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Review

From Form to Function: The Anatomy, Ecology, and Biotechnological Promise of the False-Kelp *Saccorhiza polyschides*

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Abstract

Saccorhiza polyschides is a fast-growing pioneer and opportunistic canopy-forming false-kelp belonging to the order Phyllariaceae (Ochrophyta, Phaeophyceae). The species plays a pivotal ecological role in temperate marine ecosystems and exhibits promising potential for diverse biotechnological applications. The species, however, is under growing pressure from anthropogenic disturbance. This review synthesises current knowledge regarding the biology and geographic distribution of the species, with particular emphasis on its distinctive morphology and ultrastructural features. The species' complex life cycle and marked seasonal productivity are examined concerning environmental variables. Furthermore, we explore the ecological interactions of the species, including its role as a habitat-forming species and its responses to anthropogenic stressors such as climate change and habitat degradation. Special attention is given to the state of knowledge regarding the bioactive compounds and associated bioactivities of *S. polyschides.* This includes a detailed examination of the species' phytochemical constituents, extraction and fractionation strategies, as well as in vitro and in vivo bioactivities, and potential biotechnological applications. By integrating findings from recent literature and identifying methodological and knowledge gaps, this paper seeks to provide a comprehensive understanding of *S. polyschides* as an emergent marine bioresource and to propose directions for future research and sustainable valorisation.

Keywords: morphology; distribution; ecology; life-cycle; stressors; blue biotechnology

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1. Introduction

The marine forests of the Northeast Atlantic are highly productive ecosystems, where the annual pseudo-kelp *Saccorhiza polyschides* (Lightfoot) Batters, 1902 serves as a predominant canopy-forming species [1]. This large, fast-growing brown macroalga plays a pivotal ecological role in temperate marine environments [2]. Its biological traits, life cycle, and capacity to rapidly colonise disturbed habitats render it one of the most productive and resilient kelp species along European rocky shores, particularly in areas prone to frequent disturbances [3]. However, despite its adaptability, *S. polyschides* faces significant challenges posed by climate change and anthropogenic activities [4].

Among its notable adaptive traits, *S. polyschides* exhibits a remarkable biochemical capacity, producing a range of bioactive compounds that enhance its survival under environmental stressors. These compounds provide ecological advantages, including protection against herbivores, epiphytes, and pathogens [5,6]. Additionally, they hold substantial potential for biotechnological applications, including their use in pharmaceuticals, cosmetics, and sustainable aquaculture [7,8].

Despite its ecological and biotechnological relevance, information on *S. polyschides* remains fragmented across diverse disciplines. Unlike other kelps (e.g., *Laminaria* spp.), this species has not been the subject of a dedicated review. Consolidating current knowledge is critical to support conservation strategies, sustainable exploitation, and future research directions. Hence, this paper provides a comprehensive discussion of the importance of *Saccorhiza polyschides*, covering its biology, global distribution, morphology, and ultrastructure. It also explores the distinctive features of its life cycle, the ecological role it plays within marine ecosystems, and the various environmental stressors impacting the species, particularly in the context of ongoing climate change and human activity.

2. Taxonomy, Distribution and Environmental Preferences

2.1. Phylogenetic Placement and Taxonomic Notes

Saccorhiza polyschides, commonly known as furbelows, is a member of the family Phyllariaceae within the order Laminariales (Ochrophyta, Phaeophyceae). Unlike true kelps from the family Laminariaceae, *S. polyschides* is characterised by a shorter lifespan, distinct anatomical features, and a unique translocation system. These differences, corroborated by molecular phylogenies and ultrastructural analyses, support its taxonomic separation from the more derived Laminariaceae lineages [9–11]. Phyllariaceae is considered a more basal clade among the Laminariales, with *S. polyschides* often referred to as a "false kelp" due to its annual habit and primitive traits. Despite these differences, species in both families exhibit convergent ecological functions, forming dense canopy structures in temperate reef ecosystems of the eastern Atlantic Ocean [12–14].

2.2. Ecological Function as a Marine Forest-Forming Species

Saccorhiza polyschides is a fast-growing, pioneer, and opportunistic brown seaweed. In this context, "pioneer" refers to species that are among the first to colonise newly available or disturbed substrates, initiating ecological succession. "Opportunistic" describes species with rapid growth and high reproductive output that exploit transient favourable conditions, often dominating disturbed habitats before being replaced by more competitive, long-lived species [15].

S. polyschides large, distinctive sporophyte typically reaches up to 4 m (Figure 1), though in exceptional cases it may grow as long as 10 m [16]. This species plays a crucial role in the structuring of marine ecosystems, occurring within complex benthic communities dominated by large canopy-forming macroalgae, often coexisting with other kelps such as *Laminaria hyperborea, L. ochroleuca, L. digitata* and *Saccharina latissima*. Understory species include smaller species of red (Rhodophyta), green (Ulvophyceae) and other brown seaweeds [17].

These complex ecosystems are commonly referred to as kelp forests. Due to their large size and distinctive morphology, species like *S. polyschides* significantly influence the physical properties of the ecosystem. The species modulates key factors such as light penetration, hydrodynamic conditions, sediment deposition, substrate abrasion, and local pH levels [18]. Due to its large size and dense canopy, kelps and pseudo-kelps such as *S. polyschides* reduce light penetration beneath the canopy, creating shaded microhabitats for understory species [19]. Its flexible stipes and blades attenuate wave energy, reducing near-bottom hydrodynamic stress and sediment resuspension, reducing coastal erosion. The canopy also traps suspended particles, enhancing sediment deposition in calmer zones [20].

Additionally, photosynthetic activity can locally increase pH during daylight, buffering against ocean acidification in kelp-dominated areas [21].

Figure 1. *Saccorhiza polyschides* sporophyte measuring approximately 3 m, Quebrado Beach, Peniche, Portugal, 13 July 2021.

Kelp forests dominate approximately 25% of the world's coastlines, spanning from the Arctic to temperate regions in both hemispheres [22]. They rank among the planet's most diverse and productive ecosystems, providing ecosystem services of significant ecological, economic, and social value [23,24]. These services include enhanced coastal primary and secondary productivity, as well as supporting services such as the creation of a three-dimensional habitat structure that provides food, shelter, and breeding grounds for numerous marine organisms, including other algae, invertebrates, seabirds, along with apex predators such as fish, many of which are of commercial worth [12,25,26]. Additional critical regulating services include carbon sequestration, nutrient cycling, and coastal protection, while provisioning services involve fisheries and seaweed harvesting for a multipurpose blue economy. Cultural services encompass a range of recreational activities, including scuba diving and recreational angling [27,28].

The dominant canopy-forming kelp taxa differ across latitudinal regions. The *Macrocystis* genus dominates the Pacific and South Atlantic, *Ecklonia* in the Indian Ocean, *Nereocystis* in the North Pacific, while *Laminaria/Saccharina* species prevail in the North Atlantic. *Undaria pinnatifida*, a smaller species, is native to the northwest Pacific but is invasive in the Atlantic [7], with evidence of competition between this species and indigenous macroalgae [29].

