

Comparative Phenology of *Sargassum muticum* and *Halidrys siliquosa* (Phaeophyceae: Fucales) in Limfjorden, Denmark

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Sargassum muticum (Fucales: Sargassaceae) has been present in Scandinavia since 1984. In Limfjorden, a shallow Danish sound, it has invaded the habitat of the indigenous *Halidrys siliquosa* (Fucales: Cystoseiraceae). Studies have suggested a displacement of indigenous relatives by *Sargassum muticum* and that this could be due to differences in life history strategies. Our study is the first to document the phenology of *S. muticum* at the northern part of its European distribution range (Scandinavia) and the first to document the phenology of *Halidrys siliquosa*. Thallus height and weight, species cover and tissue carbon, nitrogen and phosphorus were measured. For *Sargassum muticum* a strong seasonality with midsummer maxima, similar to previously published results from other European sites, was found. *Halidrys siliquosa* only exhibited moderate seasonality, if any. Hence, the two species were found to be functionally different and have different life histories. Our results support the idea that the competitive success of *Sargassum muticum* is caused by its pseudo-perennial life history compared to the truly perennial life histories of many indigenous relatives. Conversion factors between commonly used biometric measures were derived from the phenological data.

Introduction

Sargassum muticum (Yendo) Fensholt is indigenous to South East Asia (Yendo 1907) but it has been introduced to and invaded the American west coast for more than 50 years and European waters from the Mediterranean Sea to Scandinavia for about 30 years (Scagel 1956, Deysher and Norton 1982, Critchley *et al.* 1983, Rueness 1989, Critchley *et al.* 1990 b, Wernberg-Møller *et al.* 1998 a, Karlsson and Loo 1999, Stæhr *et al.* 2000). The invasive nature of *S. muticum* has resulted in a tremendous research effort (the bibliography of Critchley *et al.* 1990 b lists 314 publications and numerous others have been published since) covering almost every facet of the species' biology. Hence, the phenology of *S. muticum* is well described from its first establishment around the English Channel (e. g. Jephson and Gray 1977, Critchley *et al.* 1987, Givernaud *et al.* 1991). Few studies have yet been published from the northern part of its European distribution, Scandinavia, where it has been present since 1984 (Christensen 1984).

Species within the family Cystoseiraceae are common indigenous components of the habitats invaded by *Sargassum muticum* (Fletcher and Fletcher 1975 a, Jephson and Gray 1977, Gunnill 1985, Arenas *et al.* 1995, Viejo 1997, Andrew and Viejo 1998). In Denmark, the Cystoseiraceae is represented by only one species, *Halidrys siliquosa* (L.) Lyngb. (Nielsen *et al.* 1995), and it now co-occurs with *Sargassum muticum* (Knudsen 1996, Wernberg-Møller *et al.* 1998 b, Stæhr *et al.* 2000). *Halidrys siliquosa* and the other members of Cystoseiraceae are close relatives of *Sargassum muticum* (Jensen 1974, Rousseau *et al.* 1997). Some researchers have suggested a displacement of indigenous Cystoseiraceae by *Sargassum muticum* (Fletcher and Fletcher 1975 a, Viejo 1997, Stæhr *et al.* 2000), perhaps because of differences in life history strategies (Arenas *et al.* 1995, Viejo 1997). Whether the potential effects of *S. muticum* on *Halidrys siliquosa* can be explained by differences in life history strategies is unknown since the annual behavior of *H. siliquosa* basically is undescribed. Thus, the first objective of our study was to quantitatively describe and compare the phenology of *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden, a shallow Danish sound.

Different studies often use different measures of essentially the same parameter. For example, algal size may be expressed as either height (e. g. DeWreede 1978, Critchley *et al.* 1987, Espinoza 1990, Givernaud *et al.* 1991) or different forms of biomass (e. g. Yamauchi 1984, Arenas *et al.* 1995). Similarly, abundance may be expressed as either density of individuals (e. g. Deysher and Norton 1982, Gunnill

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1985, Andrew and Viejo 1998, Cosson 1999), biomass (e. g. Gorham and Lewey 1984, Critchley *et al.* 1990a, Givernaud *et al.* 1991, Núñez-López and Casas Valdez 1998, Cosson 1999) or cover (DeWreede 1983, McCourt 1984, Viejo 1997, Andrew and Viejo 1998, Wernberg-Møller *et al.* 1998b, Stæhr *et al.* 2000). Thus, the ability to extract information across studies may depend on known relationships and conversion factors between these relationships. The second objective of our study was to provide relationships and conversion factors between different biometric measures of *Sargassum muticum* and *Halidrys siliquosa*. These relationships and conversion factors will be useful in the synthesis of both past and future studies on the ecology of *Sargassum muticum* and its close relatives within the Cystoseiraceae (e. g. *Halidrys siliquosa*).

