soil amendment (Salcedo et al., 2020), as a mulch component (Merino, Salcedo, Mansilla, Casalongué, & Alvarez, 2021), a rooting promoter (Bosco et al., 2021a, b), and *U. pinnatifida* and *M. pyrifera* biomass as source of extracts with biostimulant and biofertilizer properties (Julia, Oscar, Analía, Zocolo Guilherme, & Virginia, 2020). Bioenergy production from seaweed biomass is an important research field at a global scale (Garriga, Almaraz, & Marchiaro, 2017; Ibarlucía, Córdoba, & Santalla, 2019). Finally, seaweeds could provide a wide range of valuable compounds (for most of the previously described uses), and the use of biorefinery systems (Kostas, Adams, Ruiz, Durán-Jiménez, & Lye, 2021), or multi-stream zero-effluent (MUZE) processing technologies, could improve sustainability of seaweed processing industries and be a possible pathway to develop the value-chain of seaweed biomass (Neish & Suryanarayan, 2017). We detected recent advances in biorefinery approaches for *L. vadosa* and *M. pyrifera* biomass processing (Ramos, Casoni, Estrada, & Diaz, 2021) for sorbitol and energy production. Also, the same research group explored microalgae-based biorefinery systems for the production of biodiesel, astaxanthin and PHB from *Haematococcus pluvialis* biomass (Prieto et al., 2017).

The production of phycocolloids is still one of the main industrial applications of seaweed biomass (Buschmann et al., 2017). Notwithstanding this fact, and that Argentina, the chemistry and bioactivity of seaweed polysaccharides are clearly the main fields of research on applied phycology, they were not addressed by Camurati et al. (2019). The following section extensively revises these fields.

Chemical studies on hydrocolloids and sulphated polysaccharides with biological activity from commercial seaweeds of the Argentine coast.

The first studies on seaweed hydrocolloids were performed in Argentina by Dr. A. S. Cerezo during the 1960s, working on the structure of polysaccharides from red seaweeds of the Argentine coast (Cerezo, 1967a, 1967b, 1973, 1974). For many years, his group worked exclusively on the structures of sulphated polysaccharides from red seaweeds, and are still one of the major subjects of local research (Rodríguez Sánchez et al., 2019; Hughes et al., 2018; Cosenza, Navarro, Ponce, & Stortz, 2017; Perez Recalde et al., 2016). The studies were carried out considering that not only the major polysaccharides were important, but also all the polysaccharides structure had significant biological relevance. Later, new research lines were developed, as the study of fucoidans from brown seaweeds (Feldman, Reynaldi, Stortz, Cerezo, & Damonte, 1999), and sulphated polysaccharides from green seaweeds (Ciancia et al., 2007). Here we provide detailed information on the polysaccharides structure and their actual or potential applications.

Phylum Rhodophyta

Sarcopeltis skottsbergii (as *Gigartina skottsbergii*)

Carrageenans from *S. skottsbergii* were the first polysaccharides from seaweeds studied in Argentina (Cerezo, 1967a, 1967b, 1973, 1974) from cystocarpic and tetrasporic thalli sampled in Puerto Deseado (Figure 1). Structures of carrageenans from cystocarpic and tetrasporic *S. skottsbergii* from samples collected at Bahía Camarones (Chubut Province, Figure 1) were also studied (Matulewicz, Ciancia, Noseda, & Cerezo, 1989: p. 1991; Ciancia, Matulewicz, & Cerezo, 1993, Noseda, 1994). Carrageenans were fractionated with KCl solutions showing that lambda-carrageenans also precipitate with aqueous solutions of this salt, being the major fraction obtained in the range of 0.7–0.8 M (45% of the recovered). On the other hand, the cystocarpic thalli gave similar amounts of carrageenans precipitating at 0.30–0.31 M KCl (1C1) and soluble in 2.0 M (1C3). The soluble fraction in 2.0 M KCl obtained from gametophytes (i.e., mu/nu-carrageenans), after alkaline treatment, gave a modified carrageenan insoluble at low concentrations of KCl (i.e., kappa/iota-carrageenan), whilst the major fractions from tetrasporophytes remained soluble after the alkaline modification (Matulewicz et al., 1989). The methylation procedure was unsuccessful on lambda-carrageenans showed the expected results for partially cyclized carrageenans (Matulewicz, Ciancia, Noseda, & Cerezo, 1990). The structural study of carrageenan fractions from cystocarpic individuals allowed the assignment of all the 13C NMR signals corresponding to kappa- iota- mu-, and nu-carrageenans, as well as those of the anomeric protons of the B units (Ciancia, Matulewicz, Finch, & Cerezo, 1993a). All this information allowed to determine the contribution of each carrageenan of the kappa-family to the structure of the major products biosynthesized by cystocarpic *S. skottsbergii* (Table 1).

