Type of article: review

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

Running title: *Saccharina latissima*

Nora Diehl[1], Huiru Li[2], Lydia Scheschonk[a], Bertille Burgunter-Delamare[3], Sarina Niedzwiedz[1], Silje Forbord[4], Maren Sæther[5], Kai Bischof[1], Cátia Monteiro[6,7*]

[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

[a] independent

* 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 Sac*charina 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

(GeO_2) (Kerrison *et al.* 2016; Nielsen, Kumar, *et al.* 2016). 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; Scheschonk *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; Scheschonk *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*; Scheschonk *et al.* 2023, Scheschonk 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; Scheschonk *et al.* 2023, Scheschonk 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.*

2021). 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 (Scheschonk *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 10–15ºC 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 (Olischläger *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 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 (Scheschonk *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 µmol photons m^{-2} s^{-1}) + UVR exposure (Laturnus *et al.* 2010). The impact of PAR (~10 µmol photons m^{-2} s^{-1}) and UVR were also investigated in chloroplasts of vegetative (non-soral) and fertile (soral) tissue of *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 *S. latissima* was significantly higher at high light (300 µmol photons m^{-2} s^{-1}) compared to low light conditions (3 µmol photons m^{-2} s^{-1}) (McDowell *et al.* 2015).

Sedimentation and epibiosis have a strong impact on light availability. *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 *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 *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 *S. latissima* than the various temperatures applied (0, 4, 8°C) (Scheschonk *et al.* 2019). The lower laminarin content at elevated temperatures (8°C) suggests that prolonged darkness may be a problem for *S. latissima* under future temperature trends.

In a comparable study on *S. latissima* sporophytes, low temperatures (2°C) and PAR (10 µmol 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 F_v/F_m 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, 12ºC), 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 Stekoll 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, Scheschonk, *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 B_6 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 (S_A 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 (S_A 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 intricated 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

1986). 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 CO_2 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 CO_2 (pCO_2) applied. Photophysiology, reflected by different parameters (e.g., pigments, photosynthetic O_2 evolution and CO_2 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 CO_2 uptake and O_2 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 pCO_2 levels (1200 ppm)(Iñiguez *et al.* 2016). Regarding the biochemistry, *S. latissima* was

found to utilise more CO_2 than bicarbonate (HCO_3^-) as the photosynthetic carbon source, revealed by the signatures of carbon stable isotope ($\delta^{13}C$) (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 pCO_2 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 ($\Omega_{aragonite}$) (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 pCO_2 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 pCO_2 and more likely to benefit from climate change than the temperate population, as reflected by its increased growth rates at elevated pCO_2 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- (e.g., *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.

Grazers

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 (21ºC), 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.*

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 (Evankow *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 (Scheschonk *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, pCO_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*.

Ecological forecast

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* (Scheschonk *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

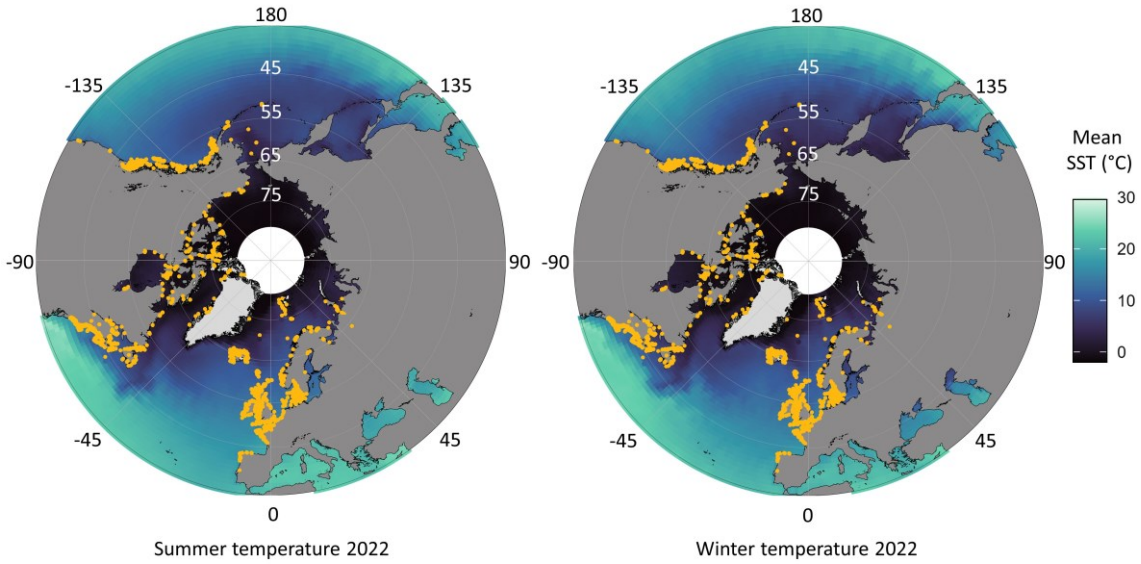

Figure 1: The worldwide distribution of *Saccharina latissima*. Occurrence data of *S. latissima* (orange dots) were collected from databases (Global Biodiversity Information Facility (http://www.gbif.org) and the Ocean Biogeographic Information System (http://iobis.org). Occurrence data cover the timeframe 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)'.

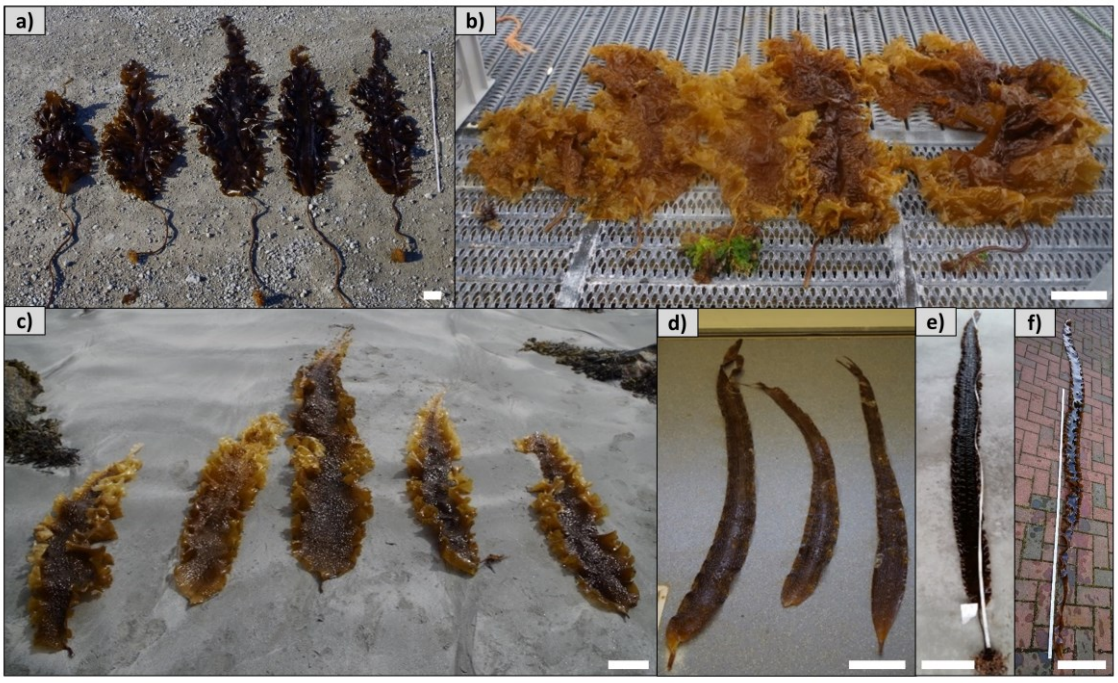

Figure 2: Morphological variability of European *Saccharina latissima* sporophytes. The white bars represent 20 cm. **a)** Ny-Ålesund, Spitsbergen; collected from the Old Pier, 10 m depth, moderate exposure (Photo: N. Diehl). **b)** Ansnas, Norway; collected in a small

bay, 1-2 m depth, protected (Photo: N. Diehl). **c)** 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). **e)** 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).

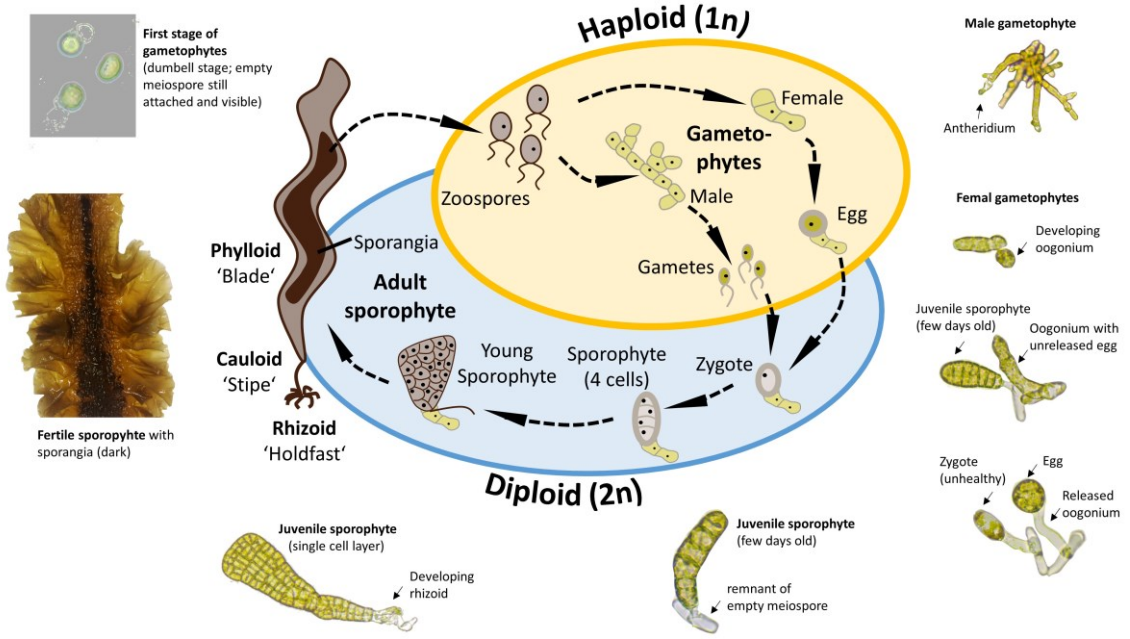

Figure 3: Life cycle of *Saccharina latissima*. The life cycle of *S. latissima* can be split into a diploid (blue) and a haploid (yellow) phase. Adult sporophytes (2n) release zoospores, which grow into either female or male gametophytes (1n). Female gametophytes release eggs (1n); male gametophytes 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.