Materials and Methods

Study site

The study was conducted from April 1997 to January 1998, in Dråby Vig (56.49.92 N 08.50.70 E; see Fig. 1), western Limfjorden (Denmark). The study site was located on an east-facing shore, protected from the predominantly westerly winds. At the location the annual variation in salinity is 25–28‰ (Grooss *et al.* 1996) and the surface temperature –1 to 25 °C (T. Wernberg, M. S. Thomsen and P. A. Stæhr, unpublished data). All *in situ* sampling was done within the main *Sargassum* bed (Wernberg-Møller *et al.* 1998b) at a depth of 2.5–3 m.

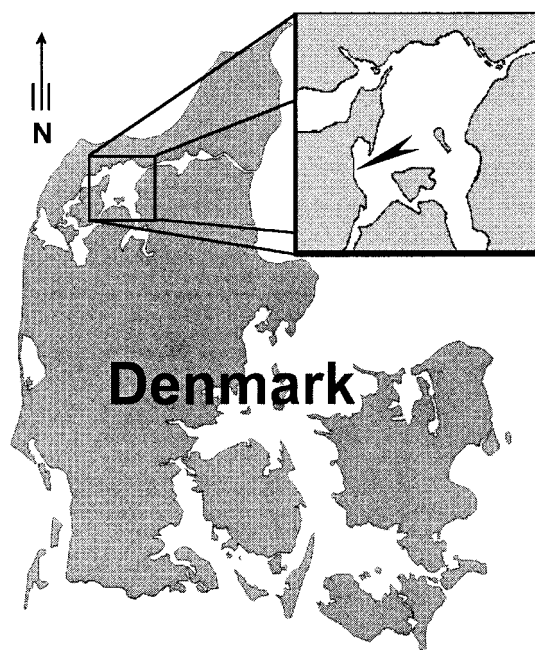


Fig. 1. Denmark and the position of the study site in Limfjorden (arrow, insert, 56.49.92 N 08.50.70 E).

Height and biomass

Each month, except October and December, 16–30 individuals of *Sargassum muticum* and 5–33 individuals of *Halidrys siliquosa* were collected haphazardly by SCUBA divers. Only individuals that could be clearly separated from each other were used in the study. Whole specimens were stored in seawater at ambient temperature until further processing, usually within 24 hours.

The total height (length) of individuals was measured as the distance from the holdfast to the tip of the longest lateral (terminology as in Jensen 1974; see also Critchley *et al.* 1990b). The biomass of individual thalli was measured as both fresh weight (FW) and dry weight (DW). Prior to FW determination large epibionts were removed from the algae, which were then rinsed in fresh water and shaken gently to remove excess water. Smaller specimens were blotted with paper towels whereas larger individuals (primarily summer) were split in portions of 50–100 g FW and spun in a mesh bag. A preliminary study showed that the two methods deviated less than 5% from each other. Dry weights were determined after drying the algal material at 105 °C until constant weight.

Percent cover and cover versus biomass relationships

At each sampling event, except April, two SCUBA divers independently estimated the percent cover of *Sargassum muticum* and *Halidrys siliquosa* within 1 m² on both sides of 68 permanent fix points, randomly distributed within a hectare (100 × 100 m). Monthly cover values for both species were calculated as the mean of all fix points (n = 68), each fix point being the mean of 2 × 2 pseudo-replicates (i. e. north/south and diver 1/diver 2 subsamples).

The relationship between cover of bottom area and standing biomass was determined at each sampling occasion for *Sargassum muticum* and in August, September, November and January for *Halidrys siliquosa*. Three SCUBA divers estimated the cover of *Sargassum muticum* or *Halidrys siliquosa* within a 0.27 m² ring in 11–17 samples of each species. In each sample all algal biomass within the ring was harvested and brought ashore for FW determination, as described above. It was sought to sample as many and as wide spread coverages as possible and thus, the sampling was not randomized.

