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Biomass dynamics of exotic *Sargassum muticum* and native *Halidrys siliquosa* in Limfjorden, Denmark—Implications of species replacements on turnover rates

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Abstract

The expansion of *Sargassum muticum* in the Danish estuary Limfjorden between 1984 and 1997 was followed by a decrease in abundance of native perennial macroalgae such as *Halidrys siliquosa*. Although commonly associated with the expansion of exotic species, it is unknown whether such structural changes affect ecosystem properties such as the production and turnover of organic matter and associated nutrients. We hypothesized that *S. muticum* possesses ‘ephemeral’ traits relative to the species it has replaced, potentially leading to faster and more variable turnover of organic matter. The biomass dynamics of *S. muticum* and *H. siliquosa* was therefore compared in order to assess the potential effects of the expansion of *Sargassum*. The biomass of *Sargassum* was highly variable among seasons while that of *Halidrys* remained almost constant over the year. *Sargassum* grew faster than *Halidrys* and other perennial algae and the annual productivity was therefore high ($P/B = 12 \text{ year}^{-1}$) and exceeded that of *Halidrys* ($P/B = 5 \text{ year}^{-1}$) and most probably also that of other perennial algae in the system. The major grazer on macroalgae in Limfjorden, the sea urchin *Psammechinus miliaris*, preferred *Sargassum* to *Halidrys*, but estimated losses due to grazing were negligible for both species and most of the production may therefore enter the detritus pool. Detritus from

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Sargassum decomposed faster and more completely than detritus from *Halidrys* and other slow-growing perennial macrophytes. High productivity and fast decomposition suggest that the increasing dominance of *S. muticum* have increased turnover of organic matter and associated nutrients in Limfjorden and we suggest that the ecological effects of the invasion to some extent resemble those imposed by increasing dominance of ephemeral algae following eutrophication.

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1. Introduction

The turnover and fate of organic matter and associated nutrients in ecosystems may depend on the type of dominant primary producer (Cebrián et al., 1998). Hence, ecosystems dominated by plants with a fast turnover of biomass support higher rates of herbivory and accumulate less carbon than systems dominated by plants with a slow turnover of biomass (Cebrián and Duarte, 1995; Cebrián et al., 1998; Cebrián, 1999). These patterns are particularly likely to apply to shallow coastal ecosystems (Duarte and Cebrián, 1996) because a number of physiological and ecological traits differ systematically among marine macroalgae with different life strategies (Littler and Littler, 1980; Steneck and Dethier, 1994). For example, many perennial macroalgae have thick thalli, grow slowly, suffer low grazing losses and decompose slowly when compared to more short-lived species (e.g. Littler and Littler, 1980; Nielsen and Sand-Jensen, 1990; Buchsbaum et al., 1991; Enriquez et al., 1993; Cebrián and Duarte, 1994; Duarte, 1995; Banta et al., 2004). Like eutrophication (Duarte, 1995; Borum and Sand-Jensen, 1996; Valiela et al., 1997), the introduction and expansion of exotic species have caused dramatic changes in algal assemblages around the world (e.g. Trowbridge, 1996; Meinesz, 1999; Stæhr et al., 2000; Boudouresque and Verlaque, 2002). It is therefore likely that exotic macroalgae have altered pathways and turnover rates of organic matter and associated nutrients (Duarte and Cebrián, 1996).

The brown macroalga *Sargassum muticum* Yendo (Fensholt) originates from north east Asia (Yendo, 1907) but has been introduced to and spread along the Pacific coast of north America and in western Europe during the last 30–40 years (Critchley, 1983; Critchley et al., 1983; Fernández et al., 1990; Rueness, 1989; Karlsson and Loo, 1999). A few individuals of *S. muticum* were discovered in the Danish estuary Limfjorden in 1984 (Christensen, 1984) but the species has since become the most dominant macroalga exceeding the abundance of all other species combined (Stæhr et al., 2000). *S. muticum* is generally regarded as a strong competitor that can affect the performance of other species negatively (e.g. Ambrose and Nelson, 1982; De Wreede, 1983; Britton-Simmons, 2004). The appearance of *S. muticum* in a new system is therefore often followed by regression of local species and subsequent changes in community structure (e.g. den Hartog, 1997; Viejo, 1997; Cosson, 1999; Stæhr et al., 2000). For example, the expansion of *S. muticum* in Limfjorden was followed by a decrease in native perennial algae such as *Laminaria saccharina* (L.) Lamouroux, *Fucus vesiculosus* (L.), *F. serratus* (L.), *Codium fragile*

(Suringar) Hariot, and in particular *Halidrys siliquosa* (L.) Lyngb. (Stæhr et al., 2000), a close relative of *S. muticum* (Rousseau et al., 1997). Thus, during the expansion of *S. muticum* between 1990 and 1997, the abundance of *H. siliquosa* decreased by more than 70% in the central parts of the estuary (Stæhr et al., 2000). Despite the taxonomical and morphological similarities between *S. muticum* and *H. siliquosa*, particularly during summer months (Wernberg et al., 2001), it cannot be assumed that they are ecologically similar per se as very little information exist for *H. siliquosa*. Given *S. muticum*'s high reproductive output, fast lengthwise growth and a large potential to colonize free space (e.g. Norton, 1976; Ambrose and Nelson, 1982; Deysher and Norton, 1982; Arenas et al., 1995; Wernberg et al., 2001) we hypothesized that its expansion and replacement of native algae had caused changes in biomass dynamics beyond the observed changes in assemblage structure (Stæhr et al., 2000). Reports on community changes following the expansion of exotic marine species are numerous (references above), yet few studies have investigated how biomass and turnover of organic matter may have been affected (Rueness, 1989; Walker and Kendrick, 1998).