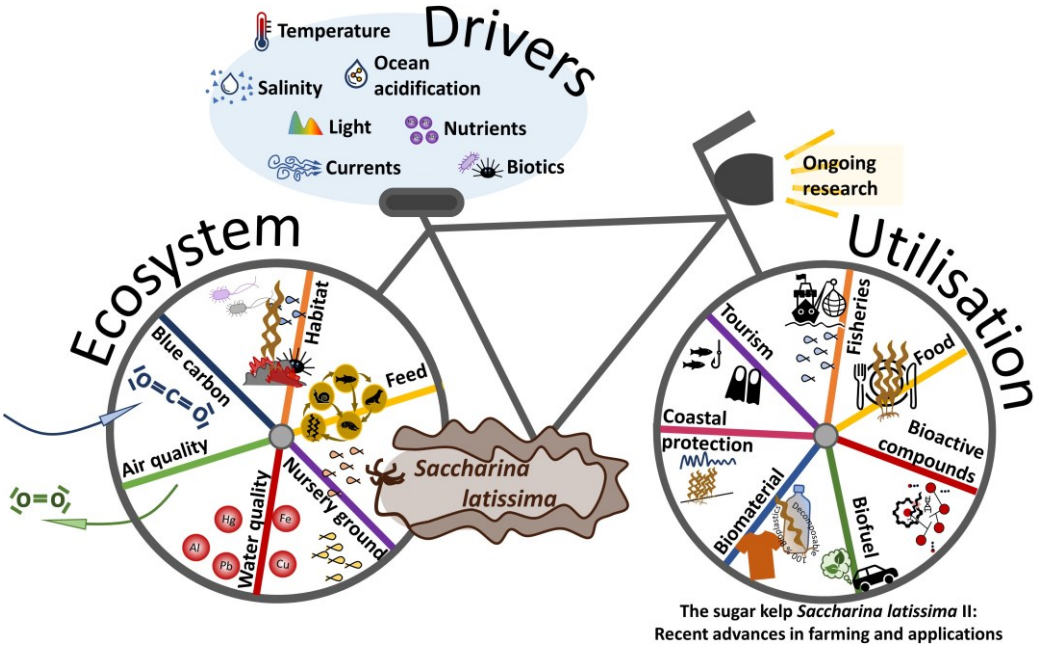

Figure 4: Research values of *Saccharina latissima* – ecosystem services, economic values, and drivers. Schematic display of the manifold ecosystem services and economic application. *S. latissima* is represented as a bicycle chain, powering many ecosystem services: providing habitat, feed and nursery 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*).

References:

Adey WH, Steneck RS. **2001**. Thermogeography over time creates biogeographic regions: A temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. *Journal of Phycology* **37**: 677–698.

Ahmed S, Cock JM, Pessia E, *et al.* 2014. A Haploid System of Sex Determination in the Brown Alga *Ectocarpus sp. Current Biology* **24**: 1945–1957.

Amsler CD. **2008**. *Algal chemical ecology*. Springer.

Anastasiadi D, Venney CJ, Bernatchez L, Wellenreuther M. **2021**. Epigenetic inheritance and reproductive mode in plants and animals. *Trends in Ecology & Evolution* **36**: 1124–1140.

Andersen GS, Moy FE, Christie H. **2018**. In a squeeze: Epibiosis may affect the distribution of kelp forests. *Ecology and Evolution* **0**.

Andersen GS, Pedersen MF, Nielsen SL. **2013**. Temperature acclimation and heat tolerance of photosynthesis in Norwegian *Saccharina latissima* (Laminariales, Phaeophyceae). *Journal of Phycology* **49**: 689–700.

Andersen GS, Steen H, Christie H, Fredriksen S, Moy FE. **2011**. Seasonal Patterns of Sporophyte Growth, Fertility, Fouling, and Mortality of *Saccharina latissima* in Skagerrak, Norway: Implications for Forest Recovery (A McMinn, Ed.). *Journal of Marine Biology* **2011**: 690375.

Araújo RM, Assis J, Aguillar R, *et al.* 2016. Status, trends and drivers of kelp forests in Europe: an expert assessment. *Biodiversity and Conservation* **25**: 1319–1348.

Armitage CS, Husa V, Petelenz-Kurdziel EA, Sjøtun K. **2017**. Growth and

competition in a warmer ocean: a field experiment with a non-native and two native habitat-building seaweeds. *Marine Ecology Progress Series* **573**: 85–99.

Assis J, Araújo MB, Serrão EA. **2018**. Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. *Global Change Biology* **24**: e55–e66.

Attridge C, Metaxas A, Denley D. **2022**. Wave exposure affects the persistence of kelp beds amidst outbreaks of the invasive bryozoan *Membranipora membranacea*. *Marine Ecology Progress Series* **702**: 39–56.

Augyte S, Lewis L, Lin S, Neefus CD, Yarish C. **2018**. Speciation in the exposed intertidal zone: the case of *Saccharina angustissima comb. nov. & stat. nov.* (Laminariales, Phaeophyceae). *Phycologia* **57**: 100–112.

Augyte S, Wikfors GH, Pitchford S, *et al.* 2020. The application of flow cytometry for kelp meiospore isolation. *Algal Research* **46**: 101810.

Badis Y, Scornet D, Harada M, *et al.* 2021. Targeted CRISPR-Cas9-based gene knockouts in the model brown alga *Ectocarpus*. *New Phytologist* **231**: 2077–2091.

Bai M, Yue S, Wang W, *et al.* 2023. Identification and Characterization of Long Non-Coding RNAs Involved in Sex-Related Gene Regulation in Kelp *Saccharina japonica*. *Journal of Ocean University of China* **22**: 755–765.

Bartsch I, Paar M, Fredriksen S, *et al.* 2016. Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biology* **39**: 2021–2036.

Bartsch I, Wiencke C, Bischof K, *et al.* 2008. The genus *Laminaria sensu lato*: recent insights and developments. *European Journal of Phycology* **43**: 1–86.

Bates AE, Helmuth B, Burrows MT, *et al.* 2018. Biologists ignore ocean weather at their peril. *Nature* **560**.

Bekkby T, Moy FE. **2011**. Developing spatial models of sugar kelp (*Saccharina*

latissima) potential distribution under natural conditions and areas of its disappearance in Skagerrak. *Estuarine, Coastal and Shelf Science* **95**: 477–483.

Bekkby T, Torstensen RRG, Grünfeld LAH, *et al.* 2023. 'Hanging gardens'—comparing fauna communities in kelp farms and wild kelp forests. *Frontiers in Marine Science* **10**.

Bernard M, Rousvoal S, Collet N, *et al.* 2019. A highly prevalent filamentous algal endophyte in natural populations of the sugar kelp *Saccharina latissima* is not detected during cultivation in Northern Brittany. *Aquatic Living Resources* **32**: 21.

Bernard M, Rousvoal S, Jacquemin B, Ballenghien M, Peters AF, Leblanc C. 2018. qPCR-based relative quantification of the brown algal endophyte *Laminarionema elsbetiae* in *Saccharina latissima*: variation and dynamics of host—endophyte interactions. *Journal of Applied Phycology* **30**: 2901–2911.

Bernard MS, Strittmatter M, Murúa P, *et al.* 2019. Diversity, biogeography and host specificity of kelp endophytes with a focus on the genera *Laminarionema* and *Laminariocolax* (Ectocarpales, Phaeophyceae). *European Journal of Phycology* **54**: 39–51.

de Bettignies T, de Bettignies F, Bartsch I, *et al.* 2021. *Background Document for Kelp Forests habitat*.

Bewick AJ, Niederhuth CE, Ji L, *et al.* 2017. The evolution of CHROMOMETHYLASES and gene body DNA methylation in plants. *Genome biology* **18**: 1–13.

Bischof K, Buschbaum C, Fredriksen S, *et al.* 2019. Kelps and Environmental Changes in Kongsfjorden: Stress Perception and Responses In: *The Ecosystem of Kongsfjorden, Svalbard*. Springer Nature Switzerland AG, 373–422.

Boderskov T, Rasmussen MB, Bruhn A. 2021. Obtaining spores for the production of

Saccharina latissima: seasonal limitations in nature, and induction of sporogenesis in darkness. *Journal of Applied Phycology*.

Boderskov T, Schmedes PS, Bruhn A, Rasmussen MB, Nielsen MM, Pedersen MF. **2016**. The effect of light and nutrient availability on growth, nitrogen, and pigment contents of *Saccharina latissima* (Phaeophyceae) grown in outdoor tanks, under natural variation of sunlight and temperature, during autumn and early winter in Denmark. *Journal of Applied Phycology* **28**: 1153–1165.

Bolton JJ. **2010**. The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. *Helgoland Marine Research* **64**: 263–279.

Bolton JJ, Lüning K. **1982**. Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Marine Biology* **66**: 89–94.

Boquete MT, Muyle A, Alonso C. **2021**. Plant epigenetics: phenotypic and functional diversity beyond the DNA sequence. *American Journal of Botany* **108**: 553–558.

Bossdorf O, Richards CL, Pigliucci M. **2008**. Epigenetics for ecologists. *Ecology letters* **11**: 106–115.

Bourdareau S, Tirichine L, Lombard B, *et al.* 2021. Histone modifications during the life cycle of the brown alga Ectocarpus. *Genome Biology* **22**: 12.

Bourlat SJ, Faust E, Wennhage H, *et al.* 2021. Wrasse fishery on the Swedish West Coast: towards ecosystem-based management. *ICES Journal of Marine Science* **78**: 1386–1397.

Breton TS, Nettleton JC, O'Connell B, Bertocci M. **2018**. Fine-scale population genetic structure of sugar kelp, *Saccharina latissima* (Laminariales, Phaeophyceae), in eastern Maine, USA. *Phycologia* **57**: 32–40.

Bringloe T, Starko S, Wade R, *et al.* 2020. Phylogeny and Evolution of the Brown

Algae. *Critical Reviews in Plant Sciences*.

Brinkhuis BH, Chung IK. **1986**. The effects of copper on the fine structure of the kelp *Laminaria saccharina* (L.) Lamour. *Marine environmental research* **19**: 205–223.

Broch O, Ellingsen I, Forbord S, *et al.* 2013. Modelling the cultivation and bioremediation potential of the kelp *Saccharina latissima* in close proximity to an exposed salmon farm in Norway. *Aquaculture Environment Interactions* **4**: 187–206.

Bruhn A, Brynning G, Johansen A, *et al.* 2019. Fermentation of sugar kelp (*Saccharina latissima*)—effects on sensory properties, and content of minerals and metals. *Journal of Applied Phycology* **31**: 3175–3187.

Bruhn A, Janicek T, Manns D, *et al.* 2017. Crude fucoidan content in two North Atlantic kelp species, *Saccharina latissima* and *Laminaria digitata*—seasonal variation and impact of environmental factors. *Journal of Applied Phycology* **29**: 3121–3137.

Bruhn A, Tørring DB, Thomsen M, *et al.* 2016. Impact of environmental conditions on biomass yield, quality, and bio-mitigation capacity of *Saccharina latissima*. *Aquaculture Environment Interactions* **8**: 619–636.

Burek KE, O'Brien JM, Scheibling RE. **2018**. Wasted effort: recruitment and persistence of kelp on algal turf. *Marine Ecology Progress Series* **600**: 3–19.