Tissue contents of carbon, nitrogen and phosphorus

Tissue contents of carbon (C), nitrogen (N) and phosphorus (P) were determined from subsamples of separate thalli, haphazardly collected at each sampling event. Because of the characteristic annual-perennial division of the *Sargassum muticum* thallus (Jensen 1974) it was decided to conduct the tissue analyses of *S. muticum* on basal and apical pieces separately. Basal pieces of *S. muticum* corresponded

to the perennial holdfast and main axis and apical pieces to the annual vegetative thallus. 3–5 basal pieces of *S. muticum* and 2–8 apical pieces of *S. muticum* and *Halidrys siliquosa* were sampled and analyzed each sampling event. Samples were dried at 105 °C and analyzed for total C and N using a Carlo-Erba NA-1500 CHN analyzer, and for total P by spectrophotometric analysis after wet oxidation with boiling H₂SO₄ (Strickland and Parson 1968).

Results

Height and biomass

The seasonal development in thallus height and biomass showed large differences between *Sargassum muticum* and *Halidrys siliquosa* (Figs 2A, 2B). The height of *Sargassum muticum* varied from 10–20 cm in spring, autumn and winter to almost 120 cm in summer, corresponding to an average elongation rate of ca. 1.5 cm day⁻¹ during spring and summer. This development in thallus height was accompanied by a distinct change in appearance and stature (see Wernberg-Møller *et al.* 1998 b). In contrast, the thallus height of *Halidrys siliquosa* remained around 30 cm throughout the entire year and retained its overall appearance. The maximum mean (\pm 95% C. L.) height of *Sargassum muticum* was found in July and amounted to 118 \pm 8 cm (range 85–165 cm, n = 27). The minimum mean height, 14 \pm 0.9 cm (range 10–21 cm, n = 30), was found in November about three months after senescence and the shedding of primary laterals. The maximum mean height of *Halidrys siliquosa*, 38 \pm 3 cm (range 25–54 cm, n = 22), and the minimum mean height, 33 \pm 5 cm (range 29–42 cm, n = 6), were found in November and May, respectively. The mean biomass of *Sargas-*

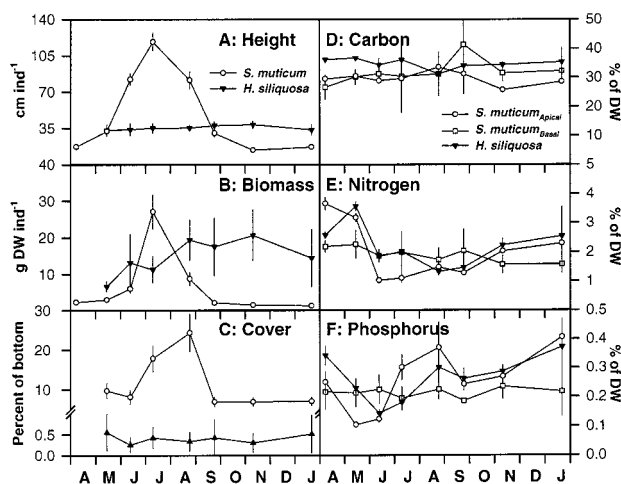


Fig. 2. Seasonal development in A) height, B) biomass, C) cover and D) carbon-, E) nitrogen- and F) phosphorus content of *Sargassum muticum* and *Halidrys siliquosa*. Error bars are 95% confidence limits. Note the broken ordinate axis in Figure 2C.

sum muticum thalli exhibited a similar seasonal pattern as for height, varying from ca. 3–30 g DW, the maximum mean of 27 \pm 5 g DW ind⁻¹ (range 12–53 g DW ind⁻¹, n = 27) found in July, but the minimum mean of 1.3 \pm 0.2 g DW ind⁻¹ (range 0.4–2.5 g DW ind⁻¹, n = 29) in January. The mean biomass of *Halidrys siliquosa* thalli, on the other hand, increased from ca. 5 g DW in spring (min. mean May, 6.6 \pm 1.4 g DW ind⁻¹, range 5–9, n = 6) to 15–20 g DW in autumn and winter (max. mean November, 21 \pm 7 g DW ind⁻¹, range 4–51, n = 22), but this trend was not statistically significant (Kruskal-Wallis; p = 0.28) as there were large variations in thallus biomass within each month.

In both *Sargassum muticum* and *Halidrys siliquosa* there was a moderate to strong correlation between thallus height and thallus biomass (Fig. 3 and Table I). Reduced major axis linear regression (Jensen 1986, McArdle 1988) on LOG X – LOG Y transformed data was used to model the relationship between thallus height and biomass (Table I) and these regression models were highly significant for both *Sargassum muticum* and *Halidrys siliquosa* (ANOVA; p < 0.0001). The rate of increase in biomass (W) of *H. siliquosa* with height (H) was more than twice that of *Sargassum muticum*.