2.3. Biogeographical Distribution and Environmental Tolerances

The northern Iberian Peninsula serves as a refuge for kelp species due to the influence of cold-water upwelling [30], as kelp distribution and survival are predominantly temperature-dependent [31]. *S. polyschides* is a warm-water-tolerant species, with its growth, reproduction, and survival primarily governed by temperature. While sporophytes thrive in temperatures ranging from 3 to 24 °C and gametophytes develop between 5 and 25 °C, optimal growth occurs in warmer waters around 17 °C. In colder conditions (~5 °C), it grows more slowly compared to other kelps like *Laminaria hyperborea* and *Saccharina latissima* [32]. Due to its preference for warmer conditions, *S. polyschides* has a more southerly distribution in Europe when compared to other *Laminaria* species, making it the most abundant kelp-like species in southern Europe [3,33].

Saccorhiza polyschides grows on rocky substrates from the lower intertidal zone to depths of over 25 m [14,34]. The depth distribution, however, is influenced by environmental factors such as light availability, sediment type, and water temperature.

The species is widely distributed across the northeast Atlantic (Figure 2), particularly in Ireland, Great Britain [3,35,36], Spain, Portugal, including the Azores archipelago [37–43], France [44,45], Belgium, the Netherlands, Denmark, and southern Finland [25]. Its northernmost occurrence has been documented in Norway [46].

In the Mediterranean, the presence of the species is rather rare and often casual populations were registered, but permanent populations can be found in the Strait of Messina (Italy) [47,48], the Alboran Sea (Morocco), and in the Strait of Gibraltar [49]. To the south, it has been registered in the Canary Islands [50] with its southernmost recorded presence in Ghana [51], however this may be a non-permanent population of *S. polyschides*.

This species is predominantly found in sheltered habitats in both gentle and strong currents. Growth in exposed environments is less frequent. It thrives on stable rocky substrates, boulders, large gravel, and artificial structures, and is also known to colonise sand-covered tide pools [52].

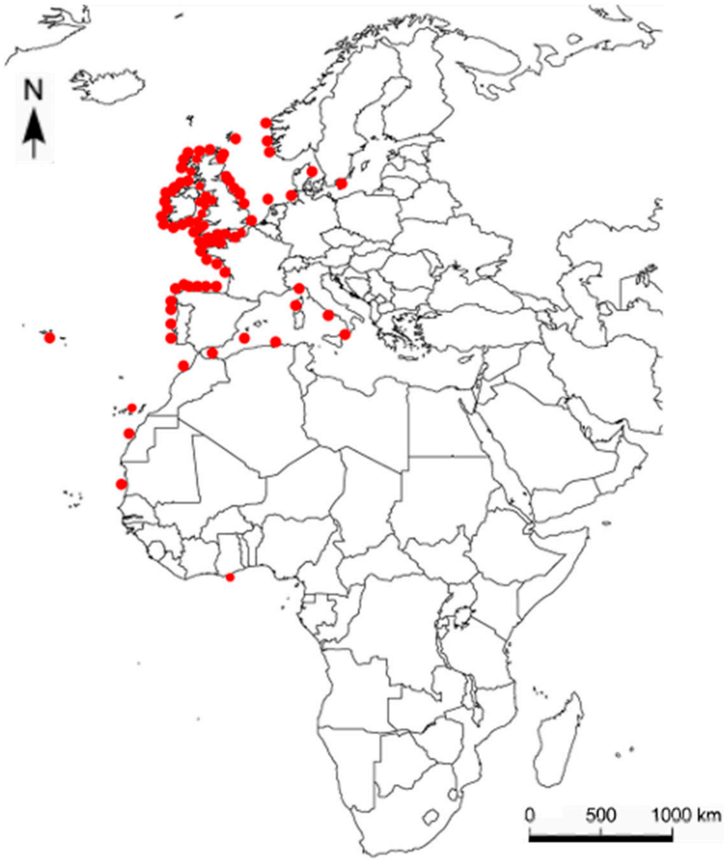

Figure 2. Global distribution of *Saccorhiza polyschides* (data from Guiry & Guiry [51]). Some Mediterranean and west Africa records are casual and do not correspond to established populations.

3. Morphology, Anatomy and Structural Adaptations

3.1. External Morphological Features

Unlike true kelps, *Saccorhiza polyschides* is an annual to biennial-like species [35]. Its young sporophytes emerge in spring (March–April) and exhibit rapid growth, achieving weekly elongation rates of up to 6.2 cm [33,53]. These rates are observed under optimal conditions of moderate water motion, high nutrient availability, and temperatures near 17 °C. Growth slows significantly under low light or nutrient limitation and at temperature extremes [3,54,55].

Typically, the thalli become fertile within 8 to 10 months and complete their life cycle within 14 months, ensuring a quick seasonal generation of spores. However, if a thallus does not become fertile during the first summer, it often survives through winter, with the holdfast bulb persisting for up to 22 months, then exhibiting a biennial-like life history. This variation is largely driven by temperature and light availability. Warmer, high-light conditions accelerate fertility, whereas cooler winters and reduced light delay reproduction, favouring persistence into a second year [52,56].

The thallus of *S. polyschides* consists of a holdfast and a stipe, topped by a large, digitated blade (lamina) resembling true kelps. The blade is broad, flattened, and dark brown, but it exhibits significant morphological variation depending on habitat conditions. In sheltered habitats with weak currents, blades are broad, whole, and heart-shaped at the base, maximising light capture; in high-energy environments, blades are narrow and deeply divided into as much as 30 digits, being triangular at the base, reducing drag and breakage risk, as in Figure 1. Growth occurs through elongation of the stipe and blade, driven by meristematic cells located at the base of the blade [34,35,55,57]. Once the meristematic tissue is lost due to blade breakage, further growth ceases [18].

The stipe is strong yet flexible, compressed into a belt-like structure approximately 4 cm wide and up to 1 m in length. Towards its base, the margins of the stipe become wavy, and the stipe itself helicoidally twists just above the holdfast. The holdfast of *S. polyschides* is particularly notable, consisting of small, unbranched rhizoids (haptera) covered by a bulbous base with numerous finger-like projections that anchor the kelp to the substrate. This bulbous base, which can reach 30 cm in diameter, provides secure attachment in the dynamic sublittoral fringe environment [34,35]. As young thalli develop, a small collar forms at the base of the stipe, eventually expanding into the characteristic bulbous base [35]. The flattened stipe and bulbous holdfast are distinctive features of this species (Figure 3).

Figure 3. Bulbous holdfast and compressed stipe base, with wavy margins of *Saccorhiza polyschides*, Leça da Palmeira, Matosinhos, Portugal, 20 September 2024.