Burgunter-Delamare B. **2022**. Etudes des interactions hôte-microbiote chez l'algue brune Saccharina latissima. *Sorbone Université, PhD thesis*.

Burgunter-Delamare B, Rousvoal S, Legeay E, *et al.* 2023. The *Saccharina latissima* microbiome: Effects of region, season, and physiology. *Frontiers in Microbiology* **13**: 1050939.

Burgunter-Delamare B, Tanguy G, Legeay E, Boyen C, Dittami SM. **2022**. Effects of sampling and storage procedures on 16S rDNA amplicon sequencing results of kelp microbiomes. *Marine Genomics* **63**: 100944.

Calosi P, De Wit P, Thor P, Dupont S. **2016**. Will life find a way? Evolution of marine species under global change. *Evolutionary Applications* **9**: 1035–1042.

Capistrant-Fossa KA, Morrison HG, Engelen AH, *et al.* 2021. The microbiome of the habitat-forming brown alga *Fucus vesiculosus* (Phaeophyceae) has similar cross-Atlantic structure that reflects past and present drivers1. *Journal of Phycology* **57**: 1681–1698.

Carrier TJ, Eddy SD, Redmond S. **2017**. Solar-dried kelp as potential feed in sea urchin aquaculture. *Aquaculture International* **25**: 355–366.

Casado-Amezúa P, Araújo R, Bárbara I, *et al.* 2019. Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern Europe. *Biodiversity and Conservation*.

Castilla-Gavilán M, Cognie B, Ragueneau E, Turpin V, Decottignies P. **2019**. Evaluation of dried macrophytes as an alternative diet for the rearing of the sea urchin *Paracentrotus lividus* (Lamarck, 1816). *Aquaculture Research* **50**: 1762–1769.

Chapman ARO. **1973**. Phenetic variability of stipe morphology in relation to season, exposure, and depth in the non-digitate complex of *Laminaria* Lamour. (Phaeophyta, Laminariales) in Nova Scotia. *Phycologia* **12**: 53–57.

Chapman AS, Stévant P, Larssen WE. **2015**. Food or fad? Challenges and opportunities for including seaweeds in a Nordic diet. *Botanica Marina* **58**: 423–433.

Charrier B, Abreu MH, Araujo R, *et al.* 2017. Furthering knowledge of seaweed growth and development to facilitate sustainable aquaculture. *New Phytologist* **216**: 967–975.

Charrier B, Barbier M, Araujo R, Holdt S, Jacquemin B, Rebours C. **2020**. Development and objectives of the PHYCOMORPH European Guidelines for the Sustainable Aquaculture of Seaweeds (PEGASUS). *Botanica Marina*.

Chavanich S, Harris LG. **2002**. The influence of macroalgae on seasonal abundance and

feeding preference of a subtidal snail, *Lacuna vincta* (montagu) (Littorinidae) in the gulf of Maine. *Journal of Molluscan Studies* **68**: 73–78.

Chen J, Zang Y, Shang S, Tang X. **2019**. The complete mitochondrial genome of the brown alga *Macrocystis integrifolia* (Laminariales, Phaeophyceae). *Mitochondrial DNA Part B* **4**: 635–636.

Christie H, Andersen GS, Bekkby T, *et al.* 2019. Shifts Between Sugar Kelp and Turf Algae in Norway: Regime Shifts or Fluctuations Between Different Opportunistic Seaweed Species? *Frontiers in Marine Science* **6**.

Christie H, Andersen GS, Tveiten LA, Moy FE. **2022**. Macrophytes as habitat for fish. *ICES Journal of Marine Science*: fsac008.

Christie H, Gundersen H, Rinde E, *et al.* 2019. Can multitrophic interactions and ocean warming influence large-scale kelp recovery? *Ecology and Evolution* **9**: 2847–2862.

Chung IK, Brinkhuis BH. **1986**. Copper effects in early stages of the Kelp,*Laminaria saccharina*. *Marine Pollution Bulletin* **17**: 213–218.

Clerc T, Boscq S, Attia R, Kaminski Schierle GS, Charrier B, Läubli NF. **2022**. Cultivation and Imaging of *S. latissima* Embryo Monolayered Cell Sheets Inside Microfluidic Devices. *Bioengineering* **9**.

Coaten DJ, Guls HD, Þorsteinsdóttir M, Halldórsson HP. **2023**. Effect of Environmental Physico-Chemical Parameters on the Biochemical Composition of Wild Icelandic *Laminaria digitata* and *Saccharina latissima* (Laminariaceae, Phaeophyceae). *Regional Studies in Marine Science* **60**: 102839.

Cock JM, Sterck L, Rouze P, *et al.* 2010. The *Ectocarpus* genome and the independent evolution of multicellularity in brown algae. *Nature* **465**: 617–621.

Coelho SM, Mignerot L, Cock JM. **2019**. Origin and evolution of sex-determination systems in the brown algae. *New Phytologist* **222**: 1751–1756.

Coleman MA, Wood G, Filbee-Dexter K, *et al.* 2020. Restore or Redefine: Future Trajectories for Restoration. *Frontiers in Marine Science* **7**.

Corrigan S, Brown AR, Tyler CR, *et al.* 2023. Development and Diversity of Epibiont Assemblages on Cultivated Sugar Kelp (*Saccharina latissima*) in Relation to Farming Schedules and Harvesting Techniques. *Life* **13**.

Daggett TL, Pearce CM, Robinson SMC, Chopin T. **2010**. Does Method of Kelp (*Saccharina latissima*) Storage Affect Its Food Value for Promoting Somatic Growth of Juvenile Green Sea Urchins (*Strongylocentrotus droebachiensis*)? *Journal of Shellfish Research* **29**: 247–252.

Davison IR, Jordan TL, Fegley JC, Grobe CW. **2007**. Response of *Laminaria saccharina* (Phaeophyta) growth and photosynthesis to simultaneous ultraviolet radiation and nitrogen limitation. *Journal of Phycology* **43**: 636–646.

Dean TA, Jewett SC. **2001**. Habitat-specific recovery of shallow subtidal communities following the Exxon Valdez oil spill. *Ecological Applications* **11**: 1456–1471.

Deiner K, Bik HM, Mächler E, *et al.* 2017. Environmental DNA metabarcoding: Transforming how we survey animal and plant communities. *Molecular Ecology* **26**: 5872–5895.

Denley D, Metaxas A, Fennel K. **2019**. Community composition influences the population growth and ecological impact of invasive species in response to climate change. *Oecologia* **189**: 537–548.

Diehl N, Bischof K. **2021**. Coping with a changing Arctic: mechanisms of acclimation in the brown seaweed *Saccharina latissima* from Spitsbergen. *Marine Ecology Progress Series* **657**: 43–57.

Diehl N, Karsten U, Bischof K. **2020**. Impacts of combined temperature and salinity stress on the endemic Arctic brown seaweed *Laminaria solidungula* J. Agardh. *Polar*

Biology.

Diehl N, Roleda MY, Bartsch I, Karsten U, Bischof K. **2021**. Summer Heatwave Impacts on the European Kelp *Saccharina latissima* Across Its Latitudinal Distribution Gradient. *Frontiers in Marine Science* **8**: 1433.

Diehl N, Steiner N, Bischof K, Karsten U, Heesch S. **2023**. Exploring intraspecific variability–Biochemical and morphological traits of the sugar kelp *Saccharina latissima* along latitudinal and salinity gradients in Europe. *Frontiers in Marine Science* **10**: 1042.

Dijkstra J, Harris L, Mello K, Litterer A, Wells C, Ware C. **2017**. Invasive seaweeds transform habitat structure and increase biodiversity of associated species. *Journal of Ecology*.

Dittami SM, Duboscq-Bidot L, Perennou M, *et al.* 2016. Host–microbe interactions as a driver of acclimation to salinity gradients in brown algal cultures. *The ISME journal* **10**: 51–63.

Doney SC, Busch DS, Cooley SR, Kroeker KJ. **2020**. The impacts of ocean acidification on marine ecosystems and reliant human communities. *Annual Review of Environment and Resources* **45**: 83–112.

Douay F, Verpoorter C, Duong G, Spilmont N, Gevaert F. **2022**. New Hyperspectral Procedure to Discriminate Intertidal Macroalgae. *Remote Sensing* **14**.

Druehl LD, Collins JD, Lane CE, Saunders GW. **2005**. An evaluation of methods used to assess intergeneric hybridization in kelps using Pacific laminariales (Phaeophyceae). *Journal of Phycology* **41**: 250–262.

Dubin MJ, Zhang P, Meng D, *et al.* 2015. DNA methylation in *Arabidopsis* has a genetic basis and shows evidence of local adaptation. *elife* **4**: e05255.

Dunlop K, Staby A, van der Meeren T, *et al.* 2022. Habitat associations of juvenile Atlantic cod (*Gadus morhua* L.) and sympatric demersal fish communities within shallow

inshore nursery grounds. *Estuarine, Coastal and Shelf Science*: 108111.

Ebbing APJ, Fivash GS, Martin NB, *et al.* 2021. In-Culture Selection and the Potential Effects of Changing Sex Ratios on the Reproductive Success of Multiannual Delayed Gametophytes of *Saccharina latissima* and *Alaria esculenta*. *Journal of Marine Science and Engineering* **9**.

Ebbing A, Pierik R, Bouma T, Kromkamp JC, Timmermans K. **2020**. How light and biomass density influence the reproduction of delayed *Saccharina latissima* gametophytes (Phaeophyceae). *Journal of Phycology* **56**: 709–718.

Ebbing APJ, Pierik R, Fivash G, *et al.* 2021. The role of seasonality in reproduction of multiannual delayed gametophytes of *Saccharina latissima*. *Journal of Phycology* **n/a**.

Eddy SD, Brown NP, Kling AL, Watts SA, Lawrence A. **2012**. Growth of Juvenile Green Sea Urchins, *Strongylocentrotus droebachiensis*, Fed Formulated Feeds with Varying Protein Levels Compared with a Macroalgal Diet and a Commercial Abalone Feed. *Journal of the World Aquaculture Society* **43**: 159–173.

Egan S, Harder T, Burke C, Steinberg P, Kjelleberg S, Thomas T. **2013**. The seaweed holobiont: understanding seaweed–bacteria interactions. *FEMS Microbiology Reviews* **37**: 462–476.

Eger AM, Layton C, McHugh TA, Gleason M, Eddy N. **2022**. *Kelp restoration guidebook: lessons learned from kelp projects around the world*. Arlington, VA, USA: The Nature Conservancy.

Eger AM, Vergés A, Choi CG, *et al.* 2020. Financial and institutional support are important for large-scale kelp forest restoration. *Frontiers in Marine Science* **7**: 535277.

Ehrig K, Alban S. **2015**. Sulfated galactofucan from the brown alga *Saccharina latissima*—variability of yield, structural composition and bioactivity. *Marine Drugs* **13**: 76–101.