Table 1. Structure of the major carrageenan samples from cystocarpic *Sarcopeltis skottsbergii.*

Fraction	Diad	Contribution to the structure
1C1	kappa- (G4S-DA)	56
0.30-0.31 M KCl	iota- (G4S-DA2S)	20
Yield 42.6 % of the recovered	nu- (G4S-D2S,6S)	11
	mu- (G4S-D6S)	4
G:DA:S 1.0:0.6:1.3	others	9
1C3	kappa- (G4S-DA)	49
Soluble in 2M KCl	nu- (G4S-D2S,6S)	29
Yield 53.9 % of the recovered	mu- (G4S-D6S)	8
	others	15
G:DA:S 1.0:0.4:1.1		

Almost 30 years later, cystocarpic *S. skottsbergii* thalli collected in Cabo Raso (Chubut Province, Figure 1) and extracted under similar conditions, showed a molar ratio of kappa-/iota-/nu-, 70:12:18. This product was assayed as anionic component of interpolyelectrolytic complexes (IPECs) (Hughes et al., 2018).

The study of the fine structure of carrageenans from tetrasporophytes was not carried out due to technical issues. So, a different approach was assayed. The autohydrolysis reaction was applied to a lambda-carrageenan and its alkali modified derivative, theta-carrageenan (Noseda & Cerezo, 1993). However, the reaction products were complex mixtures of partially hydrolysed polysaccharides, and their structures were difficult to relate with the original one. This method was also used with kappa/iota- and mu/nu- carrageenans (Ciancia et al., 1993; Stortz & Cerezo, 1991). At the same time, Piriz & Cerezo (1991) found no evident tendencies in the seasonal variation in the carrageenan yields for cystocarpic, “sterile”, and tetrasporic *S. skottsbergii* with regards to their yields, being the lowest for tetrasporophytes. Later, Estevez, Ciancia, and Cerezo (2002) confirmed that the carrageenan type was not related to ploidy.

Alkaline treatment of fractions from cystocarpic *S. skottsbergii* (Table 1) gave major amounts of gelling carrageenans of the kappa-family, as indicated above, but also small fractions of this salt (Matulewicz et al., 1989). Enantiomeric analysis of monosaccharide constituents of the latter fraction showed important quantities of (3,6-anhydro-) L-galactose units, suggesting predominance of agaran structures, together with carrageenans of the iota- and lambda-types (Ciancia et al., 1993b). Analysis of the soluble fraction gave similar results (Ciancia, Matulewicz, & Cerezo, 1997a).

In view of the great importance of the alkaline cyclization reaction, not only from the industrial perspective, but also its use in structural studies, the kinetics of this reaction were studied with fractions from *S. skottsbergii* having different substitution patterns (Ciancia, Matulewicz, & Cerezo, 1997b; Ciancia, Noseda, Matulewicz, & Cerezo, 1993c; Noseda & Cerezo, 1995). Partially cyclized nu-carrageenans treated with alkali, produced 3,6-anhydrogalactose 2-sulphate derivatives much faster than those of the lambda-family. Difference in reaction rates could be related with the absence of cyclized lambda-carrageenans in these seaweeds. For carrageenans of the kappa-family, this reaction can be performed at lower alkaline concentrations, at rates that could be still enough for potential industrial applications, and that these rates could be increased by increasing the ionic strength of the reacting solutions. This reaction is crucial from the industrial view-point in order to obtain adequate carrageenan hydrocolloids, so these results could be used directly to adjust conditions for the commercial production of these compounds. Carrageenans with non-sulphated β-D-galactose units had intermediate reaction rates (Noseda & Cerezo, 1995).

Table 2. Structure of the major carrageenan samples from cystocarpic and tetrasporic *Sarcothalia crispata*.

Fraction	Diad	Contribution to the structure
1C1 0.5-0.7 M KCl Yield 43.4 % of the recovered G:DA:S 1.0: 0.62: 1.0	kappa- (G4S-DA) iota- (G4S-DA2S) nu- (G4S-D2S,6S) mu- (G4S-D6S)	56 22 20 2
1C4 Soluble in 2M KCl Yield 53.5 % of the recovered G:DA:S 1.0:0.5: 1.1	kappa- (G4S-DA) iota- (G4S-DA2S) nu- (G4S-D2S,6S) mu- (G4S-D6S)	51 21 26 2
1T1 1.0-1.2 M KCl Yield 85.6 % of the recovered G:DA:S 1.0 :0.0: 1.2	lambda-(G2S-D2S,6S)	100

Sarcothalia crispata (as *Iridaea undulosa*)

As indicated in section 2, *Iridaea undulosa* is not found in Argentina, and possibly it has been a misidentification of *Sarcothalia crispata* (Scrosati 1991). Hence, it will be named here as *Sarcothalia crispata*.

