

Growth dynamics of *Saccharina latissima* (Laminariales, Phaeophyceae) in Aarhus Bay, Denmark, and along the species' distribution range

Mette Møller Nielsen · Dorte Krause-Jensen ·
Birgit Olesen · Rikke Thinggaard ·
Peter Bondo Christensen · Annette Bruhn

Received: 1 April 2014 / Accepted: 17 June 2014 / Published online: 3 July 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Growth dynamics of *Saccharina latissima* in a Danish embayment (56°03.793N, 10°16.148E) were investigated through an annual cycle (March 1999–March 2000) and related to patterns found in previous studies covering the distribution range of the species. The kelps exhibited meristematic growth as well as distal tissue loss all year around. Elongation rate peaked in spring (March–May, 0.75 cm day⁻¹), whereas maximum biomass growth occurred in May–July at higher insolation. *S. latissima* accumulated nitrogen (N) in November–March, when ambient N levels were high and the fast growth in March–July was followed by a depletion of these reserves. Light regimes and seasonal fluctuations of nutrients were, thus, major factors explaining the seasonal growth pattern of *S. latissima* in this temperate bay. Differences in light and exposure along depth gradients affected the growth, loss and storage product dynamics. High losses of N and carbon (C) through summer abscission of distal tissue question the efficiency of translocation, especially at shallower depths, where losses are accelerated by, e.g., high temperature. A large-scale comparison further highlighted that warming advanced the timing, increased the level of peak growth and also seemed to expand the growth period. Growth rates of the studied Danish population fell in the low end

of the range for similar latitudes and temperatures, probably due to sub-optimal salinities (avg. 23.3 psu) in combination with periodically high summer temperatures (max. 21.1 °C).

Introduction

The kelp *Saccharina latissima* (Linnaeus) (Laminariales, Phaeophyceae) is widely distributed in temperate to polar areas of the northern hemisphere where it forms key habitats in the coastal zone (Kain 1979; Steneck et al. 2002; Bartsch et al. 2008). Kelp forests are among the most productive ecosystems on the globe, and the primary production enters the food web through grazing, exudation of dissolved organic carbon and as detritus (Mann 1973; Duggins et al. 1989). The large size of kelps and the extension of kelp habitats also give kelps an important structuring role as substrate for sessile organisms as well as shelter and nursery area, thereby stimulating a high biodiversity (Dayton 1985; Bruno and Bertness 2001; Lippert et al. 2001; Steneck et al. 2002). Kelps such as *S. latissima* exhibit a pronounced seasonal pattern of growth and decay, which influences the turnover of organic matter and the structure of the kelp habitat, thereby constituting the important role of kelps in coastal ecosystems (e.g., Krumhansl and Scheibling 2011).

New kelp tissue is initiated in the basal meristematic part of the blade just above the stipe, while old tissue is lost by erosion and decay from the distal part of the blade. In general, length growth of *S. latissima* is initiated in winter, peaks in spring and is reduced during summer and autumn (Kain 1979; Lüning 1979; Sjöton 1993). The seasonal pattern of blade erosion is roughly opposite to that of length growth as it peaks in July to December (Parke

Communicated by F. Weinberger.

M. M. Nielsen (✉) · D. Krause-Jensen · R. Thinggaard ·
P. B. Christensen · A. Bruhn
Department of Bioscience, Aarhus University, Vejlsøvej 25,
8600 Silkeborg, Denmark
e-mail: meni@dmu.dk

B. Olesen
Department of Bioscience, Aarhus University, Ole Worms Allé 1,
Building 1135, 8000 Aarhus C, Denmark

1948). Seasonal fluctuations of light and ambient nutrient levels are believed to be major drivers of the growth patterns of Laminariales. At high nutrient levels and low light levels during late autumn and winter, Laminariales build up reserves of nitrogen (N) which are utilized to initiate growth in early spring when light levels increase (Chapman and Craige 1977). Rapid length growth can be sustained until late spring/early summer, after which it ceases. Instead of supporting further length growth during summer, photosynthesis products in this period are being stored for use in winter respiration and support of length growth during late winter/early spring (Black 1950; Bartsch et al. 2008). Hence, the tissue content of these carbon-based storage products peaks in late summer and declines to a minimum in late winter/early spring (Black 1950). Temperature, exerting key control on all metabolic processes, also markedly affects the production and respiration of *S. latissima* (Davison et al. 1991) and thus the seasonal growth cycle. Most studies have though focused on light and nutrient levels in explaining seasonal growth patterns and paid less attention to water temperature.

The importance of light and temperature for regulation of seasonal growth suggests that growth patterns may respond predictably to large-scale gradients in light and temperature across the species' distribution range unless variation in local factors such as nutrient levels, salinity, exposure or water depth have overriding importance and disrupts such potential large-scale relationships. Year-round availability of N in the water has been shown to suppress the storage of carbon (C) and inorganic N in *Laminaria longicruris* and hence making length growth completely coupled to the seasonality of light (Gagne et al. 1982). Low salinity may suppress growth (Spurkland and Iken 2011), and differences in wave exposure and water depth may cause further variation in growth dynamics in kelps (Mann 1973; Gerard and Mann 1979; Vadas et al. 2004). In addition, the age structure of populations is likely to influence the dynamics (Parke 1948; Mann 1972; Lüning 1979; Druehl et al. 1987; Sjötnun 1993).

Existing studies on growth dynamics in Laminariales often lack combined information on growth, loss, tissue composition, age structure and environmental conditions over entire annual cycles which limits the possibility of identifying how these aspects are related and whether they differ among sites. Furthermore, the present knowledge is still restricted to few places relative to the extensive distribution of *S. latissima*, and the vast majority of studies represent locations with high salinities which are optimal for growth of the species (27–33 psu, Gerard et al. 1987). Hence, detailed investigations describing and interpreting the ecophysiology of growth, seasonal growth and loss patterns in relation to thallus morphology, storage products,

age structure, depth and physicochemical conditions of the location are needed. This paper presents a study of seasonal growth patterns in *S. latissima*, integrating these parameters. The aim was (1) to describe the growth and biomass dynamics of an established *S. latissima* population in a Danish embayment in terms of seasonal growth and loss, age structure, morphology, dry weight (DW) and C and N dynamics, (2) to explore how dynamics of growth, loss and storage products vary with water depth, (3) to discuss the findings in relation to the physicochemical conditions of the locality and (4) to relate the observed growth dynamics to previous studies from different latitudes with the perspective of identifying large-scale patterns in growth dynamics.

Materials and methods

Study site

The study was conducted in Aarhus Bay, Denmark (56°03.793N, 10°16.148E), in the period March 1999–March 2000. Aarhus Bay is an embayment situated at the Baltic Sea–Kattegat transition where low- and high-saline waters mixes. The bay constitutes an area of roughly 610 km². The study area was restricted to an area of approximately 100 m in length where *S. latissima* was present and may not be representative for the entire bay. The seabed at the sampling site was composed of sand with scattered stones. During the period of the survey, six sampling and growth measuring events of *S. latissima* were performed at 7 m of depth. In July and September, additional measurements were conducted at 4 and 11 m of depth.

Physicochemical variables

Information on temperature, salinity, nutrient concentration and irradiance/light attenuation (Secchi depth) was obtained from the Danish National Aquatic Monitoring and Assessment Program (DNAMAP) that has monitored these variables 4–6 times per month according to common guidelines. Data were extracted from the national database on marine data (MADS) located at the Danish Centre for Environment and Energy (DCE) at Aarhus University. Values of temperature, salinity and nutrient concentration were based on measurements between 5 and 10 m depth. The light attenuation coefficient (K_d) was calculated from measurements of the Secchi depth from the equation: $K_d = 2.3/\text{Secchi depth}$. Irradiance levels at different depths were then calculated from the Lambert–Beer equation (e.g., Dennison et al. 1993): $I_z = I_0 \exp[-K_d z]$, where I_0 is the surface irradiance, K_d is the light attenuation coefficient, z is the depth, and I_z is the light at a given depth.