Eriksson BK, Johansson G, Snoeijs P. **2002**. Long-term changes in the macroagal vegetation of the inner Gullmar Fjord, Swedish Skagerrak coast. *Journal of Phycology* **38**: 284–296.

Eriksson BK, Ljunggren L, Sandström A, *et al.* 2009. Declines in predatory fish promote bloom-forming macroalgae. *Ecological Applications* **19**: 1975–1988.

Evankow A, Christie H, Hancke K, *et al.* 2019. Genetic heterogeneity of two bioeconomically important kelp species along the Norwegian coast. *Conservation Genetics* **20**: 615–628.

Fan X, Han W, Teng L, *et al.* 2020. Single-base methylome profiling of the giant kelp *Saccharina japonica* reveals significant differences in DNA methylation to microalgae and plants. *New Phytologist* **225**: 234–249.

Fan X, Xie W, Wang Y, Xu D, Zhang X, Ye N. **2020**. The complete chloroplast genome of *Saccharina latissima*. *Mitochondrial DNA Part B* **5**: 3481–3482.

Feehan C. **2014**. Disease as a control of sea urchin populations in Nova Scotian kelp beds. *Marine Ecology Progress Series* **500**: 149–158.

Feehan C, Francis F. **2014**. Harbouring the enemy: kelp holdfasts protect juvenile sea urchins from predatory crabs. *Marine Ecology Progress Series* **514**: 149–161.

Feehan CJ, Grace SP, Narvaez CA. **2019**. Ecological feedbacks stabilize a turf-dominated ecosystem at the southern extent of kelp forests in the Northwest Atlantic. *Scientific Reports* **9**: 7078.

Filbee-Dexter K. **2014**. Detrital kelp subsidy supports high reproductive condition of deep-living sea urchins in a sedimentary basin . *Aquatic Biology* **23**: 71–86.

Filbee-Dexter K, Feehan CJ, Scheibling RE. **2016**. Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Marine Ecology Progress Series* **543**: 141–152.

Filbee-Dexter K, Feehan CJ, Smale DA, *et al.* 2022. Kelp carbon sink potential

decreases with warming due to accelerating decomposition. *PLOS Biology* **20**: e3001702.

Filbee-Dexter K, Scheibling RE. **2014**. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine ecology progress series* **495**: 1–25.

Filbee-Dexter K, Smajdor A. **2019**. Ethics of Assisted Evolution in Marine Conservation. *Frontiers in Marine Science* **6**.

Filbee-Dexter K, Wernberg T, Barreiro R, *et al.* 2022. Leveraging the blue economy to transform marine forest restoration. *Journal of Phycology* **58**: 198–207.

Filbee-Dexter K, Wernberg T, Fredriksen S, Norderhaug KM, Pedersen MF. **2019**. Arctic kelp forests: Diversity, resilience and future. *Global and Planetary Change* **172**: 1–14.

Filbee-Dexter K, Wernberg T, Grace SP, *et al.* 2020. Marine heatwaves and the collapse of marginal North Atlantic kelp forests. *Scientific Reports* **10**: 13388.

Fojtová M, Kovařík A, Matyášek R. **2001**. Cytosine methylation of plastid genome in higher plants. Fact or artefact? *Plant Science* **160**: 585–593.

Forbord S, Etter SA, Broch OJ, Dahlen VR, Olsen Y. **2021**. Initial short-term nitrate uptake in juvenile, cultivated *Saccharina latissima* (Phaeophyceae) of variable nutritional state. *Aquatic Botany* **168**: 103306.

Forbord S, Matsson S, Brodahl GE, *et al.* 2020. Latitudinal, seasonal and depth-dependent variation in growth, chemical composition and biofouling of cultivated *Saccharina latissima* (Phaeophyceae) along the Norwegian coast. *Journal of Applied Phycology*.

Forbord S, Skjermo J, Arff J, *et al.* 2012. Development of *Saccharina latissima* (Phaeophyceae) kelp hatcheries with year-round production of zoospores and juvenile sporophytes on culture ropes for kelp aquaculture. *Journal of Applied Phycology* **24**: 393–399.

Førde H, Forbord S, Handå A, *et al.* 2016. Development of bryozoan fouling on cultivated kelp (*Saccharina latissima*) in Norway. *Journal of Applied Phycology* **28**: 1225–1234.

Fortes MD, Lüning K. **1980**. Growth rates of North Sea macroalgae in relation to temperature, irradiance and photoperiod. *Helgoländer Meeresuntersuchungen* **34**: 15–29.

Fossberg J, Forbord S, Broch OJ, *et al.* 2018. The potential for upscaling kelp (*Saccharina latissima*) cultivation in salmon-driven integrated multi-trophic aquaculture (IMTA). *Frontiers in Marine Science* **5**.

Fragkopoulou E, Serrão EA, De Clerck O, *et al.* 2022. Global biodiversity patterns of marine forests of brown macroalgae. *Global Ecology and Biogeography* **n/a**.

Le François NR, Tremblay-Gratton A, Drouin-Johnson C, *et al.* 2023. Nature-based coastal restoration: Development of an early-rearing production protocol of sugar kelp (*Saccharina latissima* Linnaeus) for bottom planting activities in the Gulf of St-Lawrence (Québec, Canada). *Frontiers in Marine Science* **10**.

Fredriksen S, Filbee-Dexter K, Norderhaug KM, *et al.* 2020. Green gravel: a novel restoration tool to combat kelp forest decline. *Scientific Reports* **10**: 3983.

Gerard VA. **1987**. Hydrodynamic streamlining of *Laminaria saccharina* Lamour. in response to mechanical stress. *Journal of Experimental Marine Biology and Ecology* **107**: 237–244.

Gerard VA. **1988**. Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina*. *Marine Biology* **97**: 25–36.

Gerard VA. **1990**. Ecotypic differentiation in the kelp *Laminaria saccharina*: Phase-specific adaptation in a complex life cycle. *Marine Biology* **107**: 519–528.

Gerard VA. **1997a**. The Role of Nitrogen Nutrition in High-Temperature Tolerance of the Kelp, *Laminaria Saccharina* (Chromophyta). *Journal of Phycology* **33**: 800–810.

Gerard VA. **1997b**. Environmental stress during early development of kelp sporophytes (*Laminaria saccharina*): how long do effects persist? *Journal of Applied Phycology* **9**: 5–9.

Gerard VA, Du Bois KR. **1988**. Temperature ecotypes near the southern boundary of the kelp *Laminaria saccharina*. *Marine Biology* **97**: 575–580.

Gilson AR, Smale DA, O'Connor N. **2021**. Ocean warming and species range shifts affect rates of ecosystem functioning by altering consumer–resource interactions. *Ecology* **n/a**: e03341.

Goecke F, Gómez Garreta A, Martín–Martín R, Rull Lluch J, Skjermo J, Ergon Å. **2022**. Nuclear DNA Content Variation in Different Life Cycle Stages of Sugar Kelp, *Saccharina latissima*. *Marine Biotechnology* **24**: 706–721.

Goecke F, Labes A, Wiese J, Imhoff JF. **2010**. Chemical interactions between marine macroalgae and bacteria. *Marine ecology progress series* **409**: 267–299.

Goldsmit J, Schlegel RW, Filbee-Dexter K, *et al.* 2021. Kelp in the Eastern Canadian Arctic: Current and Future Predictions of Habitat Suitability and Cover. *Frontiers in Marine Science* **8**.

González-Roca F, Gelcich S, Pérez-Ruzafa Á, Vega JMA, Vásquez JA. **2021**. Exploring the role of access regimes over an economically important intertidal kelp species. *Ocean & Coastal Management* **212**: 105811.

Gordillo FJL, Aguilera J, Wiencke C, Jiménez C. **2015**. Ocean acidification modulates the response of two Arctic kelps to ultraviolet radiation. *Journal of Plant Physiology* **173**: 41–50.

Gordillo FJL, Carmona R, Jiménez C. **2022**. A warmer Arctic compromises winter survival of habitat-forming seaweeds. *Frontiers in Marine Science* **8**: 1–18.

Graf L, Shin Y, Yang JH, *et al.* 2021. A genome-wide investigation of the effect of

farming and human-mediated introduction on the ubiquitous seaweed *Undaria pinnatifida*. *Nature Ecology & Evolution* **5**: 360–368.

Graf L, Shin Y, Yang JH, Hwang IK, Yoon HS. **2022**. Transcriptome analysis reveals the spatial and temporal differentiation of gene expression in the sporophyte of *Undaria pinnatifida*. *Algal Research* **68**: 102883.

Grant WS, Chenoweth E. **2021**. Phylogeography of sugar kelp: Northern ice-age refugia in the Gulf of Alaska. *Ecology and Evolution* **n/a**.

Guzinski J, Mauger S, Cock JM, Valero M. **2016**. Characterization of newly developed expressed sequence tag-derived microsatellite markers revealed low genetic diversity within and low connectivity between European *Saccharina latissima* populations. *Journal of Applied Phycology*: 1–14.

Guzinski J, Ruggeri P, Ballenghien M, *et al.* 2020. Seascape Genomics of the Sugar Kelp *Saccharina latissima* along the North Eastern Atlantic Latitudinal Gradient. *Genes* **11**.

Hamel KJ. **2022**. Feeding Preference of the Sea Urchin Arbacia punctulata for Algal Turf Over Kelp in a Degraded Kelp Forest Ecosystem. *Montclair State University, Msc thesis*.

Hanelt D, Tüg H, Bischof K, *et al.* 2001. Light regime in an Arctic fjord: a study related to stratospheric ozone depletion as a basis for determination of UV effects on algal growth. *Marine Biology* **138**: 649–658.

Harding APC, Scheibling RE. **2015**. Feed or flee: Effect of a predation-risk cue on sea urchin foraging activity. *Journal of Experimental Marine Biology and Ecology* **466**: 59–69.

Harley CDG, Anderson KM, Demes KW, *et al.* 2012. Effects of climate change on global seaweed communities. *Journal of Phycology* **48**: 1064–1078.

Haugland B, Rastrick S, Agnalt A, Husa V, Kutti T, Samuelsen BO. **2019**. Mortality

and reduced photosynthetic performance in sugar kelp *Saccharina latissima* caused by the salmon-lice therapeutant hydrogen peroxide. *Aquaculture Environment Interactions* **11**: 1–17.

Heinrich S, Frickenhaus S, Glöckner G, Valentin K. **2012**. A comprehensive cDNA library of light- and temperature-stressed *Saccharina latissima* (Phaeophyceae). *European Journal of Phycology* **47**: 83–94.

Heinrich S, Valentin K, Frickenhaus S, John U, Wiencke C. **2012**. Transcriptomic analysis of acclimation to temperature and light stress in *Saccharina latissima* (Phaeophyceae). *PloS One* **7**: e44342.

Heinrich S, Valentin K, Frickenhaus S, Wiencke C. **2015**. Temperature and light interactively modulate gene expression in *Saccharina latissima* (Phaeophyceae). *Journal of Phycology* **51**: 93–108.