During the 1980s, carrageenans from *Sarcothalia crispata*, collected in Puerto Deseado (Santa Cruz Province), were extracted from. Fractionation with KCl gave qualitatively similar results as those obtained for *S. skottsbergii* (Cerezo 1967b), although these studies were undertaken in greater detail (Matulewicz & Cerezo, 1980a, b; Stortz & Cerezo, 1986, 1988). The complexity of these studies of carrageenan systems from Gigartinaceae was greatly decreased, when algal samples were sorted with regard to their ploidy. The cystocarpic system of *Sarcothalia crispata*, collected close to Puerto Madryn (Chubut Province, Figure 1), was composed of comparable amounts of kappa/iota-carrageenans gelling at intermediate concentrations of KCl and soluble, mu/nu-carrageenan, while the tetrasporic system was composed mainly of a lambda-carrageenan (i.e., >90% of the total carrageenans extracted from this phase), but also a small proportion of a sulphated galactan containing L-galactose units was detected (Stortz & Cerezo, 1993). Comparison of the behaviour in KCl solutions of different carrageenan types was carried out, based on data from *S. skottsbergii* and *S. crispata*. It was clear that the same carrageenan types had different precipitation patterns in KCl solutions, when they were in mixtures obtained from unsorted algal samples, and when they were obtained from a sorted particular life-cycle generation. These data showed that a previous suggestion that the solubility of carrageenan molecules in mixtures was the same as that in homogeneous fractions was not correct, and it was concluded that the KCl precipitation range did not define the chemical structure of the carrageenan as previously assumed (McCandless & Craigie, 1979), due to possible interactions between different structures.

Later, the 1 H- and 13C NMR spectra of the kappa/iota- mu/nu- and lambda-carrageenans from *S. crispata* were carried out (Stortz et al., 1994). This was the first report of the spectra of a lambda-carrageenan in its native state. As in the case of carrageenans from *S. skottsbergii*, it was possible to determine the contribution of the different dyads to the carrageenan structure from the 1 H anomeric signals of the B-units (Table 2).

Finally, tetrasporophytes of *S. crispata* (Stortz et al. 1997) was found to be composed of lambda-carrageenans and other polysaccharide/s, which differed from carrageenans due to the presence of L-galactose and D-glucose as monosaccharide constituents, residues of 3-linked, 6-substituted and, possibly, 4-linked, 3-substituted units, and galactose side chains, were detected. It was speculated that in some fractions, 4-linked D-glucose units would replace D-galactose units.

In Flores, Stortz, Rodríguez, and Cerezo (1997), (2000)) studied the water insoluble structures of the cell walls of cystocarpic thalli of *S. crispata*. They found that the fibrillar phase, as well as the cuticle contained high quantities of proteins and/or glycoproteins, and lesser amounts of polysaccharides (i.e., cellulose, a 4-linked mannan, kappa/iota-carrageenans, and agarans). These authors also analysed histochemically the native material, as well as the residues obtained by the extraction procedure carried out using different staining techniques and found that both the cuticle and the cell walls were birefringent in intact thalli sections. Extraction of carrageenans circumscribes birefringence to the fibrillar cell wall components, especially those of medullar cells. The final residue shows intense birefringence, corresponding to fibrillar material and cuticles (Flores et al., 1997).

In a recent study, samples identified as *Sarcothalia crispata* were collected in Cabo Raso (Chubut Province). Although the authors of this publication reported their results as corresponding to a species that was not studied before for the Argentine coasts, it should correspond to the species studied before as *Iridaea undulosa*. The seaweed was extracted with water at room temperature in a high yield (i.e., 41% regarding the milled seaweed). Chemical and spectroscopic analyses showed that the carrageenans isolated from it had a structure constituted by major amounts of kappa-diads (G4S-DA, 56%), and lesser amounts of iota-diads (G4S-DA2S, 20%) and nu-diads (G4S-D2S,6S, 24%). The authors did not mention the life-cycle stage of their samples, but possibly, they were cystocarpic and/or sterile plants (see Hughes et al., 2018).

Gymnogongrus torulosus

Sulphated galactans from cystocarpic and sterile *Gymnogongrus torulosus*, collected during summer at Cabo Corrientes, Mar del Plata (Buenos Aires Province), were studied in detail by chemical and spectroscopic methods (Estevez, Ciancia, & Cerezo, 2001, 2008). As previously indicated, it was expected to obtain carrageenans of the kappa-family as major products, and this was clearly confirmed. The major carrageenan structures were of the kappa/iota-type, also a small amount of the precursor nu-carrageenan was detected. An important difference in the extraction behaviour regarding the Gigartinaceae previously studied, was that only a small amount of low molecular weight carrageenan was obtained at room temperature (5.1%), while most of the material was obtained with hot water (52.4%). Enantiomeric analysis of the hot water extracts showed very high amounts of D/L-hybrid galactans and agarans, giving a ratio of carrageenan: agaran structures of 1:0.5. Sulphated galactans were localized in the cuticle, cortex and medulla of the gametophyte thallus, being more concentrated in the intercellular matrix than in the cell walls.