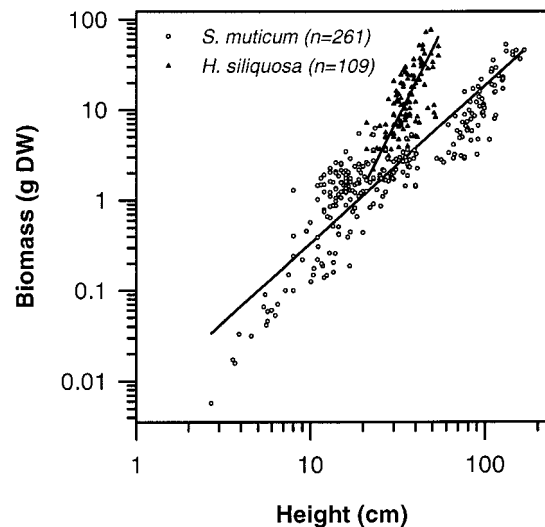


Fig. 3 The relationship between height (cm) and biomass (g DW) of individual thalli of *Sargassum muticum* and *Halidrys siliquosa*. Regression models (lines) are given in Table I.

Table I. Regression models of the relationship between algal height (H) in cm and algal biomass (W) in g dry weight (DW).

<i>Sargassum muticum</i>	$W_{\text{gDW}} = 10^{-2.2} \times H_{\text{cm}}^{1.75}$ ($r^2 = 0.80$; $p < 0.0001$; $n = 261$)
<i>Halidrys siliquosa</i>	$W_{\text{gDW}} = 10^{-4.9} \times H_{\text{cm}}^{3.87}$ ($r^2 = 0.47$; $p < 0.0001$; $n = 109$)

Percent cover

Within the 1 hectare *Sargassum* bed, *S. muticum* had a considerably higher cover than *Halidrys siliquosa* during all times of the year (Fig. 2C). The overall pattern of both species resembled that of height. *Sargassum muticum* exhibited a strong seasonal development with low cover in spring, autumn and winter (min. mean \pm 95% C. L. in September and November = 6.9% \pm 1, range 1–24%, $n = 68$) and high cover in late summer (max. mean in August = 24% \pm 5, range 1–72%, $n = 68$). *Halidrys siliquosa* remained more or less constant around 0.5% cover with no apparent seasonal tendencies (min. mean in June = 0.25% \pm 0.2, range 0–5% and max. mean in May = 0.55% \pm 0.4, range 0–12%, $n = 68$). For *Sargassum muticum* there was a one month timelag between maximum size of individual thalli (July; Figs 2A, 2B) and maximum cover (August; Fig. 2C).

Cover versus biomass

Scatter plots of cover of bottom area *versus* standing biomass of *Sargassum muticum* and *Halidrys siliquosa* suggested fitting data to a rectangular hyperbolic model. However, since none of the monthly data sets were fully saturated, a linear model was chosen because of its simplicity and the problems of curve fitting rectangular hyperbolae to non-saturated data sets (Berges *et al.* 1994). Data sets for every month were tested for homogeneity of slopes and they were found to be significantly different for *Sargassum muticum* (ANCOVA; $p < 0.0001$) but not for *Halidrys siliquosa* (ANCOVA; $p = 0.85$). Following further analysis of *Sargassum muticum* data (Tukey's multiple comparison test; $p < 0.05$) two periods with different slopes emerged: May, September, November, January (i. e. autumn, winter and spring) and June, July, August (i. e. summer). Hence, data for *S. muticum* were pooled within these two periods and data for *Halidrys siliquosa* within the entire time period. The relationship between cover of bottom area and standing biomass was modeled by reduced major axis linear regression (Jensen 1986, McArdle 1988) through the origin. The analyses of pooled data yielded highly significant regression models (ANCOVA; $p > 0.0001$) with strong regression coefficients ($r^2 = 0.71$ – 0.86) for both *Sargassum muticum* and *Halidrys siliquosa* (Table II). Thus, the linear models seemed to be adequate. The standing stock per unit area covered with *Sargassum muticum* in summer was almost 2.5 times that of the rest of the year (cf. coefficients in regression models, Table II). The relative standing biomass of *Halidrys siliquosa* was about 3/4 of that of *Sargassum muticum* during summer but almost 2 times larger over the rest of the year. Maximum standing biomass (i. e. 100% cover) was calculated as 3.7 kg FW m^{-2} for

Table II. Regression models for the relationship between algal cover (Co) in percent (%) of bottom area and biomass (W) in g FW m^{-2} .