Growth measurements

Divers collected 81 individuals of *S. latissima* from 7 m of depth on March 3, 1999. Blade length of the individuals ranged from 21 to 199 cm, with an average of 82 cm. All specimens were brought to the beach and individually tagged and measured in terms of length and width of the blade (width was measured at a distance of 10, 40, 70, 100, 130 and 160 cm from the transition of stipe to blade). The blades were kept humid by adding seawater during the measurements. Total blade area was estimated as blade length multiplied by mean width.

To enable measurements of blade elongation, two parallel holes were punched at the center of each blade 10 cm above the meristematic transition zone between blade and stipe, as described by Parke (1948). Elongation rates between sampling dates were then estimated based on the displacement of the holes from one sampling event to the next. After measuring and tagging, the specimens were returned to the sea in close proximity to their original position. As all individuals were naturally anchored by own holdfasts to smaller stones that could easily be collected together with each specimen, no artificial anchoring was needed. The site was revisited five times: May 17, 1999, July 7, 1999, September 6, 1999, November 8, 1999 and March 6, 2000. At these sampling events, the tagged specimens were measured as described above and new holes were punched. Between consecutive sampling events, there was a loss of 11–21 individuals and in May and November, the study was therefore supplemented with 24 and 16 new individuals, respectively. In July and September, the survey was expanded to include identical measurements at 4 and 11 m of depth as well. Forty individuals at each of the two depths were sampled for this purpose. Between each sampling date 12, 20–70 and 23 individuals were recovered at 4, 7 and 11 m of depth, respectively.

Density, biomass, morphometry and age determination

At each sampling date, additional individuals of *S. latissima* (7 m: $n = 17$ –52, 4 and 11 m: $n = 9$ –16) were collected for measurements of population structure (density and biomass per area), morphometry, area-specific DW, content of N and C in new and old blade tissue and determination of age. At 7 m of depth, samples were collected within 2–3 circles with a diameter of 2 m to assess the stock density. All individuals were harvested, counted and eventually dried at 60 °C to a constant weight for estimation of biomass per meter square. Due to low coverage at 4 and 11 m depth, density parameters were not rated here. Morphometric analysis included measurements of stipe length and diameter as well as age determination by counting growth rings in the stipe following the methodology of

Parke (1948). Age determination was performed for 10–37 individuals per sampling and included only plants sampled at 7 m depth.

Area-specific dry weight and carbon and nitrogen contents

By the same interval as the measurements of blade width, three disks (3.2 cm in diameter) were cut across the blade to determine the area-specific DW after drying at 60 °C for 48 h. For each date and depth, the area-specific DW was determined for 10–20 individuals, dependent on the accessibility of plants. The area-specific DW was used to convert length—and area growth to biomass units. The disks were subsequently grinded and used for the determination of C and N contents. Carbon and Nitrogen contents were analyzed on an elemental analyzer (Roboprep C/N, Europa Scientific Ltd., UK) in line with a triple collector isotopic ratio mass spectrometer (Tracermass, Europa Scientific Ltd., UK). For each sampling date, five individuals from each of the three depths were analyzed for the content of C and N given as both tissue concentration (% of DW) and as area-specific contents (mg cm^{-2}).

Large-scale patterns

Large-scale patterns in growth dynamics were assessed by comparing data on growth from the present study with literature findings at other latitudes, where growth was also typically assessed by consecutive blade-marking. The following studies covering the entire distribution range of *S. latissima* were included (latitudes in brackets): Fallis (1916) (48°N), Parke (1948) (56°N), Johnston et al. (1977) (56°N), Boden (1979) (42°N), Brady-Campbell et al. (1984) (41°N), Conolly and Drew (1985) (56°N), Dunton (1985) (70°N), Sjöton (1993) (60°N), Sjöton and Gunnarson (1995) (64°N), Lyngby and Mortensen (1996) (55°N), Schaeffelke et al. (1996) (54°N), Weile (1996) (55°N), Borum et al. (2002) (74°N), Andersen et al. (2011) (58°N) and Spurkland and Iken (2012) (60°N). Latitudes were provided directly by the cited literature or inferred from detailed descriptions of the study site. Data on average summer temperature were retrieved from the individual studies and included either as exact given values or as estimates based on graphs presented in the studies. For a few of the studies, data on depth were given as exact values as well.

Data analysis

Statistical analyses were performed with SAS-JMP 10.0 (SAS Institute Inc.). The effect of latitude, temperature and depth on large-scale growth patterns (i.e., maximum growth rate and its timing) was initially assessed with

general linear model (GLM) including depth and latitude or temperature as variables. As information of depth was only given for a few of the studies included, and it did not have any significant effect on any of the relations found (further elaboration in the results), depth was left out as an explanatory variable and the effects of latitude and temperature were subsequently assessed with linear regression.

Results are presented as mean \pm SE if not stated otherwise. The effect of sampling depth was analyzed with ANOVA after confirming the assumptions of normality and homogeneity of variance. In case of significance of treatments, a post hoc test (Tukey HSD) was conducted. Data on age structure were analyzed using linear regression.

Annual turnover ratios were calculated on a length basis as well as on a DW basis. Both calculations were based on the total annual production in relation to a weighted annual average of the biomass.

Based on the blade-marking, new length growth was compared with total lengthwise changes of the blade, making it possible to estimate loss of tissue from the distal part. Net increase in DW, C and N contents as well as losses through abscission of old tissue were estimated between each sampling date by using the C and N contents and area-specific DW in new meristematic tissue and old (distal) tissue. Thus, within a given period, loss and growth were based on the average content of C and N at start and end of the period in, respectively, old and new tissue.

Temperature, salinity, irradiance and inorganic N concentration for the study site were presented as monthly means. For temperature and salinity, minimum and maximum values for each month were given as well. Inorganic N data included measurements of ammonium, nitrate and nitrite. Irradiance data at 7 m depth were obtained using average values of surface irradiance within day hours (i.e., values of 0, representing night hours, were omitted from the analysis) in combination with the light attenuation coefficient (Fig. 1).

Results

Seasonality of physicochemical variables

The concentration of inorganic N followed an annual cycle typical for temperate areas with low levels during summer and autumn and higher levels in winter and spring months. From March to November, levels were lowest and did not exceed 1 μM inorganic N. During late autumn and winter, levels increased markedly to a peak of 14.4 μM inorganic N in January (Fig. 1a).