Heinrich S, Valentin K, Frickenhaus S, Wiencke C. **2016**. Origin matters — Comparative transcriptomics in *Saccharina latissima* (Phaeophyceae). *Journal of Experimental Marine Biology and Ecology* **476**: 22–30.

Van den Hoek C, Mann D, Jahns H. **1995**. *Algae - An Introduction to Phycology*. Cambridge University Press.

Hollants J, Leliaert F, De Clerck O, Willems A. **2013**. What we can learn from sushi: a review on seaweed–bacterial associations. *FEMS microbiology ecology* **83**: 1–16.

Holt J, Wakelin S, Lowe J, Tinker J. **2010**. The potential impacts of climate change on the hydrography of the northwest European continental shelf. *Progress in Oceanography* **86**: 361–379.

Holzinger A, Di Piazza L, Lütz C, Roleda MY. **2011**. Sporogenic and vegetative tissues of *Saccharina latissima* (Laminariales, Phaeophyceae) exhibit distinctive sensitivity to experimentally enhanced ultraviolet radiation:photosynthetically active radiation ratio.

Phycological Research **59**: 221–235.

Hsiao SIC, Druehl LD. **1973**. Environmental control of gametogenesis in *Laminaria saccharina* IV. in situ development of gametophytes and young sporophytes. *Journal of Phycology* **9**: 160–165.

Huang M, Robbins KR, Li Y, *et al.* 2023. Genomic selection in algae with biphasic lifecycles: A *Saccharina latissima* (sugar kelp) case study. *Frontiers in Marine Science* **10**.

Hurd CL, Harrison PJ, Bischof K, Lobban CS. **2014**. *Seaweed ecology and physiology*. Cambridge University Press.

Iñiguez C, Carmona R, Lorenzo MR, Niell FX, Wiencke C, Gordillo FJL. **2016**. Increased temperature, rather than elevated CO2, modulates the carbon assimilation of the Arctic kelps *Saccharina latissima* and *Laminaria solidungula*. *Marine Biology* **163**: 248.

Jevne LS, Forbord S, Olsen Y. **2020**. The Effect of Nutrient Availability and Light Conditions on the Growth and Intracellular Nitrogen Components of Land-Based Cultivated *Saccharina latissima* (Phaeophyta). *Frontiers in Marine Science* **7**.

Jueterbock A, Minne AJP, Cock JM, *et al.* 2021. Priming of Marine Macrophytes for Enhanced Restoration Success and Food Security in Future Oceans . *Frontiers in Marine Science* **8**: 279.

Jung S, Chau T V, Kim M, Na W-B. **2022**. Artificial Seaweed Reefs That Support the Establishment of Submerged Aquatic Vegetation Beds and Facilitate Ocean Macroalgal Afforestation: A Review. *Journal of Marine Science and Engineering* **10**.

Kaiser MJ. **2011**. *Marine ecology: processes, systems, and impacts*. Oxford University Press, USA.

Kang I, Lim Y, Cho J-C. **2018**. Complete genome sequence of *Granulosicoccus*

antarcticus type strain IMCC3135T, a marine gammaproteobacterium with a putative dimethylsulfoniopropionate demethylase gene. *Marine Genomics* **37**: 176–181.

Karsten U. **2007**. Salinity tolerance of Arctic kelps from Spitsbergen. *Phycological Research* **55**: 257–262.

Karsten U. **2012**. Seaweed acclimation to salinity and desiccation stress. *Seaweed biology: Novel insights into ecophysiology, ecology and utilization*: 87–107.

Kawecki TJ, Ebert D. **2004**. Conceptual issues in local adaptation. *Ecology Letters* **7**: 1225–1241.

Kerrison PD, Stanley MS, Edwards MD, Black KD, Hughes AD. **2015**. The cultivation of European kelp for bioenergy: site and species selection. *Biomass and bioenergy* **80**: 229–242.

Kerrison PD, Stanley MS, Kelly M, MacLeod A, Black KD, Hughes AD. **2016**. Optimising the settlement and hatchery culture of *Saccharina latissima* (Phaeophyta) by manipulation of growth medium and substrate surface condition. *Journal of Applied Phycology* **28**: 1181–1191.

Kim JK, Kraemer GP, Yarish C. **2015**. Use of sugar kelp aquaculture in Long Island Sound and the Bronx River Estuary for nutrient extraction. *Marine Ecology Progress Series* **531**: 155–166.

Kim JK, Kraemer G, Yarish C. **2019**. Evaluation of the metal content of farm grown *Gracilaria tikvahiae* and *Saccharina latissima* from Long Island Sound and New York Estuaries. *Algal Research* **40**: 101484.

King NG, McKeown NJ, Smale DA, Moore PJ. **2018**. The importance of phenotypic plasticity and local adaptation in driving intraspecific variability in thermal niches of marine macrophytes. *Ecography* **41**: 1469–1484.

King NG, Moore PJ, Thorpe JM, Smale DA. **2022**. Consistency and variation in the

kelp microbiota: patterns of bacterial community structure across spatial scales. *Microbial Ecology*: 1–11.

Konik M, Darecki M, Pavlov AK, Sagan S, Kowalczuk P. **2021**. Darkening of the Svalbard Fjords Waters Observed With Satellite Ocean Color Imagery in 1997–2019. *Frontiers in Marine Science* **8**.

Korb RE, Gerard VA. **2000**. Effects of concurrent low temperature and low nitrogen supply on polar and temperate seaweeds. *Marine Ecology Progress Series* **198**: 73–82.

Krause-Jensen D, Archambault P, Assis J, *et al.* 2020. Imprint of Climate Change on Pan-Arctic Marine Vegetation. *Frontiers in Marine Science* **7**.

Krause-Jensen D, Marbà N, Olesen B, *et al.* 2012. Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. *Global Change Biology* **18**: 2981–2994.

Kroth PG. **2013**. Getting a grip on genetic modification in brown algae. *Journal of Phycology* **49**: 816–818.

Krumhansl K. **2012**. Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile ssp. fragile*. *Marine Ecology Progress Series* **456**: 73–85.

Krumhansl KA, Lauzon-Guay J-S, Scheibling RE. **2014**. Modeling effects of climate change and phase shifts on detrital production of a kelp bed. *Ecology* **95**: 763–774.

Lachnit T, Blümel M, Imhoff JF, Wahl M. **2009**. Specific epibacterial communities on macroalgae: phylogeny matters more than habitat. *Aquatic Biology* **5**: 181–186.

Lämke J, Bäurle I. **2017**. Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. *Genome biology* **18**: 1–11.

Lamy T, Reed DC, Rassweiler A, *et al.* 2018. Scale-specific drivers of kelp forest communities. *Oecologia* **186**: 217–233.

Lane CE, Mayes C, Druehl LD, Saunders GW. **2006**. A multi-gene molecular

investigation of the kelp (Laminariales, Phaeophyceae) supports substantial taxonomic re-organization. *Journal of Phycology* **42**: 493–512.

Laturnus F, Svensson T, Wiencke C. **2010**. Release of reactive organic halogens by the brown macroalga Saccharina latissima after exposure to ultraviolet radiation. *Polar Research* **29**: 379–384.

Lebrun A, Comeau S, Gazeau F, Gattuso J-P. **2022**. Impact of climate change on Arctic macroalgal communities. *Global and Planetary Change*: 103980.

Lee RE. **1989**. *Phycology*. Cambridge University Press.

Lee JA, Brinkhuis BH. **1988**. Seasonal light and temperature interaction effects on development of *Laminaria saccharina* (Phaeophyta) gametophytes and juvenile sporophytes. *Journal of Phycology* **24**: 181–191.

Lewis RJ, Green MK, Afzal ME. **2013**. Effects of chelated iron on oogenesis and vegetative growth of kelp gametophytes (Phaeophyceae). *Phycological Research* **61**: 46–51.

Li H, Monteiro C, Heinrich S, *et al.* 2020. Responses of the kelp *Saccharina latissima* (Phaeophyceae) to the warming Arctic: from physiology to transcriptomics. *Physiologia Plantarum* **168**: 5–26.

Li H, Scheschonk L, Heinrich S, *et al.* 2020. Transcriptomic responses to darkness and the survival strategy of the kelp Saccharina latissima in the early Polar night. *Frontiers in Marine Science* **7**.

Liesner D, Fouqueau L, Valero M, *et al.* 2020. Heat stress responses and population genetics of the kelp *Laminaria digitata* (Phaeophyceae) across latitudes reveal differentiation among North Atlantic populations. *Ecology and Evolution*.

Liesner D, Pearson GA, Bartsch I, *et al.* 2022. Increased Heat Resilience of Intraspecific Outbred Compared to Inbred Lineages in the Kelp *Laminaria digitata*:

Physiology and Transcriptomics. *Frontiers in Marine Science* **9**.

Liesner D, Shama LNS, Diehl N, Valentin K, Bartsch I. **2020**. Thermal Plasticity of the Kelp *Laminaria digitata* (Phaeophyceae) Across Life Cycle Stages Reveals the Importance of Cold Seasons for Marine Forests. *Frontiers in Marine Science* **7**.

Lind AC, Konar B. **2017**. Effects of abiotic stressors on kelp early life-history stages. *Algae* **32**: 223–233.

Liu F, Wang W, Sun X, Liang Z, Wang F. **2014**. RNA-Seq revealed complex response to heat stress on transcriptomic level in *Saccharina japonica* (Laminariales, Phaeophyta). *Journal of Applied Phycology* **26**: 1585–1596.

Liu T, Wang X, Wang G, *et al.* 2019. Evolution of Complex Thallus Alga: Genome Sequencing of *Saccharina japonica*. *Frontiers in Genetics* **10**.

Liu Y, Wikfors GH, Clark P, *et al.* 2022. A deep dive into the epibiotic communities on aquacultured sugar kelp *Saccharina latissima* in Southern New England. *Algal Research* **63**: 102654.

Longphuirt SN, Eschmann C, Russell C. **2013**. Seasonal and species-specific response of five brown macroalgae to high atmospheric CO2. *Marine Ecology Progress Series* **493**: 91–102.

Longtin CM, Saunders GW. **2015**. On the utility of mucilage ducts as a taxonomic character in Laminaria and Saccharina (Phaeophyceae) – the conundrum of S. groenlandica. *Phycologia* **54**: 440–450.

Lubsch A, Timmermans KR. **2019**. Uptake kinetics and storage capacity of dissolved inorganic phosphorus and corresponding dissolved inorganic nitrate uptake in *Saccharina latissima* and *Laminaria digitata* (Phaeophyceae). *Journal of Phycology* **55**: 637–650.

Lüning K. **1980**. Critical levels of light and temperature regulating the gametogenesis of three Laminaria species (Phaeophyceae). *Journal of Phycology* **16**: 1–15.

Lüning K. **1984**. Temperature tolerance and biogeography of seaweeds: the marine algal flora of Helgoland (North Sea) as an example. *Helgoländer Meeresuntersuchungen* **38**: 305–317.

Lüning K. **1990a**. *Seaweeds: their environment, biogeography, and ecophysiology*. John Wiley & Sons.