3.2. Tissue and Cellular Organisation

Tissue differentiation and organisation are hallmark traits of all kelps and kelp-like species, which are large, parenchymatous organisms. Their tissue structure includes a peripheral meristoderm, underlying cortical layers, and a central medullary core. The meristoderm is composed of tightly packed, small, isodiametric cells. The cortex is divided into inner and outer layers. The outer cortex consists of cells larger than those in the meristoderm, arranged in one or more layers, with chloroplasts, large vacuoles, and, in some cases, phenolic bodies. The inner cortex contains several layers, with the innermost cells elongated and separated by numerous sieve plates [11]. The medulla, which occupies the central region of the stipe and blade, contains solenocysts and allelocysts. Solenocysts are thick-walled, highly elongated cells (up to 75 mm), responsible for long-distance symplastic translocation in the Phyllariaceae. The cell wall thickening is due to the deposition of primary and secondary fibres, differing from the callose deposition seen in the sieve filaments of true kelps (Laminariaceae). Solenocysts are interconnected by allelocysts through porous sieve plates, which are crossed by plasmodesmata. It is hypothesised that allelocysts function as lateral pumps, facilitating the loading and unloading of solutes into solenocysts via an energy-dependent mechanism. Unlike the end-to-end trumpet cells of true kelps, solenocysts exhibit numerous lateral connections through self-formed protrusions [11]. This symplastic translocation system is considered primitive, operating at a rate five times slower than that of *Macrocystis* [13].

4. Lifecycle

Saccorhiza polyschides exhibits a complex diplohaplontic lifecycle, akin to that of true kelps, characterised by the alternation between two distinct phases: a long-lived, diploid, macroscopic parenchymatous sporophytic phase and a short-lived, haploid, microscopic filamentous gametophytic phase (Figure 4).

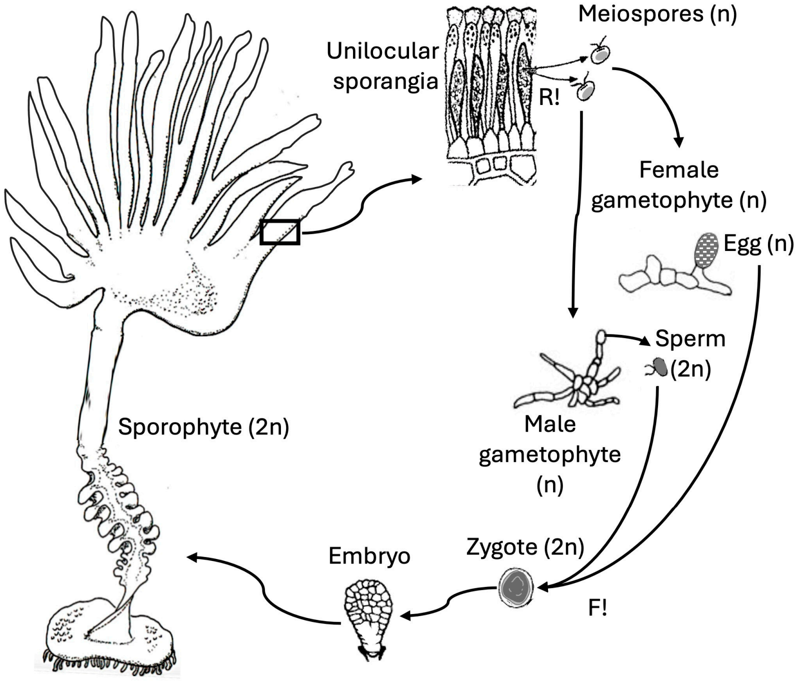

Figure 4. Diplohaplontic heteromorphic life cycle of *Saccorhiza polyschides*. F!—Fertilisation; R!—Meiosis.

4.1. Sporophyte Development and Phenology

As mentioned above, the growth of the macroscopic sporophyte is driven by an intercalary meristem situated between the stipe and the blade. This meristem secretes chemical compounds that migrate distally, suppressing the formation of spore-producing sori during the rapid spring growth of the thallus. By late summer (August) and early autumn, this chemical secretion diminishes, allowing the development of sori. Consequently, meiotic unilocular sporangia, embedded in mucilage and surrounded by paraphyses, are formed within these sori, located at the base of the lamina, stipe frills, and bulb. In contrast to true kelps, the paraphyses of *S. polyschides* sori lack thickened tips [13]. Each sporangium produces 128 two-flagellated motile meiospores, which are released through the thickening of the sporangium apex. These spores are widely dispersed, increasing the likelihood of colonising new habitats.

4.2. Gametophyte Characteristics and Fertilisation

Meiospores contain a single chloroplast and an eyespot, remaining motile for up to 48 h and are capable of travelling several kilometres. Upon settling, the meiospores develop into gametophytes [9,11,58,59]. Sexual differentiation in *S. polyschides* is determined genotypically, with females possessing a large X chromosome and males having a smaller Y chromosome. Successful recruitment of new gametophytes—marked by the appearance of the first macroscopic individuals—depends largely on the density of spore settlement. Spore density must maintain a sufficient distance between male and female gametophytes to prevent overcrowding, while still allowing proximity for fertilisation to occur [60]. Experimental studies on Laminariales indicate that successful fertilisation typically occurs when male and female gametophytes are within a few millimetres of each other (generally <5 mm), as spermatozoid motility is limited to short distances in the boundary layer [60,61].

4.3. Environmental Regulation of Reproduction

While there have been conflicting reports on whether the branched filamentous gametophytes are dioecious [13,61] or monoecious, most studies suggest the presence of separate male and female gametophytes. Male gametophytes are paler, have smaller cells, and exhibit more branching compared to females. They produce antheridia, each containing a single biflagellate spermatozoid. In contrast, female gametophytes bear oogonia, each releasing a single large, non-motile egg [9,11,58,59,62]. The mature egg secretes ectocarpene (6-but-l′-enyI-cyclohepta-l,4-diene) [61], a hormone that induces chemotactic attraction within seconds. Fertilisation leads to syngamy, producing a zygote that germinates into an embryo, eventually developing into a mature sporophyte.

Many stages of this lifecycle are regulated by environmental factors. Egg release occurs only under long-day photoperiods (16 h light/8 h dark), coinciding with late summer and early autumn intensity [54,58,59,63]. Similarly, the germination of meiospores and early gametophyte development requires relatively high light conditions, typically above 20–30 μmol photons m^{-2} s^{-1}, with optimal development reported at 40–60 μmol photons m^{-2} s^{-1} under long-day conditions [31,58]. Microscopic sporophytes also germinate only under high light intensity, reinforcing the importance of photoperiod and irradiance in controlling the timing of reproduction and recruitment in this species [54].

