Type of article: review

Title: The sugar kelp Saccharina latissima I: recent advances in a changing climate

Running title: Saccharina latissima

Nora Diehl¹, Huiru Li², Lydia Scheschonka, Bertille Burgunter-Delamare³, Sarina Niedzwiedz¹, Silje Forbord⁴, Maren Sæther⁵, Kai Bischof¹, Cátia Monteiro⁶,⁷*

¹ Marine Botany, Faculty of Biology and Chemistry, University of Bremen, 28359 Bremen, Germany
² Key Laboratory of Mariculture (Ministry of Education), Fisheries College, Ocean University of China, Qingdao 266003, China
³ Matthias Schleiden Institute of Genetics, Bioinformatics and Molecular Botany, Friedrich Schiller University Jena, 07743 Jena, Germany
⁴ Department of Fisheries and New Biomarine Industry, SINTEF Ocean AS, 7465 Trondheim, Norway
⁵ Seaweed Solutions AS, Bynesveien 50C, 7018 Trondheim, Norway
⁶ CIBIO, Research Centre in Biodiversity and Genetic Resources - InBIO Associate Laboratory, Campus of Vairão, University of Porto, Vairão, Portugal
⁷ BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus of Vairão, Vairão, Portugal

* cmonteiro@cibio.up.pt

CIBIO, Research Centre in Biodiversity and Genetic Resources - InBIO Associate Laboratory, Campus of Vairão, University of Porto,
Rua Armando Quintas nº7 4485-661 Vairão, Portugal
Abstract

• Background

The sugar kelp Saccharina latissima is a Laminariales species widely distributed in the Northern Hemisphere. Its physiology and ecology have been studied since the 1960s, given its ecological relevance in western temperate coasts. However, research interest has recently been rising, driven mainly by reports of negative impacts of anthropogenically induced environmental change and by the increased commercial interest in cultivating the species with several industrial applications for the resulting biomass.

• Scope

We reviewed peer-review research articles, reports, doctoral theses, and book chapters that targeted Saccharina latissima published from 2009 to May 2023. We include earlier publications only in the few cases where some key knowledge has not been recently supported or contested.

• Conclusions

The comprehensive view of the ecology, physiology, biochemical and molecular biology of S. latissima given here can fuel our understanding of its survival in nature and fine-tuning of cultivation methods for several specific applications, promoting a sustainable resource. Recent developments in genomics, transcriptomics and epigenomics have contributed significantly to improving the understanding of genetic diversity and molecular mechanisms underlying plasticity and local adaptation. Due to its wide distribution, S. latissima has to cope with a large variability of different environmental conditions and possible interactions between drivers. Therefore, S. latissima has developed a variety of physiological and biochemical mechanisms to adjust to environmental changes. Survival, growth, photosynthetic performance, metabolism, and
enzymatic activity are strongly affected by abiotic conditions, such as temperature, salinity, nutrient conditions or ocean acidification. Massive alterations regarding abundance, depth distribution and seasonal growth patterns of *S. latissima* have been reported recently throughout its distribution range, likely in response to climate change. These biogeographic changes are expected to continue, and although much effort has been dedicated to studying *S. latissima* responses to environmental drivers, there are still large knowledge gaps.

**keywords**: acclimation - biogeography - climate change - local adaptation - macroalgae - marine ecology - metabolites - molecular biology - omics - physiology - seaweed - warming
Introduction

Kelps – in the strict sense only including representatives of the order Laminariales – are brown macroalgae (Phaeophyceae) growing on shallow rocky shores along the Atlantic, Pacific and Indian Oceans (Wernberg and Filbee-dexter 2019). In the Northern Hemisphere, kelps are mainly represented by the genera Alaria, Laminaria and Saccharina (Bolton 2010; Wernberg and Filbee-dexter 2019). The kelp Saccharina latissima (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders (Lane et al. 2006) is a boreal-temperate kelp widely distributed across the Northern Hemisphere, from polar to temperate regions (Fig. 1). The species grows on rocky shores in the upper subtidal to depths of 15–30 m, attached to hard rock using a branched claw-like holdfast as well as boulders and cobbles (Pehlke and Bartsch 2008; Bekkby and Moy 2011; Bischof et al. 2019). S. latissima gets its common name ‘sugar kelp’ from the sweet white powder (mannitol) that remains on the surface as the seaweed dries. Controversially, a sensory study indicated that consumers rated S. latissima as the saltiest, sourest, and bitterest of the three species studied, including Laminaria digitata and Alaria esculenta (Chapman et al. 2015). The sporophyte of S. latissima changes greatly in morphology depending on exposure and environmental factors (Fig. 2) (Lüning 1990a; Van den Hoek et al. 1995). This morphological plasticity has led to misidentification and taxonomic confusion. For example, S. angustissima has only recently been elevated to species level, being until then considered a morphotype of S. latissima (Augyte et al. 2018), while both S. longicruris and S. groenlandica were synonymized with S. latissima (McDevit and Saunders 2010; Longtin and Saunders 2015). Continued taxonomic reorganisation is expected since genetic data constantly provides new insights (for more see Life cycle and phenology). Indeed, several novel -omics techniques have been applied to S. latissima recently, although we still some major constraints (more on Advances in ‘-omics’).
How *S. latissima* adjusts to its environment has been extensively studied, although unbalanced among drivers and geographical regions (see *Responses to environmental drivers*). In seaweeds, biochemical compounds, including pigments, carbohydrates, antioxidants, lipids, fatty acids and proteins, vary in composition and concentration depending on environmental conditions (summarized in Amsler 2008; Wiencke and Bischof 2012; Hurd *et al.* 2014; Zhang and Thomsen 2019). Furthermore, biological interactions with other taxa have the potential to profoundly change *S. latissima* growth and survival and are summarized in *Biotic interactions*. In addition to seasonal effects or differences on larger global scales, many environmental parameters are driven by climate change at local scales, including ocean warming, melting of snow and sea ice, or increased terrestrial run-off over land (Masson-Delmotte *et al.* 2021). Genetic divergence, phenotypic plasticity, and differential acclimation capacities of distinct populations can have major implications on the responses of *S. latissima* to climate change. Throughout the entire Northern Hemisphere, populations of *S. latissima* have undergone extensive changes in abundance and depth, including both expansions and declines (e.g. Moy and Christie 2012; Filbee-Dexter *et al.* 2016; Casado-Amezúa *et al.* 2019) (see *Biogeographic patterns*). Hence, efforts to protect and reforest kelp ecosystems are increasing, including populations of *S. latissima*. Still, there are only a few specific conservation measures for kelps, and *S. latissima* in particular (see *Conservation and restoration*).

This review (part I) focuses on knowledge generated over the past ~15 years, particularly recent developments that provide new insights into the physiology and ecology of *S. latissima*. For a review of previous work, we refer the reader to Bartsch *et al.* (2008). The second part of the review (part II) focuses on the latest applied research, farming, and applications for *S. latissima*.
Life cycle and Phenology

*Saccharina latissima*, as all Laminariales, is characterised by a haplo-diplontic (haploid-diploid) heteromorphic life cycle (Fig. 3, Coelho *et al.* 2019). Sessile macroscopic sporophytes (2n) usually grow up to 4 metres (White and Marshall 2007) and strongly vary in their morphological appearance (Fig. 2, Diehl *et al.* 2023). Bigger specimens can be found in Arctic regions (~seven metres, June 2023; pers. comm. T. Vonnahme/S. Niedzwiedz). In general, the phylloid is elongate, undivided, and without a midrib but may have bullations (wrinkled surface) and wavy rims (Fig. 2, White and Marshall 2007) (White and Marshall 2007). Under moderate wave exposure, it develops narrow fronds and solid cauloids (Lüning 1990a; Van den Hoek *et al.* 1995). In addition, sporophytes tend to develop longer and heavier stipes at greater depths to enhance light capture (Ronowicz *et al.* 2022). The adult sporophyte exhibits basal meristematic growth. Sporophytes normally have a lifespan of three years, reaching their maximum size in the second growing season. However, specimens in the intertidal zone are annuals (Lee 1989).

When mature, sporophytes of *S. latissima* sporangia accumulate into easily recognizable sori and produce microscopic spores (n) (Fig. 3, Forbord *et al.* 2012). As free-living stages, spores and gametes are the phases that allow for dispersal, although limited to usually a few metres in kelps. Therefore, spores tend to settle near parent sporophytes (Schiel and Foster 2006). Sex is expressed at the haploid stage, and gametes and gametophytes present sexually dimorphic traits. Female gametophyte cells and nuclei are larger and rounder, while male gametophytes cells are smaller and tend to form filaments with more cells (Lüning and Neushul 1978; Goecke *et al.* 2022) which allows for identification and separation of sexes in the laboratory.
After the seminal work in the 1970s and 80s by Lüning in Europe and Lee and Brinkhuis in North America (e.g. Lüning 1980; Bolton and Lüning 1982; Lee and Brinkhuis 1988), research targeting the sexual reproductive stages of *S. latissima* has stalled. Recently, the research interest has risen again, driven by the need to manipulate the sexual life cycle in aquaculture. Hence, the onset of the reproductive period can be artificially controlled in the laboratory at several stages, allowing for scientific experimentation and improving the economic sustainability of seaweed aquaculture (Charrier *et al.* 2017). Also, methodological advances have allowed examining better the development of embryos to study cellular interactions in the embryo (Clerc *et al.* 2022), quantify DNA content in different cell types (Goecke *et al.* 2022) as well as improved protocols for studying embryogenesis (Theodorou *et al.* 2021).

At the spore stage, sporogenesis (production of spores) in the wild typically peaks during winter, being negligible in summer; however, the extent of the sorus formation period is dependent on the geographical region (Bartsch *et al.* 2008; Andersen *et al.* 2011; Boderskov *et al.* 2021). In the laboratory, sporogenesis is commonly induced by applying short-day light treatments and removing the meristem's basal blade, ensuring year-round spore availability for farmers and researchers (Forbord *et al.* 2012). In turn, a recent study reported higher and faster induction of sporulation in tissues under complete darkness than in short-day treatments (Boderskov *et al.* 2021). At the gametophyte stage, gametogenesis (maturation) can be induced or prevented by manipulating both biotic and abiotic conditions (see below). When gametogenesis is prevented, gametophytes remain vegetative and continue to grow, remaining viable for several years [at least one year reported in *S. latissima* (Ebbing, Pierik, *et al.* 2021); up to 30 years in several *Laminaria* sp. (Druehl *et al.* 2005; Martins *et al.* 2019)], also referred to as delayed gametophytes. Cultures of delayed gametophytes can function as genetic diversity reservoirs if
conserved by cryopreservation successfully applied to the gametophytes of *S. latissima* (Visch *et al.* 2019). In parallel, vegetative growth of gametophyte cultures can be boosted to produce enough biomass for cultivation facilities. In the wild, delayed gametophytes might represent a marine analogous of terrestrial seed banks, preserving the algae in a resting stage during harsh environmental conditions and allowing for a quick recovery once the conditions improve (Schiel and Foster 2006). However, the high levels of gene expression reported in vegetative gametophytes rather indicate that these gametophytes are metabolically active, calling for more research on the topic (Monteiro, Heinrich, *et al.* 2019). Recent methodological advances, such as using flow cytometry to isolate gametophytes of *S. latissima*, will allow for a more cost-effective gametophyte control at a larger scale (Augyte *et al.* 2020). For more information on aquacultural approaches, see Review II.

Female gametophytes’ maturation depends on the interaction of temperature, light quality and intensity, nutrients and biotic factors. Blue light is required for female gametophytes to mature, and as temperature rises, more blue light is required until an inhibitory species-specific threshold: 20°C in *S. latissima* (Lüning and Dring 1972; Lee and Brinkhuis 1988). Therefore, under laboratory conditions, if only exposed to red light, gametophytes will tend to grow vegetatively, as growth is unaffected by light quality (Lüning and Dring 1975). Recently, a study revealed that light quality was only significant at lower intensities; at higher intensities, both red and blue light induced maturation (Ebbing, Pierik, *et al.* 2021). Concerning nutrients, it has been shown that iron is necessary for oogenesis in kelps; hence, iron is typically excluded from nutrient solutions given to stock culture meant to grow vegetatively (Motomura and Sakai 1981; Lewis *et al.* 2013). Also, nutrient enrichment favours gametophyte growth, however, caution must be taken with the proliferation of diatoms, growth which is inhibited by adding Germanium dioxide
Concerning biotic factors, an essential role of the initial gametophyte density in maturation at all temperatures and light intensities has been recently reported, with concentrations above an optimum inhibiting fertilisation (Ebbing et al. 2020). The authors ruled reduced nutrients or light intensity as the cause of inhibition of fertilisation at high concentrations, hence, the underlying mechanism remains unknown. Another relevant biotic factor was the sex-ratio of cultures, with a higher proportion of female gametophytes decreasing the reproductive yield, most relevant at high culture densities (Ebbing, Fivash, et al. 2021).

Concerning phenology, in the wild, the maturation process of *S. latissima* typically peaks in winter, with sporophytes growing at the highest rate over spring, after which they senesce over summer due to high temperatures. However, in some sites, the species is annual (Boderskov et al. 2021). While reproduction can occur over several months, reproductive success and sporophyte growth depend on the month sporogenesis occurs.

In Denmark (temperate Atlantic), the percentage of fertile sporophytes (with visible sorus formation) varied markedly over the year, peaking in November and December and reaching null values in July and September. The number of viable spores released also varied monthly, decreasing steadily from a maximum in November to February, with a surge in March and April (Boderskov et al. 2021). Meiospores of *S. latissima* (from Alaska, USA; Arctic Pacific) released in July resulted in larger gametophytes but smaller sporophytes when compared with spores released in August (Raymond and Stekoll 2021) while spores originated from *S. latissima* collected in April (from Ireland, temperate Atlantic), growth rates of gametophytes were five to ten times higher than from spores originated in February (Nielsen, Kumar, et al. 2016). Concerning sporophyte growth, seasonal variation in growth rates is notable along the coast of Norway, with sporophytes from northern Norway reaching their maximum frond length and biomass around two
months earlier than sporophytes occurring in the south of the country (Forbord et al. 2020).

The fact that recent studies (Ebbing et al. 2020; Boderskov et al. 2021) sometimes contradict previous findings and/or show a more complex control of life cycle transitions highlights the need for further research on this topic, testing for more single and interacting drivers and accounting for possible site-specific responses.