The annual average of Secchi depth was 6.1 m, monthly means ranging from 3.6 m in October to 8.9 m in September. Thus, irradiance showed considerable seasonal

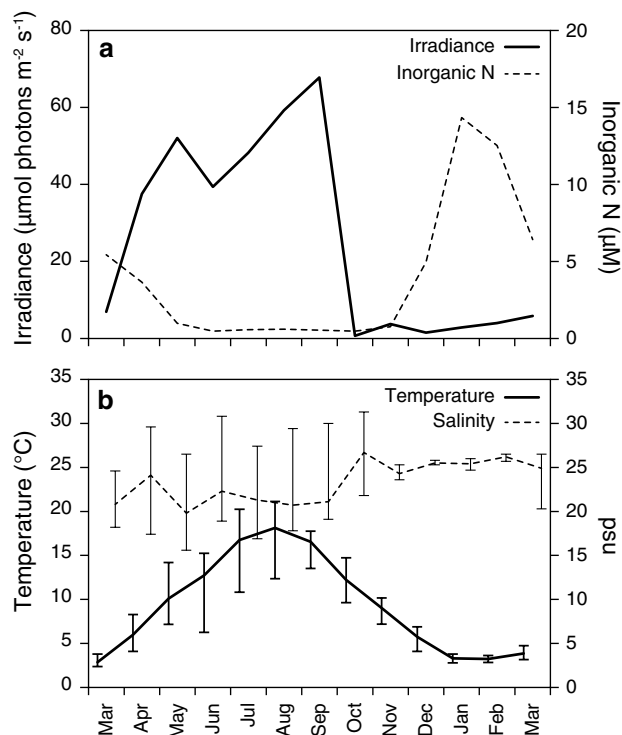


Fig. 1 **a** Seasonality of irradiance ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and inorganic nitrogen (μM) at the study site displayed as monthly averages. Irradiance data represent only averages of day hours and are calculated for 7 m depth based on surface irradiance and the light attenuation coefficient for the site at the different time points. Inorganic nitrogen data include levels of ammonium, nitrate and nitrite. **b** Seasonality of temperature ($^{\circ}\text{C}$) and salinity (psu) at the study site displayed as monthly means. Vertical lines indicate minimum and maximum values within the months. Data are from the Danish monitoring program

variation. Spring and summer irradiance at 7 m depth were in the range of 40–70 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ with maximum levels in September, while levels between October and March were below 10 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Fig. 1a). The drop in light intensity from September to October was a consequence of a massive phytoplankton bloom in early October. During summer months, when sampling was performed at different depths, the average daily light levels at 4, 7 and 11 m of depth were 128, 58 and 17 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, respectively.

Monthly averages of salinity ranged between 19.8 psu in May and 26.7 psu in October. However, at least for shorter periods, lower values were reached as indicated by minimum values of 15.6 psu in May and several occurrences of salinities below 20 psu through spring and summer months (Fig. 1b). Monthly temperature averages ranged between 2.3 and 18.1 $^{\circ}\text{C}$, with the lowest values recorded during winter and the highest during summer. Temperatures as high as 20.2 and 21.1 $^{\circ}\text{C}$ were measured in July and August, respectively (Fig. 1b).

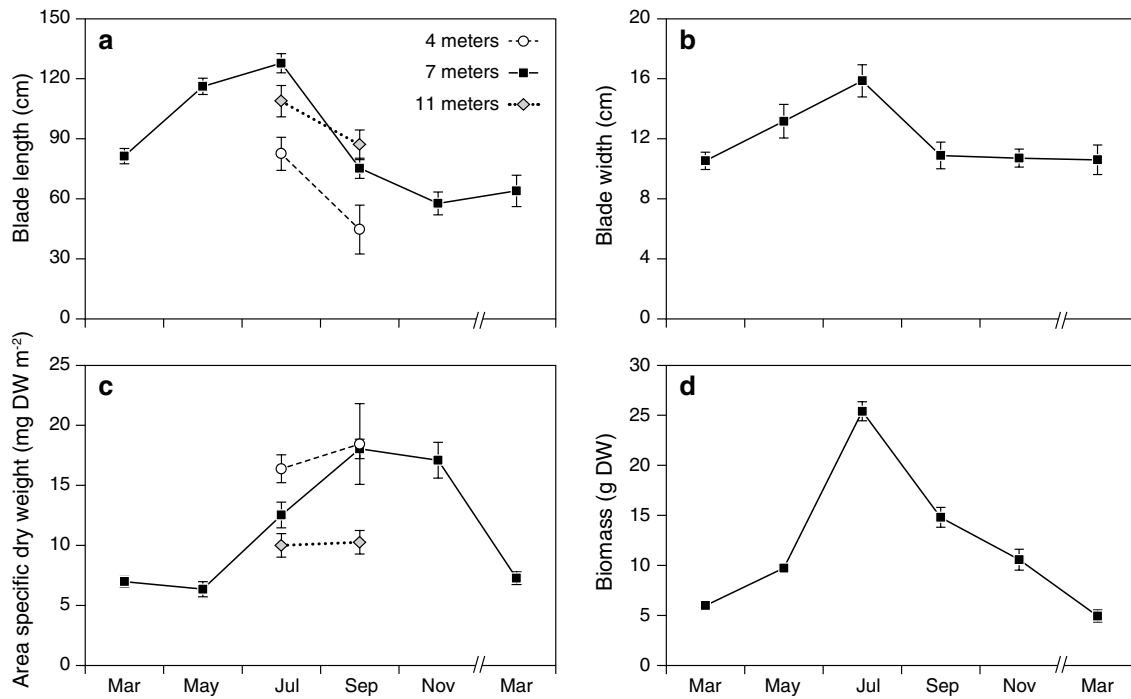


Fig. 2 Seasonal variations in **a** blade length, **b** blade width, **c** area-specific DW and **d** biomass pr. individual for *S. latissima* at different depths. Values are presented as mean \pm SE. 4 m: $n = 12\text{--}40$; 7 m: $n = 20\text{--}70$; 11 m: $n = 23\text{--}40$. Blade length and width were measured

on same individuals as used for growth measurement, whereas data on the area-specific DW were derived from individuals sampled for measurements of populations' structure. Biomass per individual represents a combination of this information. DW dry weight

Table 1 Maximum blade length and area-specific DW, daily growth and loss rates and tissue content of N and C for *S. latissima* from 4, 7 and 11 m of depth, based on data from July and September

	<i>n</i>	Period	4 m	7 m	11 m
Maximum blade length (cm)	40–52	July	83 \pm 8.2 ^a	128 \pm 4.8 ^b	109 \pm 7.8 ^b
Maximum area-specific DW (mg DW cm ⁻²)	10–18	September	18.4 \pm 3.4 ^a	18.0 \pm 0.8 ^a	10.3 \pm 1.0 ^b
Growth (cm day ⁻¹)	12–36	July–September	0.09 \pm 0.01 ^a	0.21 \pm 0.01 ^b	0.29 \pm 0.03 ^c
Loss (cm day ⁻¹)	12–36	July–September	1.00 \pm 0.01 ^a	0.90 \pm 0.06 ^b	0.75 \pm 0.13 ^b
Average N content (% of DW)	5	July–September	0.90 \pm 0.080 ^a	1.48 \pm 0.076 ^b	2.21 \pm 0.075 ^c
Average C content (% of DW)	5	July–September	38.3 \pm 0.53 ^a	36.5 \pm 0.50 ^b	34.6 \pm 0.50 ^c
Average N content (mg N cm ⁻²)	5	July–September	0.15 \pm 0.003 ^a	0.23 \pm 0.003 ^b	0.22 \pm 0.003 ^b
Average C content (mg C cm ⁻²)	5	July–September	6.25 \pm 0.14 ^a	5.61 \pm 0.07 ^a	3.48 \pm 0.05 ^b

Values represent mean \pm SE. Values in the same row with different letters differ significantly from each other (ANOVA, $p < 0.05$)

Seasonal growth and loss dynamics

At 7 m depth, blade length and width, and thereby the total thallus area, increased through the spring and reached the maximum length of 128 \pm 4.8 cm and width of 16 \pm 1.1 cm in July (Fig. 2a, b). At this time of year, the lengths of the individuals at 11 and 7 m of depth were not significantly different from each other, whereas individuals at 4 m depth generally were smaller with an average length of 82.5 \pm 8.2 cm (Table 1). From July to November, blade length decreased dramatically, with November values of