5. Ecological Role and Seasonal Dynamics

5.1. Productivity and Canopy Formation

Both semi-annual and perennial kelps are some of the most productive primary producers on the planet, and *Saccorhiza polyschides* stands out as one of the most prolific species. This species is most productive in strong currents with moderate wave action during spring and early summer when light availability is high, and water temperatures are low [22]. John [64] recorded a productivity rate of 3.9 kg/m^2/year for sublittoral populations, with a late summer biomass peak of over 13 kg of wet weight per m^2 [3]. These values highlight the pronounced seasonality of *S. polyschides* populations, showing consistent demographic trends across different sites and depths throughout the year. For comparative purposes, Table 1 presents the annual productivity of *S. polyschides* alongside that of other kelp species, highlighting its status as a prolific canopy-forming macroalgae.

In temperate latitudes, *S. polyschides* emerges as a dominant habitat-forming species on both intertidal and subtidal reefs by late summer, indicating its ecological importance. Kelp forests typically experience a decline in productivity during late summer and fall due to rising water temperatures and reduced nutrient concentrations. This decline coincides with increased erosion rates of thalli, driven by decreased tissue quality caused by sporogenesis, intensified grazing, and fouling from other organisms [22,69]. Besides seasonality, kelp forests also respond strongly to wave exposure and depth [70].

Table 1. Kelp and false-kelp species productivity in the wild and in aquaculture expressed as wet weight per square metre per year. Values for cultivated biomass may have been converted from dry weight or carbon units using standard factors (DW ≈ 15–17% of WW; C ≈ 30–35% of DW). For *S. polyschides*, cultivated values are derived from pilot-scale experiments.

Species	Life History	Productivity (kg WW m^{-2} yr^{-1})		References
		Wild	Cultivated	
Saccorhiza polyschides	Annual	3.9–13	12–15	[5,64]
Laminaria hyperborea	Perennial	2.0–3.0	8–12	[32,65]
Saccharina latissima	Perennial	1.5–2.5	10–16	[31,66,67]
Undaria pinnatifida	Annual	2.5–3.0	14–18	[31,68]

S. polyschides populations display distinct seasonal dynamics across latitudes. In northern populations (~50° N), sporophytes are present year-round, with the highest recruitment rates occurring in spring and summer. In contrast, southern populations (~41° N) exhibit shorter seasonal life cycles, with sporophytes only present between April and September [3,43]. These southern populations can be temporarily removed in winter, resulting in minimal or no standing biomass during that season [18]. As summer progresses, the oldest sections of the thalli undergo erosion. The bulbous holdfast often survives through the winter, eventually decaying and becoming detached in spring, either being washed ashore or sinking into deep-sea canyons. Decaying *S. polyschides* biomass accumulates alongside other macroalgae, contributing to detrital production, especially during intense storms or after blade degradation by grazing and epibionts. This detritus is broken down by bacteria, releasing organic carbon and nutrients, which fertilise the surrounding environment and fuel secondary productivity [52,71]. This kelp detritus can travel hundreds of kilometres, supporting marine food webs by providing essential nutrients. It may be consumed by plankton or suspension feeders, making brown seaweed detritus a vital source of nutrients for coastal ecosystems [72].

5.2. Successional Role in Disturbed Habitats

Different canopy-forming species combinations, influenced by physical and biological factors, occur at varying depths and latitudes. *S. polyschides* is considered an opportunistic pioneer species due to its rapid growth and high productivity within a single season [3,26,42,55,73]. *S. polyschides* reveals greater resilience than perennial kelps [4]. It often replaces other kelp species like *Laminaria digitata* or *L. hyperborea* due to its fast-growing nature and adaptability to disturbed environments [52,74]. Hence, *S. polyschides* plays a crucial ecological role in disturbed sublittoral rocky habitats. Its rapid growth and ability to colonise disturbed areas, such as those affected by storm surges, make it an essential species in ecological succession. It provides a dynamic, resilient habitat that supports a diverse but transient marine community.

5.3. Interactions with Epifauna and Associated Communities

The bulbous holdfasts, whether healthy or decaying, offer shelter to coastal marine fauna, with a single holdfast supporting thousands of organisms, mostly invertebrates [52]. These holdfasts are particularly important in exposed environments, providing habitat and shelter to a wide range of species [2,75]. The large volume of the bulbous holdfast explains the high diversity of epifauna associated with this species [76]. Common taxa include Mollusca (e.g., *Patella pellucida*, *Steromphala umbilicalis*, *Bittium reticulatum*, *Mytilus galloprovincialis*, *Rissoa* spp.), polychaetes (e.g., *Nereis* spp.), Echinodermata (e.g., *Ophiothrix fragilis*), Arthropoda (e.g., *Jassa* spp., *Idotea granulosa*, *Jaera* spp.), Fish (e.g., *Nerophis lumbriciformis*) as well as epiphytic algae, which use the holdfast as a fixation structure, shelter, and feeding ground [2,76,77]. Patterns of *S. polyschides* can be affected by environmental stress, especially due to the seasonal instability of its holdfasts [78], influencing the composition of associated communities.

6. Anthropogenic and Environmental Stressors

The main drivers of marine biodiversity loss include habitat destruction, overexploitation, pollution, climate change, and invasive species [12,27,34,79,80].

6.1. Climate Change and Range Shifts

Among these, rising sea temperatures due to climate change are currently the most significant factor affecting the distribution of *Saccorhiza polyschides*, particularly along the coasts of the Iberian Peninsula. The weakening of the region's cold-water upwelling due to adverse wind conditions [81,82] has led to higher summer sea temperatures and reduced nutrient availability [47,83]. As a result, cold-water kelps like *Laminaria hyperborea* are being replaced by warmer-affinity species such as *S. polyschides* in the north of the peninsula [1,56]. This shift was first recorded more than 40 years ago along the northern coast of Spain by Fernández et al. [38] and is also observed in other regions, like the northwest of France [45]. Thus, a decline in cold-temperate kelps, such as *Alaria esculenta* and *Saccharina latissima,* is ongoing, accompanied by a shift toward warmer-affinity seaweed native species. This marks a rapid process of meridionalization [84], often referred to more broadly as 'tropicalization' [73,85], reflecting the poleward expansion of warm-adapted taxa. This transition is an alarming signal of climate change's impact on kelp populations, especially in transitional regions like Iberia. Despite *S. polyschides'* adaptability to warm conditions, it faces limitations when temperatures exceed its optimal range [80]. Sudden temperature spikes and prolonged exposure to exceeding thermal thresholds can cause sporophyte collapse, significantly reduce recruitment rates or even cause immediate mortality [43,69]. As a result, population declines have been documented in the southern parts of its range, such as along the coasts of Morocco and Iberia, where rising sea temperatures are creating thermally unsuitable environments [33,86,87]. In these areas, *S. polyschides* is being replaced by more warm-tolerant species like *Cystoseira sensu lato* [88]. Conversely, at the northern limits of its range, *S. polyschides* is affected by colder winter temperatures (2–5 °C), which may negatively impact recruitment, especially when combined with long-term temperature reductions [81,82]. As a result, while the species is resilient to short-term temperature fluctuations, extreme thermal anomalies—whether heatwaves or cold spells—are reshaping its distribution.