Advances in ‘-omics’

Genomics

The decrease in sequencing costs has led to an increase in genomic resources for non-model species, such as brown algae, until recently severely understudied. Nuclear genomes are now available for some Phaeophyta species, e.g., *Ectocarpus sp.* (Cock et al. 2010), *Saccharina japonica* (Ye et al. 2015; Liu et al. 2019), *Undaria pinnatifida* (Shan et al. 2020; Graf et al. 2021) and plastid and mitochondria genomes are also mounting (e.g., Oudot-Le Secq et al. 2006; Chen et al. 2019; Rana et al. 2021). For *Saccharina latissima*, a mitochondrial genome is available (Wang et al. 2016) but not a nuclear genome, though efforts are underway (pers. comm. M. Cock; https://phaeoexplorer.sb-roscoff.fr/home/). Based on genetic data, a taxonomic reorganisation was proposed in 2006 that reassigned the previously *Laminaria saccharina* to *Saccharina latissima*, the currently accepted species name (Lane et al. 2006). Since then, other species have been synonymized with *S. latissima* (Neiva et al. 2018) highlighting the need for more extensive sampling across described and possible sites where *S. latissima* occurs to assess the intraspecific diversity better. The availability of validated DNA barcodes for the species – mitochondrial cytochrome c oxidase gene (COI) and ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (rbcL)
(Ratnasingham and Hebert 2007) is very important to confirm the identity of *S. latissima* samples. Moreover, it allows for the species to be detected in environmental DNA (eDNA) surveys, a method that allows for identification and quantification of several species from a unique sample using metabarcoding techniques (Deiner et al. 2017).

‘-Omics’ data can help describe underlying *S. latissima*’s mechanistic response to stress and hopefully help us predict adaptive potential to environmental change. Population structure, connectivity and genetic diversity in *S. latissima* have been studied using microsatellites at several regional scales (e.g., Guzinski et al. 2016; Luttikhuizen et al. 2018; Mooney et al. 2018). COI and microsatellites were applied to explore the amphi-polar distribution of the species (Neiva et al. 2018). More recently, microsatellites and double digest restriction site-associated DNA sequencing (ddRAD-seq) were used to quantify variation in single-nucleotide polymorphism (SNPs). To identify putative loci under selection in populations in the North-East Atlantic, SNPs and environmental variables (temperature, salinity, and others) were correlated in an exercise of seascape genomics (Guzinski et al. 2020). Also, novel is the application of genome-wide markers in parallel with phenotypic analysis to identify SNPs associated with traits of interest (e.g., higher growth rate) applied in NW Atlantic populations (Mao et al. 2020) an approach termed genome-wide association study (GWAS). Using a genomic selection approach, breeding values of *S. latissima*’s gametophytes were estimated and correlated with sporophytes’ phenotypic traits, especially wet and dry weight per metre; however, low genetic correlations among different years are concerning and need to be further explored (Huang et al. 2023). These approaches inform current attempts to establish breeding programs and, in the future, domesticate *S. latissima* (Yarish et al. 2017; Umanzor et al. 2021).
**Transcriptomics**

Responses of organisms to stress are often measured by physiological parameters such as survival, reproductive success, or growth, which are extremely relevant since they underlie species’ success. However, the underlying molecular mechanism often remains unknown even when significant physiological responses are found following exposure to a stressor (Bischof *et al.* 2019). Transcriptomics approaches focus on the expression of mRNA following a stimulus. Given the nature of mRNA, this approach measures a transient response that can be encoded at the DNA level or via epigenetic mechanisms (Stark *et al.* 2019). The application of this approach to non-model organisms has been rising in recent years, and methods have improved considerably in a short period. In the last decade, gene expression studies have developed from using microarray technology to RNA-sequencing, the latter providing more information at a lower cost and without relying on existing genomic knowledge as the former (Wang *et al.* 2009). Still, the use of transcriptomics in brown algae is lagging and has only been applied to a few species (e.g., *Laminaria digitata* (Liesner *et al.* 2022); *Undaria pinnatifida* (Graf *et al.* 2022) and mostly on the brown algal model *Ectocarpus* (e.g., Ahmed *et al.* 2014; Mignerot *et al.* 2019), and the commercially important *Saccharina japonica* (e.g., Liu *et al.* 2014; Zhang *et al.* 2021). While access to transcriptomic data in brown algae has been made easier by advances in (higher) model plants, namely *Arabidopsis thaliana* (e.g., Zhang *et al.* 2017), the evolutionary distance between Phaeophyceae and plants and other algae creates challenges. Namely, there is still a very low annotation rate of expressed genes in brown algae because functional studies are still not sufficiently conducted in this group as approaches such as reverse genetics are unavailable (Kroth 2013; Bringloe *et al.* 2020). However, promising advances have been made recently, and the use of CRISPR/Cas9
technology might enable a better understanding of the function of each gene in the metabolism of this group (Badis et al. 2021).

Gene expression patterns in *S. latissima* were first investigated using microarrays (Heinrich, Frickenhaus, et al. 2012; Heinrich, Valentin, et al. 2012; Heinrich et al. 2015, 2016) but more recently, RNA-sequencing was applied (Monteiro, Heinrich, et al. 2019; Monteiro, Li, et al. 2019; Pearson et al. 2019; Li, Monteiro, et al. 2020; Li, Scheschonk, et al. 2020) and reference genes for real-time-quantitative PCR (RT q-PCR) were developed (Xing et al. 2021). These studies explored interactive effects of temperature and irradiance (Heinrich, Valentin, et al. 2012), temperature and UV levels (Heinrich et al. 2015), interactive effects of temperature and salinity and its modulation by geographical variation in sporophytes (Monteiro, Li, et al. 2019; Li, Monteiro, et al. 2020); the response to darkness in sporophytes (Li, Scheschonk, et al. 2020), the interaction of temperature and sex of gametophytes (Monteiro, Heinrich, et al. 2019) as well as gene expression profiles during gametogenesis (Pearson et al. 2019) and a comparison between field and lab-cultivated sporophytes (Heinrich et al. 2016). Direct comparisons between the former studies are challenging since technologies and levels of experimental temperature applied differ. Nevertheless, these studies have revealed an intricate metabolic-wide programming of gene expression in the species in response to environmental drivers, discussed in *Responses to environmental drivers*.

Epigenomics

Epigenomics have been shown to play a crucial role in defining a phenotype (Moore et al. 2013; Anastasiadi et al. 2021). Given its sessile lifestyle, often low dispersal distances, and tendency to self-fertilise, *S. latissima* will likely rely on epigenetic mechanisms and variation. Epigenetic mechanisms play an essential role in a population’s adaptation and an individual’s coping mechanism in reaction to local conditions, ecotype differentiation...
(eco-phenotype), and rapid changes in local conditions (= local acclimation). For the aqua-/mariculture industry, knowledge regarding epigenetic mechanisms and implications of the findings already published are of value in terms of the importance of origin in spore sourcing and possibilities of priming. Priming is the exposure of preferably early life cycle stages (zygote or very young sporophytes) to a potentially lethal factor to harden the grown sporophytes for future encounters (Jueterbock et al. 2021).

The known, non-exclusive epigenetic mechanisms encompass non-coding RNA (ncRNA), histone modification, and DNA cytosine methylation (Boquete et al. 2021). They have been shown to play a role in establishing, maintenance and control of gene expression without changes to the DNA sequence (Anastasiadi et al. 2021), hence play a key role in the eco-evolutionary dynamics of a species (Calosi et al. 2016; Anastasiadi et al. 2021). Epigenetic modulation is tissue-specific and induced in reaction to local, abiotic, and biotic factors (Bossdorf et al. 2008; Richards et al. 2010; Lämke and Bäurle 2017). While all mechanisms become effective within a single generation, they can be stable across generations. In plants and hence, likely algae, very few epigenetic markers have been found that do not get transmitted to at least F1 and F2 generations (Anastasiadi et al. 2021). Research on epigenetic modulation and variation thereof is well-established in plant biology (Richards et al. 2017). However, in kelp, the study of epigenetics just gained momentum, with presently just a handful of studies (Phaeophyceae; (Cock et al. 2010; Liu et al. 2019; Fan, Han, et al. 2020; Teng et al. 2021; Schesonk et al. 2023). Regarding epigenetic mechanisms in the genus Saccharina, or the species S. latissima, only DNA cytosine methylation has been investigated so far (Liu et al. 2019; Fan, Han, et al. 2020; Teng et al. 2021; Schesonk et al. 2023). ‘DNA methylation’ in plants and algae describes the methylation of a cytosine in the DNA (5′-methylcytosine, 5-mC). DNA Cytosine methylation can occur within and outside genes in the sequence context.
of CG, CHG or CHH (‘H’ any base except G; (Bewick et al. 2017)). Genes are typically methylated in the CG context in animals (Schmitz et al. 2019), and methylation of the CG context in gene bodies of nuclear DNA is between 2 % and 86 % across Viridiplantae (Bewick et al. 2017). Methylations in the CG, CHG, and CHH contexts were found to act in silencing transposable elements in and outside of genes (Zhou et al. 2020) or to act in regulation of transcript expression (Dubin et al. 2015; L Zhang et al. 2018; Boquete et al. 2021). With this, they are important to consider as aspects of acclimation and adaptation processes. Moreover, it has been proposed in plants that CG methylation regulates the inheritance of other types of epigenetic information (Mathieu et al. 2007).

In terrestrial plants, DNA methylation of the chloroplast genome is uncommon in general (Fojtová et al. 2001), but in the kelp S. japonica, evidence for DNA methylation of the chloroplast genome has recently been published (Teng et al. 2021). Due to the putative direct influence on photosynthesis, evidence of methylation in the chloroplast genome is of particular interest regarding adaptation processes to rising temperatures.

Within brown algae, there seem to be group-specific occurrences regarding the types of epigenetic mechanisms. Histone modification has been observed in Ectocarpus siliculosus (Cock et al. 2010; Bourdareau et al. 2021), while DNA cytosine methylation was found to be negligible, which led to the assumption that DNA methylation is negligible in brown algae (Cock et al. 2010). However, in the kelps S. latissima and S. japonica, methylation playing a significant role in gene expression has recently been established, both for the nuclear and chloroplast genome (e.g. Fan et al. 2020; Yang et al. 2021; Scheschonk et al. 2023). Hence, the totality of epigenetic modifications of importance in S. latissima can likely only be assessed with testing for the respective mechanism in the species, or possibly the congener species (S. japonica), but cannot per se be implied by findings from other genera within the group of Phaeophyceae. The
studies focusing on *Saccharina* investigated the impact of cytosine methylation on both life cycle stages at transcriptomic level (*S. japonica*; Liu *et al.* 2019; Fan *et al.* 2020; Teng *et al.* 2021) and differences in cytosine methylation due to cultivation and latitudinal location (possibly heritable traits) observable on sporophyte stage (*S. latissima*; Schesonk *et al.* 2023, Schesonk unpubl. res.). Cytosine methylation was shown to influence gene expression in both life cycle stages (predominantly the non-heritable methylation variant CHH; ~56%, Yang *et al.* 2021), with higher methylations found in the gametophyte stage for both nuclear and chloroplast genome (Fan, Xie, *et al.* 2020; Teng *et al.* 2021). In both life cycle stages and genomes (nuclear and chloroplast), high levels of cytosine DNA methylation led to the silencing of the respective DNA sequence, acting as an additional control mechanism in gene expression (Fan, Han, *et al.* 2020). On population level, differences in cytosine methylation were observed to differ between latitudes in populations regardless of cultivation status (laboratory and wild; Schesonk *et al.* 2023, Schesonk unpubl. res.). This implies hereditary additional control imposed via cytosine methylation. As in other sequences, regions only became methylated during the cultivation process in both origins and DNA cytosine methylations likely are a mechanism of rapid adaptation, as changes in habitat (wild to cultivation) initiated epigenetic changes within a generation.

**Responses to environmental drivers**

**Temperature**

The composition and biogeographical distribution patterns of macroalgal communities are largely determined by temperature (Lüning 1984; Adey and Steneck 2001; Wiencke and Bischof 2012). Thus, climate change, particularly warming and marine heatwaves (MHWs), is a major threat to marine forests (e.g., Harley *et al.* 2012; Smale 2020). The
use of the term ‘MHW’ differs in different studies. In this review, we refer to the wording
of the individual studies.

Much is known about the general thermal characteristics of *Saccharina latissima*, mainly
in terms of survival, reproduction, photosynthesis and growth (Bartsch *et al.* 2008). Like
other kelps, *S. latissima* is a cold-temperate organism (Araújo *et al.* 2016). Sporophytes
from Helgoland presented optimum growth between 10 and 15°C (Bolton and Lüning
1982), although they tolerated an extensive range of temperature from 0–23°C for shorter
periods, with highly increasing mortality rates >20°C (Fortes and Lüning 1980; Lüning
1984, 1990b). Gametophytes of *S. latissima* exhibited a broader thermal tolerance
surviving temperatures down to -1.5°C and up to 23–25°C (tom Dieck 1993). Furthermore, sporophytes of *S. latissima* from Nova Scotia were found to have decreasing
growth rates with increasing temperatures between 11–21°C, high mortality at 18°C and
no survival at 21°C already after two weeks (E J Simonson *et al.* 2015). Contrary, *S.
latissima* sporophytes from Brittany survive up to 25°C for more than a week (Diehl *et
al.* 2021). Susceptibility to high temperature was shown to vary with environmental
thermal history, thus between seasons and years (Niedzwiedz *et al.* 2022). Differences in
temperature sensitivity were also found between laboratory cultures and field sporophytes
(Heinrich *et al.* 2016) and male and female gametophytes (Monteiro, Heinrich, *et al.*
2019). Consequently, generalisations about thermal limits based on a few studies should
be handled carefully.