<i>Sargassum muticum</i> (summer)	$W_{gFWm^{-2}} = 36.9 \times Co\%$ ($r^2 = 0.71$; $p > 0.0001$; $n = 45$)
<i>Sargassum muticum</i> (autumn, winter, spring)	$W_{gFWm^{-2}} = 14.5 \times Co\%$ ($r^2 = 0.83$; $p > 0.0001$; $n = 49$)
<i>Halidrys siliquosa</i> (all year)	$W_{gFWm^{-2}} = 28.5 \times Co\%$ ($r^2 = 0.86$; $p > 0.0001$; $n = 45$)

S. muticum in summer, 1.5 kg FW m^{-2} for *S. muticum* the rest of the year and 2.9 kg FW m^{-2} for *Halidrys siliquosa*.

C, N, P content

Carbon content remained constant throughout the year around 30% of DW in *Sargassum muticum* and 35% in *Halidrys siliquosa* (Fig. 2D, Table III). There were no significant differences between the C content of basal (perennial) and apical (vegetative) parts of *Sargassum muticum* (Kruskal-Wallis, Dunn's method; $p > 0.05$) but the C content of *Halidrys siliquosa* was significantly different from both of these (do.; $p < 0.05$). In contrast to C, N content and P content exhibited large seasonal variations in both species (Figs 2E, 2F, Table III). Apical parts of *Sargassum muticum* and *Halidrys siliquosa* followed the same general seasonal pattern and were not found to be significantly different with regard to either N or P (Kruskal-Wallis; $p > 0.05$). Nitrogen content varied from a maximum of 3–4% of DW in April–May to a minimum of 1–2% in summer (June, July, August). Phosphorus content varied from a minimum of 0.1–0.2% of DW in May–June to a maximum of 0.3–0.4% in August. Although the statistical results were somewhat ambiguous, there was a tendency of less (no) seasonality of nutrient contents in basal parts of *Sargassum muticum*. There was no overall statistical difference between the N content of basal parts of *S. muticum*, apical parts or *Halidrys siliquosa* (Kruskal-Wallis; $p = 0.22$). Phosphorus content was significantly different between basal parts of *Sargassum muticum* and *Halidrys siliquosa* (Kruskal-Wallis; $p < 0.05$) but not between apical and basal parts of *Sargassum muticum* (Kruskal-Wallis; $p > 0.05$). Hence the N content in basal parts of *S. muticum* remained around 2% of DW and P content around 0.2%. Although the statistical analyses did not find any general differences in N- and P content between apical parts of *S. muticum* and *Halidrys siliquosa*, there was a tendency for *Sargassum muticum* to display a faster and stronger seasonal change. During spring, N contents dropped much faster in apical *S. muticum* than in *Halidrys siliquosa* and the values stayed lower until late summer. Similarly, apical *Sar-*

Table III. Seasonal development in weight-based (A) and molar ratios (B) of fresh weight (FW), dry weight (DW), carbon (C), nitrogen (N) and phosphorus (P). Values are mean ratios \pm relative 95% confidence limits (% of mean ratio). For *Sargassum muticum* n = 16–30 for FW:DW and 4–8 for C:N:P. For *Halidrys siliquosa* n = 5–33 for FW:DW and n = 2–8 for C:N:P.