58 \pm 5.7 cm at 7 m depth. The same pattern was found for the blade length of individuals at 4 and 11 m depth from July to September (Fig. 2a). Only minor changes were observed in blade length and width from November to March at 7 m depth. In comparison with length and width development (Fig. 2a, b), the seasonal pattern for the area-specific DW was slightly displaced with maximum values in September. However, combining the blade area and the area-specific DW to determine the seasonal variation of the biomass expressed as DW per individual, the maximum biomass was found in July (Fig. 2d), when the area was

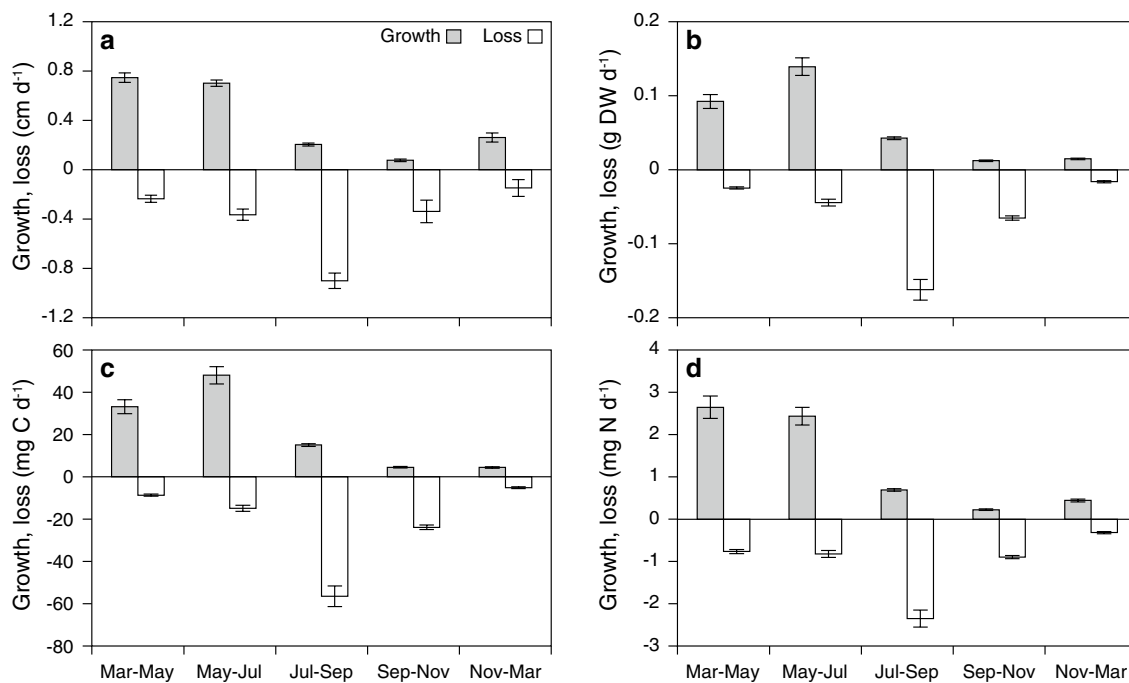


Fig. 3 Seasonal growth and loss dynamics of *S. latissima* expressed as average daily changes of **a** blade length, **b** dry weight (DW), **c** C content and **d** N content. Only data from 7 m depth are included. Values are presented as mean \pm SE. $n = 20$ –70. Data are obtained by

combining growth measurements with average values of area-specific DW and C and N contents from the area-specific sampling. *Growth* represents new meristematic tissue, whereas *loss* represents distal tissue

the largest even though the area-specific DW had not yet reached its maximum (Fig. 2c). In September, when area-specific DW peaked, no significant differences in area-specific DW were found between blades from 4 to 7 m depth, whereas blades from 11 m exhibited significantly lower values (Table 1).

From March to July, daily growth in blade length, biomass and C and N contents in new meristematic tissue exceeded the daily loss through tissue abscission (Fig. 3a–d). Meristematic tissue exhibited the fastest rates of length growth (0.75 ± 0.04 cm day⁻¹) (Fig. 3a) and N incorporation (2.7 mg N day⁻¹ individual⁻¹) (Fig. 3d) during spring (March–May), while the fastest daily increase in biomass (0.14 ± 0.012 g DW day⁻¹ individual⁻¹) (Fig. 3b) and C content (50 mg C day⁻¹ individual⁻¹) (Fig. 3c) occurred in early summer (May–July) at higher insolation (Fig. 1a). By contrast, from July to November, loss rates exceeded growth—and incorporation rates of all variables, with maximum loss rates during summer months, along with a reduction in growth and C and N incorporation. From November to March, rates of length growth and N incorporation in the new tissue exceeded loss rates, whereas growth and loss in terms of DW and C balanced each other (Fig. 3). Comparisons in July–September across the depth gradient showed a pattern of faster length growth but lower loss rates in deep compared to shallower water (Table 1).

Nitrogen and carbon dynamics

The average N content of the blade (% of DW) showed distinct seasonal variation. It reached maximum in March (3.16 ± 0.12 and 3.48 ± 0.22 % of DW in March 1999 and 2000, respectively) and was reduced during summer to a minimum of 1.27 ± 0.04 % of DW in September (Fig. 4a). Area-specific N content did not show as pronounced seasonality, but overall, it increased from May to November and decreased during winter and spring (Fig. 4b).

The patterns of the C content were exactly the opposite. Carbon concentrations only varied slightly throughout the year with maximum levels of 37.7 ± 0.56 % of DW in November and minimum levels in March (34.8 ± 0.65 % of DW in 1999 and 22.7 ± 0.72 % of DW in 2000, Fig. 4a). However, during most of the study period, levels were in the range of 33–38 % of DW. In contrast, the area-specific content of C showed more marked variations throughout the year (Fig. 4b). Between May and November, the area-specific C content more than doubled from 2.43 ± 0.15 mg C cm⁻² in May to 6.45 ± 0.57 mg C cm⁻² in November, after which it decreased dramatically toward March 2000 to a minimum level of 1.65 ± 0.12 mg C cm⁻². The seasonality of the C and N contents resulted in a peak atomic C/N ratio of 25 in September and minimum ratio of 9.4 and 5.6 in March 1999 and 2000, respectively.

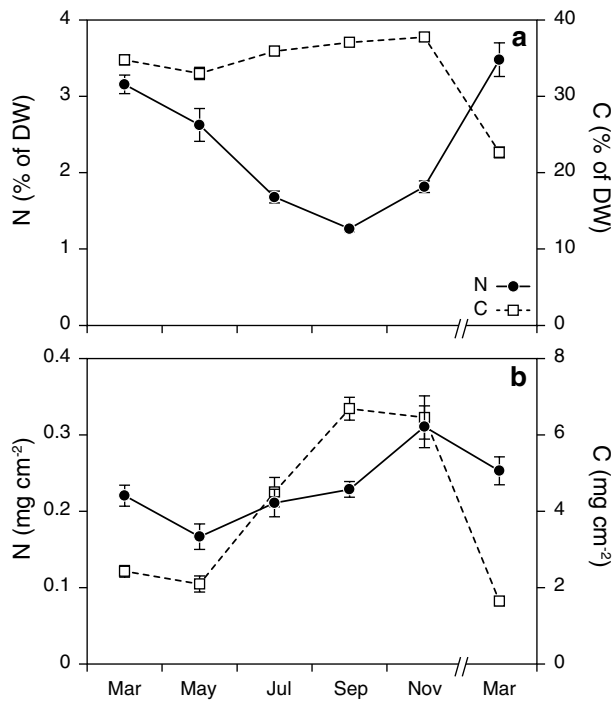


Fig. 4 Seasonal variation of N and C contents of *S. latissima* presented as **a** percentage of dry weight (DW) and **b** the area-specific content (mg cm⁻²). Each data point represents mean \pm SE of five individuals, for which the average of 3–6 measurements along the blade length has been calculated

Between July and September, the average tissue N concentration (% of DW) showed a significant increase toward deeper water, whereas the opposite was found for the C concentration (Table 1). The same tendencies occurred for the area-specific C and N contents (mg cm⁻²) (Table 1). At all depths, minimum values of N concentrations were found in September, amounting to 0.75 % of DW, 1.27 % of DW and 2.11 % of DW, respectively, for plants from 4, 7 and 11 m.