The aim of the present study was to compare and contrast the biomass dynamics (standing stock, growth, grazing and decomposition) of the exotic *S. muticum* and the native *H. siliquosa*. We focused on *H. siliquosa* because of its taxonomical and morphological closeness to *S. muticum* and because it was one of the species with the largest change in relative abundance following *S. muticum*'s expansion in Limfjorden. However, we also included other slow-growing perennial algae from Limfjorden for which data were available in the literature. Data on seasonal development of biomass, growth and productivity were obtained from a field study carried out in Dråby Vig (Limfjorden), while grazing and decomposition were studied in laboratory experiments. Our findings were used to discuss the potential effects on the fate and turnover of organic matter and associated nutrients following the expansion of *S. muticum* in Limfjorden, Denmark.

2. Materials and methods

The study was carried out in Dråby Vig, Limfjorden, Denmark (56.49.92 N, 8.50.70 E). Dråby Vig is a small (area: ca. 18 km²) shallow bay, reaching a depth of only 6 m approximately 1 km from the shoreline. The substratum in Dråby Vig is composed mainly of sand and gravel (~75% cover) with scattered stones >10 cm in diameter (~25% cover) (Wernberg et al., 1998).

Data on surface irradiance were obtained from a nearby meteorological station while data on salinity, water temperature, secchi-depth and concentrations of dissolved inorganic nutrients were provided by the county of Viborg as an integrated part of the Danish monitoring program under the action plan for the aquatic environment (Kronvang et al., 1993).

Algal cover and biomass was quantified within a permanent plot (100 m × 100 m) situated between 2.7 and 3.4 m depth about 160 m from the shoreline. The plot was overlaid by a permanent 5 m × 5 m grid of nylon wires. Samples were collected seven times between April 1997 and February 1998. The biomass of *S. muticum* and *H. siliquosa* was determined from non-destructive estimates of algal cover at 68 fixed sampling points

within the permanent plot, followed by a conversion of cover to dry weight biomass. Sampling points were situated at 5 m × 5 m grid intersections and were assigned in a proportional stratified random manner (Andrew and Mapstone, 1987) to each quarter of the plot. At each sampling event, two SCUBA divers independently estimated the percent cover of *S. muticum* and *H. siliquosa* within 1 m² to the left and to the right of each sampling point. To reduce the effect of variability among observers, the divers switched sides and repeated the cover estimates. Thus, the overall sample grain at each of the 68 points was 2 m², and the obtained value for each sample was calculated as the mean of four sub-samples (i.e. left and right, two divers). The relationship between percent cover and dry weight biomass was determined at each sampling event. Three SCUBA divers independently estimated the cover of each species within 11–17 circular plots (area: 0.27 m²) just outside the permanent plot. All algae within these plots were harvested, sorted, rinsed and dried to constant weight at 105 °C. Reduced major axis regression (model 2 regression) on ln(x + 1)-transformed data (Quinn and Keough, 2002) was used to determine the relationship between cover and dry weight biomass. Data were transformed to reduce heteroscedasticity and obtain linear relationships between the dependent (dry weight) and independent (cover) variables. Relationships obtained at different sampling dates were pooled when slopes and intercepts were indistinguishable (ANCOVA, Zar, 1996). Seasonal changes in biomass were tested by Friedman's test for repeated measures because several zero values in the data sets prevented the use of parametric analysis of variance (Zar, 1996).

In situ growth rates of *S. muticum* and *H. siliquosa* were determined from the increase in biomass of apical fronds. Fronds (ca. 10 g fresh weight) were collected, rinsed and the initial fresh weight (FW₀) determined. The initial dry weight (DW₀) of each sample was estimated from a DW:FW ratio obtained from five sacrificed samples for each species. The algal samples ($n = 8$ for each species) were then incubated within the permanent plot at ca. 3 m depth in cylindrical translucent PVC cages (20 cm long, 10 cm in diameter). The cages were closed at both ends with 0.5 mm mesh to permit water exchange but limit entry of grazers and loss of algal material (Geertz-Hansen et al., 1993). The algae were left to grow for 8–10 days while the cages were inspected and rinsed every second day. By the end of the period the algae were collected, rinsed and dried at 105 °C to constant weight (DW_t). Net growth rates (μ) were calculated from changes in DW biomass according to Eq. (1) assuming exponential growth:

$$\mu = (\ln DW_t - \ln DW_0)t^{-1} \quad (1)$$

where DW₀ and DW_t are the initial and final DW biomass of algal samples and t is the incubation time in days. Temporal variations in growth rates were examined for each species by Kruskal–Wallis ANOVA because of heterogeneous of variances (Levenes test, $p \ll 0.05$) (Zar, 1996). The overall growth rates of *S. muticum* and *H. siliquosa* were compared by Wilcoxon's test for the same reason (Zar, 1996).