Callophyllis variegata

Previously in this review, it was generalized that lambda-carrageenans were only biosynthesized by tetrasporophytes from members of Gigartinaceae and Phyllophoraceae. However, its cyclized derivative (i.e., theta-carrageenan, Figure 1), as well as other highly sulphated galactans of related structures were obtained from seaweeds of the genus *Callophyllis* (Kallymeniaceae, Gigartinales), as *C. variegata* from Puerto Deseado (Santa Cruz Province) (Rodríguez et al., 2005). The main fraction obtained by extraction with water at room temperature and fractionation of the extract with KCl was soluble at a 2.0 M concentration of this salt. These galactans were D/L-hybrids, as 10% of the total monosaccharides were L-galactose units. β-D-Galactose 2-sulphate linked to α-D-galactose 2,3,6-trisulfate and β-D-galactose 2,4-disulphate linked to 3,6-anhydro-α-D-galactose 2-sulphate were the major structures. This is a very highly sulphated galactan structure, containing 4–3 sulphate groups per disaccharidic unit (compare with kappa, iota, and lambda, which have 1, 2, and 3 sulphate groups per idealized disaccharidic unit).

Gracilaria gracilis

It is remarkable that, although *G. gracilis* was the main seaweed resource in Argentina since the 1960s, the first reports about characteristics of the agar from this species were not published until 1997 (Rebello, Ohno, Ukeda, Kusunose, & Sawamura, 1997). Results obtained for samples from different locations were compared, as well as with those obtained for other species, including also some species of *Gracilariopsis* (Rebello et al., 1997), and it was found that *G. gracilis* from Argentina gave the greatest yield in the different alkaline conditions used (32.6–39.5%).

The polysaccharides from summer-collected specimens of *G. gracilis* from Bahía Bustamante (Chubut Province, Figure 1) were isolated by sequential extraction with water at room temperature, i.e., 70 and 90°C, and studied regarding their structure and properties (Rodríguez, Matulewicz, Noseda, Ducatti, & Leonardi, 2009). The best yield was obtained for the first water extract obtained at 70°C (26.7%). This extract had low sulphate and protein content and remarkably high weight-average molecular weight (Mw) of 541 800 Da. The gel strength was 437 g cm^{-2} and the gelling and melting temperatures were 31°C and 85°C, respectively, for the major extract. On the other hand, extracts obtained with water at 90°C had a lower sulphate content, but higher protein and glucose content, the latter, which derived from floridean starch, represented 16% of the total carbohydrates. As expected, the 13C NMR spectrum of the room temperature water extracts gave the signals corresponding to agarose and to precursor units, typical of agarans of low gelling capacity.

Pyropia columbina (as *Porphyra columbina*)

Alkaline cyclization in agarans was studied by Noseda, Viana, Duarte, & Cerezo (2000), from a gametophytes extract of *Porphyra columbina*, collected in Comodoro Rivadavia (Chubut Province, Figure 1). This sample contained 15.6% sulphate and the monosaccharide analysis showed galactose (38.6 mol%), its 6-*O*-methyl-derivative (38.7 mol%), and 3,6-anhydrogalactose (22.7 mol%) as constituent units. The alkali-treated derivative was composed of agarose and its 6-*O*-methylated derivative in a molar ratio of 3:7, a small amount of non-cyclized B units was detected (i.e., 1.7 mol%), due to the conditions of the alkaline reaction. Anomeric signals of the 13C NMR spectra of the porphyran and its alkali treated derivative, agarose, were assigned.

The alkaline cyclization of the α-L-galactopyranosyl 6-sulphate units to 3,6-anhydro-α-L-galactose residues in this porphyran gave a rate constant value intermediate between that measured for a partially cyclized mu/nu-carrageenan and a lambda-carrageenan, in agreement with the accelerating effects of the 4-sulphate (Ciancia et al., 1993), and the retarding effects of the 2-sulphate groups (Noseda & Cerezo, 1995), on the β-D-units, and was in the same range as that determined for carrageenans in which non-sulphated A units predominated.

In other research, the galactans from *P. columbina* obtained with water at room temperature were studied regarding the configuration of the (3,6-anhydro-) galactose units (Navarro & Stortz, 2003). Slightly more D-units than L-units were obtained (i.e., 54:46), suggesting the possible presence of small amounts of D/L-hybrids. Thus, an alkaline treatment, followed by determination of the configuration of the 3,6-anhydrogalactose units was carried out. Although most of the 3,6-anhydrogalactose that was produced by the alkaline treatment (i.e., 35% of the total sugars) belonged to the L-series, and about 3–4% of these units corresponded to the D-series, although there was no 3,6-anhydro-D-galactose in the original polysaccharide. These results clearly confirmed that the native polysaccharide obtained from *P. columbina* with water at room temperature was a D/L-hybrid (or a mixture of two polysaccharides).

Sulphated polysaccharides of an extensive group of species not considered as seaweed resources in this work, were also studied. They included agarans obtained from different species of the order Ceramiales, which have variable sulphation patterns, and also calcareous red seaweeds of the order Corallinales, known as corallinans (Cases, Stortz, & Cerezo, 1994), which are sulphated xylogalactans with an agaran backbone, usually devoid of 3,6-anhydrogalactose. A detailed list of these studies is included in Supplementary Material.

Antiviral activity of sulphated polysaccharides from red seaweeds of the Argentine coast

Sulphated polysaccharides (SPs) are believed to be of potential therapeutic importance because they can mimic heparan sulphates (HS) present in animal extracellular matrices, which are essential points for viral entry in susceptible cells. It has been postulated that SPs can compete for binding sites normally occupied by HS and thus inhibit these processes.