Population structure and production

Length and diameter of *S. latissima* stipes did not differ significantly over the season (ANOVA, $P > 0.22$, data not shown), and data from all sampling events were therefore pooled to analyze relationships between stipe dimensions and age (Fig. 5). The number of visible stipe growth rings varied from 1 to 3 for all collected specimens for the entire period of the survey, indicating that *S. latissima* in Aarhus Bay did not exceed the age of 3 years. There were significant correlations between stipe diameter and number of stipe growth rings (linear regression, $r^2 = 0.27$, $F_{1,110} = 40.44$, $P < 0.0001$) as well as between stipe length and number of stipe growth rings (linear regression, $r^2 = 0.14$, $F_{1,110} = 18.04$, $P < 0.0001$) (Fig. 5), suggesting

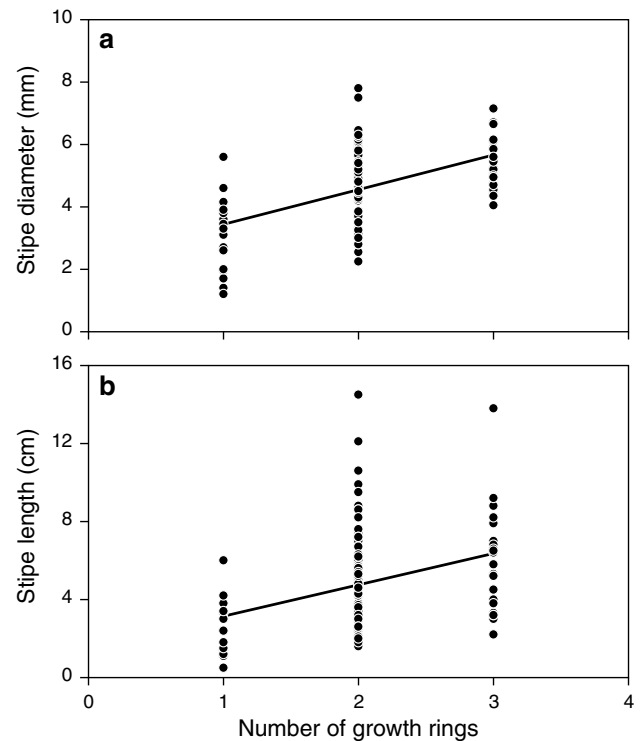


Fig. 5 Diameter (**a**) and length (**b**) of *S. latissima* stipes as a function of the number of growth rings. Data are from March to November 1999 at 7 m of depth. $n = 112$. Statistics of the fitted lines: **a** $r^2 = 0.27$, $F_{1,110} = 40.44$, $P < 0.0001$; **b** $r^2 = 0.14$, $F_{1,110} = 18.04$, $P < 0.0001$

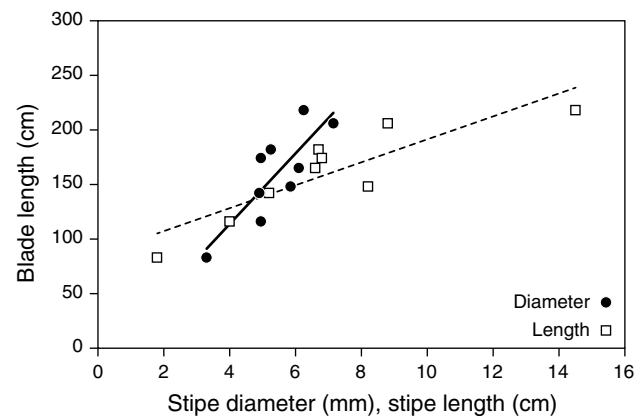


Fig. 6 Blade length of *S. latissima* as a function of stipe diameter and stipe length, respectively. Data are from July 1999, 7 m of depth. $n = 9$. Statistics of the fitted lines: stipe diameter, $r^2 = 0.69$, $F_{1,7} = 15.77$, $P = 0.0054$; stipe length, $r^2 = 0.77$, $F_{1,7} = 22.84$, $P = 0.002$

that both parameters reflected the age of *S. latissima*. In addition, when blade length reached its maximum in July and loss through distal erosion was still limited, both stipe diameter and stipe length were significantly correlated to the length of the blade (Fig. 6), hence indicating that

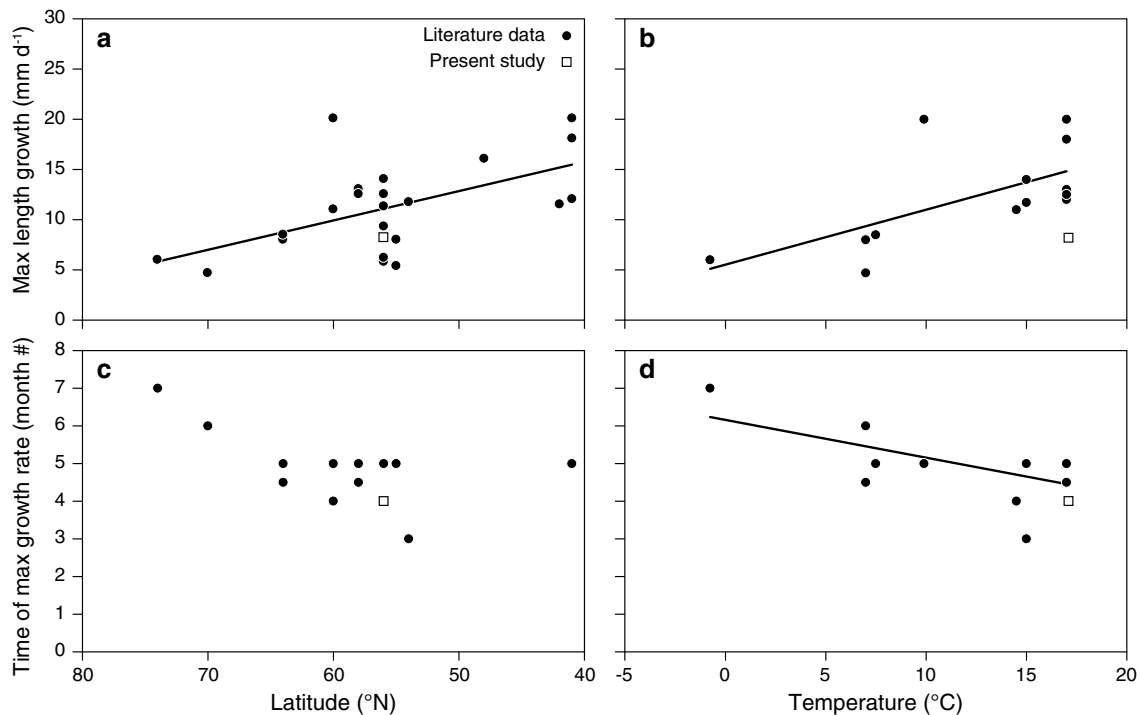


Fig. 7 Maximum length growth rate (**a**, **b**) and time of maximum growth rate (**c**, **d**) of *S. latissima* as a function of latitude (**a**, **c**) and average summer temperature (July–September) (**b**, **d**) across the entire geographical distribution of the species. Function of the fitted lines: **a** $y = -0.29x + 27.2$, **b** $y = 0.47x + 5.96$, **c** $y = -0.11x + 6.19$. Statistic of the fitted lines: **a** $r^2 = 0.32$, $F_{1,21} = 9.73$, $P = 0.0052$; **b** $r^2 = 0.30$, $F_{1,12} = 5.22$, $P = 0.0414$;

d $r^2 = 0.40$, $F_{1,12} = 8.05$, $P = 0.015$. No significant correlation between time of maximum growth rate and latitude was found; hence, no fitted line is displayed in **c**. Data from the present study (open squares) are compared with literature values (filled circles) where growth was also typically assessed based on consecutive blade-marking

maximum blade length increased with age, at least until the age of three.