Feeding preference and grazing rates of the dominant meso-grazer in Dråby Vig, the sea urchin *Psammechinus miliaris* Müller, were investigated in a multiple-choice experiment. Sea urchins were collected in Dråby Vig in June 1997 and brought to the laboratory where they were kept in aquaria at 15 °C under a 19:5 h light:dark cycle (ca. 100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) for 1 week before the start of the experiment. About 10 g FW of both *S. muticum*

and *H. siliquosa* were placed in each of eight aquaria (17 L) with seawater collected at the sampling site. Four equally sized sea urchins (ca. 11 g FW and 32 mm test diameter) were assigned to each of four aquaria while the remaining aquaria were used to measure algal growth in the absence of grazers. The experiment was terminated after 7 days of incubation. Algal growth rates with and without the presence of grazers were estimated from changes in biomass as described for growth rates. The relative grazing rate per grazer (g) was subsequently estimated as:

$$g = [(\ln DW_t^{(-)} - \ln DW_t^{(+)}) - \ln DW_0] \times t^{-1} \times \text{number of grazers}^{-1} \quad (2)$$

where DW_0 represents the initial algal biomass and $DW_t^{(+)}$ and $DW_t^{(-)}$ are the final algal biomasses after t days of growth with and without grazers, respectively. Daily consumption rates per individual animal were estimated from these rates and combined with data on sea urchin density (Wernberg et al., 2004) in order to estimate potential in situ grazing losses.

Decomposition rates of *S. muticum* and *H. siliquosa* were obtained from a litterbag experiment. Thirty samples (20–30 g FW each) of each species were collected, rinsed and weighed (FW_0) and were then placed in mesh litterbags (mesh size: 1 mm). Three samples of each species were initially sacrificed and dried for determination of the initial DW:FW ratio. The litterbags were buried in sediment to a depth of ca. 5 cm in aquaria containing water (ca. 20 L) and sediment from the sampling site. The aquaria were kept in darkness at a constant temperature (15 °C) and the water was exchanged with freshly collected seawater each month. For each species, three litter bags were retrieved periodically and the contents rinsed for sand, weighed (FW_t), dried at 105 °C for 24 h and weighed (DW_t). Decomposition rates were calculated for DW assuming exponential decay, using non-linear regression:

$$B_t = B_0 \times \exp(-k \times t) + G_R \quad (3)$$

where B_t and B_0 are the final and initial DW biomass, respectively, k is the decay rate, t is the number of days elapsed since the initiation of the experiment and, G_R is the approximate size of the residual (i.e. non-reactive) fraction of the detritus (Westrich and Berner, 1984).

Net changes in algal biomass ($\Delta B_{t-[t+1]}$) between two successive sampling events was calculated as:

$$\Delta B_{t-[t+1]} = B_{t+1} - B_t \quad (4)$$

Daily gross production m^{-2} (P) was calculated from the observed growth rates and biomass as:

$$P = B_{t+1}^* - B_t \quad (5)$$

where B_t is the observed biomass of *S. muticum* or *H. siliquosa* at time t and, B_{t+1}^* is the estimated biomass on the following day, B_{t+1}^* being estimated from:

$$B_{t+1}^* = B_t e^{(\mu \times t)} \quad (6)$$

where μ is the growth rate (obtained from Eq. (1)) and t is the time (i.e. 1 day). Total production m^{-2} between two successive sampling events ($P_{t-[t+1]}$) was calculated as:

$$P_{t-[t+1]} = \left(\frac{P_t + P_{t+1}}{2} \right) \times t \quad (7)$$

where P_t and P_{t+1} are the daily production m^{-2} at two successive sampling events and t is the number of days elapsed between sampling events. The loss of biomass m^{-2} between two successive sampling events ($L_{t-[t+1]}$) was calculated as:

$$L_{t-[t+1]} = \Delta B_{t-[t+1]} - P_{t-[t+1]} \quad (8)$$

where $\Delta B_{t-[t+1]}$ is the change in biomass in g DW m^{-2} (obtained from Eq. (4)) and $P_{t-[t+1]}$ is the integrated production in g DW m^{-2} (obtained from Eq. (7)). Standard errors and confidence limits related to the combined results of Eqs. (4)–(8) were estimated from standard methods (Meyer, 1975).

3. Results

Daily surface irradiance ranged from 1 mol photons m^{-2} in January to 59 mol photons m^{-2} in June (Fig. 1A). Light availability at the bottom within the permanent plot averaged 15–20% of the surface irradiance (not shown). Water temperature followed roughly the pattern of surface irradiance and ranged from 0 to 25 °C (Fig. 1B) while salinity remained constant at about 28‰ (Fig. 1B). The concentration of dissolved inorganic nitrogen (NO_3^- , NO_2^- and NH_4^+) was high ($>20 \mu\text{M}$) in winter, spring and autumn, but low ($<3 \mu\text{M}$) during summer (Fig. 1C). The concentration of dissolved inorganic phosphorus (PO_4^{3-}) ranged from $<0.5 \mu\text{M}$ in spring to just below $5 \mu\text{M}$ in August/September (Fig. 1D). The molar DIN:DIP ratio was always less than 16 and remained below 1 during most of the summer suggesting potential N limitation of primary production from April to late September. Total external (i.e. land based plus atmospheric) nutrient loading to the central part of Limfjorden averages 13 g total N m^{-2} and 0.3 g total P m^{-2} annually (10 years average, Limfjordsovervågningen, 1996).