6.2. Storm Disturbances and Erosion

Climate change is also expected to intensify storms, which pose additional threats to kelp forests [17]. Strong storms can break or dislodge entire kelp beds [69], affecting the distribution and abundance of kelp species. As stated above, warm-water tolerant species like *S. polyschides* and *L. ochroleuca* are becoming more dominant. However, because *L. ochroleuca* is less tolerant of wave action, it is more susceptible to being dislodged by storms, being quickly replaced by *S. polyschides* [89]. *S. polyschides*, being an annual species, is particularly vulnerable, as it depends on the seasonal maturity of sporophytes to produce spores, while perennial kelps produce spores year-round. Extreme storms, hence, may hamper annual spore production or dispersal, making coastal population recruitment reliant on subtidal areas [4]. Moreover, storms also affect subcanopy kelp individuals, reducing their density and hindering kelp forest recovery [90].

The spread of non-native marine species is another concern for kelp beds in Europe. For instance, the Japanese kelp *Undaria pinnatifida* (Wakame) has been introduced in various regions, including Europe, where it competes with native species like *S. polyschides* due to similarities in their recruitment and growth patterns. Both species exhibit opportunistic strategies, but their dominance depends on environmental context. *U. pinnatifida* tends to prevail in sheltered, nutrient-enriched waters, whereas *S. polyschides* maintains an advantage in moderately exposed coastal habitats [91,92].

6.3. Invasive Species and Herbivory Pressure

Grazing by sea urchins, whose populations have surged due to the removal of their predators, is a significant factor in kelp canopy loss, especially at higher water temperatures [28,73]. Sea urchins feed primarily on young kelp recruits, and their grazing activity plays a major role in determining kelp distribution globally [18]. Kelp persistence in such regions depends on the availability of topographic refugia to protect young recruits from herbivory [93].

6.4. Impacts of Harvesting and Anthropogenic Pressure

Finally, where harvesting is concerned, while seaweed harvesting has been practised by local communities for millennia [94], recent decades have seen a rise in the commercial demand for seaweed products [95]. Although seaweed harvesting is still in use in many parts of the world, the macroalgae market has been supplied by the growth of aquaculture. Therefore, when properly regulated—through measures such as licencing, biomass-based quotas, seasonal restrictions, and rotational harvesting to maintain resource sustainability and ecosystem integrity—wild harvesting can remain sustainable for many years [96].

7. Bioactive Compounds and Bioactivities

The marine environment, particularly its macroalgae, has emerged as a prolific source of structurally diverse and biologically active compounds with promising biotechnological applications. The increasing demand for natural and sustainable solutions to the challenges currently facing the pharmaceutical, cosmetics and food industries has recently led to the investigation of marine organisms as potential sources of bioactive compounds [97,98]. Marine macroalgae have demonstrated significant biotechnological potential due to the abundance of secondary metabolites, low toxicity and high seasonal availability [97,99,100]. Within the brown seaweed, the species *Saccorhiza polyschides* has gained prominence due to its functional versatility and distinctive biochemical profile. From a biochemical perspective, *S. polyschides*, like other brown algae, contains a variety of biologically active compounds, including sulphated polysaccharides (such as alginates and fucans), phlorotannins, polyunsaturated fatty acids, sterols and antioxidant pigments, such as fucoxanthin [101–103]. The composition of the algae can vary seasonally and according to whether it is wild or cultivated, which might have a direct influence on its bioactivity [104,105]. Historically underexplored compared to other brown seaweeds such as *Fucus vesiculosus* and *Laminaria digitata*, *S. polyschides* is now recognised for its considerable biomass productivity, ecological versatility, and bioactive metabolite content. Recent studies have demonstrated that solvent-partitioned extracts of *S. polyschides* exhibit significant antioxidant, antimicrobial and anti-inflammatory activities, positioning the species as a promising candidate for applications in cosmeceuticals and nutraceuticals [7]. The biotechnological potential of *S. polyschides* is further reinforced by its role as a green substrate for the biosynthesis of gold and silver nanoparticles that show antiproliferative and immunostimulant activity or its biostimulant effect, which enhances plant resistance to abiotic stressors [106,107]. Despite these advances, comprehensive evaluations of the species' chemical diversity, extraction protocols, biological mechanisms, and innovative applications remain limited. Moreover, challenges persist regarding extract standardisation, in vivo bioavailability data, and regulatory validation for human or agricultural use.

At a functional level, *S. polyschides* extracts have demonstrated multiple biological activities, including antioxidant activity (through neutralisation of reactive oxygen species and protection against cellular oxidative stress), anti-inflammatory activity (through the inhibition of pro-inflammatory mediators in cellular models), antimicrobial effects (through inhibition of pathogenic microorganisms, including Gram-positive and Gram-negative bacteria), hypoglycaemic action (associated with modulation of digestive enzymes and glucose metabolism) and anti-enzymatic activity (particularly the inhibition of tyrosinase, that has potential application in depigmenting cosmetics) [108]. These bioactivities make *S. polyschides* a valuable source of natural ingredients with functional applications, in line with the principles of the blue economy and marine sustainability. However, it is necessary to organise and critically analyse the current information on bioactive compounds present in *S. polyschides*, reinforcing the strategic value of this seaweed in the marine biotechnology landscape by bringing together scattered evidence and identifying research gaps.

7.1. Phytochemical Composition of Saccorhiza polyschides

The bioactivity of *S. polyschides* is intimately linked to its unique and diverse phytochemical profile. As a member of the brown algae, it produces a wide range of primary and secondary metabolites with documented pharmacological and ecological roles (Table 2). These compounds include polyphenols (notably phlorotannins), sulphated polysaccharides (such as fucoidans and laminarins), alginate, carotenoids (especially fucoxanthin), fatty acids, sterols, and terpenoids. The concentration and distribution of these compounds vary with environmental conditions, harvesting season, and the polarity of the extraction solvent employed [7,104,105]. Phlorotannin levels tend to increase under high light and UV stress [109], whereas fucoidan content is strongly influenced by salinity and nutrient availability [110]. Solvent polarity also plays a critical role in extraction efficiency, with intermediate-polarity solvents such as ethanol and methanol achieving higher phenolic recovery compared to aqueous extraction [111].

Table 2. Classes of phytochemical compounds identified in *Saccorhiza polyschides* and other brown seaweed and their biological activities.