In general, sulphated polysaccharides exhibiting antiviral potential are highly sulphated. Those obtained from some seaweed species have shown promising activity against a variety of animal enveloped viruses, such as herpes simplex virus (HSV) types 1 and 2, human immunodeficiency virus (HIV), human cytomegalovirus (HCMV), dengue virus (DENV), respiratory syncytial virus (RSV), human papillomavirus (HPV), and influenza A virus, by shielding off the positively charged sites of the viral envelope glycoprotein, which are necessary for virus attachment to cell surface heparan sulphate, a primary binding site, before more specific binding occurs to the cell receptors (Damonte, Matulewicz, & Cerezo, 2004).

Variations in the viral envelope´s glycoprotein region may result in differences in the susceptibility of different enveloped viruses to these sulphated polysaccharides. Other studies showed that these polysaccharides did not interfere with viral attachment or penetration, but they prevented viral protein synthesis (Pujol, Carlucci, Matulewicz, & Damonte, 2007).

HSV was one of the first viruses to be reported as susceptible to the antiviral action of SPs more than 50 years ago (Nahmias & Kibrick, 1964; Takemoto & Fabisch, 1964). From these initial studies and based on the need to find new antiviral strategies against herpetic infections, human pathogens of the family

Herpesviridae, such as HSV type 1 (HSV-1), HSV type 2 (HSV-2), and HCMV were thoroughly investigated. SPs extracted from red seaweeds represent the most extensively analysed type of polyanionic virus inhibitors. In this group, the highly effective antiherpesvirus compounds include: xylomannans from *Nothogenia fastigiata* (Damonte et al., 1994; Kolender, Matulewicz, & Cerezo, 1995; Kolender, Pujol, Damonte, Matulewicz, & Cerezo, 1997; Pujol, Matulewicz, Cerezo, & Damonte, 1998), *Nemalion helminthoides* (Perez Recalde et al. 2009; Pérez Recalde et al., 2012), and carrageenans from *Sarcopeltis skottsbergii* (Carlucci et al., 1997; Carlucci, Scolaro, & Damonte, 1999; Carlucci, Scolaro, Noseda, Cerezo, & Damonte, 2004; Mateu et al., 2011; Pujol et al., 2006), *Gymnogongrus torulosus* (Pujol et al., 2002), *Callophyllis variegata* (Rodríguez et al., 2005) from the Argentine coast. However, their efficacy *in vivo* in animal and human systemic infections has undesirable drawbacks, such as poor absorption, toxic side effects, inability to reach target tissues, and anticoagulant properties. SPs have been tested in clinical trials as topical microbicides to prevent sexually transmitted diseases caused by viruses, and they are considered suitable tools to prevent viral infections in humans (Carlucci et al., 2004; Shahzad, Farooq, Aslam, & Umer, 2017).

Sulphated polysaccharides from red seaweeds represent the most potent and selective antiviral agents able to block HSV replication in cell culture at concentrations as low as 0.1 μg ml^{-1} without causing cell toxicity at concentrations up to 1–5 mg ml^{-1}, with a selectivity index (SI) in the order 1,000–50,000, values not easy to afford for any antiviral agent. Furthermore, carrageenans and other related galactans are effective inhibitors of herpes viruses, independently of the antiviral assay and their effectiveness is not significantly affected by the input multiplicity of infection. An important advantage of these antiviral SPs is that they can be prepared and made available in large quantities at low cost (Damonte et al., 2004; Pujol et al., 2007). Nowadays, the antiviral activity of carrageenans against enveloped RNA viruses, such as influenza virus and coronavirus, is particularly important (Leibbrandt et al., 2010; Jang et al., 2021). It has been shown that iota-carrageenan can inhibit the cell entry of the SARS-CoV-2 spike pseudotyped lentivirus in a dose-dependent manner, as well as various rhino- and endemic coronaviruses. Recently, a nasal spray containing iota-carrageenan demonstrated a reduction of severity and duration of symptoms of common cold caused by various respiratory viruses (Morokutti-Kurz et al., 2021).

Another major biological activity tested with sulphated polysaccharides has been the immunomodulatory effect of these biopolymers. Immunity refers to the biological protection of organisms against foreign harmful substances. The immune function of the body is accomplished through the interaction of lymphocytes, monocytes, and other related cells and their products (Huang, Shen, Morris, & Xie, 2019; Jiao, Yu, Zhang, & Ewart, 2011).

Sulphated polysaccharides have become one of the hotspots in the field of polysaccharide research in recent years due to their action as immune regulators with immunomodulatory function. They can maintain homoeostasis by regulating macrophages, T/B lymphocytes, natural killer cells (NK cells), and complement systems, increasing the release of cytokines and regulating the immune system (Huang et al., 2019).