The cover of *S. muticum* in the permanent plot was much higher than the cover of *H. siliquosa* (data not shown, but see Wernberg et al., 2001 for details). The relationships between cover and dry weight biomass of *S. muticum* could be arranged in three groups; one including the data obtained in May, August, September and January, one containing the data from June and July and one containing the data from November (Table 1). The relationships between cover and biomass for *H. siliquosa* did not differ significantly between sampling events (ANCOVA, $p > 0.05$) and were therefore pooled (Table 1). The annual mean biomass of *S. muticum* was seven-fold higher than that for *H. siliquosa* (34.5 versus 3.8 g DW m^{-2} , Fig. 2) but it varied substantially over the year (Friedmans test, d.f. = 7, $p < 0.001$), ranging from 13.7 g DW m^{-2} in November to 76.1 g DW m^{-2} in July. In contrast, the biomass of *H. siliquosa* remained rather constant during the entire study (range: 3.1–4.4 g DW m^{-2} ; Friedmans test, d.f. = 7, $p = 0.597$). The strong seasonal variation in biomass of *S. muticum* relative to that of *H. siliquosa* was evident when

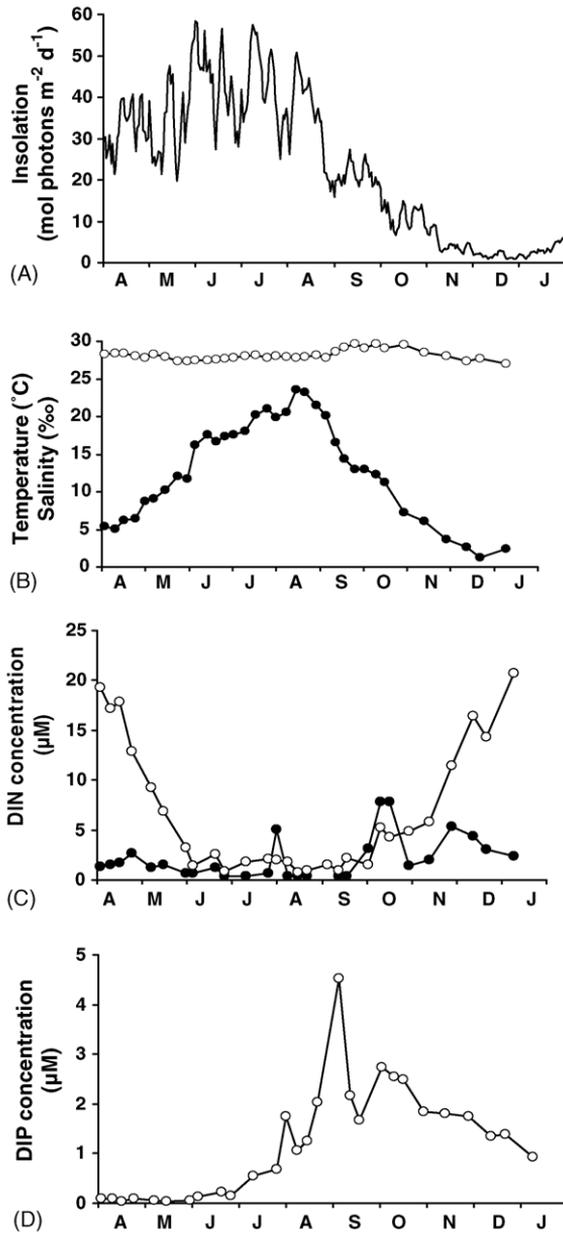


Fig. 1. Seasonal variation in environmental parameters in Dråby Vig 1998: (A) surface irradiance; (B) water temperature and salinity; (C) concentrations of dissolved inorganic nitrogen (closed symbols: NH_4^+ , open symbols: NO_3^- plus NO_2^-); and (D) concentrations of dissolved inorganic phosphorus.

Table 1

Linear models (reduced major axis regression) used to describe relationships between percent cover and dry weight biomass for *Sargassum muticum* and *Halidrys siliquosa*

	Slope	Intercept	R ²	p-value
<i>Sargassum muticum</i>				
April, May, August, September and January	1.089	0.685	0.834	<0.001
June and July	1.074	1.171	0.877	<0.001
November	0.986	0.648	0.840	<0.001
<i>Halidrys siliquosa</i>				
All sampling dates	1.123	1.152	0.835	<0.001

The relationships were based on $\ln(x + 1)$ -transformed data. Data from different sampling events were pooled when ANCOVA showed that they did not differ significantly from each other.

comparing the relative variations across season ($CV_{\text{season}} = 0.70$ and 0.13 for *Sargassum* and *Halidrys*, respectively).