Average annual length growth and blade length of *S. latissima* were, respectively, 132 and 84 cm, leading to a turnover ratio of 1.6 year⁻¹ when calculated on a length basis. Likewise, the annual biomass turnover was 1.1 year⁻¹ when calculated as the ratio between the average annual biomass production (17.8 g DW year⁻¹) and weight per individual (16.2 g DW). The *S. latissima* population had an average density of 4.8 individuals m⁻² on the scattered stones at 7 m depth and with an average weight of 16.2 g DW per individual, the area-specific biomass amounted to 77.5 g DW m⁻² as an annual average. Maximum biomass of 122 g DW m⁻² was found in July, whereas minimum biomass was found in March, being 24 g DW m⁻² in March 2000 and 29 g DW m⁻² in March 1999. Overall, the *S. latissima* population exhibited an annual blade production of 85.5 g DW m⁻² at 7 m depth.

Large-scale patterns

Comparison of maximal daily elongation rates of this study (0.75 cm day⁻¹ in March–May) with data covering

the entire distribution range of *S. latissima* showed a four-fold variation across the distribution range with a general increase from north to south (Fig. 7a). On average, maximum daily growth rates increased 0.29 mm day⁻¹ per latitudinal degree southwards. The comparison further indicated that the elongation rates of the Danish population studied here fell in the lower range of those registered at similar latitudes (Fig. 7a). The seasonal timing of the maximum elongation rate of the Danish kelp population fell within the range (March–May) identified for other populations within the latitude range of 45–60°N (Fig. 7c). By contrast, the maximum elongation rates in arctic regions occurred later in summer (June and July). Both the maximum elongation rate and its timing were correlated with water temperature (Fig. 7b, d), increasing the maximum growth rate with 0.47 mm and advancing it by 3.4 days/° temperature increase. The large-scale comparison of *S. latissima* growth patterns included studies conducted at different depths—the vast majority at depths of <10 m. Though testing was only allowed for a few of these studies of which the exact depth was given, there were no indications that differences in depth influenced any of the general relations found in Fig. 7a (GLM, $F_{1,9} = 1.47$, $P = 0.2556$),

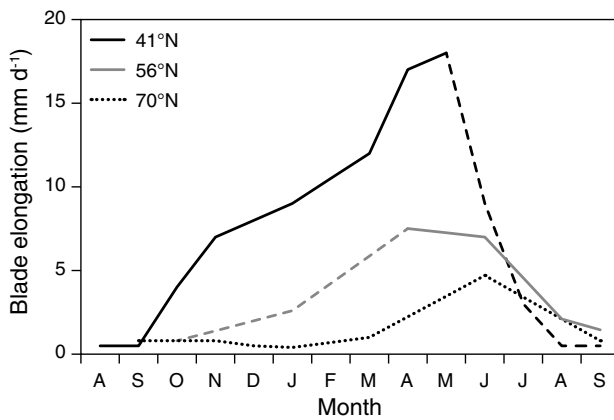


Fig. 8 Blade elongation rate (mm day^{-1}) throughout the year at three different latitudes. The three curves are based on the following studies: 41°N —Brady-Campbell et al. 1984, 56°N —present study, 70°N —Dunton 1985. Dashed lines indicate that data are obtained from different growth seasons

Fig. 7b (GLM, $F_{1,8} = 0.62$, $P = 0.4521$) or Fig. 7d (GLM, $F_{1,8} = 0.15$, $P = 0.7070$).

Comparing the course of growth curves from the present study and from northern and southern areas of the distribution range of *S. latissima* (based on the work of Brady-Campbell et al. 1984 and Dunton 1985) suggests additional differences between populations inhabiting the north and south (Fig. 8): (1) Onset of growth occurs earlier in southern populations, (2) growth is terminated slightly earlier in southern populations, (3) the growth period has a longer extend in southern populations, and (4) summer growth declines faster in southern populations (Fig. 8).

Discussion

Growth patterns: global and local regulators

The latitudinal patterns identified in the global comparison (Fig. 7) suggest that large-scale factors are important in regulating growth dynamics in *S. latissima*. Water temperature and light (irradiance and photoperiod) are key candidates for inducing these latitudinal differences in seasonality and peaks of kelp growth (Kain 1989). The global comparison indicated that both the maximum growth rate and its timing are affected by temperature (Fig. 7b, d), thus stressing its importance as a large-scale parameter regulating growth dynamics in *S. latissima*. It is believed that critically high summer temperatures are also responsible for determining the species southern distribution boundary (van den Hoek 1982; Breeman 1988), and the fact that growth rates increase with latitude without any decline near the southern limit of distribution (Fig. 7a) indicates that the

expansion is not prevented by growth of the sporophyte, but more likely coupled to the survival of earlier developmental stages (i.e., spores and gametophytes) and/or sporogenesis, which requires a period of minimum 4 weeks with short daylengths at 15°C or lower to occur (Müller et al. 2009). The identified effects of temperature support earlier indications that *S. latissima* may expand northwards in a warmer future (Müller et al. 2009; Krause-Jensen et al. 2012). Furthermore, warming might entail earlier timing and probably also longer extent of the growth season in addition to increased peak production. In contrast, populations at the southern end of the distribution range may experience increased temperature stress and loss of biomass in late summer. A recent study on the seasonality of eelgrass populations along large-scale gradients also suggests earlier timing of the growth season with higher temperature, but no indications of longer growth season, increased peak biomass or production in warmer waters (Clausen et al. 2014).

Besides temperature, sea ice cover has also been identified as a major regulator of the growth of *S. latissima* in arctic regions (Krause-Jensen et al. 2012) and is together with long polar winters a factor known to confine kelp growth to a short period during summer where light conditions are sufficient (Dunton 1985; Borum et al. 2002). These factors most probably contribute to the later timing of maximum growth as well as the shorter growth period identified for arctic regions as compared to more temperate areas in this study (Figs. 7c, 8).

In addition to large-scale parameters, the huge variation in growth rate within narrow geographical ranges ($55\text{--}56^{\circ}\text{N}$) (Fig. 7a) implies that growth dynamics are also influenced by parameters varying on a local scale, for instance high summer temperatures and suboptimal salinities. Marked reductions of growth at only 5° deviations from the optimum temperature range for *S. latissima* ($10\text{--}15^{\circ}\text{C}$) have been reported previously (Kain 1979; Bolton and Lüning 1982; Andersen et al. 2013). Thus, it is plausible that the productivity of *S. latissima* in Aarhus Bay was periodically inhibited during the study period by non-optimal temperatures at the extreme of the recorded range from 2.4°C (minimum value of March 1999) to 21.1°C (maximum value of August 1999). It seems that high summer temperatures were more detrimental in the regulation of productivity than low winter temperatures, considering that the lowest growth rates and the highest loss rates coincided with high temperatures during summer, whereas a similar relationship was not apparent during cold winter months, where loss rates were low (Figs. 1b, 3a–b). This pattern is in accordance with previous findings that high temperatures (20°C) lead to reduced net photosynthesis along with increased tissue deterioration as compared to lower temperatures (10 and 15°C) (Andersen et al. 2013). Krumhansl and Scheibling (2011) also found this effect

of temperature but further pinpointed the coverage of epiphytes as an enhancer of blade tissue loss. For this present study, however, no notable epiphytes were seen and hence were not considered problematic in that term.