Phylum Ochrophyta

Three groups of polysaccharides are abundant in brown seaweeds, i.e., alginic acid, fucoidan and laminaran (Cosenza et al., 2017, Ponce & Stortz 2020). The most abundant are the alginic acids with wide applications in medicine, food and biotechnological industries. Three kelp species are the main brown seaweed resources in Argentina: *Macrocystis pyrifera, Lessonia flavicans* and the exotic *Undaria pinnatifida*. Some pioneer works from the 1970s and 1980s studied different techniques on yield and quality of final alginate content of the two native kelps (Duville & Duville, 1974, 1975, 1975, Barrales 1974) and bioactivity of different polysaccharides of *M. pyrifera* (Larripa et al. 1987, Mayer et al., 1987b, 1987a). More recently, some other applications of alginates, or aqueous extracts, from *M. pyrifera* and *U. pinnatifida* were performed (Gomez, Lambrecht, Lozano, Rinaudo, & Villar, 2009; Cazón et al., 2014; Diaz et al. 2017).

Fucoidans are a class of sulphated polysaccharides from brown seaweeds. In recent years, the number of publications devoted to the biological properties of fucoidans has greatly increased. However, the chemical exploration of these polysaccharides developed appreciably more slowly (Usov & Bilan, 2009).

Fucoidans from four species of the Argentine coast were studied in pioneer works by the group of Stortz and co-workers: *Leathesia marina* (Lyngbye) Decaisne 1842 (as *Leathesia difformis*) (Feldman et al., 1999), *Adenocystis utricularis* (Bory) Skottsberg (Ponce, Pujol, Damonte, Flores, & Stortz, 2003, Trinchero et al. 2009), and *Scytosiphon lomentaria* (Lyngbye) Link, nom. cons. 1833 (Ponce et al., 2019) from the order Ectocarpales, and *Dictyota dichotoma* (Hudson) J.V.Lamouroux 1809

(Rabanal, Ponce, Navarro, Gómez, & Stortz, 2014) from the order Dictyotales (Supplementary Material). These species are not considered as commercial resources and further details of those works are not included in this review. More recently a detailed revision of the fucoidan composition from a chemotaxonomic perspective was published by Ponce & Stortz (2020).

The seasonal fluctuations of fucoidan content and composition of *Undaria pinnatifida* sporophylls from Patagonia (42.75° Lat S) were recently reported (Arijón et al., 2021). These fucoidans were composed mainly of fucose and galactose (galactofucan) and the monosaccharide profile varied slightly between the studied seasons (November-March). The average fucoidan content was 18.1% of the dry weight, and slightly increased with season and in senescent individuals. The average sulphate content in fucoidan extracts was 20.3% dry wt. which decreased significantly with month and development of thalli.

Phylum Chlorophyta

Sulphated polysaccharides from green seaweeds show a great variety of chemical structures. They can be divided into two main groups, based on the early classification of Percival and McDowell (1981): p. 1) Sulphated glucuronoxylorhamnans and glucuronoxylorhamnogalactans, also divided into two different subgroups according to whether the uronic acids are part of the main backbone, or they appear as side-chains and 2) Sulphated xyloarabinogalactans, which have positive optical rotation.

Order Bryopsidales

The first structural study on the sulphated polysaccharides from *Codium fragile* was carried out by Love and Percival (1964). Bilan, Vinogradova, Shashkov, and Usov (2006, 2007) and Ciancia et al. (2007) studied the sulphated polysaccharides of *Codium fragile* var. *novae zelandiae*, collected in Puerto Deseado (Santa Cruz Province, Figures 1 and 1C. *vermilara*, collected in San Antonio Oeste (Buenos Aires Province, Figure 1). In the latter work, it was found that the first room temperature water extract was rich in galactose and arabinose, however, arabinans predominate in that from *C. vermilara* (V1), while galactans, in that of *C. fragile* (A1). It was found that β-L-arabinopyranose residues formed linear chains of 3-linked units, heavily sulphated, especially those from V1, in which the disulfated units predominated. This extract showed high anticoagulant activity (APTT and TT), in a dose-dependent way, lower, but of the same order as that of heparin. In addition, these fractions, when mixed with normal platelet-rich plasma, induced platelet aggregation *per se*. Hence, these sulphated polysaccharides showed controversial effects on the haemostatic system: inhibition of coagulation pathways and induction of platelet activation. This work was the basis of further detailed investigation regarding these polymers, especially those from *C. vermilara*. Extract V1 was fractionated by precipitation with 0.115 M KCl, and the product which remained soluble was a pure sulphated (1→3)(1→6)-β-D-galactan (Fernández, 2012; Fernández et al., 2013). The fraction that precipitated with KCl was constituted by a 3-linked pyranosic β-L-arabinan, highly sulphated on C2 and C4, which gave a high anticoagulant activity (Ab1, 54.1% sulphate). Ab1 exerted its activity through direct and indirect inhibition of thrombin. Direct thrombin inhibition was studied in detail, showing a mechanism different to those found previously for other sulphated polysaccharides (Fernández et al., 2013).