The growth rate of both species varied seasonally (Kruskall–Wallis; $k_{Sm} = 7$, $H_{Sm} = 48.47$, $p_{Sm} < 0.001$ and $k_{Hs} = 7$, $H_{Hs} = 38.25$, $p_{Hs} < 0.001$), both being low in spring and autumn and higher in June and July (Fig. 3). The growth rate of *S. muticum* ranged from

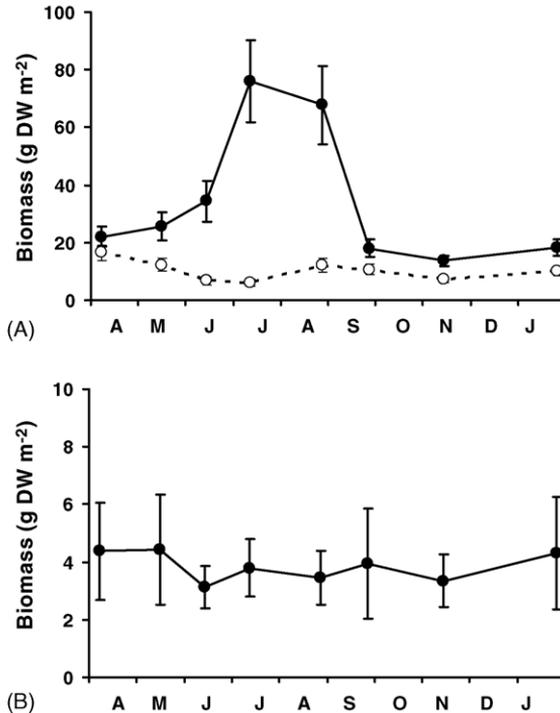


Fig. 2. Seasonal variations in biomass for: (A) *Sargassum muticum* (total biomass: closed symbols, perennial biomass: open symbols) and (B) *Halidrys siliquosa* in Dråby Vig, Limfjorden, Denmark. Values are mean \pm 95% CL.

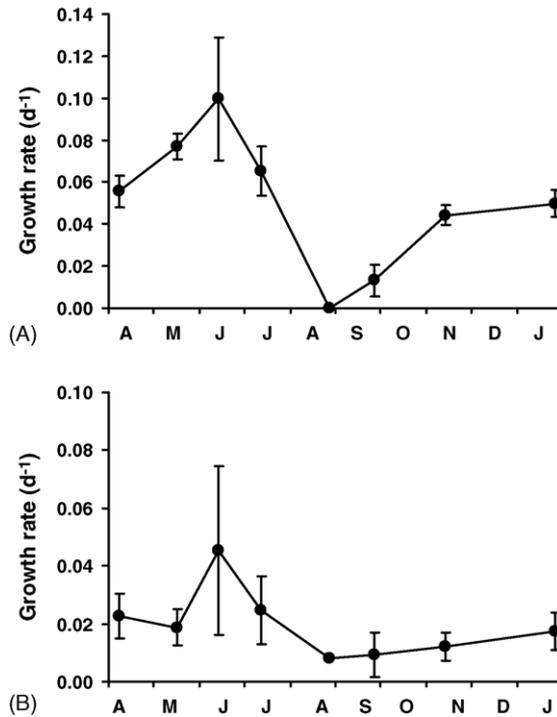


Fig. 3. Seasonal variation in relative growth rate (RGR) for: (A) *Sargassum muticum* and (B) *Halidrys siliquosa* in Dråby Vig, Limfjorden, Denmark. Values are mean \pm 95% CL.

0.000 day⁻¹ in September to 0.100 day⁻¹ in June with an annual mean value of 0.051 day⁻¹. *H. siliquosa* grew significantly slower than *Sargassum* (WilCoxons test; $Z = 2.24$, $p = 0.025$) the growth rate ranging from 0.008 day⁻¹ in August to 0.045 day⁻¹ in June (mean: 0.020 day⁻¹). The relative variation in growth rates across seasons were similar for the two species ($CV_{\text{season}} = 0.64$ and 0.60 for *Sargassum* and *Halidrys*, respectively).

The daily productivity of *S. muticum* (Fig. 4A) ranged from 0 g DW m⁻² in August to 5.1 g DW m⁻² in July ($CV_{\text{season}} = 1.03$). Annual production (April 1997 to January 1998) reached 449 g DW m⁻², corresponding to an annual P/B ratio of about 12. Losses of *Sargassum* biomass (Fig. 4A) achieved the same magnitude as the production on an annual basis (453 g DW m⁻²) but approximately 60% of these losses appeared during a short period between July and September as the algae lost their laterals. The daily productivity of *H. siliquosa* ranged from 0.0 g DW m⁻² in August to 0.2 g DW m⁻² in June (Fig. 4B) and was less variable across season ($CV_{\text{season}} = 0.62$). The annual productivity of *H. siliquosa* reached 18 g DW m⁻², corresponding to a P/B ratio of 5 while annual losses of biomass reached 18 g DW m⁻².