Detrimental effects of suboptimal high temperatures on *S. latissima* include often
compromised growth (e.g., Bolton and Lüning 1982; E. J. Simonson *et al.* 2015), but it
can also lead to weakening the tissue structure (E. J. Simonson *et al.* 2015), increasing
blade erosion (Krumhansl *et al.* 2014; E. J. Simonson *et al.* 2015), enhanced biofouling
and epiphytism (Andersen *et al.* 2013; Forbord *et al.* 2020), complex modifications in
photosynthetic mechanisms, lowered chlorophyll \( a \) and fucoxanthin concentrations (Andersen et al. 2013), strongly increased de-epoxidation state of the xanthophyll cycle (DPS) (Nepper-Davidsen et al. 2019; Diehl et al. 2021) and reduced kelp carbon decomposition (Filbee-Dexter, Feehan, et al. 2022). In fact, exposure to elevated, though not lethal, temperature is harmful in the long term for \( S. \) latissima (Andersen et al. 2013; Nepper-Davidsen et al. 2019). Warming in the Arctic, however, might promote kelp populations, with densities higher in warmer areas than at comparable colder sites (Wiktor et al. 2022). At the warmer sites, \( S. \) latissima was also found at slightly greater depths. It is increasingly relevant to look at MHWs impact on seaweeds (Straub et al. 2019). Nevertheless, few studies simulating MHW scenarios were conducted on \( S. \) latissima (see Nepper-Davidsen et al. 2019; Diehl et al. 2021; Niedzwiedz et al. 2022). Strong correlations between MHW events over the last 60 years and loss of \( S. \) latissima forests in the North and West Atlantic were found (Filbee-Dexter et al. 2020). After a simulated three-week MHW event in Danish waters, most samples died within a few days at 24°C, and impairing effects of high but sub-lethal temperatures (18 and 21°C) were observed in a two-week recovery phase (Nepper-Davidsen et al. 2019). Thereby, interrelationships were demonstrated between reduced growth, reduced photosynthetic performance, carbon uptake, and pigment composition. At the same temperatures (11, 18, 21°C), no changes in C:N and phlorotannins were detected in specimens from Nova Scotia, USA (E. J. Simonson et al. 2015). The impact of local MHWs in summer on five European \( S. \) latissima populations ranging from southern Brittany to Spitsbergen revealed strong physiological and biochemical divergences between the populations. Increased mortality and decreased photosynthetic performance at the higher temperature amplitude treatments were detected exclusively in the rear-edge populations from Helgoland (German Bight) and Brittany, while the Arctic population was unaffected (Diehl et al.
In Norway, strong differences in the physiological condition of *S. latissima* were observed, showing, e.g. decreased growth and more erosion in a hot year compared to a cooler year (Armitage *et al.* 2017). The impact of MHWs also varies by year and season, as shown for field sporophytes from Helgoland (Niedzwiedz *et al.* 2022). *S. latissima* was more sensitive to high temperatures at the end of summer and during an extremely warm year.

High and excessively low temperatures alter physiological and biochemical properties of *S. latissima*. Overall, wild *S. latissima* from Iceland revealed positive correlation between carbohydrates and negative correlations of proteins with the environmental temperature (Coaten *et al.* 2023). Lower pigment concentrations were found at temperatures <10°C, whereas DPS was significantly higher compared to higher temperature treatments (Olischläger *et al.* 2017; Monteiro, Li, *et al.* 2019; Li, Monteiro, *et al.* 2020) and higher phosphorylation rates of mitogen-activated protein kinases were measured at 2 than at 7°C (Parages *et al.* 2013). Additionally, strongly enhanced mannitol concentrations were detected in young sporophytes from Brittany after 0°C treatment, indicating a strong anti-freezing response of the species (C Monteiro *et al.* 2020). Consequently, *S. latissima* will most likely rather benefit from the predicted rising temperatures in subpolar and polar regions (Filbee-Dexter *et al.* 2019; Diehl and Bischof 2021) as physiological functions of *S. latissima* will be enhanced (Iñiguez *et al.* 2016). Yet, darkness during the polar night seems to outcompete the positive effects of warming (Schieshonk *et al.* 2019), and low water temperature is a requirement for survival (Gordillo *et al.* 2022). Warming in winter accelerated weight loss of young sporophytes over four months of darkness, with approx. 50% at 8°C and 40% at 3°C (Gordillo *et al.* 2022). Further, dark respiration of Arctic *S. latissima* sporophytes increased with increasing temperatures (3, 7, 11°C) (Niedzwiedz and Bischof 2023).
Arctic *S. latissima* gametophytes did not survive 20°C in the lab but grew at 15°C and below, with higher growth rates between 10–15°C than 5°C (measured in length of both male and female gametophytes) (Park *et al.* 2017). Another laboratory study targeting Arctic gametophytes showed that they survive at 20°C through heat stress mechanisms that were extensively induced at the transcriptomic level at that temperature, while at 4 and 12°C, which did not occur (Monteiro, Heinrich, *et al.* 2019). If we consider spore germination, a higher temperature of 9°C increased the germination rate of spores compared to 5°C for Arctic individuals (Zacher *et al.* 2016). In an experiment with individuals from North America, at temperatures between 4 and 12°C, lower temperatures negatively influenced the size of gametophytes and sporophytes and the production of eggs and young sporophytes (Raymond and Stekoll 2021). When looking at sexual reproduction, sex-biased responses to temperature were found, with male gametophytes being more resilient to higher temperatures than females – females grew at a slower rate, and pathways related to fecundity were repressed (Monteiro, Heinrich, *et al.* 2019). Similarly, higher temperatures increased the proportion of male gametophytes in an earlier study (Lee and Brinkhuis 1988), but not more recently (Park *et al.* 2017). Recently, the impact of increasing temperatures in the Arctic in combination with decreased salinity (Monteiro, Li, *et al.* 2019; Diehl and Bischof 2021), increased pCO$_2$ (Olschläger *et al.* 2014, 2017; Iñiguez *et al.* 2016), UV radiation stress (Parages *et al.* 2013), increased sedimentation (Zacher *et al.* 2016) or increased nutrient conditions (Diehl and Bischof 2021) were investigated. All these studies showed that growth, photosynthetic performance, biochemical composition and also transcriptomics of *S. latissima* were strongly affected by temperature. The species would rather benefit from higher temperatures in Arctic regions, whereas the impact of the other drivers was less pronounced, or there was no impact at all. On the other hand, the early stages of *S.
*latissima* appear vulnerable to strong warming and interaction with other factors in the Arctic. Overall, strong interactions between light and temperature were also detected in different microstages, highlighting UV-B radiation’s impairing effect (Müller et al. 2008, 2012). Increased production of superoxide anion radicals (O$_2^*$) was measured in gametophytes under increasing temperatures between 2 and 18°C and slightly under UV radiation (Müller et al. 2012). Temperatures up to 21°C combined with hyposalinity diminished the spore settlement of *S. latissima* from Alaska (Lind and Konar 2017). While higher temperatures generally lead to higher germination rates of Arctic *S. latissima* spores, temperature and grazing had an interactive effect (Zacher et al. 2016). At 5°C, germination rate was higher when grazers were present, and at 9°C, the reverse happened. The same pattern holds for the density of juvenile sporophytes. The species-specific interactive effects revealed a differential response between co-occurring kelps in the Arctic.

Large ecosystem shifts from kelp canopies to turfs or barrens have been reported. Generally, the loss of *S. latissima* populations has been attributed to warming to a certain extent. In Norway, *S. latissima* communities were observed to be replaced by ephemeral, filamentous turf algae (Moy and Christie 2012; Christie, Andersen, et al. 2019). This ecosystem shift was proposed to have been mainly driven by extraordinarily high temperatures over summer, in combination with eutrophication (Moy and Christie 2012). Loss of *S. latissima* beds and shifts to turf-dominated ecosystems were also observed in Nova Scotia, Canada, caused by increased temperature and diverse unbalanced multitrophic interactions (Filbee-Dexter et al. 2016). Yet, the impacts of interactions between MHWs and biota on kelp forests appear to be extremely dynamic and complex (e.g., Christie, Gundersen, et al. 2019; McPherson et al. 2021). Thus, multifactorial experimental set-ups are of major importance in identifying the complexity of climate change.
change reactions and local anthropogenic stressors (Strain et al. 2014). Overall, much research has been done on Arctic and Norwegian populations of S. latissima. Contrary, the knowledge about the acclimation potential of southern populations has been scarce and should receive particular attention in future studies.

**Hydro-optics**

As photosynthetic organisms, seaweeds are dependent on light availability to survive. Irradiance effects on S. latissima have already been well studied for decades and summarised in Bartsch et al. (2008). Both extremely high and low Photosynthetic Active/Available Radiation (PAR) and mainly UV radiation (UVR) cause modifications in multiple biochemical and physiological processes in S. latissima, with early-life stages and adult sporophytes showing differences in susceptibility.

More recent studies demonstrated that reduced irradiance negatively affects the growth performance of sporophytes in situ (Spurkland and Iken 2011; Forbord et al. 2020) without diminishing the photosynthetic performance (Spurkland and Iken 2011) but still promoting biofouling (Forbord et al. 2020). The maximum modelled distribution depth of S. latissima in Arctic fjords followed the extent of the meltwater plume, being shallower close to the glaciers and deeper in outer fjord regions (Niedzwiedz and Bischof 2023). Pronounced variability was found in different parts of the phylloid regarding the long-term storage of carbohydrate laminarin in Arctic field sporophytes between October and early February (Scheshonk et al. 2019). Also, other biochemical components, such as mannitol or nitrogen, strongly declined during the dark season. Interestingly, darkness appeared to be optimal for artificial sporogenesis of Danish S. latissima compared to other light levels (20-120 μmol photons m⁻² s⁻¹) (Boderskov et al. 2021).

A few studies suggest that other response variables, beyond the main physiological and biochemical parameters, are involved in acclimating to light variations in S. latissima.
Enhanced release of organic iodine and reduced release of reactive organic bromine and chlorine were found after PAR (23 \(\mu\)mol photons m\(^{-2}\) s\(^{-1}\)) + UVR exposure (Latumus et al. 2010). The impact of PAR (~10 \(\mu\)mol photons m\(^{-2}\) s\(^{-1}\)) and UVR were also investigated in chloroplasts of vegetative (non-soral) and fertile (soral) tissue of \textit{S. latissima} (Holzinger et al. 2011). While fertile tissue cells were not affected by PAR + UVR, negative effects were found in vegetative parts. For instance, decreased optimum quantum yields (\(F_v/F_m\)) were measured under UVR treatment, and the chloroplast structure was altered, i.e., including more physodes. Another study revealed that the oxygen consumption rate of \textit{S. latissima} was significantly higher at high light (300 \(\mu\)mol photons m\(^{-2}\) s\(^{-1}\)) compared to low light conditions (3 \(\mu\)mol photons m\(^{-2}\) s\(^{-1}\)) (McDowell et al. 2015).

Sedimentation and epibiosis have a strong impact on light availability. \textit{S. latissima} can withstand short-term sediment cover (Roleda and Dethleff 2011; Picard et al. 2022), whereas longer burial negatively affects its vitality and morphology (Roleda and Dethleff 2011). Furthermore, it was shown that sediment from melting ice weakened the recruitment of \textit{S. latissima} (Zacher et al. 2016). The overgrowth with epibionts, and consequent shading, can reduce growth and survival of the species (Andersen et al. 2018).

Polar night imposes very special conditions for Arctic \textit{S. latissima}, especially when combined with future increases in winter temperatures. Treatments of light/dark or darkness alone seem to have a greater effect on \textit{S. latissima} than the various temperatures applied (0, 4, 8°C) (Scheshonk et al. 2019). The lower laminarin content at elevated temperatures (8°C) suggests that prolonged darkness may be a problem for \textit{S. latissima} under future temperature trends.

In a comparable study on \textit{S. latissima} sporophytes, low temperatures (2°C) and PAR (10 \(\mu\)mol photons m\(^{-2}\) s\(^{-1}\)) + UVR treatments activated the rapid phosphorylation of mitogen-
activated protein kinases, while UVR generally impaired the photosynthetic performance (Parages et al. 2013). A study in juvenile Arctic sporophytes revealed that Fv/Fm remained unchanged in low PAR treatments (~24 µmol photons m⁻² s⁻¹), even with the addition of UVR, and that it decreased under high light stress (~110 µmol photons m⁻² s⁻¹), especially combined with UVR (Heinrich, Valentin, et al. 2012; Heinrich et al. 2015). Remarkably, the photosynthetic performance was particularly severely reduced at high PAR × high temperatures (17 vs. 2 and 7°C) (Heinrich, Valentin, et al. 2012), whereas when UVR was included in a comparable set-up, the strongest inhibition occurred in the high PAR + UVR treatment at 2°C, compared to 7 and 12°C (Heinrich et al. 2015). Thus, high temperatures appear to mitigate the impairing effects of UVR on S. latissima sporophytes. However, these observations were more pronounced in laboratory cultures than in field sporophytes (Heinrich et al. 2015).

Investigating the effects of irradiance (<10 and 30–50 µmol photons m⁻² s⁻¹), temperature (4, 8, 12°C), and season on gametophyte growth and reproduction of S. latissima, revealed that gametophyte length, sporophyte length, fraction of female gametophytes with eggs, and fraction of female gametophytes with sporophytes were all mainly altered by temperature and season (Raymond and Stekol 2021). Irradiance significantly affected all response parameters except for gametophyte length; however, interactions were only found for sporophyte length (irradiance × temperature).