From the hot water extract of the same seaweed, a (1→4)-β-D-mannan, sulphated mainly on C2 (23.2% of the mannose units), and in minor amounts with side chains or sulphate on C6. This backbone corresponded to that of the fibrillar polysaccharide of the same seaweed (Fernández, 2012).

A very similar general pattern regarding the sulphated polysaccharides was found for *Codium decorticatum*, collected from a fresh beach-cast at Punta Ambrosetti (Nuevo gulf, Chubut Province), with some structural differences: 1) Pyruvate ketals were linked, not only to C3 and C4 of terminal β-D-galactose units, but also to C4 and C6 of 3-linked β-D-galactose units in a ratio of 1.0:1.2. 2) Sulphated 3-linked ®-L-arabinans with sulphate on C2 and, mainly, C2 and C4 and possible single stubs of arabinose, and 3) 4-linked β-D-mannans with a low degree of sulphation on C2. In this case, the galactan and the arabinan could not be separated by a simple precipitation with KCl solutions, instead, a cumbersome anion exchange chromatography was needed (Fernández, Raffo, Alberghina, & Ciancia, 2015).

The system of cell wall polysaccharides from *C. fragile* was also studied in detail (Estevez, Fernández, Kasulin, Dupree, & Ciancia, 2009). It comprised 31% (w/w) of linear (1→4)-β-D-mannans, 9% (w/w) of pyruvylated arabinogalactan sulphates, and small amounts of hydroxyproline-rich glycoprotein epitopes (HRGPs), similar to those found in land plants. This was the first report of these compounds in the cell walls of any kind of seaweed. In situ chemical imaging by synchrotron radiation Fourier transform infrared (SR-FTIR) microspectroscopy and immuno-labelling using antibodies revealed that β-D-mannans and the sulphated polysaccharides were placed in the middle part of the cell wall, whereas HRGP epitopes were located on the wall boundaries, especially in the utricle apical zone (Estevez et al., 2009). For *C. vermilara*, HRGPs were also detected. The utricle cell wall showed by TEM a sandwich structure of two fibrillar-like layers of similar width delimiting a middle amorphous-like zone. The *in situ* distribution of (1→4)-β-D-mannans and HRGP-like epitopes was shown to consist of two distinct cell-wall layers, whereas the sulphated polysaccharides were distributed in the middle area of the wall. The overall cell-wall polymer arrangement in the utricles was different from that of *C. fragile*, despite both being phylogenetically very close (Fernández, Ciancia, Miravalles, & Estevez, 2010). The pattern of distribution for the main components of the utricle cell wall of *C. decorticatum* agreed with this model (Fernández et al., 2010, 2015).

Samples from three different populations of *C. vermilara* from the Argentine coast, i.e., La Farola (Buenos Aires Province), San Antonio Oeste (Río Negro Province) and Bahía Arredondo (Chubut Province). Showed (i) an important variation in the relative arabinan content, which increased from north to south, and (ii) a measurable degree of cell wall variability in the sulphate distribution between the different sulphated polysaccharides (Fernández, Ciancia, & Estevez, 2011). When cell wall composition was analysed over three consecutive years in La Farola, the quantity of mannans and overall sulphate content remained constant, whereas the galactan:arabinan molar ratio changed over the time. Besides, similar cell wall composition was found between actively growing (apical) and resting (basal) zones of the thallus, suggesting that cell wall composition was independent of growth stage and development. It was suggested that *C. vermilara* developed a mechanism to adjust the total level of cell wall sulphation by modulating the arabinan; galactan:mannan sulphates molar ratios, and also by adjusting the sulphation level in each type of polymer, whereas non-sulfated fibrillar mannans, as the main structural polysaccharides, did not change over the time or growing stage. In conclusion, the cell wall carbohydrate polymers from three of the four species of *Codium* reported for the Argentine coast (Boraso de Zaixso, 2004), were studied in detail.

Discussion

Seaweed production in Argentina developed between the late 1950s and 1970s and then went through a long period of decline until the 21st century, in which production fell down to virtually zero. However, during the 1970s, basic and applied seaweeds research lines were established by government research institutions by the 1970´s. As a result, seaweed diversity has been described along the Argentine coast, with a focus mainly on the Patagonian region, where the largest number of seaweed species with commercial interest were found. Knowledge generated from these studies provided a standard for future the taxonomical, biological phenological, geographical distributional and chemical seaweed studies of some which are still used as relevant references (Halperin et al. 1973, Boraso de Zaixso 2013).

Only two out of seventeen taxa here reviewed (*M. pyrifera* and *G. gracilis*) have been studied with an emphasis on the geographical and seasonal variations of biological and ecological characteristics, which may be evident throughout their distribution range. As a consequence, for most of the reviewed seaweed resources, very little is known about their ecological role, detailed distribution, stock size or the seasonal variations of their chemical composition. Taxonomic studies of seaweed species were mainly done on the basis of their morphological characteristics. Only the taxonomy of few species have been updated and in many cases, it is still necessary to re-examine these materials considering the morphological variation throughout the seaweed species distribution range along the Argentinean coast, as well as through genetic studies (i.e., *P. columbina, Lessonia* spp., *Ulva* spp., *Sarcothalia* spp.). The latter of which may provide a plethora of data, as complementary genetic studies could also help to solve the cryptogenic status of some species (i.e., *G. gracilis*) before considering its potential management or aquaculture (Meinesz 2007, Guillemin et al., 2014).

