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Spatio-temporal distribution patterns of the invasive macroalga *Sargassum muticum* within a Danish *Sargassum*-bed

Abstract *Sargassum muticum* was first observed in Scandinavia in Limfjorden (Denmark) in 1984, where it is now the most abundant and conspicuous macroalga. Despite the ecological importance of *Sargassum*, few studies have described seasonal patterns within Scandinavian *Sargassum* beds. We quantified the dynamics of macroalgae among years and seasons along a depth transect through a typical *Sargassum* bed in Limfjorden. The annual investigations (summer transects 1989–1999) showed a gradual increase in the dominance of *Sargassum*, especially at the 2–4-m depth interval. Significant seasonal dynamics in macroalgal abundance and assemblage structure were observed in this depth interval; the mean cover of *Sargassum* varied from ca. 5% (autumn and winter) to 25% (mid-summer). In comparison, encrusting algae had high and relatively stable covers throughout the year (ca. 20%). Other perennial macroalgae had low mean covers ($<2\%$) characterized by a few patches of higher abundances. Except from a spring bloom, filamentous algae had low covers throughout the year. Within this relatively uniform bed, *Sargassum* abundance was positively related to boulders >10 cm in diameter and species richness was negatively correlated to depth and stones <10 cm in diameter, and non-correlated to other algal form-groups or grazer densities. Thus, in Limfjorden, the distribution of *Sargassum* is determined by large- (>6 m) and small-scale (<1 m) depth differences where low light limits *Sargassum* at depth, physical disturbance and sediment stress limits *Sargassum* in shallow waters, and the presence of stable boulder substratum facilitate *Sargassum*. Competition for space from other macroalgae and herbivory are probably of minor importance.

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Introduction

Invasion of alien marine species has caused serious ecological problems throughout the world (Carlton 1996; Walker 1998; Meinesz 1999). In particular, *Sargassum muticum* (Yendo) Fensholt (hereafter *Sargassum*), a brown canopy forming macroalga originating from Asia, is considered one of the most aggressive of the marine invaders (Norton 1976; Boudouresque and Verlaque 2002). *Sargassum* was first observed in Scandinavia in 1984 (Christensen 1984) and subsequent studies have indicated that its invasion has significantly altered shallow hard bottom communities there (Rueness 1985, 1989; Karlsson 1988; Thelin 1989; Arenas et al. 1995; Karlsson and Loo 1999; Stæhr et al. 2000; Wernberg et al. 2001, 2004; Bjaerke and Frederiksen 2003; Steen 2003). In Denmark, the first plant was found in the large sound Limfjorden (Christensen 1984), and today *Sargassum* is the most conspicuous and abundant macroalga there (Stæhr et al. 2000). Despite Scandinavian studies suggesting important habitat changes with the formation of distinct '*Sargassum*-beds', no studies have quantified the spatio-temporal community dynamics within such beds. Rather, Scandinavian studies have focused on qualitative descriptions (Christensen 1984; Rueness 1985, 1989; Karlsson 1988; Thelin 1989), laboratory experiments (Steen 2003), aut-ecological aspects (Wernberg et al. 2001), associated flora and fauna (based on *Sargassum* individuals, not area-based,

Bjaerke and Frederiksen 2003; Wernberg et al. 2004) or large-scale mid-summer distribution patterns (presence–absence or simple dominance scales, Karlsson and Loo 1999; Stæhr et al. 2000). It is well established that *Sargassum* has a seasonally variable appearance (Critchley et al. 1987; Wernberg et al. 2001) but it is unknown if and how this seasonality manifests itself in distribution patterns of associated flora and fauna within Scandinavian *Sargassum* beds. Our objective was therefore to quantify macroalgal distribution patterns within a typical *Sargassum*-locality and, in particular, to relate the spatio-temporal variability of *Sargassum* to depth, substratum, other algae and grazers.

Methods

Study site

Based on 11 years of monitoring data from throughout Limfjorden (Denmark) (Stæhr et al. 2000) and numerous exploratory dives, we selected Dråby Vig (56°49′92″N 8°50′70″E) as a representative *Sargassum* bed. Dråby Vig is a shallow bay, with the 6-m depth contour 1 km from the coastline. Salinity and temperature vary annually from 25 to 28‰ and –1 to 25°C, respectively. There are no major tidal fluctuations. Underwater visibility ranges from 5 to 10 m in winter and early spring to less than 2 m during summer (personal observation).

Annual changes

To describe the overall macroalgal assemblage and the invasion of *Sargassum*, summer abundance of macroalgae from 1989 to 1999 was obtained from the Danish Monitoring Program under the Action Plan for the Aquatic Environment (MPAPAE, Station 10, Limfjorden, Denmark). The sampling methods have been discussed extensively elsewhere (Middelboe et al. 1998; Laursen et al. 2000; Stæhr et al. 2000), but, in short, a diver estimated the proportion of hard substratum covered by macroalgae using a rank dominance scale (corresponding to ca. 0, 1, 14, 38, 63 and 88% cover of hard substratum, Stæhr et al. 2000) within each of six depth intervals.