		<i>Sargassum muticum</i> (apical)					<i>Sargassum muticum</i> (basal)					<i>Halidrys siliquosa</i>				
		FW	DW	C	N	P	FW	DW	C	N	P	FW	DW	C	N	P
Apr	A	8.1	1.0 \pm 5%	0.29 \pm 1%	0.037 \pm 5%	0.0025 \pm 12%	5.6	1.0 \pm 4%	0.27 \pm 11%	0.022 \pm 6%	0.0022 \pm 19%	5.1	1.0 \pm 4%	0.36 \pm 1%	0.026 \pm 3%	0.0034 \pm 8%
	B	–	–	304	32	1	–	–	317	22	1	–	–	275	17	1
May	A	9.7	1.0 \pm 2%	0.30 \pm 1%	0.032 \pm 4%	0.0010 \pm 4%	5.7	1.0 \pm 3%	0.30 \pm 6%	0.023 \pm 15%	0.0021 \pm 16%	5.8	1.0 \pm 3%	0.37 \pm 1%	0.036 \pm 3%	0.0023 \pm 6%
	B	–	–	752	67	1	–	–	365	23	1	–	–	412	34	1
Jun	A	8.5	1.0 \pm 2%	0.29 \pm 2%	0.010 \pm 7%	0.0012 \pm 8%	5.3	1.0 \pm 3%	0.31 \pm 2%	0.019 \pm 5%	0.0023 \pm 15%	6.0	1.0 \pm 6%	0.34 \pm 6%	0.019 \pm 9%	0.0014 \pm 6%
	B	–	–	602	18	1	–	–	358	18	1	–	–	632	29	1
Jul	A	8.1	1.0 \pm 2%	0.30 \pm 3%	0.011 \pm 10%	0.0030 \pm 11%	5.1	1.0 \pm 3%	0.30 \pm 29%	0.020 \pm 25%	0.0019 \pm 15%	5.7	1.0 \pm 5%	0.36 \pm 7%	0.020 \pm 11%	0.0018 \pm 9%
	B	–	–	254	8	1	–	–	403	23	1	–	–	517	25	1
Aug	A	8.3	1.0 \pm 3%	0.34 \pm 8%	0.015 \pm 11%	0.0037 \pm 17%	4.4	1.0 \pm 5%	0.31 \pm 15%	0.017 \pm 14%	0.0023 \pm 11%	5.8	1.0 \pm 3%	0.31 \pm 9%	0.013 \pm 8%	0.0030 \pm 13%
	B	–	–	234	9	1	–	–	357	17	1	–	–	268	10	1
Sep	A	4.7	1.0 \pm 7%	0.31 \pm 4%	0.013 \pm 4%	0.0024 \pm 8%	4.5	1.0 \pm 6%	0.41 \pm 25%	0.020 \pm 22%	0.0019 \pm 3%	6.0	1.0 \pm 3%	0.34 \pm 1%	0.015 \pm 7%	0.0026 \pm 11%
	B	–	–	330	12	1	–	–	572	24	1	–	–	338	12	1
Nov	A	9.2	1.0 \pm 3%	0.26 \pm 2%	0.020 \pm 3%	0.0027 \pm 6%	5.1	1.0 \pm 6%	0.31 \pm 7%	0.016 \pm 13%	0.0024 \pm 13%	5.7	1.0 \pm 3%	0.34 \pm 2%	0.022 \pm 8%	0.0029 \pm 6%
	B	–	–	247	17	1	–	–	345	15	1	–	–	306	17	1
Jan	A	8.8	1.0 \pm 8%	0.28 \pm 2%	0.023 \pm 5%	0.0011 \pm 4%	5.4	1.0 \pm 5%	0.32 \pm 7%	0.016 \pm 14%	0.0022 \pm 7%	4.6	1.0 \pm 3%	0.35 \pm 7%	0.025 \pm 7%	0.0037 \pm 12%
	B	–	–	693	48	1	–	–	383	16	1	–	–	247	15	1

gassum muticum displayed the fastest and strongest seasonal change in P content.

Fresh weight (FW):dry weight (DW) and C:N:P ratios

Ratios between FW, DW and C, N and P reflected the seasonality illustrated in Figs 2 D–2 E (Table III). Fresh weights of apical parts of *Sargassum muticum* were 8.1–9.7 times the DW, except for September when there was a somewhat lower value. Basal parts of *S. muticum* had a significantly higher DW content than apical parts (Kruskal-Wallis; $p < 0.05$), and their FW varied between 4.4–5.7 times the DW. The FW:DW ratio of *Halidrys siliquosa* varied from 4.6–6.0, with the lower values in April and January. Molar ratios of tissue C, N, P showed some seasonal variation in apical *Sargassum muticum* and *Halidrys siliquosa*, but appeared to be more constant in basal *Sargassum muticum*. The average molar C:N:P was found to be 427:26:1, 388:20:1 and 374:20:1 for apical, basal *S. muticum* and *Halidrys siliquosa*, respectively. Maximum molar C:P and C:N was found in May and June respectively for apical *Sargassum muticum* (752:1 and 33:1) and in June and September for *Halidrys siliquosa* (632:1 and 28:1). Maximum molar N:P was found in January for apical *Sargassum muticum* (48:1) and in May for *Halidrys siliquosa* (34:1) and minimum molar N:P in July (8:1) and August (10:1) for the two species, respectively.

Discussion

This study has revealed considerable differences between the phenology of *Sargassum muticum*, a recently introduced species in Limfjorden (Christensen 1984), and *Halidrys siliquosa*, an indigenous species present in the habitat now successfully invaded by *Sargassum muticum* (Stæhr *et al.* 2000). Generally, the phenology of *S. muticum* showed large seasonal variation and the phenology of *Halidrys siliquosa* moderate to no seasonal variation. The differences in seasonality between these two closely related macroalgae (Jensen 1974, Rousseau *et al.* 1997) indicate differences in growth strategy which could offer an explanation for the relative success of *Sargassum muticum*.