In the last decade, transcriptomic responses of S. latissima to different light conditions have been investigated (Heinrich, Valentin, et al. 2012; Heinrich et al. 2015, 2016; Li, Scheselonk, et al. 2020; Xing et al. 2021). On the time scale of 24 h exposure, the combination of high temperature and high photosynthetically active radiation (PAR) induced more transcriptomic regulation than low temperature and low PAR. High PAR and high temperature widely downregulated genes involved in photosynthesis, including
photosystem I/II components, thylakoid protein and light harvest complex proteins with strong folds (up to 60-fold). In contrast, genes encoding reactive oxygen species (ROS) scavenging enzymes, oxygen heat shock proteins (HSPs), and proteins involved in proteolysis were upregulated under high PAR and high-temperature conditions. On the other hand, the combination of high PAR and low temperature generally upregulated genes encoding photosynthesis, ROS, and HSPs, whereas downregulated genes encoded proteolysis-related protein. The 24 h exposure to UVR also induced a wide regulation of gene expression, mainly including photosynthetic components, DNA repair, vitamin B₆ biosynthesis and ROS scavengers, which supported that UVR negatively affected photosynthesis and damaged DNA (Heinrich, Valentin, et al. 2012). The long-term (14 days) exposure to PAR, UVR and temperature combinations resulted in large transcriptomic reprogramming, which did not cause physiological adjustments. The combination of high PAR and UVA caused more gene regulation than the single exposure to high PAR or UVR and mainly upregulated genes encoding photosynthetic components, pigment metabolisms, glycine, serine and threonine metabolism and ROS scavenging enzymes. The transcriptomic responses of *S. latissima* to 14 days of darkness at two temperatures revealed that darkness induced more regulated genes than increased temperature (Li, Scheschonk, et al. 2020). Darkness downregulated genes encoding enzymes involved in glycolysis and metabolite biosynthesis. Some energy-consuming processes, e.g., photosynthetic components and transporters' biosynthesis were also repressed. On the contrary, genes coding for the catabolism of lipid and laminarin, glyoxylate cycle and signalling were upregulated in darkness, pointing out the possible energy source of *S. latissima* during the polar night.
Salinity

Coastal salinity frequently varies with tidal ranges, precipitation, freshwater plumes from rivers or terrestrial run-offs (Lüning 1990a), increasing with climate change (Holt et al. 2010; Masson-Delmotte et al. 2021). Salinity variation is particularly relevant for the physiology of *S. latissima* in Arctic fjord systems due to enhanced sea ice and glacier melting (Hanelt *et al*. 2001; Svendsen *et al*. 2002; Sundfjord *et al*. 2017). Fluctuations in salinity lead to osmotic stress with consequences on the physiological and biochemical level, which is overall well studied for seaweeds (see Karsten 2012 and references therein) but not on *S. latissima*. Even though *Laminaria sensu lato* is considered a rather stenohaline genus (Bartsch *et al*. 2008), *S. latissima* is known to physiologically tolerate broad ranges of salinities between $S_A$ 5 and 60 (Karsten 2007), although young sporophytes were shown to have a tolerance of down to $S_A$ 11 under laboratory conditions (Karsten 2007; Peteiro and Sánchez 2012), which allows the species to inhabit Brackish waters (Nielsen, Paulino, *et al*. 2016; Mortensen 2017). Still, hyposalinity results in decreased growth (e.g., Spurkland and Iken 2011; Marinho *et al*. 2015; Bruhn *et al*. 2016; Forbord *et al*. 2020), diminished photosynthetic performance (e.g., Karsten 2007; Spurkland and Iken 2011; Peteiro and Sánchez 2012), and loss of pigmentation (Karsten 2007; Peteiro and Sánchez 2012). Furthermore, decreased carbon dioxide exchange rates were detected at low salinities (Mortensen 2017). Generally, salinity has a strong effect on the biochemical composition of *S. latissima*. For instance, the content of sulfated fucose-rich polysaccharides, measured with fucoidan, generally increased at absolute salinities ($S_A$ 15-25) in the Baltic Sea, however, the pattern did not hold for all locations (Bruhn *et al*. 2017). Samples of *S. latissima* from an Atlantic population hold higher content of fucose-containing sulfated polysaccharides than a Baltic one, which experiences lower salinity variation than the former population (Ehrig and Alban 2015).
Along the Baltic Sea’s salinity gradient, salinity's effects were observed in various carbohydrates, proteins, pigments and nitrogen contents (Nielsen, Kumar, et al. 2016). However, it should be noted that these observations were not necessarily consistent between different populations or experimental frameworks (Manns et al. 2017; Diehl et al. 2023).

Little is known about the interaction between salinity and other factors in *S. latissima*, with only salinity × temperature investigated so far. Recent studies revealed that hyposalinity is potentially highly stressful for *S. latissima* in combination with temperature variation. In the Baltic Sea, low salinity in combination with high summer temperatures decreases the productivity of *S. latissima* due to high physiological stress in cultivated seaweed (Nielsen et al. 2014). Arctic field adult sporophytes of *S. latissima*, however, were almost unaffected by temperature increase (4°C to 10°C) and hyposalinity (SA 25) under mimicked field conditions (Diehl et al. 2020), even though slightly increased growth and photosynthetic performance ($F_v/F_m$) were detected at higher temperatures. In contrast to adult sporophytes, more pronounced effects of both parameters and some interaction of salinity and temperature are detectable in the early life stages of *S. latissima*. For instance, elevated temperatures and low salinities decreased spore settlement and gametophyte growth (Lind and Konar 2017). The impact of temperature × salinity interaction was investigated in young sporophytes from Brittany and the Arctic by running comparable experiments on specimens from both locations (Monteiro, Li, et al. 2019; Li, Monteiro, et al. 2020; C Monteiro et al. 2020). Remarkably, almost similar effects were observed in young sporophytes from the two regions. Lower salinities had little negative impact on growth and $F_v/F_m$ and modified the xanthophyll-cycle pigment pool. The effects of different temperatures were more pronounced, revealing ameliorating effects of higher and diminishing effects of lower temperatures.
At the transcriptomic level, an ameliorating effect of high temperature was observed for algae from Brittany and Svalbard (Monteiro, Li, et al. 2019; Li, Monteiro, et al. 2020). The treatments at low salinity (SA 20) at 0°C and 8°C elicited more differentially expressed genes than at 15°C and low salinity. Geographical variation also played an important role as the combination of low salinity and low temperature was especially stressful for sporophytes from Brittany (not exposed to 0°C in their environment of origin) than Svalbard. In response to low salinity, metabolic pathways such as photosynthesis and carbon assimilation were down-regulated, and some gene coding enzymes contributed to the xanthophyll cycle and cell wall metabolism. Moreover, genes coding for heat shock proteins and enzymes involved in the synthesis of mannitol and proline were not significantly regulated during this experiment, revealing perhaps that the stress was mild or that the regulation of salt stress is more intricate than expected, involving several other pathways than already described for other environmental drivers.

**Nutrients**

The macronutrients nitrogen (N) and phosphorus (P) serve as essential elements for photosynthesis and growth, of which N is considered the main limiting resource for macroalgal productivity (Roleda and Hurd 2019). An overarching overview of nutrient physiology and factors affecting nutrient uptake in seaweeds is given by Roleda and Hurd (2019). Effects of various nutrient regimes have been well investigated for Laminariales, including *Saccharina latissima* (summarised in Bartsch et al. 2008). Laminariales can accumulate nutrient reserves over winter when nutrient conditions are favourable (Bartsch et al. 2008; Lubsch and Timmermans 2019) and have an optimum environmental nitrate concentration of about 10 μM but also tolerate oligotrophic conditions (Kerrison et al. 2015). Still, nutrient depletion is already long known to have negative impacts on the physiological status of *S. latissima*, resulting, for instance, in lower growth rate and
lower photosynthetic performance (Williams and Herbert 1989; Gerard 1997a; b; Korb and Gerard 2000; Roleda and Hurd 2019). A recent study revealed that young sporophytes' development, density, and length growth were also diminished under nutrient-poor conditions (Raymond and Stekoll 2021). Nitrate (NO$_3^-$) uptake rates are linearly related to the substrate concentrations for both N-limited and N-saturated young sporophytes, indicating that *S. latissima* requires high ambient nitrate concentrations in the environment to have rapid growth. The sporophytes with deficient internal nitrogen pools exhibited higher uptake rates of NO$_3^-$ than sporophytes with higher internal nitrogen pools (Forbord *et al.* 2021). As a result, the growth of *S. latissima* decreases significantly over summer, yet it can continue to grow for some time even under low nutrient conditions (Nielsen *et al.* 2014; Lubsch and Timmermans 2019; Forbord *et al.* 2020). The species’ ability to store nutrients is also considered an advantage in direct competition for habitat with other seaweeds (Armitage *et al.* 2017). Several physiological parameters of *S. latissima* are also limited by bioavailable P (Bruhn *et al.* 2016). Comparing the effect of P enrichment on spores and gametophytes in February and April showed that growth was supported by elevated P levels (23–69 μM), and earlier gametophyte development appeared under P-treatment in April (Nielsen, Kumar, *et al.* 2016). Sufficient or slightly enhanced N supply is reported to have beneficial effects on the response of *S. latissima* with respect to several environmental stressors. For instance, it was found that UV damage in *S. latissima* can be mitigated or prevented by enriched (50 μM) N supply (Davison *et al.* 2007). Recent studies on nutrient × light interactions showed the high importance of nutrients (N + P). Specimens were overall not much altered by the different natural light intensities, but growth and intracellular N were positively affected by elevated nutrient conditions (Boderskov *et al.* 2016; Jevne *et al.* 2020). The contents of total C decreased, and chlorophyll *a* and fucoxanthin increased under nutrient-rich
conditions and varying between frond parts (Boderskov et al. 2016). No distinct interaction of light and nutrients were determined. Yet, interactions of nutrients and light were found regarding sterolic compounds (de Jong et al. 2021). Highest sterol content was measured at low nutrient and high light, though enhanced nutrient conditions combined with high light resulted in unchanged or even decreased concentrations. However, the authors attribute the results to reduced photosynthetic function rather than nutrient fluctuations.

A recent study on the interaction of nutrient availability and wave exposure revealed that fronds grow narrow under high wave exposure and high nutrient concentrations and wider under low nutrient concentrations (Zhu et al. 2021). Additionally, the frond surface’s biomass, shape, and C:N ratio were affected by waves, nutrients, and their interaction. Thereby, specific morphological changes can compensate for nutrient-poor conditions.

Eutrophication has become a common phenomenon in coastal regions, mainly triggered by anthropogenic nutrient input (Skjoldal 1993; Norderhaug et al. 2015). Moderate enhanced N (~3–20 µM) supply was already reported to positively influence the physiology of S. latissima (e.g., Chapman et al. 1978; Conolly & Drew 1985; Gerard 1997). However, severe eutrophication levels combined with high temperatures are detrimental (Moy and Christie 2012). Contrary, Arctic primary production was reported to be limited due to low nutrient availability (< 1 µM), but nutrient concentrations are expected to increase and alter seasonal patterns as melting, and thus freshwater run-off, increases and occurs earlier (Zacher et al. 2009; Filbee-Dexter et al. 2019). Only marginal positive effects of nutrient enrichment on the physiological and biochemical status were reported (Gordillo et al. 2006; Diehl and Bischof 2021). Temperature effects outcompeted nutrient supply, and no significant interactions of temperature and nutrients were determined (Diehl and Bischof 2021).
Saccharina latissima can act as a bioremediator. In investigating the potential of S. latissima to remove nutrients from eutrophic brackish fjord systems and the parallel effects on several chemical compounds of the species, it was found to survive hyposalinity under elevated nutrient conditions (Mortensen 2017). Higher protein and tissue N content and lower contents of β-glucans and iodine were found in young S. latissima maintained in brackish water with nutrient supplementation compared to conditions in seawater with adequate nutrient supply. Furthermore, the study revealed that the beneficial effects of increased nutrient levels were greater in young sporophytes than in older ones.

Regarding aquaculture research, the nutrient regime is of prominent importance. The potential of algae to sequester nutrients poses great potential for establishing integrated multi-trophic aquaculture, which aims to reduce eutrophication caused by intensive fish farming (Kim et al. 2015; Marinho et al. 2015). While removing large amounts of N from the environmental system, S. latissima benefits from the elevated nutrient conditions by enhancing its growth by up to 50% compared to a reference site (e.g., Sanderson et al. 2012; Broch et al. 2013; Wang et al. 2014; Fossberg et al. 2018). Different studies describe enhanced growth, photosynthetic activity, N (protein) concentration and pigment content, resulting in higher biomass quality of cultivated S. latissima (Sanderson et al. 2012; Wang et al. 2014; Rugiu et al. 2021) (see Saccharina latissima II for further information).

The effects of micronutrients on S. latissima are still largely unexplored. Trace metals are essential for various metabolic functions in seaweeds but can also be harmful at higher concentrations (Stengel et al. 2005 and references therein). The only studies on the effects of microelements, e.g., iodine or copper, on S. latissima were conducted more than 30 years ago (Hsiao and Druehl 1973; Brinkhuis and Chung 1986; Chung and Brinkhuis
However, for other Laminariales, iodine has been shown to support osmotic functions (Nitschke and Stengel 2014), iron had a strong impact on gametogenesis (Raymond and Stekoll 2021), and copper modified the transcriptomic profile (Zhang et al. 2019). To what extent abiotic factors and distribution patterns affect the concentration of microelements in *S. latissima* is unknown. In addition, the fact that *S. latissima* accumulates micronutrients from the environment (e.g., Schiener et al. 2015; Bruhn et al. 2016; Nielsen, Manns, et al. 2016) is of high relevance to the food industry as concentrations above certain thresholds can exclude *S. latissima* biomass from human consumption (e.g., Bruhn et al. 2019; Kim et al. 2019; Roleda et al. 2019).

**pH**

Ocean acidification (OA) refers to the ongoing decrease in seawater pH and variations in carbonate chemistry resulting from the substantial marine uptake of CO₂ since the Industrial Revolution (Doney et al. 2020). Studies about the effects of OA on *Saccharina latissima* have mainly focused on growth, photo-physiology and biochemistry. OA has been reported to increase (Gordillo et al. 2015; Olischläger et al. 2017; Young and Doall 2021), not affect (Iñiguez et al. 2016; Olischläger et al. 2017) or even decrease (Swanson and Fox 2007) the growth rates of *S. latissima* according to the duration of the experiment and the levels of partial pressure of CO₂ (pCO₂) applied. Photophysiology, reflected by different parameters (e.g., pigments, photosynthetic O₂ evolution and CO₂ uptake, and chlorophyll *a* fluorescence), also showed various responses under OA conditions. For example, in some studies, it was shown that OA (about 1000 and 800 ppm, respectively) significantly increased the rates of photosynthetic CO₂ uptake and O₂ evolution rates (Longphuirt et al. 2013; Nunes et al. 2016), whereas another study failed to detect differences in net photosynthesis rates between ambient (390 ppm) and increased pCO₂ levels (1200 ppm)(Iñiguez et al. 2016). Regarding the biochemistry, *S. latissima* was
found to utilise more CO₂ than bicarbonate (HCO₃⁻) as the photosynthetic carbon source, revealed by the signatures of carbon stable isotope (δ¹³C) (Young and Doall 2021). The contents of soluble carbohydrates, nitrogen, and lipids changed in sporophytes of a temperate population of S. latissima whereas remained stable in the Arctic samples when pCO₂ increased alone (Olischläger et al. 2014). Saccharina latissima has been found to mitigate the negative effects of OA on farmed bivalves by increasing pH and the saturation state for aragonite (Ωaragonite) (Young et al. 2022). Thereby, the co-cultivation of bivalves and S. latissima is likely a promising integrated multi-trophic aquaculture approach to generate synergistic benefits in future OA scenarios.