Lüning K. **1990b**. Seaweed vegetation of the cold and warm temperate regions of the Northern Hemisphere In: *Seaweeds: their environment, biogeography, and ecophysiology*. USA: John Wiley & Sons, .

Lüning K, Dring MJ. **1972**. Reproduction induced by blue light in female gametophytes of *Laminaria saccharina*. *Planta* **104**: 252–256.

Lüning K, Dring MJ. **1975**. Reproduction, growth and photosynthesis of gametophytes of *Laminaria saccharina* grown in blue and red light. *Marine Biology* **29**: 195–200.

Lüning K, Neushul M. **1978**. Light and temperature demands for growth and reproduction of laminarian gametophytes in southern and central California. *Marine Biology* **45**: 297–309.

Luttikhuizen PC, van den Heuvel FHM, Rebours C, Witte HJ, van Bleijswijk JDL, Timmermans K. **2018**. Strong population structure but no equilibrium yet: Genetic connectivity and phylogeography in the kelp *Saccharina latissima* (Laminariales, Phaeophyta). *Ecology and Evolution* **8**: 4265–4277.

Malakhoff KD, Miller RJ. **2021**. After 15 years, no evidence for trophic cascades in marine protected areas. *Proceedings of the Royal Society B: Biological Sciences* **288**: 20203061.

Manns D, Nielsen MM, Bruhn A, Saake B, Meyer AS. **2017**. Compositional variations of brown seaweeds *Laminaria digitata* and *Saccharina latissima* in Danish waters. *Journal of Applied Phycology* **29**: 1493–1506.

Mao X, Augyte S, Huang M, *et al.* 2020. Population Genetics of Sugar Kelp Throughout the Northeastern United States Using Genome-Wide Markers. *Frontiers in Marine Science*.

Marinho GS, Holdt SL, Birkeland MJ, Angelidaki I. **2015**. Commercial cultivation and bioremediation potential of sugar kelp, *Saccharina latissima*, in Danish waters. *Journal of Applied Phycology* **27**: 1963–1973.

Martínez B, Arenas F, Trilla A, Viejo RM, Carreño F. **2015**. Combining physiological threshold knowledge to species distribution models is key to improving forecasts of the future niche for macroalgae. *Global Change Biology* **21**: 1422–1433.

Martins N, Pearson GA, Gouveia L, Tavares AI, Serrão EA, Bartsch I. **2019**. Hybrid vigour for thermal tolerance in hybrids between the allopatric kelps *Laminaria digitata* and *L. pallida* (Laminariales, Phaeophyceae) with contrasting thermal affinities. *European Journal of Phycology*: 1–14.

Masson-Delmotte V, Zhai P, Pirani A, *et al.* 2021. *IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge.

Mathieu O, Reinders J, Čaikovski M, Smathajitt C, Paszkowski J. **2007**. Transgenerational stability of the Arabidopsis epigenome is coordinated by CG methylation. *Cell* **130**: 851–862.

Maturilli M, Herber A, König-Langlo G. **2015**. Surface radiation climatology for Ny-Ålesund, Svalbard (78.9 N), basic observations for trend detection. *Theoretical and Applied Climatology* **120**: 331–339.

McDevit DC, Saunders GW. **2010**. A DNA barcode examination of the Laminariaceae (Phaeophyceae) in Canada reveals novel biogeographical and evolutionary insights. *Phycologia* **49**: 235–248.

McDowell RE, Amsler MO, Li Q, Lancaster Jr JR, Amsler CD. **2015**. The immediate wound-induced oxidative burst of *Saccharina latissima* depends on light via photosynthetic electron transport. *Journal of Phycology* **51**: 431–441.

McKeown DA, Schroeder JL, Stevens K, *et al.* 2018. Phaeoviral infections are present in *Macrocystis*, *Ecklonia* and *Undaria* (Laminariales) and are influenced by wave exposure in Ectocarpales. *Viruses* **10**: 410.

McKeown DA, Stevens K, Peters AF, *et al.* 2017. Phaeoviruses discovered in kelp (Laminariales). *The ISME Journal* **11**: 2869–2873.

McPherson ML, Finger DJI, Houskeeper HF, *et al.* 2021. Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. *Communications Biology* **4**: 298.

Meneghesso C, Seabra R, Broitman BR, *et al.* 2020. Remotely-sensed L4 SST underestimates the thermal fingerprint of coastal upwelling. *Remote Sensing of Environment* **237**: 111588.

Mignerot L, Avia K, Luthringer R, *et al.* 2019. A key role for sex chromosomes in the regulation of parthenogenesis in the brown alga *Ectocarpus*. *Plos Genetics* **15**: e1008211.

Monteiro C, Heinrich S, Bartsch I, *et al.* 2019. Temperature Modulates Sex-Biased Gene Expression in the Gametophytes of the Kelp *Saccharina latissima*. *Frontiers in Marine Science* **6**.

Monteiro C, Li H, Bischof K, *et al.* 2019. Is geographical variation driving the transcriptomic responses to multiple stressors in the kelp *Saccharina latissima*? *BMC Plant Biology* **19**: 513.

Monteiro C, Li H, Diehl N, *et al.* 2020. Modulation of physiological performance by temperature and salinity in the sugar kelp *Saccharina latissima*. *Phycological Research*.

Monteiro J, Rey, Melo, *et al.* 2020. The unique lipidomic signatures of *Saccharina*

latissima can be used to pinpoint their geographic origin. *Biomolecules* **10**: 107.

Mooney KM, Beatty GE, Elsäßer B, *et al.* 2018. Hierarchical structuring of genetic variation at differing geographic scales in the cultivated sugar kelp *Saccharina latissima*. *Marine Environmental Research* **142**: 108–115.

Moore LD, Le T, Fan G. **2013**. DNA methylation and its basic function. *Neuropsychopharmacology* **38**: 23–38.

Mortensen LM. **2017**. Diurnal carbon dioxide exchange rates of *Saccharina latissima* and *Laminaria digitata* as affected by salinity levels in Norwegian fjords. *Journal of Applied Phycology* **29**: 3067–3075.

Motomura T, Sakai Y. **1981**. Effect of chelated iron in culture media on oogenesis in *Laminaria angustata*. *Nippon Suisan Gakkaishi* **47**: 1535–1540.

Moy FE, Christie H. **2012**. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. *Marine Biology Research* **8**: 309–321.

Müller R, Desel C, Steinhoff FS, Wiencke C, Bischof K. **2012**. UV-radiation and elevated temperatures induce formation of reactive oxygen species in gametophytes of cold-temperate/Arctic kelps (Laminariales, Phaeophyceae). *Phycological Research* **60**: 27–36.

Müller R, Laepple T, Bartsch I, Wiencke C. **2009**. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Botanica Marina* **52**: 617.

Müller R, Wiencke C, Bischof K. **2008**. Interactive effects of UV radiation and temperature on microstages of Laminariales (Phaeophyceae) from the Arctic and North Sea. *Climate Research* **37**: 203–213.

Neiva J, Paulino C, Nielsen MM, *et al.* 2018. Glacial vicariance drives phylogeographic diversification in the amphi-boreal kelp *Saccharina latissima*. *Scientific Reports* **8**: 1112.

Nepper-Davidsen J, Andersen DT, Pedersen MF. **2019**. Exposure to simulated heatwave scenarios causes long-term reductions in performance in *Saccharina latissima*. *Marine Ecology Progress Series* **630**: 25–39.

Nicotra AB, Atkin OK, Bonser SP, *et al.* 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* **15**: 684–692.

Niedzwiedz S, Bischof K. **2023**. Glacial retreat and rising temperatures are limiting the expansion of temperate kelp species in the future Arctic. *Limnology and Oceanography* **68**: 816–830.

Niedzwiedz S, Diehl N, Fischer P, Bischof K. **2022**. Seasonal and inter-annual variability in the heatwave tolerance of the kelp *Saccharina latissima* (Laminariales , Phaeophyceae). *Phycological Research* **70**: 212–222.

Nielsen MM, Krause-Jensen D, Olesen B, Thinggaard R, Christensen PB, Bruhn A. **2014**. Growth dynamics of *Saccharina latissima* (Laminariales, Phaeophyceae) in Aarhus Bay, Denmark, and along the species' distribution range. *Marine Biology* **161**: 2011–2022.

Nielsen MM, Kumar JP, Soler-Vila A, Johnson MP, Bruhn A. **2016**. Early stage growth responses of *Saccharina latissima* spores and gametophytes. Part 1: inclusion of different phosphorus regimes. *Journal of Applied Phycology* **28**: 387–393.

Nielsen MM, Manns D, D'Este M, *et al.* 2016. Variation in biochemical composition of *Saccharina latissima* and *Laminaria digitata* along an estuarine salinity gradient in inner Danish waters. *Algal research* **13**: 235–245.

Nielsen MM, Paulino C, Neiva J, Krause-Jensen D, Bruhn A, Serrão EA. **2016**. Genetic diversity of *Saccharina latissima* (Phaeophyceae) along a salinity gradient in the North Sea–Baltic Sea transition zone. *Journal of Phycology* **52**: 523–531.

Nitschke U, Stengel DB. **2014**. Iodine contributes to osmotic acclimatisation in the kelp

Laminaria digitata (Phaeophyceae). *Planta* **239**: 521–530.

Norderhaug KM, Gundersen H, Pedersen A, *et al.* 2015. Effects of climate and eutrophication on the diversity of hard bottom communities on the Skagerrak coast 1990-2010. *Marine Ecology Progress Series* **530**: 29–46.

Norderhaug KM, Nedreaas K, Huserbråten M, Moland E. **2021**. Depletion of coastal predatory fish sub-stocks coincided with the largest sea urchin grazing event observed in the NE Atlantic. *Ambio* **50**: 163–173.

Norway M of C and E (Ed.). **2001**. Svalbard Environmental Protection Act.

Nunes J, McCoy SJ, Findlay HS, *et al.* 2016. Two intertidal, non-calcifying macroalgae (*Palmaria palmata* and Saccharina latissima) show complex and variable responses to short-term CO2 acidification. *ICES Journal of Marine Science* **73**: 887–896.

O'Brien BS, Mello K, Litterer A, Dijkstra JA. **2018**. Seaweed structure shapes trophic interactions: A case study using a mid-trophic level fish species. *Journal of Experimental Marine Biology and Ecology* **506**: 1–8.

O'Brien JM, Scheibling RE. **2016**. Nipped in the bud: mesograzer feeding preference contributes to kelp decline. *Ecology* **97**: 1873–1886.

Olischläger M, Iñiguez C, Gordillo FJL, Wiencke C. **2014**. Biochemical composition of temperate and Arctic populations of *Saccharina latissima* after exposure to increased pCO2 and temperature reveals ecotypic variation. *Planta* **240**: 1213–1224.