Kelps are recognized for their value in providing multiple ecosystem services (Smale, Burrows, Moore, O'Connor, & Hawkins, 2013), and in turn, may be affected by global change factors, such as climate change (Smale, 2020). Along the Patagonian coast, there are three kelp genera/species. While two have been harvested both from natural beds and from the shore line (*M. pyrifera* and *U. pinnatifida*), only one species was collected solely from the shore line (*Lessonia* sp). Out of these species, *M. pyrifera* and *Lessonia* spp. would be considered as native species, however, *U. pinnatifida* is considered a highly invasive species with multiple effects on the invaded habitat. Due to *U. pinnatifida´*s invasive nature, much of the ecological information available is focused on this last species. This bounty of information is in stark contrast to the research information available for *M. pyrifera* and for *Lessonia* spp. which has shown to be either outdated or with no ecological information available. With such a deep lack of knowledge and baseline information, it is urgent to conduct more updated research considering all the ecosystem services as well as the disservices to not only guarantee the adequate and sustainable management of the seaweeds resources, but also of the sustainability of the whole ecosystem.

In order to effectively execute the inclusion of more holistic and accurate information, it is important to note that sustainable harvesting of seaweed species requires management and regulation strategies based on scientific information both from population and ecosystem perspectives (Mac Monagail, Cornish, Morrison, Araújo, & Critchley, 2017). In this review, we only found information focused on harvesting effect for two species (*M. pyrifera* and *P. columbina*). Both are the only species that are allowed to be harvested directly from wild populations according Chubut province legislation. This current legal framework is based on outdated scientific studies without considering the monitoring of population and community parameters. In addition to this, the remaining reviewed taxa have been historically collected from beach cast, and thus far we have not found studies assessing the impact of the beach cast harvesting on natural seaweed beds and stock availability. An example could be the case of *G. gracilis*, where large volumes of wet biomass were historically harvested from the coast, however, there is no information on how this could affect the population dynamics of natural beds (i. e. by harvesting before spore release of reproductive thalli). In this sense, our lack of updated research and knowledge may have caused or helped cause the drastic population decline of the *G. gracilis* biomass.

Currently, seaweed biomass production in Argentina is at very low levels, and most of the produced biomass is exported as raw material for food production and for fucoidan extraction. Historically, the main harvested species, *G. gracilis*, seems scarcely available at present. In tandem, the main industry that processed that biomass for agar production went bankrupt recently. This sublimation of seaweed studies in Argentina has shifted the main research areas on seaweed from the chemistry of phycocolloids like carrageenan, agar and alginate, to the chemistry and bioactivity of polysaccharides with health or biomedical applications, like fucoidans and ulvans.

We detected only three companies processing seaweed biomass in Argentina. Two were processing seaweed mainly for biofertilizer and biostimulant production (mainly from *U. pinnatifida* and *M. pyrifera*) for agricultural uses, as well as for the production of feeding supplements and cosmetic products. The third company produces food products (based on *Ulva*, *Pyropia*, and *Undaria* biomass) and algae-based cosmetics. However, we found scarce published research on agricultural applications. Considering the importance of the agro-industry in Argentina, in our opinion agricultural applications could have, in the internal market, the traction to upscale algal production and processing in the country. Consequently, we found that an increase in research efforts on this issue could be valuable for the seaweed industry development. Although edible seaweed products most likely not have a huge market in Argentina, we found that this market could represent another way to increase and diversify algal production with local value added (Solana et al. 2017, Dellatorre et al., 2021). We reported several publications focused on proximate composition and food safety parameters of biomass of different seaweed species. However, information about seasonal and geographical fluctuations on these parameters is scarce (Dellatorre, Solana, & Castaños, 2017). Also, the processing parameters and sensorial attributes of food products have been scarcely addressed from a scientific perspective (Dellatorre, Solana, Roldán, Davies, & Pallavedino, 2019; Solana, Tomás, Ixtaina, Castaños, & Dellatorre, 2019).

In conclusion, the history of seaweed resources exploitation in Argentina has developed exclusively from the harvest of natural beds, based on an industry towards the production of phycocolloids (agar). The variation on biomass availability through the time, together with the lack of adequate management, regulation and policies, led to a current scenario where the seaweed activity is scarce. There is a clear need to increase the attention to ecosystem-based management, and to find new forms of governance linking scientific, private and public sector to manage seaweed resources (Naylor et al., 2021). In this sense, policy is essential both to promote scientific research and seaweed activity and to protect natural resources from overharvesting. Furthermore, considering the great potential for seaweed aquaculture of the Argentinean coast, an alternative to achieve sustainable management of wild resources could be seaweed farming. In this sense, seaweed aquaculture could improve the livelihoods of many coastal communities, as artisanal fisheries and provide several ecosystem services.

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