Exposure to sea urchins caused a significant reduction in the growth rate of both algae. The growth rate of *S. muticum* was reduced from 0.032 day⁻¹ (without grazers) to -0.030 day⁻¹ in the presence of sea urchins, giving a relative grazing rate of 0.063 ± 0.012 day⁻¹ corresponding to a daily consumption rate of 16 mg DW algae urchin⁻¹. The growth rate of

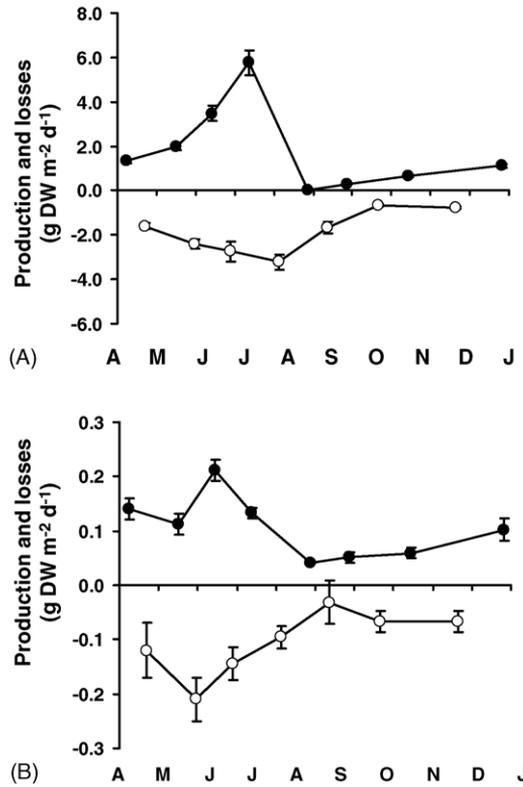


Fig. 4. Seasonal variations in production (closed symbols) and losses (open symbols) of biomass for *Sargassum muticum* (A) and *Halidrys siliquosa* (B) in Dråby Vig, Limfjorden, Denmark. Values are mean \pm 95% CL.

H. siliquosa was reduced from 0.007 day^{-1} (without grazers) to 0.000 day^{-1} in the presence of grazers, corresponding to a relative grazing rate of $0.007 \pm 0.002 \text{ day}^{-1}$ and a daily consumption rate of $0.2 \text{ mg DW algae urchin}^{-1}$. Estimated daily consumption of *S. muticum* in the field ranged from 5 to 24 mg DW m^{-2} , with an integrated annual consumption of 4 g DW m^{-2} corresponding to about 1% of the production. Estimated in situ consumption of *H. siliquosa* corresponded to ca. $0.4 \text{ g DW m}^{-2} \text{ year}^{-1}$ which is equivalent to approximately 1.5% of the production.

The decomposition of *S. muticum* followed a first-order exponential decay model (Fig. 5). Detritus from *S. muticum* decomposed with a rate of 0.016 day^{-1} (Table 2) and was almost complete within 120 days. The decomposition of *H. siliquosa*, in contrast,

Table 2
Decomposition of *Sargassum muticum* and *Halidrys siliquosa* as determined from litter bag experiments

	k (day^{-1})	p -value	G_R (percentage of initial DW)	p -value	R^2
<i>Sargassum muticum</i>	-0.016 ± 0.002	<0.001	-4 ± 3	<0.001	0.945
<i>Halidrys siliquosa</i>	-0.019 ± 0.011	0.085	68 ± 4	<0.001	0.600

Coefficients (\pm S.E.) from the exponential decay model based on data expressed in units of dry weight (DW).

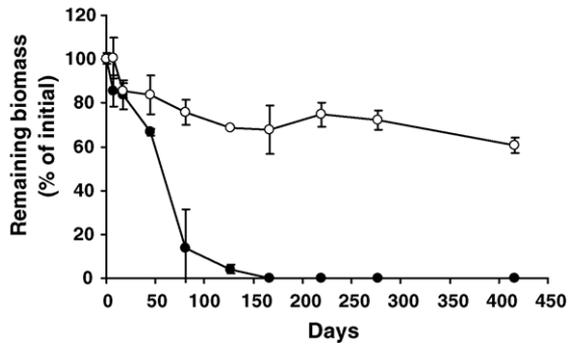


Fig. 5. Loss of dry weight biomass through decomposition in litterbag experiments carried out over 416 days for *Sargassum muticum* (closed symbols) and *Halidrys siliquosa* (open symbols), respectively. Values are mean \pm S.E. ($n = 3$).

followed a first-order exponential decay model with a residual fraction. The initial decomposition rate was similar to that of *S. muticum* ($k = 0.019 \text{ day}^{-1}$, Table 2) but decomposition ceased almost completely after 100–150 days, leaving about 68% of the original material after 400 days (Fig. 5). The amount of detritus decomposed and accumulated within a year after its production was simulated for each species using a dynamic model which applied the observed decomposition rates on the amount of detritus produced day by day. *S. muticum* produced $449 \text{ g detritus m}^{-2}$ in a year and 88% (395 g m^{-2}) of that was decomposed within the same period while *H. siliquosa* produced $18 \text{ g detritus m}^{-2}$ annually of which only 28% was decomposed within a year of its production. A larger proportion of the organic matter produced by *H. siliquosa* may thus accumulate as detritus within the system.