Low and fluctuating salinity, typical for inner Danish waters, may also have contributed to the relatively low production, as osmotic stress can exert physiological stress on kelps. During this study, monthly averages of salinity ranged between 19.8 and 26.7 psu, which are somewhat below the optimal range for *S. latissima* of 27–33 psu reported by Gerard et al. (1987). Periodically, salinities were as low as 15.6 psu, which may have affected the growth negatively and contributed to the low production in the area. Low growth of *S. latissima* has also been found in another Danish study (5.4 mm day⁻¹, Weile 1996) conducted in an area of low salinity (annual average <14 psu, data obtained from DNAMAP) reinforcing the linkage of low growth and low salinity.

Annual production and turnover

In average, *S. latissima* exhibited an annual length growth of 132 cm at 7 m depth. A global comparison of the annual length growth reveals a tendency of increasing values in a north to south direction (Krause-Jensen et al. 2012) as was also found for maximum growth rates in this work. Within this global data comparison of annual length growth, Danish data once again fall in the lower range.

Based on the blade length, the annual turnover amounted to 1.6 year⁻¹ on average, whereas the turnover based on DW was somewhat lower, 1.1 year⁻¹, stressing that the correlation between length and weight is not linear and that as an individual grows longer, it also gets wider and thicker. Turnover rates are prone to vary with age (Mann 1972), but since determinations of age and blade elongation (i.e., production) were not made for the same individuals in the present study, an exact comparison of turnover values between age classes was not possible. However, we found that blade length increased with age (Figs. 5, 6) and assuming that absolute length growth was similar in all age classes (Mann 1972), data indicated a reduced turnover in older individuals. Our results thus support previous statements concerning the influence of cohort distribution within a population on growth dynamics of Laminariales (Parke 1948; Mann 1972; Lüning 1979; Sjöton 1993).

Standing stock and area production

The average standing stock of *S. latissima* in Aarhus Bay (77.5 g DW m⁻²) was low compared to kelp biomasses reported from elsewhere (Bartsch et al. 2008). A major reason for this was a limitation of suitable substratum. The scattered stones of the study site only allowed an average

density of 4.8 individuals m⁻², whereas rocky shores can host much denser populations (Mann 1972). In addition, the size of the individuals (weighted length average: 83.8 cm; weighted biomass average: 16.1 g DW individual⁻¹) was also relatively modest compared to specimens found elsewhere (i.e., Parke 1948; Gaevart et al. 2001; Krause-Jensen et al. 2012) and thus contributed to the low standing stock in the area. It is probable that the relatively small stones which composed the substratum could not support larger individuals. The limited standing stock along with the moderate turnover ratio implied that annual area production (85.5 g DW m⁻²) was also modest relative to levels realized for kelp beds elsewhere (Mann 1973; Lüning 1990; Vadas et al. 2004).

Carbon and nitrogen dynamics

Generally, the lamina contained more C during summer and autumn than during spring months, corresponding to the suggestion that *S. latissima* stores carbohydrates during summer for use in winter growth (Black 1950). Also, the increase in blade length from November to March (Fig. 3a) simultaneously with a decrease in the C content (Fig. 4a, b) indicated a consumption of stored carbohydrates. These findings are comparable to what has been described for Laminariales elsewhere (Mann 1973; Sjöton 1993). However, our study also showed that considerable amounts of the C were lost through abscission of distal tissue during summer months (Fig. 3c), hence proposing that the ability to translocate C from old tissue to new meristematic tissue was not complete.

The tissue C content decreased with increasing depth paralleling the decline in irradiance (Table 1), merely indicating that the ability to store carbohydrates was influenced by the light conditions, thus again stressing the important role of light for the biomass dynamics of *S. latissima*. Depth also influenced loss rate (Table 1); the highest loss rates were found at 4 m depth presumably as a consequence of a higher degree of exposure to pressures—in terms of waves, low salinity and high temperatures. Despite a higher C content in these shallow growing algae, the high loss of distal blade tissue reduces the translocation of stored C for new meristematic growth and consequently, this might along with the higher exposure to pressures reduce their growth performance.

From September to March, the total N content in *S. latissima* increased as indicated by a dramatic increase in tissue N concentration as well as an overall increase in the area-specific N content (Fig. 4a, b). This increase coincided with the period of maximum ambient nutrient levels (Fig. 1b) and verified the ability of the species to build up N reserves under such conditions. On the contrary, between March and September, nutrient levels were low in Aarhus

Bay (Fig. 1b). At this time of the year, the N tissue concentration dropped dramatically (Fig. 4a) simultaneously with an occurrence of marked growth in blade area and biomass (Fig. 2a, b). Hence, the decline of tissue N concentration was a consequence of N being diluted as new tissue was formed. In other words, internally stored N was utilized to support new growth in this period. However, as with C, considerable amounts of N were lost from the distal tissue during summer (Fig. 3d) and the ability of *S. latissima* to recover N from the distal tissue was not complete. High growth presumably based on internal N reserves was only maintained until July, after which it ceased (Fig. 3a, b). In this same period, the internal N concentration decreased to 1.3 % of DW, which is below the critical N value (1.7 % of DW) necessary to maintain maximum growth reported for other brown seaweeds (Pedersen and Borum 1996). It therefore seems reasonable to assume that growth decline during summer was partly related to N limitation, as ambient nutrient levels at this time a year were low (Fig. 1a) and internal storages were exhausted (Fig. 4a).

At 11 m of depth, the minimum tissue N concentration was 2.1 % of DW, somewhat higher than the critical N value (Pedersen and Borum 1996) and hence, the same exhaustion of N did not seem to occur in deeper waters despite higher elongation rates. The presence of a pycnocline between 7 and 11 m of depth during summer months may have caused this pattern by enhancing nutrient availability, and hence nutrient uptake, below the pycnocline as compared to above it. Further expected benefits of a summer pycnocline in terms of increased salinity and reduced temperature did not seem to enhance the overall growth performance of the plants at 11 m depth, as even though they had a higher elongation rate, their low area-specific DW (Table 1) merely indicated an increase in the blade area rather than a real growth in biomass. Increasing the blade area could be an adaptation to better light exploitation in this low light environment ($17 \mu\text{mol photons m}^{-2} \text{s}^{-1}$).

In summary, our study confirms earlier findings that seasonal growth and loss dynamics of *S. latissima* are indeed regulated by annual fluctuations in light and N levels. However, differences in light and exposure along depth gradients also affect the dynamics, and high losses of both N and C through summer abscission of distal tissue question the efficiency of translocation in *S. latissima*, especially where late summer losses are accelerated by, e.g., high temperature. Our large-scale comparisons further highlight that warming advances the timing and increases the level of peak growth and also seems to expand the growth period. It is suggested that local factors such as low salinity and periodically high summer temperature may contribute to explaining why maximum growth rate in the present study falls in the low range of values measured in other *S. latissima* populations from similar latitudes.

Acknowledgments This study was funded by The Danish Council of Strategic Research and carried out as a part of the MacroAlgae Biorefinery (MAB3) project. Morten Foldager Pedersen, Roskilde University, is thanked for valuable comments to an earlier version of the manuscript.