In Limfjorden *Sargassum muticum* had a rapid growth (elongation of the vegetative thallus) from May to July after which it was senescent at the time of maximum fertility. A similar growth pattern has been demonstrated for *S. muticum* around the world (Spain: Arenas *et al.* 1995, France: Givernaud *et al.* 1991, Netherlands: Critchley *et al.* 1987, U. K.: Jephson and Gray 1977, Gorham and Lewey 1984, Canada: DeWreede 1978) although there are some latitudinal differences in the timing of the growth cycle (see Norton and Deysher 1989) probably due to environmental stimuli (Norton 1977, Norton and Deysher 1989, Hales and Fletcher 1990, Arenas *et al.* 1995).

The maximum mean height (118 cm) and range (85–165 cm) of *S. muticum* thalli found in Limfjorden compares well to general findings of ca. 75 cm (DeWreede 1978, Gorham and Lewey 1984, Espinoza 1990, Givernaud *et al.* 1991) to ca. 150 cm (Jephson and Gray 1977, Critchley *et al.* 1987, Espinoza 1990, Givernaud *et al.* 1991) although considerable exceptions exist (5 m: Gorham and Lewey 1984; 2.5–10 m: Belsher and Pommellec 1988; 4.2 m: Karlsson and Loo 1999). The maximum mean biomass of *S. muticum* in Limfjorden (27 g DW ind⁻¹) was lower than the range 60–80 g DW ind⁻¹ reported by Yamauchi (1984) from Japan (in culture) and Critchley *et al.* 1990 a from the Netherlands, but corresponded well to the ca. 17–25 g DW ind⁻¹ reported by DeWreede (1978) and Arenas *et al.* (1995) from Canada and Spain, respectively.

In contrast to *Sargassum muticum*, *Halidrys siliquosa* has been poorly studied. To our knowledge, this study is the first to present quantitative phenological data on this species, except for the recordings of thal- lous components (e. g. vesicles, receptacles etc.) by Moss and Lacey (1963). The findings, by Moss and Lacey (1963), of a phenological pattern for *H. siliquosa* somewhat similar to *Sargassum muticum* with ‘a rapid vegetative growth during the spring and early summer’ were not supported by the findings of this study. However, we did observe a tendency to increasing biomass during summer and a loss in winter, probably due to the loss of higher order laterals (Reinke 1876 quoted in Fritsch 1981) during storms as indicated by large amounts of drift *Halidrys siliquosa* on the beach in January. Nevertheless, it appears that the *H. siliquosa* population at our study site is made up of small individuals since descriptions of the species mention heights of up to 1–1.5 m (Oltmanns 1889, Rueness 1977) which has also been observed elsewhere in Danish coastal areas (pers. obs. T. Wernberg, M. S. Thomsen and P. A. Stæhr).

When disregarding the generally small seasonal variations in FW:DW, mean values for both *Sargassum muticum* (4.4–9.7) and *Halidrys siliquosa* (4.6–6.0) are in the proximity of 4.8–6.9 found in earlier studies of *Sargassum muticum* (Gorham and Lewey 1984, Yamauchi 1984, Critchley *et al.* 1990 a) and other Fucales [*Fucus vesiculosus* L.: 6.1, *Asco- phyllum nodosum* (L.) LeJol.: 4.5 (Brinkhuis 1977)]. However, the apical (vegetative) thallus of *Sargassum muticum* generally had a lower DW content (higher FW:DW) than reported by other studies, possibly reflecting that the spinning method of removing excess water prior to FW determination, removed less water than rigorous drying by towels. The remarkably low September FW:DW value for apical (vegetative) parts of *S. muticum* (4.7) can be explained by an increased presence of epibionts that were hard to remove, such as newly settled calcareous tube worms (*Pomatoceros triqueter* L.) and hydroids (*Obelia* sp.), on the remaining senescent laterals (pers. obs. T. Wernberg, M. S. Thomsen and P. A. Stæhr).