4. Discussion

This study represents the first attempt to quantify annual biomass dynamics and productivity of the newly introduced macroalga, *S. muticum*, in Danish coastal waters. The expansion of *S. muticum* during the 80's and 90's was followed by a decline of local perennial macroalgae and *S. muticum* is now the most abundant macroalga in Limfjorden (Stæhr et al., 2000) suggesting that it has become a significant contributor to total primary production.

In Limfjorden, *S. muticum* is taxonomically and morphologically most similar to *H. siliquosa*, which it to a large extent has replaced. Based on our measurements of changes in biomass, growth, grazing, and decomposition, *S. muticum* clearly had more 'ephemeral' traits compared to *H. siliquosa*. Thus, the biomass of *S. muticum* was highly variable among seasons ($\text{CV}_{\text{season}} = 0.70$) whereas that of *H. siliquosa* remained more constant ($\text{CV}_{\text{season}} = 0.13$), resembling the typical pattern of most perennial macroalgae (e.g. Sfriso et al., 1992). The large seasonal variation in *S. muticum* biomass relative to that of *H. siliquosa* was driven by high growth rates in spring and early summer and by shedding of annual laterals in late summer, which caused a substantial loss of biomass within few

weeks. The highest mean biomass of *S. muticum* in Dråby Vig was observed in mid-summer. This biomass was considerably lower than previously reported within dense meadows (range: 230–1200 g DW m⁻², Critchley et al., 1990; Knudsen, 1995), probably reflecting the low availability of suitable substrates in the area (i.e. large stones). The cover of *S. muticum*, however, exceeded that of all other macrophytes in the area (Wernberg et al., 1998) and presumably therefore also the biomass of all other macroalgae, although relationships between biomass and cover may vary when compared across species.

The significant accumulation of *S. muticum* biomass in spring and early summer was based on rapid growth early in the growth season. The maximum growth rate of *S. muticum* ($\mu_{\max} = 0.100 \text{ day}^{-1}$) was significantly higher (Student's *t*-test; d.f. = 13, $t = 3.85$, $p = 0.002$) than for *H. siliquosa* ($\mu_{\max} = 0.045 \text{ day}^{-1}$) and most other perennial macroalgae in Danish coastal waters which typically have growth rates between 0.019 and 0.042 day⁻¹ (Table 3). The growth rates of *S. muticum* and *H. siliquosa* were closely correlated to surface irradiance and water temperature suggesting that these factors, rather than low nutrient availability, controlled the overall seasonal growth pattern although low DIN concentrations and low DIN:DIP ratios (<1) between June and September indicated potential N-limitation of primary production during summer (Pedersen and Borum, 1996).

The combination of high biomass and fast growth resulted in a relatively high productivity of *S. muticum* in the permanent plot (449 g DW m⁻² year⁻¹) suggesting that *Sargassum* plays a significant role for total system productivity. We have no direct estimate of total primary production in Dråby Vig, but total system productivity of many shallow

Table 3

Maximum growth rates for a number of different macroalgal species (representing ephemeral and perennial species, respectively) in Danish coastal waters

Species	Range in relative growth rate (day ⁻¹)
Ephemeral species	
<i>Cladophora</i> sp.	0.251–0.300
<i>Ulva lactuca</i>	0.210–0.343
<i>Pilayella littoralis</i>	0.151–0.270
<i>Enteromorpha</i> sp.	0.144–0.260
<i>Chaetomorpha linum</i>	0.190–0.218
<i>Ceramium</i> sp.	0.039–0.223
<i>Polysiphonia</i> sp.	0.070–0.151
Perennial species	
<i>Sargassum muticum</i>	0.100
<i>Codium fragile</i>	0.083
<i>Chondrus crispus</i>	0.021–0.048
<i>Fucus spiralis</i>	0.036
<i>Fucus evanescens</i>	0.035
<i>Fucus vesiculosus</i>	0.020–0.065
<i>Fucus serratus</i>	0.019–0.066
<i>Halidrys siliquosa</i>	0.051
<i>Laminaria digitata</i>	0.046

Data from Nielsen and Sand-Jensen (1990), Pedersen and Borum (1996), Pedersen and Borum (1997), M.F. Pedersen (unpublished) and this study.

coastal ecosystems average 1000–1200 g DW m⁻² year⁻¹ (Borum and Sand-Jensen, 1996). Further, the productivity of *S. muticum* was relatively high when compared to the productivity of other major groups of primary producers in Limfjorden, e.g. annual productivity of phytoplankton ranges between 400 and 900 g DW m⁻² (depending on depth) in the central parts of Limfjorden (Limfjordsovervågningen, 1996), while the productivity of eelgrass (*Zostera marina* L.) ranges between 831 and 1284 g DW m⁻² within dense meadows (Olesen and Sand-Jensen, 1994). The 1–4 m depth interval, in which *S. muticum* is dominant, constitutes about 50% of the total area in Dråby Vig and *S. muticum* should thus be able to contribute with 15–30% to total primary production, while phytoplankton and seagrasses would contribute with about 40–80% and 7–13% each (seagrasses covering about 10% of the substrate between 0.5 and 2 m of depth). *S. muticum* may thus contribute significantly to the production of organic matter in Dråby Vig and the fate of the produced matter may be important for the total turnover within the system.