Olischläger M, Iñiguez C, Koch K, Wiencke C, Gordillo FJL. **2017**. Increased pCO2 and temperature reveal ecotypic differences in growth and photosynthetic performance of temperate and Arctic populations of *Saccharina latissima*. *Planta* **245**: 119–136.

van Oppen MJH, Coleman MA. **2022**. Advancing the protection of marine life through genomics. *PLOS Biology* **20**: e3001801.

Oudot-Le Secq M-P, Loiseaux-de Goer S, Stam WT, Olsen JL. **2006**. Complete

mitochondrial genomes of the three brown algae (Heterokonta: Phaeophyceae) *Dictyota dichotoma*, *Fucus vesiculosus* and *Desmarestia viridis*. *Current genetics* **49**: 47–58.

Parages ML, Heinrich S, Wiencke C, Jiménez C. **2013**. Rapid phosphorylation of MAP kinase-like proteins in two species of Arctic kelps in response to temperature and UV radiation stress. *Environmental and Experimental Botany* **91**: 30–37.

Park J, Kim JK, Kong J-A, Depuydt S, Brown MT, Han T. **2017**. Implications of rising temperatures for gametophyte performance of two kelp species from Arctic waters. *Botanica Marina* **60**: 39–48.

Pearson GA, Martins N, Madeira P, Serrão EA, Bartsch I. **2019**. Sex-dependent and -independent transcriptional changes during haploid phase gametogenesis in the sugar kelp *Saccharina latissima*. *PloS One* **14**: e0219723.

Pehlke C, Bartsch I. **2008**. Changes in depth distribution and biomass of sublittoral seaweeds at Helgoland (North Sea) between 1970 and 2005. *Climate Research* **37**: 135–147.

Peleg O, Blain C, Shears N. **2023**. Long-term marine protection enhances kelp forest ecosystem stability. *Ecological Applications*: e2895.

Peteiro C, Freire Ó. **2013a**. Epiphytism on blades of the edible kelps *Undaria pinnatifida* and *Saccharina latissima* farmed under different abiotic conditions. *Journal of the World Aquaculture Society* **44**: 706–715.

Peteiro C, Freire Ó. **2013b**. Biomass yield and morphological features of the seaweed *Saccharina latissima* cultivated at two different sites in a coastal bay in the Atlantic coast of Spain. *Journal of Applied Phycology* **25**: 205–213.

Peteiro C, Sánchez N. **2012**. Comparing salinity tolerance in early stages of the sporophytes of a non-indigenous kelp (*Undaria pinnatifida*) and a native kelp (*Saccharina latissima*). *Russian Journal of Marine Biology* **38**: 197–200.

Picard MMM, Johnson LE, Ferrario F, *et al.* 2022. Drivers of kelp distribution in the Gulf of St. Lawrence: insights from a transplant experiment. *Marine Biology* **169**: 50.

De Pooter D, Appeltans W, Bailly N, *et al.* 2017. Toward a new data standard for combined marine biological and environmental datasets - expanding OBIS beyond species occurrences. *Biodiversity Data Journal* **5**: e10989.

Potter KA, Arthur Woods H, Pincebourde S. **2013**. Microclimatic challenges in global change biology. *Global Change Biology* **19**: 2932–2939.

Rana S, Valentin K, Riehl J, *et al.* 2021. Analysis of organellar genomes in brown algae reveals an independent introduction of similar foreign sequences into the mitochondrial genome. *Genomics* **113**: 646–654.

Ratnasingham S, Hebert PDN. **2007**. BARCODING: bold: The Barcode of Life Data System (http://www. barcodinglife. org). *Molecular Ecology Notes* **7**.

Raymond AET, Stekoll MS. **2021**. Conditions for staggering and delaying outplantings of the kelps *Saccharina latissima* and *Alaria marginata* for mariculture. *Journal of the World Aquaculture Society* **52**: 1135–1157.

Reed TE, Schindler DE, Waples RS. **2011**. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology* **25**: 56–63.

Ribeiro PA, Næss T, Dahle G, *et al.* 2022. Going With the Flow – Population Genetics of the Kelp *Saccharina latissima* (Phaeophyceae, Laminariales). *Frontiers in Marine Science* **9**.

Richards CL, Alonso C, Becker C, *et al.* 2017. Ecological plant epigenetics: Evidence from model and non-model species, and the way forward. *Ecology letters* **20**: 1576–1590.

Richards CL, Bossdorf O, Verhoeven KJF. **2010**. Understanding natural epigenetic variation. *The New Phytologist* **187**: 562–564.

Rinde E, Christie H, Fagerli CW, *et al.* 2014. The Influence of Physical Factors on Kelp and Sea Urchin Distribution in Previously and Still Grazed Areas in the NE Atlantic. *PLOS ONE* **9**: e100222.

Robinson LM, Elith J, Hobday AJ, *et al.* 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography* **20**: 789–802.

Roleda MY, Dethleff D. **2011**. Storm-generated sediment deposition on rocky shores: Simulating burial effects on the physiology and morphology of *Saccharina latissima* sporophytes. *Marine Biology Research* **7**: 213–223.

Roleda MY, Hurd CL. **2019**. Seaweed nutrient physiology: application of concepts to aquaculture and bioremediation. *Phycologia* **58**: 552–562.

Roleda MY, Marfaing H, Desnica N, *et al.* 2019. Variations in polyphenol and heavy metal contents of wild-harvested and cultivated seaweed bulk biomass: Health risk assessment and implication for food applications. *Food Control* **95**: 121–134.

Ronowicz M, Kukliński P, Włodarska-Kowalczuk M. **2022**. Morphological variation of kelps (*Alaria esculenta*, cf. *Laminaria digitata*, and *Saccharina latissima*) in an Arctic glacial fjord. *Estuarine, Coastal and Shelf Science* **268**: 107802.

Rugiu L, Hargrave MS, Enge S, Sterner M, Nylund GM, Pavia H. **2021**. Kelp in IMTAs: small variations in inorganic nitrogen concentrations drive different physiological responses of *Saccharina latissima*. *Journal of Applied Phycology* **33**: 1021–1034.

Sanderson JC, Dring MJ, Davidson K, Kelly MS. **2012**. Culture, yield and bioremediation potential of *Palmaria palmata* (Linnaeus) Weber & Mohr and *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders adjacent to fish farm cages in northwest Scotland. *Aquaculture (Amsterdam, Netherlands)* **354**–**355**: 128–135.

Scheschonk L, Becker S, Hehemann JH, Diehl N, Karsten U, Bischof K. **2019**. Arctic kelp eco-physiology during the polar night in the face of global warming: a crucial role for laminarin. *Marine Ecology Progress Series* **611**: 59–74.

Scheschonk L, Bischof K, Kopp MEL, Jueterbock A. **2023**. Differences by origin in methylome suggest eco-phenotypes in the kelp *Saccharina latissima*. *Evolutionary Applications* **16**: 262–278.

Schiel DR, Foster MS. **2006**. The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. *Annual Review of Ecology, Evolution, and Systematics* **37**: 343–372.

Schiener P, Black KD, Stanley MS, Green DH. **2015**. The seasonal variation in the chemical composition of the kelp species *Laminaria digitata*, *Laminaria hyperborea*, *Saccharina latissima* and *Alaria esculenta*. *Journal of Applied Phycology* **27**: 363–373.

Schlegel RW, Darmaraki S, Benthuysen JA, Filbee-Dexter K, Oliver ECJ. **2021**. Marine cold-spells. *Progress in Oceanography* **198**: 102684.

Schmitz RJ, Lewis ZA, Goll MG. **2019**. DNA methylation: shared and divergent features across eukaryotes. *Trends in Genetics* **35**: 818–827.

Schroeder DC, Mckeown DA. **2021**. Viruses of Seaweeds. *Studies in Viral Ecology*: 121–138.

Seabra R, Wethey DS, Santos AM, Lima FP. **2015**. Understanding complex biogeographic responses to climate change. *Scientific reports* **5**: 1–6.

Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T. **2014**. Ecological value of coastal habitats for commercially and ecologically important species. *ICES Journal of Marine Science* **71**: 648–665.

Shan T, Yuan J, Su L, *et al.* 2020. First genome of the brown alga *Undaria pinnatifida*: chromosome-level assembly using PacBio and Hi-C technologies. *Frontiers in genetics*

11: 140.

Shunatova N, Nikishina D, Ivanov M, *et al.* 2018. The longer the better: the effect of substrate on sessile biota in Arctic kelp forests. *Polar Biology* **41**: 993–1011.

Simonson E J, Metaxas A, Scheibling RE. **2015**. Kelp in hot water: II. Effects of warming seawater temperature on kelp quality as a food source and settlement substrate. *Marine Ecology Progress Series* **537**: 105–119.

Simonson E. J., Scheibling RE, Metaxas A. **2015**. Kelp in hot water: I. Warming seawater temperature induces weakening and loss of kelp tissue. *Marine Ecology Progress Series* **537**: 89–104.

Skjoldal HR. **1993**. Eutrophication and algal growth in the North Sea. In: Symposium Mediterranean Seas 2000.

Smale DA. **2020**. Impacts of ocean warming on kelp forest ecosystems. *New Phytologist* **225**: 1447–1454.

Smale DA, Moore PJ. **2017**. Variability in kelp forest structure along a latitudinal gradient in ocean temperature. *Journal of Experimental Marine Biology and Ecology* **486**: 255–264.

Spurkland T, Iken K. **2011**. Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic *Saccharina latissima* (Laminariales, Laminariaceae). *Botanica Marina* **54**: 355–365.

Spurkland T, Iken K. **2012**. Seasonal growth patterns of *Saccharina latissima* (Phaeophyceae, Ochrophyta) in a glacially-influenced subarctic estuary. *Phycological Research* **60**: 261–275.

Stark R, Grzelak M, Hadfield J. **2019**. RNA sequencing: the teenage years. *Nature Reviews Genetics* **20**: 631–656.

Staufenberger T, Thiel V, Wiese J, Imhoff JF. **2008**. Phylogenetic analysis of bacteria

associated with Laminaria saccharina. *FEMS Microbiology Ecology* **64**: 65–77.

Stengel DB, McGrath H, Morrison LJ. **2005**. Tissue Cu, Fe and Mn concentrations in different-aged and different functional thallus regions of three brown algae from western Ireland. *Estuarine, Coastal and Shelf Science* **65**: 687–696.

Strain EMA, van Belzen J, van Dalen J, Bouma TJ, Airoldi L. **2015**. Management of Local Stressors Can Improve the Resilience of Marine Canopy Algae to Global Stressors. *PLOS ONE* **10**: e0120837.

Strain EMA, Thomson RJ, Micheli F, Mancuso FP, Airoldi L. **2014**. Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Global Change Biology* **20**: 3300–3312.

Strand HK, Christie H, Fagerli CW, Mengede M, Moy F. **2020**. Optimizing the use of quicklime (CaO) for sea urchin management — A lab and field study. *Ecological Engineering* **143**: 100018.

Straub SC, Wernberg T, Thomsen MS, *et al.* 2019. Resistance to obliteration; responses of seaweeds to marine heatwaves. *Frontiers in Marine Science* **6**: 763.