References

- 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. *J Mar Biol*. doi:10.1155/2011/690375
- Andersen GS, Pedersen MF, Nielsen SL (2013) Temperature acclimation and heat tolerance of photosynthesis of Norwegian *Saccharina latissima* (Laminariales, Phaeophyceae). *J Phycol* 49:689–700
- Bartsch I, Wiencke C, Bischof K, Buchholz CM, Buck BH, Eggert A, Feuerpfeil P, Hanelt D, Jacobsen S, Karez R, Karsten U, Molis M, Roleda MY, Schubert H, Schumann R, Valentin K, Weinberger F, Wiese J (2008) The genus *Laminaria* sensu lato: recent insight and development. *Eur J Phycol* 43(1):1–86
- Black WAP (1950) Seasonal variation in weight and chemical composition of the common British Laminariaceae. *J Mar Biol Assoc UK* 29:45–72
- Boden GT (1979) The effect of depth on summer growth of *Laminaria saccharina* (Phaeophyta, Laminariales). *Phycologia* 18:405–408
- Bolton JJ, Lüning K (1982) Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species in culture. *Mar Biol* 66:89–94
- Borum J, Pedersen MF, Krause-Jensen D, Christensen PB, Nielsen K (2002) Biomass, photosynthesis and growth of *Laminaria saccharina* in a high-arctic fjord, NE Greenland. *Mar Biol* 141:11–19
- Brady-Campbell MM, Campbell DB, Harlin MM (1984) Productivity of kelp (*Laminaria* spp.) near the southern limit in the northwestern Atlantic Ocean. *Mar Ecol Prog Ser* 18:79–88
- Breeman AM (1988) Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. *Helgoländer Meeresunters* 42:199–241
- Bruno JF, Bertness MD (2001) Habitat modification and facilitation in the benthic marine communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer Associates, Sunderland, Massachusetts, pp 201–218
- Chapman ARO, Craige JS (1977) Seasonal growth in *Laminaria longicruris*: relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Mar Biol* 40:197–205
- Clausen KK, Krause-Jensen D, Olesen B, Marba N (2014) Seasonality of eelgrass biomass across gradients in temperature and latitude. *Mar Ecol Prog Ser*. doi:10.3354/meps10800
- Conolly NJ, Drew EA (1985) Physiology of Laminaria. III. Effect of a coastal eutrophication gradient on seasonal growth and tissue composition in *L. digitata* Lamour. and *L. saccharina* (L.) Lamour. *Mar Ecol* 6:181–195
- Davison IR, Greene RM, Podolak EJ (1991) Temperature acclimation of respiration and photosynthesis in the brown alga *Laminaria saccharina*. *Mar Biol* 110:449–454
- Dayton PK (1985) Ecology of kelp communities. *Annu Rev Ecol Syst* 16:215–245
- Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA (1993) Assessing water quality with submerged aquatic vegetation habitat requirements as barometers of Chesapeake Bay health. *Bioscience* 43:86–94

- Druehl LD, Cabot EL, Lloyd KE (1987) Seasonal growth of *Laminaria groenlandica* as a function of plant age. *Can J Bot* 65:1599–1604
- Duggins DO, Simenstad CA, Eestes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170–173
- Dunton KH (1985) Growth of dark-exposed *Laminaria saccharina* (L.) Lamour. and of *Laminaria solidungula* J. Ag. (Laminariales: Phaeophyta) in the Alaskan Beaufort Sea. *J Exp Mar Biol Ecol* 94:181–189
- Fallis AL (1916) Growth in some Laminariaceae. *Puget Sound Mar Stn Publ* 1:1–17
- Gaevert F, Davoult D, Creach A, Kling R, Janquin M-A, Seuront L, Lemoine Y (2001) Carbon and nitrogen content of *Laminaria saccharina* in the eastern English Channel: biometrics and seasonal variations. *J Mar Biol UK* 81:727–734
- Gagne JA, Mann KH, Chapman ARO (1982) Seasonal patterns of growth and storage in *Laminaria longicuris* in relation to differing patterns of availability of nitrogen in the water. *Mar Biol* 69:91–101
- Gerard VA, Mann KH (1979) Growth and production of *Laminaria longicuris* (Phaeophyta) population exposed to different intensities of water movements. *J Phycol* 15:33–41
- Gerard AA, DuBois K, Green R (1987) Growth responses of two *Laminaria saccharina* populations to environmental variation. *Hydrobiology* 151:229–232
- Johnston CS, Jones RG, Hunt RD (1977) A seasonal carbon budget for a laminarian population in a Scottish sea-loch. *Helgoländer Wiss Meeresunters* 30:327–345
- Kain JM (1979) A view of the genus *Laminaria*. *Oceanogr Mar Biol Ann Rev* 17:101–161
- Kain JM (1989) The seasons in the subtidal. *Br Phycol J* 24:203–215
- Krause-Jensen D, Marbá N, Olesen B, Sejr MK, Christensen PB, Rodrigues J, Renaud PE, Balsby TJS, Rysgaard S (2012) Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. *Glob Chang Biol* 18:2981–2994
- Krumhansl K, Scheibling R (2011) Detrital production of Nova Scotian kelp beds: patterns and processes. *Mar Ecol Prog Ser* 421:67–82
- Lippert H, Iken K, Rachor E, Wiencke C (2001) Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). *Polar Biol* 24:512–522
- Lüning K (1979) Growth strategies of three *Laminaria* species (Phaeophyceae) inhabiting different depth zones in the sublittoral region of Helgoland (North Sea). *Mar Ecol Progr Ser* 1:195–207
- Lüning K (1990) *Seaweeds: their environment, biogeography, and ecophysiology*. Wiley, New York
- Lyngby JE, Mortensen SM (1996) Effects of dredging activities on growth of *Laminaria saccharina*. *Mar Ecol* 17:345–354
- Mann KH (1972) Ecological energetics of the sea-weed zone in a marine bay in the Atlantic coast of Canada. II. Productivity of the seaweeds. *Mar Biol* 14:199–209
- Mann KH (1973) Seaweeds: their productivity and strategy for growth. *Science* 182:975–981
- Müller R, Laepple T, Bartsch I, Wiencke C (2009) Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Bot Mar* 52:617–638
- Parke M (1948) Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. *J Mar Biol Assoc UK* 27:651–709
- Pedersen MF, Borum J (1996) Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Mar Ecol Prog Ser* 142:261–272
- Schaeffelfe B, Peters AF, Reusch TBH (1996) Factors influencing depth distribution of soft bottom inhabiting *Laminaria saccharina* (L.) Lamour. in Kiel Bay, Western Baltic. *Hydrobiology* 326/327:117–123
- Sjötun K (1993) Seasonal lamina growth in two age groups of *Laminaria saccharina* L. Lamour in western Norway. *Bot Mar* 36:433–441
- Sjötun K, Gunnarson K (1995) Seasonal growth of an Icelandic *Laminaria* population (section *Simplices*, Laminariaceae, Phaeophyta) containing solid- and hollow-stiped plants. *Eur J Phycol* 30:281–287
- Spurkland T, Iken K (2011) Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic *Saccharina latissima* (Laminariales, Laminariaceae). *Bot Mar* 54:355–365
- Spurkland T, Iken K (2012) Seasonal growth patterns of *Saccharina latissima* (Phaeophyceae, Ochrophyta) in a glacially-influenced subarctic estuary. *Phycol Res* 60:261–275
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29(4):436–459
- Vadas RL Sr, Beal BF, Wright WA, Nickl S, Emerson S (2004) Growth and productivity of sublittoral fringe kelps (*Laminaria longicuris*) Bach. Pyl. In Cobscook Bay, Maine. *Northeast Nat* 11:143–162
- van Den Hoek C (1982) The distribution of benthic marine algae in relation to the temperature regulation of their life histories. *Biol J Linn Soc* 18:81–144
- Weile K (1996) Baseline study of *Laminaria* populations in Øresund. Doc. nr. 95/120/1E. By VRI/Toxicon AB for Øresundskonsortiet