The effects of OA on S. latissima have been investigated in interaction with temperature (Olischläger et al. 2014, 2017; Iñiguez et al. 2016) and ultraviolet radiation (UVR) (Gordillo et al. 2015). The effects of increased pCO₂ on growth, biochemical composition, and photosynthetic performances of S. latissima were generally less pronounced than those of increased temperature (Olischläger et al. 2017). Furthermore, Arctic S. latissima was more resilient to increased pCO₂ and more likely to benefit from climate change than the temperate population, as reflected by its increased growth rates at elevated pCO₂ and higher temperatures (Olischläger et al. 2014, 2017). The interactive effects of OA and UVR illustrated that OA increased the growth of S. latissima, meanwhile, inhibited a series of UVR-driven responses (e.g., pigments and photosynthetic electron transportations) (Gordillo et al. 2015). Due to the various responses of S. latissima to OA discussed above, more work is needed to understand how it is and will affect S. latissima. Besides, no studies on the molecular mechanisms regulating responses of S. latissima to OA are available to date. Transcriptomics and/or metabolomics must be applied to understand the gene regulation and related metabolic pathways of S. latissima under OA conditions.
Biotic interactions

Microbiome

Macroalgal functioning must be considered as the result of the interactions between the algal hosts and their associated microbiota, forming a singular entity, the algal holobiont (Egan et al. 2013). Algal microbial partners can be prokaryotes like viruses, Archaea, or bacteria and eukaryotes like fungi. Bacterial partners regulate and support macroalgal health and fitness (Goecke et al. 2010), pathogen resistance (Wiese et al. 2009), acclimation to a changing environment (Dittami et al. 2016), and metabolism (Burgunter-Delamare et al. 2020).

Saccharina latissima microbiota has only become a subject of interest in recent years (Vallet et al. 2018; Tourneroche et al. 2020; King et al. 2022; Liu et al. 2022; Burgunter-Delamare et al. 2023). Bacteria associated with S. latissima are also classically found in other brown macroalgae (Hollants et al. 2013) and belong predominantly to the Proteobacteria and Bacteroidota phyla (Tourneroche et al. 2020; Burgunter-Delamare et al. 2023). At the class level, Alphaproteobacteria and Gammaproteobacteria (Liu et al. 2022; Burgunter-Delamare et al. 2023), Deltaproteobacteria, Bacilli, Flavobacteriia, Planctomycetia, and Verrucomicrobiae (Liu et al. 2022) were found. Bacterial strain isolation experiments determined that strains were affiliated with Actinobacteria, Bacteroidetes, Firmicutes, Alpha-, Beta-, and Gammaproteobacteria and belonged to 21 genera (Wiese et al. 2009). The genera Marinobacter, Psychromonas, Litorimonas, and Aquimarina were also exclusively found attached to the blade of S. latissima and not in the surrounding seawater (Liu et al. 2022). The bacterial composition gradually changes along the blade, shifting from a lower to higher alpha-diversity from the meristem to the distal part, reflecting the age gradient (Staufenberger et al. 2008; Burgunter-Delamare et
al. 2022, 2023). The degree of colonization is partially linked to the type of metabolites released by the algae (Tourneroche et al. 2020). As such, epibiotic bacteria are considered specialized metabolizers (Staufenberger et al. 2008; Liu et al. 2022).

The bacterial core of *S. latissima* is independent of the specimens’ geographical origin, season, or physiologic state. When looking at the meristematic part, a small core comprising the four genera *Granulosicoccus* sp., *Litorimonas* sp., *Hellea* sp., and *Blastopirellula* sp. was found in two studies - (8/13 ASVs and 4/9 genera (King et al. 2022); four genera (Burgunter-Delamare et al. 2023). Five additional ASVs (*Croceitalea* sp., *Robiginitomaculum* sp., *Gammaproteobacteria* sp., OM190 sp., and KI89A_clade sp.) were also found in this blade region (King et al. 2022). The bacterial core composition also shows the shifts from low to higher diversity along the blade at the genus level. Indeed, the distal bacterial core comprises the four genera found in the meristem core plus the five genera *Algitalea*, *Arenicella*, *Portibacter*, *Tenacibaculum*, and *Bdellovibrio* (Burgunter-Delamare et al. 2023). In addition, when looking at the core community and the ASVs found specifically attached to a particular tissue, particularly *Granulosicoccus* and *Litorimonas*, ecology and genome profiles suggest that they may be functionally necessary for the host (King et al. 2022; Burgunter-Delamare et al. 2023).

For example, the *Granulosicoccus* genus might help its host by providing vitamins (e.g. vitamin B12) and reduced nitrogen (Kang et al. 2018; Capistrant-Fossa et al. 2021; Weigel et al. 2022).

Fungi infect the blade more often than other parts, and fungal communities comprise principally Ascomycota and Basidiomycota (Vallet et al. 2018; Tourneroche et al. 2020), with a predominance of *Dothideomycetes* and *Sordariomycetes* (Vallet et al. 2018) or *Psathyrellaceae* (Tourneroche et al. 2020). Additionally, *S. latissima* is colonised by viruses classified as Phaeovirus (*Saccharina latissima virus*, SlatV, family
Phycodnaviridae (Schroeder and McKeown 2021). They are latent double-stranded DNA viruses that insert their genome into those of their host (McKeown et al. 2017) and spread in three sub-groups A, B, and C. Phaeoviruses are geographically widespread in the Laminariales (McKeown et al. 2018). In particular, Laminaria and Saccharina genera are infected by Phaeovirus from sub-group C (McKeown et al. 2017). Identifications of these viruses are supported by novel Phaeovirus major capsid protein (mcpl MCP) sequences found in kelp (by PCR) (McKeown et al. 2017, 2018; Schroeder and Mckeown 2021).

Environmental factors influence microbiota composition. Those factors interact altogether and affect bacterial communities (King et al. 2022). Several studies compared the bacterial population of different geographical origins and found regional structuring in S. latissima [Baltic and North Sea (Staufenberger et al. 2008; Lachnit et al. 2009), North and West Scotland, Wales, and South England (King et al. 2022); Brittany, Helgoland, and Skagerrak (Burgunter-Delamare et al. 2023)]. The global epibacterial communities of S. latissima were differentiated between the Baltic and North Sea (Staufenberger et al. 2008; Lachnit et al. 2009). Differences regarding salinity, tidal range, and bacterioplankton composition between sampling sites likely explain this. A regional structuring across British sites (North, West Scotland, Wales, and South England) was also discovered, where bacterial communities in Wales differ from those in North and West Scotland. Here, the temperature is not the responsible factor, but rather that the variable portion of the microbiota reflects random and determinant processes within the host environment (King et al. 2022), as reef habitats are highly dynamic and influenced by several factors that vary across multiple scales [wave exposure, light and nutrient availability, sedimentation rates, salinity;(Kaiser 2011; Lamy et al. 2018)]. In the same way, samples from Brittany, Helgoland, and Skagerrak cluster according to their region of origin (Burgunter-Delamare et al. 2023). Abiotic factors can lead to cellular
stress and senescence and thus will create a new ecological niche for specific bacterial
groups (Burgunter-Delamare et al. 2023). Also, algal genotypes differ depending on the
region (see Biogeographic patterns) (Guzinski et al. 2016, 2020) and can impact bacterial
communities. Chemical and lipid content in membranes also varies with environmental
factors (see Responses to environmental drivers), so attractiveness for bacteria is
influenced (Burgunter-Delamare et al. 2023). Furthermore, the associated microbial
communities can vary with seasonality. Regardless of the mechanisms, seasonal changes
may vary from site to site, and therefore, any conclusions drawn about seasonality are
valid only for the studied area. Differences between winter and spring were found at the
blades and rhizoid levels of S. latissima from the Baltic Sea (Staufenberger et al. 2008).
In Brittany (Roscoff, France), the abundance of Firmicutes, Actinobacteria, and Alpha-
and Gammaproteobacteria were impacted, with an increase in autumn for the Firmicutes
and Alphaproteobacteria, in summer for the Actinobacteria and in spring for the
Gammaproteobacteria. The seasonal changes were linked to the nutrient content of
seawater and the algae’s chemical composition (Burgunter-Delamare et al. 2023).
Even though the biological impact of viruses on their hosts is mainly unknown,
researchers are working on the microbial effects on the host regarding potential
pathogens. By performing co-culture experiments with bacteria specifically isolated from
S. latissima, it has been shown that a disruption in the microbiota composition (dysbiosis)
is correlated to an increase in Quorum Sensing molecules (bacterial ability to detect and
respond to cell population density through gene regulation) and a decrease in algal growth
(Burgunter-Delamare et al. 2022). Also, Aquimarina, Parcubacteria, and
Peronosporomycetes were suggested as potential pathogens of S. latissima (Liu et al.
2022). Conversely, first-time evidence that fungal partners of brown macroalgae may
protect their host in vivo by producing molecules as an active chemical defence has
already been given (Vallet et al. 2018). Thus, the algal microbiota might manage the infection rate of pathogenic microbes in the phycosphere.

**Mobile biota**

Kelps are essential coastal habitats for many commercially important fish and crustacean species (Seitz et al. 2014). However, specific associations between fish/crustaceans and *S. latissima* have been poorly assessed. One study found 358 individuals of fish and crustaceans associated with *S. latissima* communities in Southern Norway, higher than the number of individuals associated with eelgrass and turf algae but lower than the specimens caught in *Laminaria hyperborea* (700). Regarding species richness and diversity, eelgrass beds held higher diversity than *S. latissima* and the other habitats (Christie et al. 2022). Habitat preferences of fish are species-specific and vary with life stages. Young (< 1 year old) cod in Norwegian waters prefers red algae and eelgrass over *S. latissima* dominated habitats, however, cod older than one year used all seaweed and seagrass habitats equally. In turn, the fishes Goldsinny wrasse (*Ctenolabrus rupestris*) and corkwing wrasse (*Symphodus melops*) preferred *S. latissima* and red algae over eelgrasses (Dunlop et al. 2022). In the Northwest Atlantic, the residential fish cunner (*Tautogolabrus adspersus*) uses *S. latissima* and other large blade Phaeophyta for foraging and refuge (O’Brien et al. 2018). *S. latissima* offers a better refuge for fish (>1 cm) but lower quality habitat for meso-invertebrates than other morphologically different macroalgae, such as turf (Ware et al. 2019). On the other hand, the decline of large predatory fish has cascading effects throughout the food-web, ultimately reinforcing the decline of *S. latissima* in some regions (Eriksson et al. 2009).

**Epi- and Endobiota**

*Saccharina latissima*, like other kelps, can serve as a substratum for smaller algae and animals to grow on (epiphytes) or inside (endophytes) of its thalli (Bartsch et al. 2008).
Considering epiphytes, both macro- (*Ectocarpus siliculosus*, *Ulva lactuca*, and *Champia parvula*) and microalgae (e.g., pennate diatoms including genera *Licmophora*, *Navicula*, and *Nitzschia*) were observed on the surface of *S. latissima* (Liu et al. 2022). Considering endophytes, microscopic brown algae with filamentous thalli, mostly *Ectocarpales sensu lato*, are common in kelps (reviewed by Bartsch et al., 2008) and in *S. latissima* (Bernard et al. 2018). A study revealed that 88 % of endophyte algae from kelps belonged to the genera *Laminarionema* and *Laminariocolax*, with two isolates belonging to the genera *Ectocarpus* (MS Bernard et al. 2019). Furthermore, the most common endophyte in European *S. latissima* is *Laminarioema elsbetiae* (M Bernard et al. 2019). The infection rates of endophytic algae in wild *S. latissima* along the European coasts were found to be up to 100 % (Bernard et al. 2018). The occurrence and abundance of epi-/endophytic algae were affected by both environmental factors, such as seasons and locations, and characters of *S. latissima*, such as age and position (Peteiro and Freire 2013a; MS Bernard et al. 2019; Corrigan et al. 2023). For example, the abundance of epiphytes on *S. latissima* was observed to be significantly higher for fronds growing in the sheltered area of the bay compared to those farmed at the exposed location, and the greatest quantities of epiphytes were on the apical parts of *S. latissima* blades (Peteiro and Freire 2013a). Besides, the cultivated *S. latissima* in Northern Brittany was not found to be affected by *Laminarioema elsbetiae*, which is highly prevalent in the wild populations of European *S. latissima* (Bernard et al. 2019a). The infection with epibionts can reduce the photosynthesis of *S. latissima* by hindering up to 90 % of available light revealed under laboratory conditions (Andersen et al. 2018). In addition to causing morphological changes, endophytic algae also adversely impacted the physiological and biochemical traits of kelps, such as growth and reproduction. The transcriptomic analysis demonstrated that *S. latissima* upregulated many cell-wall modification-related genes and...
stress response-related genes during the infection of endophytes *L. elsbetiae*, suggesting that endophytic algae damaged the cell wall and induced oxidative stresses in *S. latissima* (Xing et al. 2021). In Norway, cultivated *S. latissima* sustains a heavy load of epibionts, up to 90% of available area, causing light deprivation driven mainly by epiphytic algae and ascidians and to a less extent by bryozoans (Andersen et al. 2018). The lack of *S. latissima* populations at the Skagerrak coast was suggested to be due to heavy epiphytism rather than the direct effect of abiotic factors on *S. latissima*, as transplanted sporophytes were able to grow and mature until epiphyte load increased in the summer (Andersen et al. 2011). The reduced growth and survival of kelp populations in shallow waters are also driven by the heavy load of epibionts, driving *S. latissima* populations deeper down and reducing their vertical distribution. This impact is seasonal and site-specific; hence it probably interacts with other environmental factors to drive the ongoing decline of *S. latissima* populations (Andersen et al. 2018).