The annual losses of biomass from *S. muticum* and *H. siliquosa* were of the same magnitude as the production. Losses of biomass may either occur through grazing or through shedding or breakage of annual laterals which, in the latter case, represents a direct input to the detritus pool within the system. We do not know the extent of *S. muticum* grazing in situ, but the laboratory experiments showed that sea urchins preferred *S. muticum* over *H. siliquosa*. Moreover, estimated urchin grazing accounted for only a few percent of the total losses of biomass for both species. These numbers may of course underestimate true grazing losses due to additional grazers such as gammarids and gastropods. Regardless, sea urchins are the largest and most abundant grazer of macroalgae in Dråby Vig (Wernberg et al., 2004) and grazing losses for both *S. muticum* and *H. siliquosa* must therefore be relatively low. Low grazing losses correspond well to the presence of relatively high levels of phenolic compounds in *Sargassum* (Gorham and Lewey, 1984; Hay and Fenical, 1988) and the low to intermediate grazer preference found in other Sargassaceae (e.g. Nicotri, 1980; Duffy and Hay, 1991). Most of the annual production of *S. muticum* and *H. siliquosa* is likely channeled directly into the detritus pool, via shedding of annual laterals in autumn (only *S. muticum*), pruning and dislodgment during storms, and ice-scour in winter.

The steady state standing stock of detritus in an ecosystem depends on both the input rate and the rate by which the detritus is decomposed (Banta et al., 2004). The input of macroalgal detritus to the detritus pool should remain more or less unaffected by the expansion of *S. muticum* if we assume that the productivity of *S. muticum* balances the lost productivity of the species it has replaced and, that the proportion of the production that is grazed is approximately the same for *S. muticum* and these species. The size and turnover rate of the detritus pool will therefore mainly be affected if decomposition differs markedly between *S. muticum* and the species it has displaced.

Dead *S. muticum* decomposed completely within 120 days at a rate of 0.017 day⁻¹. This rate is markedly slower than for phytoplankton and most ephemeral macroalgae, but comparable to those of most perennial macroalgae and leaves of *Z. marina* (Table 4). The decomposition of *S. muticum* was, however, complete within a relatively short time whereas detritus from many other perennial macrophytes often contain a refractory component that undergo very slow decomposition (Buchsbaum et al., 1991; Banta et al.,

Table 4

Examples of decomposition rates (k) and size of the refractory pool (G_R) in different marine primary producers (range given for literature values of natural phytoplankton communities, nd not determined)

Species/type	k (day ⁻¹)	G_R (percentage of initial mass)	References
Natural phytoplankton	-0.010 to -0.068	nd	Enriquez et al. (1993)
<i>Ulva lactuca</i>	-0.040	0	Banta et al. (2004)
<i>Ceramium rubrum</i>	-0.038	0	Banta et al. (2004)
<i>Sargassum muticum</i>	-0.016	0	This study
<i>Fucus vesiculosus</i>	-0.028	7	Banta et al. (2004)
<i>Halidrys siliquosa</i>	-0.019	68	This study
<i>Zostera marina</i> (leaves)	-0.033	15	Banta et al. (2004)
<i>Zostera marina</i> (rhizomes)	-0.013	57	Banta et al. (2004)

2004). The presence of refractory compounds in the detritus means that initial decomposition occurs quickly followed by one or more phases with much slower decomposition (years to decades). The net result is that complete decomposition takes much longer for *Halidrys*, *Fucus*, etc. than for *S. muticum*, although decomposition rates measured over shorter time scales (weeks–months) may appear similar. The decomposition pattern of *S. muticum* is thus more similar to that of ephemeral macroalgae which decompose fast and almost completely (e.g. Buchsbaum et al., 1991; Banta et al., 2004).

We have shown that *S. muticum* possesses several ‘ephemeral’ traits (large fluctuations in biomass among seasons, growth, grazing and decomposition) when compared to the perennial macroalgae it has replaced. Based on these findings we suggest that the expansion of *S. muticum* and the concurrent regression of other true perennial macroalgae may have had significant ecosystem consequences beyond changes in community structure (Stæhr et al., 2000). Increased dominance of *S. muticum* has led to a shift such that true perennial and slow-growing macrophytes contribute less to total system productivity. The increased importance of an alga with a faster biomass turnover has led to large inputs of detritus over a relatively narrow time-window, to some extent resembling the boom and crash cycling of ephemeral algae (e.g. Valiela et al., 1997). In addition, detritus from *S. muticum* undergo faster and more complete decomposition than detritus from the macrophytes it replaced and the turnover and regeneration of nutrients has therefore increased. The net effect is likely to have been a larger, faster and more fluctuating flow of organic matter and associated nutrients, less accumulation of nutrients in slowly decomposable matter and, hence, more open and fluctuating nutrient cycles. In conclusion, the overall effect of increased dominance of *S. muticum* on turnover of organic matter and nutrients seems to resemble that of increasing dominance by ephemeral algae, where irregular amounts of detritus is produced and decomposed quickly, typically followed by large fluctuations in nutrient and oxygen concentrations (Duarte, 1995; Borum and Sand-Jensen, 1996; Valiela et al., 1997).

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