The C:N:P contents (30–35%:1–4%:0.1–0.4% of DW) and ratios (grand mean molar ratio 396:22:1) found in this study were within the range of what has previously been reported for *Sargassum muticum* and species resembling *Halidrys siliquosa* (Cystoseiraceae spp. and Fucaceae spp.), as well as other macroalgae in general (Atkinson and Smith 1983, Yamauchi 1984, Duarte 1992, Lapointe *et al.* 1992, Arenas *et al.* 1995, Rico and Fernández 1997). Low internal N:P ratios (< 10) during summer and high N:P ratios (> 30) during spring could indicate that both species experienced nutrient limited growth (Atkinson and Smith 1983, Lapointe *et al.* 1992) during these periods, P being limiting in spring and N in summer, and more so in *Sargassum muticum* than in *Halidrys siliquosa*. A similar result was obtained by Rico and Fernández (1997) for *Sargassum muticum* and *Cystoseira nodicaulis* (Whit.) Roberts, a very close relative of *Halidrys siliquosa* (Rousseau *et al.* 1997), in Spain and by Lyngby (1990) for *Ceramium rubrum* (Huds.) C. Agardh [now *C. nodulosum* (Lightf.) Ducluz. (Nielsen *et al.* 1995)] in Limfjorden. Because nutrient limitation depends as much on actual concentrations as ratios (Duarte 1992), low/high N:P ratios do not prove its presence. However, it does seem plausible as seasonal nutrient limitation (particularly N) has been frequently demonstrated for macroalgae in coastal waters (e. g. Lyngby 1990, Fong *et al.* 1993, Pedersen 1995, Taylor *et al.* 1995, Pihl *et al.* 1996). The relatively constant C:N:P content of the basal (perennial) part of *Sargassum muticum* indicates that this part of the thallus does not take part in the annual outburst of growth.

Sargassum muticum and *Halidrys siliquosa* are both large macroalgae, characterized as 'thick and leathery' (*sensu* Littler *et al.* 1983 a; see Littler *et al.* 1983 a, b, Viejo 1997). Despite the common ecological properties of *Sargassum muticum* and *Halidrys siliquosa* implied by this shared designation, this study has shown that the two algae are functionally different. *Halidrys siliquosa* is a truly perennial macroalgae, more or less retaining its thallus throughout the season, whereas *Sargassum muticum* has a perennial holdfast which produces an annual vegetative thallus, a strategy which has been referred to as pseudo-perennial (Ang and Trono 1987). This annual-perennial hybrid life strategy of *S. muticum* has been suggested to be important by several authors (Norton 1976, Paula and Eston 1987, Rueness 1989, Fernández *et al.* 1990, Viejo 1997), as it has several advantages enhancing competitive abilities. By producing an annual vegetative thallus, *S. muticum* avoids investing energy into protecting and maintaining large long-lived structures. Less structural tissue is probably what is reflected in the lower C content of *S. muticum* (ca. 30% of DW) compared to *Halidrys siliquosa* (ca. 35% of DW) (Duarte 1992). Hence, more energy can be allocated for elongation, securing availability of light, and subsequently reproduction (Carpenter

1990). This is an important feature, since many, although not all, of the systems successfully invaded by *Sargassum muticum* are shallow turbid estuary-type systems presumed to have high or elevated nutrient levels. In such systems light often becomes limited during summer and therefore it is essential for any alga to get as close to the surface as possible (Duarte 1995). Furthermore, the annual shedding of the vegetative thallus makes the species more persistent (Fletcher and Fletcher 1975 b, Norton 1976) because the retained holdfast is less vulnerable to potentially detrimental events such as winter storms. Also, maintaining the holdfast secures suitable substratum already occupied. Because of the large number of vesicles and monoecious receptacles, shedding the reproductive laterals increases *S. muticum*'s effective dispersal range (Norton 1977, Deysher and Norton 1982, van den Hoek 1987, Norton 1992) and may enhance a supply of propagules to new suitable areas. In contrast, lack of long-range dispersal success in *Halidrys siliquosa* is thought to be responsible for its highly regionalized distribution in the northeastern Atlantic Ocean (van den Hoek 1987).

Conversion factors and relationships between commonly used biometric measures were provided for both *Sargassum muticum* and *Halidrys siliquosa*. This was possible from the quantification of several vegetative aspects of both species. Since several authors have reported phenotypic variation in thallus morphology of *Sargassum muticum* (DeWreede 1978, Critchley 1983, Lewey and Gorham 1984, Norton and Deysher 1989, Viejo *et al.* 1995) and *Halidrys siliquosa* (Moss and Lacey 1963) the value of these conversion factors and relationships can be questioned. However, for trying to compare data across studies it is better to have a questionable relationship than none at all (McArdle 1988). Furthermore, as there do not seem to be any major discrepancies between the general phenological patterns and algal characteristics found in this study and what has previously been reported in the literature (see above) we conclude that the given conversion factors and relationships are widely applicable. Obviously, they should only be applied critically, particularly if extrapolating outside the dimensions of the algae in this study.

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