In the wild, the bryozoan *Membranipora membranacea* – epiphyte on *S. latissima* – has negative effects on populations of *S. latissima* in the Northwest (NW) Atlantic, namely tissue weakening, breakage and ultimately kelp biomass loss (Attridge et al. 2022). Populations of this bryozoan, invasive in the Northeast (NE) Atlantic, are expected to increase under climate change scenarios, further impacting *S. latissima* populations in the area (Denley et al. 2019). In the NE Atlantic, *M. membranacea* is a common native bryozoan, and although very little is known for natural populations, impacts of this species on cultivated *S. latissima* are already reported (e.g., Førde et al. 2016; Forbord et al. 2020). Another common bryozoan on kelps is *Electra pilosa*, however, this species has a slower growth rate and less substrate preference than *M. membranacea* and seems to have a more benign effect on kelps, including *S. latissima*. A pattern that holds on both sides of the Atlantic (Yorke and Metaxas 2011; Førde et al. 2016).
Mobile and epiphytic communities associated with *S. latissima* farms in Norway were shown to be significantly different from wild stands, holding less biodiversity and a smaller number of individuals (Bekkby et al. 2023). The dominant species also differed between farmed and wild stands, with isopods being abundant in farmed *S. latissima* and nearly absent in the wild sporophytes. Also, kelp farms represent an additional, richer habitat than the surrounding water column (Bekkby et al. 2023). A *S. latissima* farm in Sweden had a significantly positive impact on the amount and diversity of benthic infauna and attracted a similar number of mobile taxa as the nearby wild sites (Visch et al. 2020).

In a field study in Ireland comparing the associated biota of four macroalgae (*S. latissima*, *Halydris siliquosa*, *Fucus serratus* and *Sargassum muticum*), *S. latissima* held the lowest epiphytic algae’s biomass of the four species (Strong et al. 2009). *S. latissima* supported a broad epiphytic faunal community (significantly different from the other macroalgae) with the species *Gibbula umbilicalis*, *Corophium volutator* and *Ischyrocarus anguipes* being characteristic of the thallus of *S. latissima*. In turn, the grazer amphipod *Dexamine spinosa* was considerably more abundant in *S. muticum* than *S. latissima* and had no significant effect on *S. latissima*’s growth. *S. latissima* also showed more resilience to fouling (with only 9% of biomass loss) when compared to the invasive *S. muticum* (with mean losses of 70%) (Strong et al. 2009). The biota associated with *S. latissima* in Kongsfjorden, a high Arctic fjord on the west coast of Spitsbergen, was assessed (Shunatova et al. 2018). 111 sessile taxa were reported for the complex stone with *S. latissima* in 2018 – 80 animals (of these 56 were Bryozoa) and 30 algae taxa (of these 36 were Phaeophyceae and 11 Florideophyceae) (Shunatova et al. 2018). Species richness associated with *S. latissima* was higher than in nearby sediment substrates. Both species richness and biomass varied with microhabitat and season, being considerably higher on holdfast compared to blades and stipes and in January compared to May and September.
Although *S. latissima* contains high levels of phlorotannins that decrease the species’ digestibility, several animals can still graze directly on it. Among them is the snail *Lacuna vincta* (O’Brien and Scheibling 2016; Young and Doall 2021). A comparative study revealed that *S. latissima* is one of the preferred food sources for *L. vincta* and the macroalgae that elicits a higher growth rate (Chavanich and Harris 2002). This snail prefers reproductive over vegetative tissue, probably due to lower levels of phlorotannins in the first, compromising the reproductive success of *S. latissima* (O’Brien and Scheibling 2016). *L. vincta* also consumes *S. latissima* at higher rates when pre-treated with high temperatures (21°C), probably because the tissue is easier to consume (weaker, more fragile at higher temperatures) (E J Simonson *et al.* 2015). *L. vincta*’s grazing rate is apparently unaffected by changing temperatures (E J Simonson *et al.* 2015) but decreased under ocean acidification conditions (Young and Doall 2021).

A significant group in the coastal food web are sea urchins. Across the globe, events of mass grazing by sea urchins have decimated kelp forests and give rise to sea urchin barrens (Filbee-Dexter and Scheibling 2014). Several studies have shown that grazing pressure of the green sea urchin *Strongylocentrotus droebachiensis* led to the decline of *Laminaria hyperborea* (e.g., Rinde *et al.* 2014) in several areas in NE Atlantic and of *Saccharina longicruris*, now *S. latissima*, in NW Atlantic. Although field studies studying the direct link between *S. droebachiensis* and *S. latissima* are rare, laboratory experiments show that *S. droebachiensis* indeed feeds on *S. latissima* (Daggett *et al.* 2010; Eddy *et al.* 2012) and growth rates of the sea urchins fed *S. latissima* or other macroalgae species is similar (Carrier *et al.* 2017). The growth and survival of *S. droebachiensis* are, in turn, controlled by its predators (Norderhaug *et al.* 2021) and by disease outbreaks (Feehan 2014). A field and laboratory study in Nova Scotia showed that the presence of the crab
Cancer borealis did not change the foraging behaviour of the sea urchin on S. latissima. A greater proportion of sea urchins around cages with S. latissima than without was also determined, revealing some response to a food cue (Harding and Scheibling 2015). Another study revealed that juveniles of S. droebachiensis inhabiting S. latissima holdfasts are 20-30% less likely to be predated by crabs Cancer borealis and C. irroratus when compared to treatments with no refuge (Feehan et al. 2019). Also, there was a correlation between S. latissima volume and the size of sea urchin juveniles, showing that S. latissima serves as food, habitat, and refuge for S. droebachiensis (Feehan and Francis 2014). Moreover, S. latissima detritus remains a main food source even for deep-living sea urchins (60 m) that can maintain a good reproductive status (Filbee-Dexter 2014). In a laboratory experiment with samples of S. latissima from Alaska, a high sediment load (as in a land-terminating glacier) led to a sharp decrease in grazing rates of S. droebachiensis on S. latissima. In the same experiment, increasing temperature had no effect on grazing rates (Traiger 2019). Other species of sea urchin feed on S. latissima, such as Arbacia punctulata, even though they prefer turf algae over S. latissima (Hamel 2022). The purple sea urchin Paracentrotus lividus also feeds on S. latissima (Castilla-Gavilán et al. 2019), although the best growth performance is achieved when fed on the red alga Palmaria palmata. A set of mesocosm experiments compared respiration and consumption rates of several grazers under medium and increased temperatures (Gilson et al. 2021). While the common sea urchin Echinus esculentus preferred the combination of S. latissima and L. digitata over L. ochroleuca and Saccorhiza polyschides, the gastropod Steromphala umbilicalis consumed more of the latter and the amphipod Gammarus spp. did not show preference. In addition, both E. esculentus and Gammarus spp. increased their respiration rates under warming but only Gammarus spp. increased its consumption rates. In turn, S. umbilicalis increased growth with warming but not the
other two species. Another animal group feeding on *S. latissima* are fish, such as wrasses, although *S. latissima* only represents a small percentage of their diet (Bourlat *et al.* 2021). However, more studies looking at fish’s gut content are necessary to understand better the pressure exerted by this group of grazers.

A recent study revealed that kelp forests have recovered (*L. hyperborea* and *S. latissima* considered together) along the northern Norwegian coast (Christie, Gundersen, *et al.* 2019). It was suggested as the result of complex interactive effects of temperature on the food-web. In the southern part of the previous sea urchin barren, the recovery of kelp is due to a decline in sea urchins following direct and indirect effects of increasing temperature. While in the northernmost section, the recovery seems to be driven by top-down control. Higher crab abundances, led by lower abundance of cod and higher temperatures, led to higher predation of sea urchins, which released kelp beds from their grazing pressure (Christie, Gundersen, *et al.* 2019). Given the diversity of animals feeding on *S. latissima* and the unknowns related to their interactions with other species and physical factors, more work is necessary to clarify the impact of grazing on *S. latissima*.

**Algal competitors**

*Saccharina latissima* disappeared in the early 2000s from several sites in Norway and has been replaced by turf algae (Moy and Christie 2012). Since then, several studies have tried to understand the underlying mechanisms and monitor any changes (e.g., Andersen *et al.* 2018; Christie, Andersen, *et al.* 2019; Christie, Gundersen, *et al.* 2019). Although some studies have reported that a regime shift has occurred (*S. latissima* was no longer able to recover and had been replaced by turf algae), recent monitoring efforts have revealed some recovery, although temporal and spatially variable. Given that this region is closely monitored (Moy and Christie 2012; Christie, Andersen, *et al.* 2019; Christie, Gundersen, *et al.* 2019), this could be an ideal opportunity to understand shifts between
phases and determine what actions are successful in recovering *S. latissima* populations – knowledge that can then be applied to less studied regions. A similar regime shift has occurred in the NW Atlantic, off Nova Scotia, Canada’s kelp biomass (mainly composed of *Laminaria digitata* and *S. latissima*) decreased 85–99% recently when compared to the first monitoring campaigns in 1949 (Filbee-Dexter *et al.* 2016). In the Gulf of Maine, a phase shift from canopy algae (including *S. latissima*) to ephemeral turf algae has occurred, and now 50–90% of the bottom is dominated by red and green algae that were not common in the 1980s (Dijkstra *et al.* 2017). Associated biota was found in lower numbers in *S. latissima* and other canopy species than in highly branched and filamentous algae. Nevertheless, high numbers of several gastropods were associated with *S. latissima*, including *Lacuna vincta, Margarite helicinus, and Mitrella* (Dijkstra *et al.* 2017). The presence of turf algae further reduced *S. latissima* populations by competing for space. *S. latissima* is increasingly recruiting from turf algae, but the individuals are smaller, the survival rate lower, and are more likely to be dislodged by wave action than sporophytes attached to rocky reefs, hence decreasing the health of the populations (Burek *et al.* 2018; Feehan *et al.* 2019). It was suggested that individuals are smaller because energy is diverted to larger holdfasts required to stabilise sporophytes in a more unstable substratum (turfs compared to rocks). Detachment rates of turf-attached *S. latissima* are more pronounced at high-wave action sites or after storm events. This pattern was consistent throughout the distributional range of *S. latissima* in NW Atlantic.

A field study in Northern Ireland revealed that the invasive *Sargassum muticum* did not compete with *S. latissima* stands (Strong and Dring 2011). Another potential competing species is the invasive green alga *Codium fragile ssp. fragile*. A study in Nova Scotia compared *C. fragile* with *S. latissima* in terms of composition of its detritus and contribution to the detrital food chain (Krumhansl 2012), revealing that degradation in *S.*
*S. latissima* was faster and resulted in higher mass loss than *C. fragile*. The C:N ratio was higher in *S. latissima* than in *C. fragile* throughout decomposition, resulting in a lower nutritional value of *S. latissima* than in *C. fragile*. This resulted in associated macrofauna that was more abundant but less diverse on *S. latissima* than on *C. fragile*.

**Biogeographic patterns**

Population differentiation at genetic level

Population structure, genetic diversity and connectivity of populations of *Saccharina latissima* have been explored in recent years (Guzinski *et al.* 2016, 2020; Nielsen, Paulino, *et al.* 2016; Luttikhuizen *et al.* 2018; Mooney *et al.* 2018; Neiva *et al.* 2018; Grant and Chenoweth 2021). Overall, population differentiation, low within-genetic diversity, and low connectivity have been observed, although regional and local patterns can differ.

Only one study compared samples across oceans, identifying four differentiated phylogroups – A) including specimens from Northwest (NW) Pacific (Japan, as *S. coriacea*), Northeast (NE) (British Columbia) Pacific and Greenland and Hudson Bay in NW Atlantic; B) NE Atlantic; C) NW Atlantic and D) samples from Russia previously identified as *S. cichorioides* (Neiva *et al.* 2018). Together with recent findings on individuals in NE Pacific and Bering Sea (Grant and Chenoweth 2021), the hypothesis of a northern refugium during the Last Glacial Maximum for the species is gaining support, in contrast to the previous hypothesis of recolonisation from southern European populations, as it has been suggested for other seaweed species (Bringloe *et al.* 2020).

Further differentiation of *S. latissima* populations exists within the NE Atlantic phylogroup with quite distinct ‘northern’ and ‘southern’ clusters (Neiva *et al.* 2018). Authors suggest that speciation might be in progress within these phylogroups, in
accordance with another study determining population differentiation between seven European populations (Luttikhuizen et al. 2018). Furthermore, it was shown that within-population genetic diversity is the lowest for the southern populations (Spain and Portugal) and the isolated island population on Helgoland, German Bight and highest in Spitsbergen (Guzinski et al. 2016). This was also confirmed by a more recent study employing both microsatellites and a more recent method, ddRAD-seq, to explore the genetic diversity of eleven populations in the NE Atlantic (Guzinski et al. 2020).

At smaller scales, populations of S. latissima revealed low genetic diversity within a brackish population (Denmark), while significant differences were observed between brackish and marine populations (Denmark vs. Norway and Sweden) (Nielsen, Paulino, et al. 2016). In the Irish Sea, populations from Scotland, the Isle of Man and Northern Ireland were also shown to be differentiated (Mooney et al. 2018). In Norway, isolation-by-distance has been observed in S. latissima, however, the grouping seems to differ by method of analysis due to the use of different genetic markers and sampling sites and sizes. In general, northern populations (Svalbard and Lofoten) are observed to be genetically distinct, suggesting that a physical barrier (islands) drives genetic differentiation. Overall, along the Norwegian coastline, results range from three different genetic groups (Evanckow et al. 2019) to generally connected populations (Ribeiro et al. 2022). Local adaptation has been discussed for the general connection, as including a locus under positive selection altered the results of the genetic structure, even in the face of gene flow (Ribeiro et al. 2022). Like European populations, a differentiation in ‘cold’ and ‘temperate’ clusters was found in the NW Atlantic phylogroup, though less pronounced (Neiva et al. 2018). Fine-scale genetic structure and low within-genetic diversity have been found for populations along the eastern Maine region in the NW Atlantic (Breton et al. 2018). However, comparing the same markers, lower allelic
richness and heterozygosity were reported in NW Atlantic than in NE populations (Guzinski et al. 2016). Lower genetic diversity in NW Atlantic compared to NE has been reported for other benthic taxa (Wares and Cunningham 2001). A recent study in S. latissima with more sampling sites revealed a biogeographic barrier at Cape Cod separating the Gulf of Maine and Southern New England’s populations (Mao et al. 2020). Despite the apparent wealth of studies targeting population structure of S. latissima, they differ in locations studied and methods applied, preventing a wide comparison and global conclusions. All studies generally show that within-population genetic diversity is low, which is concerning since it indicates that populations might not have the adaptive potential to face increasing environmental change at sites where it is most extreme. Moreover, they report low connectivity that could result from stretches of land, waves and currents and salinity variation depending on the site that restricts colonisation of disturbed populations. For a successful conservation and/or restoration plan for the species, the data on population differentiation obtained so far suggest it is crucial to apply the same methodology to a large number of locations covering the geographical distribution but also spatial heterogeneity at smaller scales (e.g., islands or other isolated populations).