Compound Class	Main Example(s)	Biological Activities	Potential Applications	References
Polyphenols	Phlorotannins	Antioxidant, anti-inflammatory, antimicrobial	Anti-ageing and skin cosmetics; nutraceuticals; functional foods	[112–115]
Sulphated polysaccharides	Fucoidans, laminarins	Anticoagulant, antiviral, immunomodulatory, antioxidant	Pharmaceutical agents; nutraceuticals; functional foods	[102,116]
Structural polysaccharides	Alginate	Gelling agent, stabiliser	Food industry; biomedical (wound dressings, drug delivery); tissue engineering	[117–119]
Carotenoids	Fucoxanthin	Antioxidant, anti-obesity, anti-tumour	Nutraceuticals; anti-ageing skincare; cancer-preventive supplements	[120,121]

Table 2. *Cont.*

Compound Class	Main Example(s)	Biological Activities	Potential Applications	References
Fatty acids	EPA, DHA	Anti-inflammatory, cardioprotective, nutraceutical	Functional foods; dietary supplements; dermatological formulations	[122,123]
Sterols	Fucosterol	Antioxidant, anti-inflammatory, neuroprotective	Nutraceuticals for brain health; anti-inflammatory supplements	[124,125]
Terpenoids	Sesquiterpenes, diterpenes	Antibacterial, antifungal, cytotoxic	Pharmaceutical leads (antimicrobial, anticancer); agricultural biocontrol	[126]

7.1.1. Phlorotannins

Saccorhiza polyschides contains predominantly phlorotannins, which are a type of polyphenol synthesised exclusively by brown algae. Phlorotannins are polymeric molecules synthesised via the acetate-malonate (polyketide) pathway. They play a vital role in defending algae against herbivory, ultraviolet rays, and oxidative stress. These compounds are composed of phloroglucinol units (1,3,5-trihydroxybenzene) connected via C–C and/or C–O–C couplings. They are classified into subclasses such as fucols, phlorethols, fucophlorethols and eckols based on their inter-phloroglucinol linkages [127]. In *S. polyschides*, phlorotannins have been detected in both crude extracts and semi-purified fractions, particularly in the ethyl acetate and diethyl ether fractions, which exhibit high radical-scavenging and enzyme-inhibitory properties [7]. Moreover, it has been demonstrated that extraction with solvents of intermediate polarity, such as ethanol and methanol, is an effective method for obtaining phlorotannin-rich extracts with high biological activity [114]. These compounds are of notable interest due to their capacity to modulate oxidative stress, inflammation, and microbial viability, also showing neuroprotective, anti-diabetic and anticancer activities [127–130]. The chemical structure and bioactivity of phlorotannins can vary depending on the environmental conditions of the macroalgae habitat. Factors such as salinity, light exposure and temperature can significantly affect the phenolic composition.

7.1.2. Sulphated Polysaccharides: Fucoidans and Laminarins

Brown algae represent a significant source of sulphated polysaccharides, with fucoidans and laminarins being among the most prominent. These compounds are branched heteropolymers, rich in fucose, and characterised by varying degrees of sulfation. The structure of fucoidans, complex and heterogeneous, directly influences their biological activity. Fucoidans are fucose-rich, sulphated polysaccharides known for their anticoagulant, antiviral, immunomodulatory and anticancer properties [131]. Fucoidans are integral components of the algal cell wall matrix, which have been shown to decrease the digestibility of carbohydrates and proteins by inhibiting digestive enzymes and by forming insoluble resistant complexes [132]. Their effect on different metabolic pathways is determined by the presence of sulphate groups and the monosaccharide composition. Laminarins, in turn, are β-glucans with antioxidant and prebiotic properties. This type of polysaccharide serves as an energy reserve in brown algae and is mainly accumulated under favourable growing conditions.

Studies in animal models and in vitro experiments suggest a positive impact on lipid and glucose metabolism regulation, as well as modulation of the gut microbiota [133,134]. Dietary supplementation with 5% aqueous extract of the brown alga *S. polyschides* over eight months significantly reduced weight gain and fat mass in mice fed a high-fat, highsugar diet [128]. These improved metabolic parameters led to changes in gut microbiota composition, including increased abundance of beneficial bacteria such as bifidobacteria and elevated production of short-chain fatty acids (SCFAs), which may contribute to improved energy homeostasis. The beneficial effects are attributed primarily to the high content of bioactive polysaccharides in the extract, which modulate digestive enzyme activity, enhance distal bile acid absorption, and support favourable microbial fermentation processes [132].

7.1.3. Alginate

Alginate is one of the primary structural polysaccharides found in the cell walls of brown algae, including in *S. polyschides* [135]. It is a linear copolymer composed of β-D-mannuronic acid (M) and α-L-guluronic acid (G) residues arranged in sequences that determine its physical properties [117]. While alginates have been studied extensively in species such as *Laminaria digitata* and *Ascophyllum nodosum*, *S. polyschides* is also recognised as a promising source of high-quality alginate [136]. Nonetheless, yield and composition of alginate in this species can vary depending on environmental conditions, seasonal factors and the maturity of the algal tissue [137]. Alginate extracted from *S. polyschides* exhibits excellent gel-forming ability, particularly in the presence of divalent cations such as calcium, making it valuable in a range of industrial applications [117,135]. These include its use as a gelling agent, thickener and stabiliser in the food industry, and as a biocompatible material in the pharmaceutical and biomedical fields [117]. Specifically, alginate's capacity for water absorption, film formation, and controlled release of active compounds makes it suitable for use in wound dressings, drug delivery systems, and cosmetic formulations [138]. As a natural, biodegradable and renewable marine biopolymer, alginate from *S. polyschides* represents a sustainable alternative for innovative applications in health, nutrition and bioengineering.

It is therefore pivotal to expand the range of applications for alginate beyond its traditional use as a gelling agent, thickener and stabiliser in the food industry. Its emerging uses in the pharmaceutical and biomedical fields are particularly notable, including in tissue engineering, controlled drug delivery systems and smart dressings, where its biofunctional properties are exploited to promote healing and cell regeneration. Kenny et al. [139] emphasise the importance of integrating sustainability principles into every stage of the alginate production process, from harvesting the algae to manufacturing the final product, to ensure its long-term economic and environmental viability. This approach establishes alginate as a strategic biomaterial for multiple sectors, aligning with the current demand for sustainable and innovative solutions, which involve selective harvesting, seasonal rotation, and integration of life-cycle assessment (LCA) and eco-certification, alongside valorisation of by-products for agricultural use.

7.1.4. Carotenoids: Fucoxanthin

Fucoxanthin is the most abundant carotenoid in *Saccorhiza polyschides* and represents one of the main photosynthetic pigments of brown algae, being responsible for their characteristic olive-brown pigmentation. Its chemical structure includes a unique allenic bond and conjugated carbonyl groups, which enhances singlet oxygen capture and results in significantly higher antioxidant capacity compared to other dietary carotenoids. This compound has attracted increasing interest due to its potent antioxidant activity, as well as the anti-obesity, anti-diabetic, and anticancer properties evidenced in experimental studies [121,140–142]. The ability of fucoxanthin to modulate the expression of genes involved in lipid metabolism and cellular apoptosis has been explored in clinical and preclinical trials. The concentration of fucoxanthin in *S. polyschides* is influenced by light intensity, harvest depth and composition of the marine environment.