Strong JA, Dring MJ. **2011**. Macroalgal competition and invasive success: testing competition in mixed canopies of *Sargassum muticum* and *Saccharina latissima*. *Botanica Marina* **54**: 223.

Strong JA, Maggs CA, Johnson MP. **2009**. The extent of grazing release from epiphytism for *Sargassum muticum* (Phaeophyceae) within the invaded range. *Journal of the Marine Biological Association of the United Kingdom* **89**: 303–314.

Sundfjord A, Albretsen J, Kasajima Y, *et al.* 2017. Effects of glacier runoff and wind on surface layer dynamics and Atlantic Water exchange in Kongsfjorden, Svalbard; a model study. *Estuarine, Coastal and Shelf Science* **187**: 260–272.

Svendsen H, Beszczynska-Møller A, Hagen JO, *et al.* 2002. The physical environment

of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar research* **21**: 133–166.

Swanson AK, Fox CH. **2007**. Altered kelp (Laminariales) phlorotannins and growth under elevated carbon dioxide and ultraviolet-B treatments can influence associated intertidal food webs. *Global Change Biology* **13**: 1696–1709.

Teng L, Han W, Fan X, *et al.* 2021. Integrative analysis of chloroplast DNA methylation in a marine alga—*Saccharina japonica*. *Plant molecular biology* **105**: 611–623.

Theodorou I, Opsahl-Sorteberg H-G, Charrier B. **2021**. Preparation of Zygotes and Embryos of the Kelp *Saccharina latissima* for Cell Biology Approaches. *Bio-protocol* **11**: e4132.

tom Dieck I. **1993**. Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications. *Marine Ecology Progress Series* **100**: 253.

Tourneroche A, Lami R, Burgaud G, *et al.* 2020. The bacterial and fungal microbiota of *Saccharina latissima* (Laminariales, Phaeophyceae). *Frontiers in Marine Science* **7**: 587566.

Traiger SB. **2019**. Effects of elevated temperature and sedimentation on grazing rates of the green sea urchin: implications for kelp forests exposed to increased sedimentation with climate change. *Helgoland Marine Research* **73**: 5.

Tsiamis K, Salomidi M, Gerakaris V, *et al.* 2020. Macroalgal vegetation on a north European artificial reef (Loch Linnhe, Scotland): biodiversity, community types and role of abiotic factors. *Journal of Applied Phycology* **32**: 1353–1363.

Umanzor S, Li Y, Bailey D, *et al.* 2021. Comparative analysis of morphometric traits of farmed sugar kelp and skinny kelp, *Saccharina spp.*, strains from the Northwest Atlantic. *Journal of the World Aquaculture Society*.

Vallet M, Strittmatter M, Murúa P, *et al.* 2018. Chemically-mediated interactions between macroalgae, their fungal endophytes, and protistan pathogens. *Frontiers in Microbiology* **9**: 3161.

Vihtakari M. **2022**. ggOceanMaps: Plot Data on Oceanographic Maps using "ggplot2", R package version 1.3.4. *https://CRAN.R-project.org/package=ggOceanMaps*.

Visch W, Kononets M, Hall POJ, Nylund GM, Pavia H. **2020**. Environmental impact of kelp (*Saccharina latissima*) aquaculture. *Marine Pollution Bulletin* **155**: 110962.

Visch W, Rad-Menéndez C, Nylund G, Pavia H, J. Ryan M, Day J. **2019**. Underpinning the development of seaweed biotechnology: cryopreservation of brown algae (*Saccharina latissima*) gametophytes. *Biopreservation and Biobanking*.

Wang X, Blikra MJ, Evensen TH, Skipnes D, James P. **2021**. Effects of site, depth and sori origin on the growth and minerals composition of cultivated *Saccharina latissima* (Phaeophyceae) in the north of Norway. *Journal of Applied Phycology*.

Wang X, Broch OJ, Forbord S, *et al.* 2014. Assimilation of inorganic nutrients from salmon (*Salmo salar*) farming by the macroalgae (*Saccharina latissima*) in an exposed coastal environment: implications for integrated multi-trophic aquaculture. *Journal of Applied Phycology* **26**: 1869–1878.

Wang S, Fan X, Guan Z, *et al.* 2016. Sequencing of complete mitochondrial genome of *Saccharina latissima* ye-C14. *Mitochondrial DNA Part A* **27**: 4037–4038.

Wang Z, Gerstein M, Snyder M. **2009**. RNA-Seq: a revolutionary tool for transcriptomics. *Nature Reviews Genetics* **10**: 57.

Ware C, Dijkstra J, Mello K, Stevens A, O'Brien B, Ikedo W. **2019**. A novel three dimensional analysis of functional-architecture that describes the properties of macroalgae as refuge. *Marine Ecology Progress Series* **608**: 93–103.

Wares JP, Cunningham CW. **2001**. Phylogeography and historical ecology of the North

Atlantic intertidal. *Evolution* **55**: 2455–2469.

Weigel BL, Miranda KK, Fogarty EC, Watson AR, Pfister CA. **2022**. Functional insights into the kelp microbiome from metagenome-assembled genomes. *Msystems* **7**: e01422-21.

Wernberg T, Filbee-dexter K. **2019**. Missing the marine forest for the trees. *Marine Ecology Progress Series* **612**.

White N, Marshall CE. **2007**. Saccharina latissima - *Sugar kelp*. https://www.marlin.ac.uk. 14 Jan. 2022.

Wiencke C, Bischof K. **2012**. *Seaweed biology - Novel Insights into Ecophysiology, Ecology and Utilization*. Springer-Verlag.

Wiese J, Thiel V, Nagel K, Staufenberger T, Imhoff JF. **2009**. Diversity of antibiotic-active bacteria associated with the brown alga *Laminaria saccharina* from the Baltic Sea. *Marine Biotechnology* **11**: 287–300.

Wiktor JM, Tatarek A, Kruss A, Singh RK, Wiktor JM, Søreide JE. **2022**. Comparison of macroalgae meadows in warm Atlantic versus cold Arctic regimes in the high-Arctic Svalbard. *Frontiers in Marine Science* **9**: 1–16.

Williams SL, Herbert SK. **1989**. Transient photosynthetic responses of nitrogen-deprived *Petalonia fascia* and *Laminaria saccharina* (Phaeophyta) to ammonium resupply. *Journal of phycology* **25**: 515–522.

Wilson KL, Skinner MA, Lotze HK. **2019**. Projected 21st-century distribution of canopy-forming seaweeds in the Northwest Atlantic with climate change. *Diversity and Distributions*.

Winters G, Nelle P, Fricke B, Rauch G, Reusch T. **2011**. Effects of a simulated heat wave on photophysiology and gene expression of high- and low-latitude populations of Zostera marina. *Marine Ecology Progress Series* **435**: 83–95.

Witman JD, Lamb RW. **2018**. Persistent differences between coastal and offshore kelp forest communities in a warming Gulf of Maine. *PloS One* **13**: e0189388.

Xing Q, Rousvoal S, Leblanc C. **2021**. Transcriptome-wide identification and evaluation of optimal reference genes for RT-qPCR expression analysis of *Saccharina latissima* responses to biotic and abiotic stress. *Journal of Applied Phycology* **33**: 617–627.

Yang X, Wang X, Yao J, Duan D. **2021**. Genome-Wide Mapping of Cytosine Methylation Revealed Dynamic DNA Methylation Patterns Associated with Sporophyte Development of Saccharina japonica. *International Journal of Molecular Sciences* **22**: 9877.

Yarish C, Kim JK, Lindell S, Kite-Powell H, Articles EEB. **2017**. *Developing an environmentally and economically sustainable sugar kelp aquaculture industry in southern New England: from seed to market*.

Ye N, Zhang X, Miao M, *et al.* 2015. *Saccharina* genomes provide novel insight into kelp biology. *Nature communications* **6**: 6986.

Yesson C, Bush LE, Davies AJ, Maggs CA, Brodie J. **2015**. Large brown seaweeds of the British Isles: Evidence of changes in abundance over four decades. *Estuarine, Coastal and Shelf Science* **155**: 167–175.

Yorke AF, Metaxas A. **2011**. Interactions between an invasive and a native bryozoan (*Membranipora membranacea* and *Electra pilosa*) species on kelp and *Fucus* substrates in Nova Scotia, Canada. *Marine Biology* **158**: 2299–2311.

Young C, Doall M. **2021**. Dual benefit of ocean acidification for the laminarialean kelp *Saccharina latissima*: enhanced growth and reduced herbivory. *Marine Ecology Progress Series* **664**: 87–102.

Young CS, Sylvers LH, Tomasetti SJ, *et al.* 2022. Kelp (Saccharina latissima) Mitigates Coastal Ocean Acidification and Increases the Growth of North Atlantic Bivalves in Lab

Experiments and on an Oyster Farm . *Frontiers in Marine Science* **9**.

Zacher K, Bernard M, Bartsch I, Wiencke C. **2016**. Survival of early life history stages of Arctic kelps (Kongsfjorden, Svalbard) under multifactorial global change scenarios. *Polar Biology* **39**: 2009–2020.

Zhang L, Cui C, Li Y, Wu H, Li X. **2018**. A genome screen for the development of sex-specific DNA markers in *Saccharina japonica*. *Journal of Applied Phycology* **30**: 1239–1246.

Zhang J, Li Y, Luo S, Cao M, Zhang L, Li X. **2021**. Differential gene expression patterns during gametophyte development provide insights into sex differentiation in the dioicous kelp *Saccharina japonica*. *BMC Plant Biology* **21**: 335.

Zhang P, Shao Z, Li L, Liu S, Yao J, Duan D. **2018**. Molecular characterisation and biochemical properties of phosphomannomutase/phosphoglucomutase (PMM/PGM) in the brown seaweed <i>Saccharina japonica</i. *Journal of Applied Phycology* **30**: 2687–2696.

Zhang X, Thomsen M. **2019**. Biomolecular composition and revenue explained by interactions between extrinsic factors and endogenous rhythms of *Saccharina latissima*. *Marine Drugs* **17**: 107.

Zhang Y, Wang X, Shan T, Pang S, Xu N. **2019**. Transcriptome profiling of the meristem tissue of *Saccharina japonica* (Phaeophyceae, Laminariales) under severe stress of copper. *Marine Genomics*: 100671.

Zhang S-S, Yang H, Ding L, *et al.* 2017. Tissue-specific transcriptomics reveals an important role of the unfolded protein response in maintaining fertility upon heat stress in *Arabidopsis*. *The Plant Cell* **29**: 1007–1023.

Zhou W, Liang G, Molloy PL, Jones PA. **2020**. DNA methylation enables transposable element-driven genome expansion. *Proceedings of the National Academy of Sciences*

117: 19359–19366.

Zhu G, Ebbing A, Bouma TJ, Timmermans KR. **2021**. Morphological and physiological plasticity of *Saccharina latissima* (Phaeophyceae) in response to different hydrodynamic conditions and nutrient availability. *Journal of Applied Phycology*.