However, most studies on population differentiation neglected the epigenetic component of local adaptation, which is strong in S. latissima across latitudes (Schesonk et al. 2023). They might explain the general capacity of this species to adjust to rapid changes and colonise very different habitats. Hence, even with the apparent low genetic diversity, epigenetic differences might be high, and therefore it is crucial that they are considered in future studies.
Phenotypic plasticity and local adaptation

Phenotypic plasticity refers to the ability of a single genotype to modify its phenotype in response to changing conditions (Nicotra et al. 2010; King et al. 2018). Contrary, ecotypes are locally adapted populations that are phenotypically and genetically differentiated for adaptive traits, meaning they perform better at the local conditions than another population from a distant location with other local environmental factors (Kawecki and Ebert 2004; Nicotra et al. 2010). Ecotypes can emerge by long-term exposure to selective environmental pressures (Nicotra et al. 2010), such as temperature ecotypes in different climate zones. For example, stress responses and recovery towards ocean warming and heat waves were shown to differ between organisms and across latitudes (Winters et al. 2011; Liesner, Fouqueau, et al. 2020). By local adaptation and acclimation mechanisms, species can vary in tolerance and performance to biotic and abiotic factors. In models or simulations, broadly distributed species are usually treated as single homogenous physiological units (Reed et al. 2011). However, seaweeds such as *S. latissima* can exhibit different specific responses to distinct environmental conditions, of which temperature is a key factor (Lüning 1990a; Adey and Steneck 2001, see also Responses to environmental drivers). Overall, influences of various abiotic factors on the morphology, physiology and biochemical composition of *S. latissima* have been extensively studied, and a high degree of acclimation capacity has been found. Only little is known about how geographical patterns influence the species’ acclimation capacity. Morphological plasticity is linked with adjustments to local conditions in different sites (Lüning 1990a; Peteiro and Freire 2013b; Visch et al. 2020; Zhu et al. 2021; Diehl et al. 2023). Effects of wave exposure on the frond length and width of *S. latissima* have been described in the field (Chapman 1973) and under laboratory conditions (Gerard 1987; Zhu et al. 2021). Sporophytes typically form narrow blades with solid stipes in more
wave-exposed habitats, while blades are broader with hollow stipes in sheltered habitats (Lüning 1990a). Controlled laboratory experiments revealed an interaction between wave action and nutrient availability (Zhu et al. 2021). Under wave action, S. latissima sporophytes developed a rough, more intricate frond surface that allowed for a higher nutrient and light uptake, resulting in high biomass and frond length even under low nutrient conditions (Zhu et al. 2021). Additionally, sporophytes from a glacier-influenced area in Alaska have been described as narrower and longer than oceanic individuals (Spurkland and Iken 2012), while in Svalbard (European Arctic), biomass and size of S. latissima were lower in glacier-influenced sites. In the same fjord, sporophytes of S. latissima were longer and heavier at greater depths (Ronowicz et al. 2022). For lab-grown individuals (from the gametophyte stage), sporophytes from the Arctic were narrower and longer than sporophytes from Brittany (Monteiro, Li, et al. 2019), indicating eco-phenotypes (see further down). Morphological plasticity is very common in S. latissima and has led to misidentifications. For example, S. angustissima, formerly considered a morphotype of S. latissima (Augyte et al. 2018), is endemic to Maine (USA). Very exposed conditions result in narrow blades; otherwise, it is morphologically very similar to S. latissima but shows genetic divergence. Recent studies investigated the biochemical plasticity of field-grown sporophytes of S. latissima. By comparing the lipidomic composition and other parameters such as total carbon, lipid, protein, and carbohydrate contents of S. latissima, it was possible to distinguish populations from France, Norway and the United Kingdom (J Monteiro et al. 2020). High intraspecific variability and habitat-specific phenotypes in morphology and biochemical composition were also found in field sporophytes of S. latissima across its entire distribution range in Europe, although without apparent geographic patterns (Diehl et al. 2023).
In addition, different populations of *S. latissima* were shown to vary in sensitivity to environmental factors, such as temperature (Olischläger et al. 2014, 2017; Monteiro, Li, et al. 2019; Diehl et al. 2021, 2023). The existence of ecotypes regarding specific local parameters such as temperature, salinity, $p$CO$_2$ and light have been postulated for the Northeast and Northwest Atlantic (Lüning and Dring 1975; Gerard 1987, 1988, 1990; Gerard and Du Bois 1988; Müller et al. 2008; Spurkland and Iken 2012; Olischläger et al. 2014, 2017). Contrary, other studies did not find evidence for ecotypic differentiation and rather suggested high phenotypic plasticity in *S. latissima* (Bolton and Lüning 1982; Spurkland and Iken 2011). Several studies have proposed ecological differentiation between populations from Spitsbergen and Helgoland (Müller et al. 2008; Olischläger et al. 2014, 2017). Differences in biochemical composition and physiological performance were reported under different temperature and CO$_2$ treatments (Olischläger et al. 2014, 2017). In a multiple-stressor experiment on laboratory cultures of *S. latissima* from Brittany and the Arctic, results suggest the existence of ecotypes in *S. latissima* (Monteiro, Li, et al. 2019; Li, Monteiro, et al. 2020). Responses to salinity and temperature variation diverged between Brittany and the Arctic, resulting in variations in morphology, differences in growth rate and pigment content and gene expression profiles. At the transcriptomic level, short-term responses differed between sporophytes from the two sites in magnitude and in involved metabolic pathways, which correlated to some degree with the local conditions (Monteiro, Li, et al. 2019).

Along the Norwegian coast (58 to 69°N), populations of cultivated *S. latissima* display higher blade length and biomass in central and northern regions that peak later in the season than for individuals in the south (Forbord et al. 2020). Increased growth in north and central populations was coupled with higher protein content and delayed onset of biofouling.
Concerning vertical distribution, cultivated *S. latissima* sporophytes in Norway display higher biomass yields and frond length at 1-2 m depth compared to 8-9 m (Forbord *et al.* 2020). However, this is not the case for the Baltic coast of Denmark, where frond size and dry matter reached the highest values at depths over 11 m (Nielsen, Manns, *et al.* 2016).

To date, it has been shown that *S. latissima* is adapted to local conditions throughout its wide geographic distribution. As several studies attempt to look at regional differences, evidence of high intra-regional – among sites differences are evident (e.g., Smale and Moore 2017; Wang *et al.* 2021; Diehl *et al.* 2023), which complicates the analysis of latitudinal effects on *S. latissima* but reveals its acclimation ability. Adjustments to abiotic drivers are site-specific and, therefore, cannot be generalised from one population to the entire species complex. Still, definite ecotypes could not be confirmed yet, and the question of whether *S. latissima* exhibits ecotypes or not is still not fully resolved. In addition, most studies conducted on ecotypes so far have been focused on the genetic level as an explanation for the intra-specific variability (phenotypes as local expression of a genotype). However, epigenetic mechanisms have been shown to control gene expression (Richards *et al.* 2017), and first data are available on epigenetic mechanisms in *S. latissima* (Scheschonk *et al.* 2023). These findings show that, like the concept of phenotypic plasticity, the epigenome of *S. latissima* likely plays a vital role in local acclimation and adaptation in this species. To highlight the importance of non-genetic gene control for local adaptation/acclimation processes, the term ‘eco-phenotype’ has been suggested (Scheschonk *et al.* 2023). It indicates epigenetic mechanisms (within and across generations, see *Epigenomics*) to be involved in the variation of the phenotype in response to local parameters.
Phylogeographic differentiation of *S. latissima* populations has been reported across the Northern Hemisphere, also on small geographical distances (see *Population differentiation at genetic level*). Though it is hypothesised that the European *S. latissima* species complex has not reached an equilibrium, the emergence of ecotypes can occur and eventually lead to different species (Luttikhuizen *et al.* 2018; Neiva *et al.* 2018). However, this might be precluded by the rapid changes in its habitats due to climate change. The fact that there is evidence that divergence between different populations is expressed at transcriptomic and epigenetic levels (Monteiro, Li, *et al.* 2019; Scheschonk *et al.* 2023) suggests that ecotypes may emerge at phenotypic level (or as more pronounced eco-phenotypes) in future or may be revealed with more extreme environmental pressure or different parameters tested.

The variability in phenotypic plasticity and formation of ecotypes in *S. latissima* described above is based on different approaches (various laboratory experiments, *in situ* measurements, reciprocal transplants), environmental criteria (temperature, salinity, irradiance), and response parameters (growth, survival, fitness, biochemical composition). These differences complicate a systematic comparison of results and warrant a discussion of which parameter is most helpful in assessing phenotypic plasticity or local adaptation. ‘Common garden experiments’, or reciprocal transplants of field specimens from distinct populations, are needed to clarify ecotypes’ existence in *S. latissima* (Kawecki and Ebert 2004). However, reciprocal transplants cannot be applied in protected areas, such as Spitsbergen (Norway 2001), and concerns regarding genetic contamination are warranted (Guzinski *et al.* 2016; Luttikhuizen *et al.* 2018). Again, assessing and comparing the epigenome might shed light on the complex topic of eco-evolutionary dynamics in *S. latissima.*
Climate change, especially global warming, has affected the distribution and abundance of many kelps (Smale 2020; Fragkopoulou et al. 2022). Kelps are projected to continuously shift northwards in the future (Wilson et al. 2019; Krause-Jensen et al. 2020). *Saccharina latissima* has already been observed and estimated to decrease in Nova Scotia (Filbee-Dexter et al. 2016), Gulf of Maine (Witman and Lamb 2018), Rhode Island (Feehan et al. 2019), Norway (Bekkby and Moy 2011; Moy and Christie 2012), Sweden (Eriksson et al. 2002), Helgoland: (Pehlke and Bartsch 2008), Iberian Coast: (Casado-Amezúa et al. 2019) whereas increasing in biomass in Greenland (Krause-Jensen et al. 2012, 2020) and Svalbard (Bartsch et al. 2016) (Distribution see Fig. 1).

Species distribution models (SDMs) have been regarded as an effective tool for predicting marine species distribution shifts, using the species occurrence data and environmental variables available (Robinson et al. 2011). In the last decade, SDMs have been applied to evaluate the distribution of *S. latissima* in Norway (Bekkby and Moy 2011) and the British Isles (Yesson et al. 2015). Furthermore, other models considered the effect of climate change on *S. latissima* distribution and projected its future distribution trends (Müller et al. 2009; Assis et al. 2018; Goldsmit et al. 2021). The northward shift of *S. latissima* was first projected by relating the temperature requirements of *S. latissima* and the modelling of sea surface temperature isotherms in 2080-2099 (Müller et al. 2009). By constructing SDMs of kelp forests in the year 2100 under the future scenario (RCP 8.5), *S. latissima* was projected to extend to higher latitudes and inhabit the entire Arctic coast while retreating from its southern limits in Nova Scotia, northwest Iberia, and Brittany towards Newfoundland and southwest Ireland (Assis et al. 2018). In the Eastern Canadian Arctic, under RCP 8.5, *S. latissima* was projected to have the largest gain (64,000 km$^2$) of suitable habitats in 2050 and second largest gain (17,000 km$^2$) in 2100 of the kelps.
studied (Goldsmit et al. 2021). Still, some areas were projected to be lost in 2100, such as north of Baffin Bay, Foxe Basin, and Hudson Bay (Goldsmit et al. 2021).

Although SDM is a powerful tool to predict the potential distribution of species under future climate scenarios, the accuracy of predictions is often disputed. For example, few studies have taken into the account physiological limits in SDMs of seaweeds, although this has proven useful for modelling macroalgal distribution (Martínez et al. 2015). Besides, the discrepancy between model predictions and long-term field observations of Arctic kelps abundance suggests that SDMs might overestimate the northern expansion potential of kelps in the short-term (Filbee-Dexter et al. 2019). The possible reasons may be the extensive gaps between available substrates, the limited dispersal ability of kelps, and other abiotic factors, such as turbidity and light penetration (Filbee-Dexter et al. 2019; Smale 2020). Hence, it is critical to track the occurrence and absence of *S. latissima* throughout the whole distributional limit in the future to improve the precision of model predictions. Modelling exercises that include physiological data generated from experiments and considering possible local adaptation are also worth considering. To achieve more accurate predictions, it is also essential to improve the spatial resolution of environmental data layers available to consider the variable physical landscape of the intertidal and shallow subtidal where *S. latissima* occurs and account for regional patterns that might override large-scale warming patterns, e.g., upwelling (Potter et al. 2013; Meneghesso et al. 2020).

**Conservation and restoration**

Given the severe decline of kelp forests globally, the need for conservation has called for action. Threats to *S. latissima* have been discussed in previous sections – effects of abiotic and biotic factors largely driven by climate change. Evidence of the impacts of other
anthropogenic activities, such as pollution, on S. latissima are scarce. These rare examples include hydrogen peroxide on salmon farms that significantly induced mortality and reduced photosynthetic efficiency of nearby S. latissima juveniles (Haugland et al. 2019). In contrast, S. latissima juveniles at sites impacted by the Exxon Valdez oil spill presented higher densities than reference sites two years after the spill, and populations recovered ten years later (Dean and Jewett 2001).

Kelp forests have been included in conventions aiming to protect habitats – the Convention of Bern and the Habitats Directive, both at the European level and in the list of threatened species and habitats of the Convention for the Protection of the Marine Environment of the Northeast Atlantic (OSPAR) (de Bettignies et al. 2021). Nevertheless, specific measures targeting conservation of kelps and, more specifically, S. latissima are rare. Marine Protected Areas (MPAs) in the Atlantic have not yet been designed to protect kelp forests, but many include areas with kelp forests, providing some protection as harvest is forbidden. This is the case in some MPAs in Norway, France, the United Kingdom and Germany. However, the effects of these measures have not been evaluated, and little is known about the efficiency of MPAs in conserving kelps (de Bettignies et al. 2021). A study in California, USA, revealed that after 15 years, the abundance of sea urchins inside the MPA remained unchanged and giant kelp populations did not differ between inside and outside the MPA (Malakhoff and Miller 2021). However, another study in a 30-year-old marine reserve in New Zealand demonstrated that the MPA effectively conserves populations of the kelp Ecklonia radiata. Outside MPAs, where fishing still occurred, sites were dominated by sea urchins and turf algae, while inside the MPA, healthy populations of E. radiata are present (Peleg et al. 2023). MPAs in Chile have successfully preserved intertidal populations of the commercially harvested Lessonia spp. (González-Roca et al. 2021). These are encouraging results and call for
similar actions for *S. latissima* if aiming for the protection and/or restoration of its populations. Considerable baseline information will be required to evaluate the effect of MPAs and other conservation measures, such as reducing local pollution inputs or limiting coastal construction, on the conservation of *S. latissima*.