7.1.5. Fatty Acids

Lipids, particularly polyunsaturated fatty acids (PUFAs), play a vital role in many biological processes. Although macroalgae typically contain only 1–5% lipids by dry weight, their PUFA content can be comparable to, or even greater than, that of terrestrial plants [101]. These fatty acids are essential as they are the precursors of bioactive mediators in humans, such as prostaglandins and leukotrienes [8]. The brown alga *Saccorhiza polyschides* has a diverse lipid profile, with a high proportion of PUFAs. The major PUFAs identified include eicosapentaenoic acid (EPA, 20:5 n-3), which has well-documented anti-inflammatory, cardiovascular and neuroprotective properties; arachidonic acid (AA, 20:4 n-6), a precursor of pro-inflammatory eicosanoids; linoleic acid (LA, 18:2 n-6), which is essential for maintaining membrane structure; and alpha-linolenic acid (ALA, 18:3 n-3), a metabolic precursor of EPA and DHA. These lipids contribute to the anti-inflammatory and cardioprotective bioactivity of macroalgae extracts, also acting as precursors of eicosanoids and other lipid mediators [122,143]. EPA is typically the dominant PUFA in *S. polyschides*, contributing to its strong anti-inflammatory and antioxidant potential. PUFAs represent approximately 25–35% of the total fatty acid composition in this species, often exhibiting a nutritionally beneficial omega-3 to omega-6 ratio greater than 1. Functionally, these PUFAs act as natural emollients, supporting the restoration of the skin's lipid barrier, mitigating inflammation, and aiding tissue regeneration. They are also associated with systemic health benefits, including improved cardiovascular and cognitive function, and the regulation of oxidative stress through modulation of inflammatory signalling pathways [144]. Seasonal and environmental factors strongly affect the lipid profile of *S. polyschides*, along with developmental stage and tissue type. The composition of PUFAs is particularly sensitive to environmental conditions: colder waters generally increase EPA levels, whereas elevated temperatures and nutrient limitation reduce overall lipid content and alter omega-3/omega-6 ratios [1]. Additionally, cultivation parameters have a significant impact on the synthesis and accumulation of specific fatty acids [5]. Lastly, the extraction of fatty acids is favoured by organic solvents such as chloroform-methanol, and this method is widely used for gas chromatography analysis [123].

7.1.6. Sterols and Terpenoids

Sterols are lipophilic compounds found in several species of algae, with structural functions in the cell membrane. In *Saccorhiza polyschides*, the presence of fucosterol is particularly relevant, given its antioxidant, anti-inflammatory, and antitumor activity documented in several studies [129,145]. Fucosterol also shows potential in the regulation of lipid metabolism and neuroprotection and is considered a promising compound for the development of nutraceuticals [124]. In addition to sterols, *S. polyschides* produces a variety of terpenoids with ecological and pharmacological functions. These compounds include diterpenes and sesquiterpenes with antibacterial, antifungal and cytotoxic activities, whose properties are still little explored in the specific literature for this species. The development of selective extraction methods and identification by mass spectrometry has contributed to the structural elucidation of these compounds [126]. Although less extensively studied, terpenoids and other halogenated secondary metabolites have been reported in related brown algae and are presumed to be present in *S. polyschides*. These compounds are thought to contribute to antimicrobial defence and allelopathic interactions in marine environments [146]. GC-MS analyses suggest the presence of mono- and sesquiterpenes [135].

7.2. Bioactive Properties

The biochemical composition and pharmacological activities of *Saccorhiza polyschides* led to a full range of bioactivities, namely antioxidant, antimicrobial, anti-inflammatory, anticancer, anti-obesity and cytoprotective properties [7,123,128,131,147]. The evidence shows a promising candidate for functional food ingredients, pharmaceutical development and cosmeceutical applications. Nevertheless, much of the existing data derive from in vitro studies. Further in vivo and clinical studies are needed to validate the potential of these compounds.

7.2.1. Antioxidant Effects

The antioxidant properties of brown seaweeds are primarily attributed to phlorotannins, which have demonstrated potent radical scavenging activity in various in vitro assays [8]. Although specific studies on *Saccorhiza polyschides* remain limited, recent research has confirmed that ethanolic extracts of this species exhibit antioxidant capacity, as measured by DPPH and FRAP assays, likely due to their rich content of phenolic compounds [7]. Ferreira et al. [123] quantified polyphenols and determined antioxidant activity by FRAP in methanolic extracts obtained from different biomasses. *S. polyschides* had a polyphenol content of 4.94 mg $GAE \cdot g^{-1}$ of extract and showed Fe^{3+} reducing activity (FRAP). However, studies conducted by Meirelles and colleagues [147] do not indicate that the species *S. polyschides* has DPPH antioxidant capacity. The authors of this study suggest that the observed differences may be related to the types of extract under study and their respective methods of extraction. Notably, there are other studies using different methodologies that have detected antioxidant activity [106,148]. The methanolic extract of *S. polyschides* has a low phenolic content of 2.07 ± 0.12 mg GAE/g DW and a low flavonoid content of 10.45 ± 0.6 mg quercetin/g DW [148]. Nevertheless, in the same study, *S. polyschides* demonstrated significant antioxidant activity in FRAP (25.6 ± 1.39 mg TE g^{-1} DW) and DPPH (EC_{50} of 0.045 mg/mL) assays, suggesting its potential as an antioxidant. These results point to a potential application in nutraceutical or cosmetic formulations, highlighting that the origin of the biomass, but also the methods used, can significantly influence antioxidant activity.

7.2.2. Antimicrobial Effect

Susano et al. [7] investigated the effect of different extracts of *Saccorhiza polyschides* on the growth of three microorganisms associated with dermatological conditions. The results indicated that although the fractions have an antimicrobial effect, their potency is relatively low compared to established pharmacological agents. The results obtained indicate that *S. polyschides* extracts have specific antimicrobial activity, being more effective against *Cutibacterium acnes*, a microorganism relevant in the pathogenesis of acne vulgaris. However, the activity observed is moderate, implying that the isolated use of these fractions may not be sufficient for clinical treatments. Nevertheless, they may represent potential adjuvants or sources of compounds for pharmacological development.

In terms of antifungal activity, the alga exhibited significant activity against the fungi *Botrytis cinerea* and *Penicillium digitatum*, but this activity varied according to the season, being stronger in autumn [148]. Therefore, *S. polyschides* could be a promising source of bioactive compounds to replace synthetic fungicides and contribute to more sustainable agricultural practices. Nonetheless, further studies are needed to purify and identify the bioactive compounds responsible for the antifungal and antibacterial activities.