In case conservation actions fail, restoration may be the way to go. One strategy to recover populations is to plant new individuals where it has been lost/decreased, aiming to restore the populations. A few studies aiming to find the best techniques for restoration have been performed on *S. latissima* (Fredriksen *et al.* 2020; Tsiamis *et al.* 2020; Le François *et al.* 2023). In a trial in Quebec, Canada, the production of *S. latissima* sporophytes was successful and worked best on artificial substrate and using a binder-based method for spraying gametophytes (Le François *et al.* 2023). In contrast, a study in Scotland revealed that the abundance of *S. latissima* and other kelps in an artificial reef was low, and in turn, turf seaweeds were abundant (Tsiamis *et al.* 2020). This is in accordance with a review on artificial seaweed reefs that concluded that the success of reforesting macroalgae is variable and depends on scale, structural composition, materials employed and surface complexity (Jung *et al.* 2022). A trial in Norway was also successful using the ‘green gravel’ method – stones are seeded in the laboratory and only planted in the field when sporophytes reach 2-3 cm (Fredriksen *et al.* 2020). Another strategy for restoration of kelps is grazer control. A study in Norway showed that sea urchin decline following treatment with quicklime allowed for kelp forest recovery, including *S. latissima* (Strand *et al.* 2020). Other strategies not yet tested for *S. latissima* include the harvest of grazers and destructive hammering of sea urchin populations (Eger *et al.* 2022). Up to this moment, research on restoration practices in *S. latissima* is scarce, and no large-scale restoration plan has been attempted.
Scientific debate is ongoing on whether assisted evolution (or assisted adaptation) is warranted when restoring degraded and vulnerable populations. Assisted evolution entails that genetic diversity of populations is artificially increased, either by moving new genotypes to a population, boosting genetic diversity within, using intra-specific hybrid vigour or heterosis or genome editing (Coleman et al. 2020; van Oppen and Coleman 2022). These methods raise important ethical questions that might limit their use (Filbee-Dexter and Smajdor 2019). Given all stated above, this is an area of research that we expect will get a lot of attention in the near future as the need to restore degraded habitats becomes evident, and best practices need to be discussed.

Conclusions

All in all, Saccharina latissima has intensively been studied over the last 15 years, and important new insights have been gained (Fig. 4). Nevertheless, new findings usually raise new questions, and we will highlight below the most current research priorities. Generally, as already stated in the review of the genus Laminaria by Bartsch et al. (2008), microscopic life-history phases have received considerably less research attention than the sporophyte stage. Direct comparisons between life-history stages have to be included in future studies to identify phase-specific responses to environmental drivers. Spores, stages of gametophyte development, gametes, and microscopic sporophytes should all be studied more intensely. Also, studies on differences in gametophyte sexes and sporophyte maturity are largely underrepresented. Only by examining the sensitivity throughout the entire life cycle of S. latissima a comprehensive understanding of the species' resilience to climate change will be possible.

Regarding climate change, most attention has been given to the impact of warming and marine heat waves. However, other weather extremes, such as marine cold spells
(Schlegel et al. 2021) or climate change-related increases in storm surges, can have a huge impact and should be considered in future studies. Furthermore, to date, studies investigating the impact of irradiation on *S. latissima* mainly focused on changes in PAR and the effect of UVR. However, increased sediment input along all coastal regions (meltwater run-off, river outflows, precipitation) not only leads to a reduction of PAR but also affects the spectral composition in the water column. Especially in Arctic regions, the environmental light spectrum changes drastically due to accelerating glacial melt and permafrost thaw, reducing the photosynthetically available (Niedzwiedz and Bischof 2023). Therefore, in further experimental and modelling research on *S. latissima*, the spectral composition of radiation should be incorporated.

The strongest impact of climate change on marine life has been observed in the Arctic (Masson-Delmotte et al. 2021), where pronounced seasonal light conditions exist. Overall, seaweeds in Arctic regions have been intensively studied (Lebrun et al. 2022). Still, adaptive responses to polar day, polar night, and the respective transitions are poorly investigated. Furthermore, melting sea ice and glaciers change salinity or result in coastal darkening (Konik et al. 2021), which can result in additional stress for Arctic *S. latissima* and should be further analysed. In addition, increasing temperatures are especially pronounced during Arctic winters with significant environmental consequences (Maturilli et al. 2015). However, only very little winter data for Arctic *S. latissima* are available. In this context, transgenerational effects in cold acclimation have been shown for *Laminaria digitata* (Liesner, Shama, et al. 2020) and the same may hold for *S. latissima*. Data on growth rates, stress response and biotic interactions for the rear edge populations of *S. latissima* is also lacking. The uneven distribution of studies across the species' distributional range – focusing on central populations in Germany, United Kingdom and mainland Norway- limits our understanding of the species' acclimation potential to
various environmental conditions. To date, the question of whether *S. latissima* exhibits
different ecotypes remains unanswered and requires further research.

When testing the consequences of climate change, an important and very complex topic
is the interaction of drivers. Hence, multifactorial approaches are increasingly applied but
are still a minority, despite their high ecological relevance. The interplay of various
altering factors might have synergistic or antagonistic impacts on the resilience and
susceptibility of *S. latissima*, and hence are key to understanding survival and success in
the future. Experiments testing the impact of ongoing climate change mostly use average
values over large scales, e.g., average sea surface temperature increase, and fail to include
relevant temporal and spatial variability at different scales (Seabra et al. 2015; Bates et
al. 2018). Different intensities, duration and recovery periods in marine heatwave
experiments result in different responses of *S. latissima*. Moreover, inter-annual and
seasonal variability on the thermal stresses of *S. latissima* was already shown
(Niedzwiedz et al. 2022). In general, seasonality strongly impacts physiological and
biochemical parameters of *S. latissima*, still, little is known about how phenology changes
across the distributional range and how it is affected by climate change. Future research
needs to include more intricate experimental designs that address more variability and
how it may affect the survival of *S. latissima*.

The application of ‘omics’ to *S. latissima* is expected to sharply increase soon as costs
decrease, and technologies quickly improve. Still, ‘omics’ approaches to *S. latissima* and
other kelps lag behind other major taxonomic groups and there is still much to be
explored. Recent work on the transcriptomic responses in *S. latissima* should be expanded
to include more abiotic and biotic drivers and complex interactive responses to climate
change. In addition, transcriptomic studies should be combined with metabolomics and
proteomics to understand how regulation occurs fully. Still, a major caveat to these
approaches is the lack of functional annotation that limits our interpretation of results. More efforts in the molecular and biochemical characterisation of genes are necessary, and knowledge generated for *S. japonica* (a closely related species) will help to streamline progress in *S. latissima* (e.g., Zhang *et al.* 2018). Another severe knowledge gap is how epigenetic mechanisms modulate responses in *S. latissima*. The modulation of DNA methylation in response to environmental stimulus has recently been demonstrated in *S. latissima* (Schesonk *et al.* 2023) but if non-coding RNAs and histone modifications are also involved has not yet been tested. As these last two mechanisms have been demonstrated in other brown algae (Bourdareau *et al.* 2021; Bai *et al.* 2023), studies examining these patterns in *S. latissima* will surely follow. In addition, active gene modulation would be required to assess the definite impact of any given epigenetic modulation on the actual gene expression. Regarding the microbiome, most microbiota studies for *S. latissima* have focused on describing the microbial partners. Consequently, there is a need to expand the research on co-cultures to investigate causal relations. Specific isolates of interest, such as bacterial core, specialised metabolisers, and pathogens, can be used to study their impact on algal growth and morphology (Burgunter-Delamare 2022). Furthermore, more research is needed on the impact of potential pathogens on the physiological state of *S. latissima* and the composition of its whole microbiota. *In silico* predictions of beneficial metabolic network complementarity are a way to identify specific interactions between *S. latissima* and its microbiota. There is also a need to start cataloguing genes and their functions for both the microbiome and the host, which will require a combination of metagenomic and metatranscriptomic studies linking microbial and host gene expression. Viruses have been recently described in Laminariales and reported to infect two-thirds of the host populations (McKeown *et al.* 2017), highlighting the importance of incorporating viruses in studies on algal microbiota.
All the ‘omic’ data recently generated is being used to improve breeding of macroalgae that still lags far behind plant crops. Several of these land crop techniques are expected to be applied to *S. latissima* as investment in aquaculture facilities is rising on both sides of the North Atlantic. However, these techniques may raise social and ethical issues that will need to be discussed with society in the next decades (more on Charrier *et al.* 2020).

Although the distribution of *S. latissima* is fairly well documented in some regions, repeated monitoring and detailed distribution data are still lacking in other regions, e.g. south of Europe, Russian waters. New technologies, such as remote sensing, drone imagery, video by underwater vehicles, but also eDNA approaches can greatly assist in monitoring the occurrence of *S. latissima* (e.g. De Pooter *et al.* 2017; Douay *et al.* 2022).

Studies across the biogeographic distribution range of *S. latissima* will help to distinguish between present phenotypic plasticity and adaptation patterns present in the species and how it may be affected by climate change scenarios.

Despite overwhelming evidence that *S. latissima* populations are declining and that this compromises the ecosystem services they provide, there are still few management actions in place. Moreover, if present, these are country- or region-specific, without international perspective and guidance. Hence, the effectiveness of management actions already applied to other macroalgae has not been tested for *S. latissima*. It is imperative that this will be put into action if we aim to maintain the remaining populations and restore some of the others. Management actions tested in other seaweeds that may also prove successful with *S. latissima* include improving water quality (by decreasing nutrient load, for example), Marine Protected Areas, grazer control, and others (Strain *et al.* 2015; Eger *et al.* 2022; Peleg *et al.* 2023). As political interest and societal benefits in recovering kelp populations are rising, securing the financial and logistical means to undergo large-scale
restoration efforts might become more reachable (Eger et al. 2020; Filbee-Dexter, Wernberg, et al. 2022).

Acknowledgements

CM is supported by FutureMARES (grant number 869300) and previously by ThermalBuffer (PTDC/BIA-BMA/31088/2017 and PTDC/BIA-BMA/31088/2017). The contributions of ND and SN were conducted in the frame of the project FACE-IT (The Future of Arctic Coastal Ecosystems – Identifying Transitions in Fjord Systems and Adjacent Coastal Areas). FACE-IT has received funding from the European Union’s Horizon 2020 research and innovation programme under grant agreement No 869154. BBD received funding from the collaborative research centre SFB1127/2/3 ChemBioSys (Deutsche Forschungsgemeinschaft - Project ID 239748522) and previously by a joint PhD scholarship from the Brittany region (Project HOSALA) and Sorbonne University (ED227).

Figure legends
Figure 1: The worldwide distribution of *Saccharina latissima*. Occurrence data of *S. latissima* (orange dots) were collected from databases (Global Biodiversity Information Facility (http://www.gbif.org) and the Ocean Biogeographic Information System (http://iobis.org). Occurrence data cover the timeframe between 1903–2020. Note that the point size is increased to allow visualisation at this large scale and does not display the real area extent. Sea surface temperature data (colour gradient) from 2022 a) summer temperature (21.03–21.09.2022) and b) winter temperature (01.01–21.03.2022 & 21.09–31.12.2022) were downloaded from the NOAA database (https://coastwatch.pfeg.noaa.gov/erddap/). The maps integrate the monthly temperature mean with latitude and longitude averaged as integers. White areas around the North Pole: projection makes data interpolation impossible. Maps were created with the R package ‘ggOceanMaps(Vihtakari 2022)’.

Figure 2: Morphological variability of European *Saccharina latissima* sporophytes. The white bars represent 20 cm. a) Ny-Ålesund, Spitsbergen; collected from the Old Pier, 10 m depth, moderate exposure (Photo: N. Diehl). b) Ansnas, Norway; collected in a small
bay, 1-2 m depth, protected (Photo: N. Diehl). e) Runde, Norway; collected from rocks surrounded by sand, 1-2 m depth, moderate exposure (Photo: N. Diehl). d) Runde, Norway; collected in a Laminaria digitata forest, 1-3 m depth, exposed (Photo: N. Diehl).

c) Locmariaquer, France; collected from rocky shores, high tidal range, 3-5 m depth, moderate exposure (Photo: L. Fouqueau). f) Helgoland, Germany; collected from rocky shores, 5 m depth, exposed (Photo: A. Wagner). Figure modified from (Diehl et al. 2023).

Figure 3: Life cycle of Saccharina latissima. The life cycle of S. latissima can be split into a diploid (blue) and a haploid (yellow) phase. Adult sporophytes (2n) release zoospores, which grow into either female or male gametophytes (1n). Female gametophytes release eggs (1n); male gametophytes release gametes (1n). Egg and gametes fuse to a zygote (2n), which grows into sporophytes (2n). Sporophyte photo: S. Forbord. Microscopic photos and description: I. Bartsch.
Figure 4: Research values of *Saccharina latissima* – ecosystem services, economic values, and drivers. Schematic display of the manifold ecosystem services and economic application. *S. latissima* is represented as a bicycle chain, powering many ecosystem services: providing habitat, feed and nursery ground for the associated micro- and macrofauna (*Biotic interactions*); improving the water quality accumulating high concentrations of harmful elements; improving the air quality by releasing oxygen; and sequestering carbon (*Conservation and restoration*). These ecological values lead to a multitude of economic values. In nature, *S. latissima* provides coastal protection by reducing wave energy, increasing fishing and diving tourism, and enhancing fisheries by serving as a nursery group for economically important fish species (*Biotic interactions*). Harvested *S. latissima* is utilised for food; feed; extraction of bioactive compounds, with applications in pharmaceutical, medical, cosmetics, paper and processed food industries, among others (see more in Review II); development of biofuels and biomaterial (see more in Review II). The main drivers of *S. latissima* survival and growth are temperature (*Microbiome*), light availability (*Mobile biota*), salinity (*Epi- and endobiota*), nutrients (*Grazers*), and biotic factors (*Biotic interactions*), that significantly modify ecological and
economic services provided. Ongoing research leads the way for a deeper understanding
of kelp ecosystems and new applications (Conclusion).

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