7.2.3. Anti-Inflammatory and Immunomodulatory Activities

Brown algae-derived polysaccharides such as fucoidans have been extensively studied for their immunomodulatory effects, including the suppression of pro-inflammatory cytokines and enhancement of macrophage activity [131]. Preliminary investigations into *Saccorhiza polyschides* extracts suggest that they may have similar activity profiles, but the results are limited. However, there is a lack of mechanistic insights and comparative analyses with other brown algae species.

7.2.4. Anticancer Potential

Using marine extracts, such as those from *Saccorhiza polyschides*, to synthesise nanoparticles is a sustainable and innovative approach in experimental oncology. Innovative solutions reduce the use of toxic chemicals and increase the biocompatibility of the resulting nanoparticles, rendering them safer for biomedical applications [106]. The demonstrated anticancer activity is likely related to the presence of bioactive compounds in the extract, such as polyphenols and phlorotannins. These compounds act as reducing and stabilising agents during nanoparticle synthesis and have intrinsic therapeutic properties. While the in vitro results are promising, further research is needed in the form of in vivo studies and clinical trials to evaluate the safety, bioavailability and therapeutic efficacy of these nanoparticles. Future studies should also clarify the specific molecular mechanisms involved in anticancer and immunomodulatory activity.

7.2.5. Plant Biostimulant Potential

Agricultural applications have also been explored. A subcritical water extract of *Saccorhiza polyschides*, produced via green, solvent-free techniques, was characterised for mineral (macro and micronutrients), organic matter, nitrogen, iodine and other elements, supporting its suitability as a biofertilizer [149]. The extracts contain high concentrations of macronutrients, such as potassium (K), sodium (Na), sulphur (S), calcium (Ca) and magnesium (Mg), as well as essential micronutrients, including iron (Fe), zinc (Zn), manganese (Mn), copper (Cu) and selenium (Se). According to the same study [149], levels of potentially toxic elements such as cadmium, lead, nickel, arsenic and selenium are below phytotoxicity limits, rendering the extracts safe for agricultural use. The authors also emphasise that, due to the presence of elements such as iron, zinc, calcium, magnesium, iodine and selenium, the extracts can be used in biofortification strategies to enhance the nutritional content of food crops. The extracts can also be used as foliar or soil fertilisers, providing an alternative to conventional chemical fertilisers. These results suggest that *S. polyschides* extracts have the potential to be used in fertilisation and agricultural biofortification products.

A follow-up study [107] found that applying an aqueous crude seaweed extract to *Phaseolus vulgaris* (common bean) under saline stress (68 mM NaCl) improved plant growth, photosynthetic activity, nutrient uptake, and the activities of antioxidant enzymes. The extract spray produced the most consistent benefits in terms of IAA induction, soluble sugars and enzyme activities.

8. Biotechnological Applications

In recent years, *Saccorhiza polyschides* has attracted growing interest as a source of bioactive compounds and biostimulant materials. Sequential extraction has revealed notable antioxidant, anti-enzymatic, antimicrobial, anti-inflammatory and photoprotective properties. The extracts exhibited a high phenolic content and strong radical scavenging activity (DPPH, ORAC and FRAP), as well as potent tyrosinase inhibition and pronounced antimicrobial activity against *Cutibacterium acnes* ($IC_{50} \approx 12.4$ µg/mL) and *Malassezia furfur* [7]. There were no apparent cytotoxic effects, and some extracts also demonstrated photoprotective capacity.

Its agricultural applications have also been explored. A subcritical water extract of *S. polyschides*, produced using green, solvent-free techniques, was characterised for its mineral content (macro- and micronutrients), organic matter, nitrogen, iodine and other elements [149]. This supports its suitability as a biofertilizer. A follow-up study found that applying aqueous crude seaweed extract (SPE) to *Phaseolus vulgaris* (common bean) under saline stress improved plant growth, photosynthetic activity, nutrient uptake, and antioxidant enzyme activities [107].

Preliminary investigations into nanoparticle synthesis also suggest that *S. polyschides* extracts can act as reducing and capping agents in the green synthesis of gold and silver nanoparticles [106]. These nanoparticles may exhibit further biological activity due to fucoidan, a sulphated polysaccharide that is abundant in brown algae. However, detailed characterisation of nanoproducts and their bioactivities remains limited.

Overall, the evidence indicates that *S. polyschides* has considerable biotechnological potential. The antioxidant and anti-enzymatic activities of *S. polyschides* extracts underpin their use in dermatological formulations for anti-ageing and skin-brightening, whereas their biostimulant properties support agricultural applications, enhancing plant stress tolerance and nutrient assimilation [7,107]. Nevertheless, the isolation of bioactive compounds, the scalability of extraction protocols, toxicological profiling and in vivo validation remain important areas that have not yet been robustly addressed in the current literature.

9. Future Prospects

Despite increasing recognition of *Saccorhiza polyschides* as a key ecological and biotechnological species, considerable knowledge gaps persist regarding its physiology, chemical ecology, and potential for large-scale valorisation. Addressing these gaps requires integrative, multidisciplinary research efforts spanning molecular biology, chemical ecology, and applied blue biotechnology.

From an ecological perspective, the species' responses to environmental stressors—such as heatwaves, shifting upwelling regimes, storm frequency, and biological invasions—remain insufficiently characterised. The relative contribution of phenotypic plasticity versus genetic adaptation in determining local resilience is not well understood, especially near distributional edges [1,4]. Future research should incorporate longitudinal population monitoring, reciprocal transplant experiments, and genomic tools to explore adaptation across environmental gradients.

On the biotechnological front, the current understanding of *S. polyschides*' secondary metabolism is largely based on crude extracts and in vitro bioassays, which limit mechanistic insights and commercial translation. There is a pressing need to standardise extraction protocols, quantify seasonal and ontogenetic variation in metabolite content, and characterise bioactivities through in vivo and clinical models [7,147]. Advanced analytical platforms (e.g., metabolomics, proteomics, HPLC-MS/MS, NMR) should be coupled with bio-guided fractionation to isolate and elucidate lead compounds.

Furthermore, sustainable exploitation models for *S. polyschides* remain undeveloped. The species' fast growth and high biomass turnover suggest strong potential for low-impact harvesting or controlled cultivation, yet there are no published protocols for the aquaculture of this species. Only one pilot study was found that assessed the quality of the biomass produced in inland and offshore aquaculture, and determined that cultivation of the species is viable in both situations [5]. Further studies are therefore needed to determine nutrient supplementation and yield optimisation in coastal environments, ensuring the production of biomass for the industry and, at the same time, the protection of wild populations.

Finally, the potential of *S. polyschides* to contribute to blue circular economy models—as a source of nutraceuticals, green nanomaterials, and agricultural biostimulants—must be balanced against regulatory, environmental and socioeconomic considerations. The development of eco-certification frameworks, life-cycle assessments (LCA), and value chain analyses would help to guide responsible innovation and policy integration [27].

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