Distribution from the beach

To identify the position of the main *Sargassum* bed relative to the coastline and to determine relationships between substratum, depth and macroalgal assemblages, a line transect was sampled perpendicular to the coastline (from west to east) in September 1997 and July 1999. Percent cover of macroalgae and substrata (mud/sand, stones < 10 cm in diameter, and boulders > 10 cm) were visually estimated 0.5 m to either side of the transect.

The first sample was taken on the beach at the water line and subsequent samples were collected at regular intervals except around abrupt changes in either substratum and/or algae where extra samples were collected. Abrupt change in algae were typically associated with obvious changes in conditions of substrata.

Distribution within the Sargassum-bed

As documented by the beach transects, the main *Sargassum* beds are located within the 2–4-m depth range approximately 160 m from the coastline. Within this bed, percent cover of *Sargassum*, other macroalgae and substrata were quantified in May, June, July, August, September and November 1997 and July 1998. In addition, cover of *Sargassum* was quantified in January 1998 and July 1999. Depth was recorded once with a dive computer (± 0.1 m) in June 1997. At each sampling event two divers independently estimated percentage cover of macroalgae and substratum within 1 m^2 on both sides of 68 permanently fixed points within a 100×100 m^2 area (17 points randomly distributed at 5 m grid intersections within each quarter of the hectare). To reduce observer bias, divers switched sides and repeated the cover estimates. Thus, each sample consisted of paired 1 m^2 observations where the cover values were averaged between the two divers. Inconspicuous and sub-dominant algae were only identified to genus or grouped into form-functional units (cf. Table 1). Three divers were involved with the surveys, and prior to each survey a calibration dive was carried out. To visualize the spatial distribution patterns of *Sargassum* within the bed, maps of cover values were plotted for each month using an inverse distance interpolation technique (nearest neighbor and exponent 2) (Caloz 1997). Within the *Sargassum* bed, line-transects were added to quantify the continuous distribution of *Sargassum* and encrusting algae, a group that was abundant but inconspicuous and often partly buried. All algae that touched these lines, in a perpendicular view, were recorded. Three transects (154, 130 and 100 m) were surveyed for *Sargassum* in September 1997 and two (59 and 59 m) in July 1999. Nine transects (all 2 m) were surveyed for encrusting algae in September 1997. Finally, to estimate grazer densities, the two main grazers, the gastropod *Littorina littorea* and the echinoid *Psammechinus miliaris* (unpublished data, Wernberg et al. 2004) were counted in 0.25 m^2 quadrats at a random subset of the fixed points in May, June, July, August, September and November 1997, January and July 1998 and July 1999 ($N = 23, 37, 35, 20, 24, 24, 23, 41, 15$).

Correlation analysis

Correlation analyses were conducted to determine if the abundance of *Sargassum* within the bed correlated with depth, substratum, abundance of other macroalgae or

grazers. Pearson's correlation coefficients r (Quinn and Keough 2002) were calculated for each month between percentage cover of *Sargassum* and corresponding depth, cover of stones and boulders, dominant grazers (the sum of *Littorina* and *Psammechinus* densities) and cover of macroalgae classified into form-functional groups (thick leathery, coarsely branched, filaments and sheet-like or encrusting/calcified groups) (Stæhr et al. 2000). Form-groups were used because the infrequent occurrence of most individual species would obscure correlation patterns. Further, we suspected that any correlation patterns would reflect the functional properties of each of these groups in competition for light, nutrients and space. Some variables were not normally distributed even after attempted transformation. However, Kolmogorov-Smirnov tests (Quinn and Keough 2002) indicated strong non-normality only for the thick-leathery and coarsely branched form groups, which, even after pooling individual species, were characterized by many zeros. Still, reporting coefficients of determination remain useful for comparing the relative importance of the different co-variables (Underwood 1997).

Results

Annual changes

A total of 33 species of macroalgae were observed in Dråby Vig over the 11 years of summer monitoring. *Sargassum* was the most abundant species followed by *Enteromorpha* spp., *Dictyota dichotoma* (another relatively new species in Danish waters, Lund 1949) and *Ralfsia verrucosa* (pooling year and depth, Table 1). Plots of the abundance of form-groups for specific depth intervals (Fig. 1) showed that *Sargassum* became dominant in the early 1990s, but only at 2–4 m. Furthermore, only a few algae were present and with relatively low cover at 1–2 and 4–6 m (mainly ephemeral filamentous and sheet-like forms), and very few algae were found deeper than 6 m. Except for the initial invasion of *Sargassum* in the 2–4-m depth interval, fluctuations in algal

abundances were high and apparently non-directional. Overall, the MPAPAE data did not indicate any form-groups to be detrimentally affected by the invasion of *Sargassum*, although the thick leathery algal group did decrease in abundance in the 2–4 m depth interval.

Distribution from the beach

The line transects from the beach suggested that lack of hard substrata (stones and boulders) limits algal distribution at certain depths (Fig. 2), partially explaining the low cover values shown in Fig. 1c. The presence of stones and boulders (Fig. 2b) clearly co-varies with abundance (Fig. 2c) and algal richness (Fig. 2d–e). The high *Sargassum* cover (ca. 30%) at shallow depth in September consisted of a dense mat of newly settled 3–10 cm recruits (for photo cf. Wernberg-Møller et al. 1998). However, hardly any of these shallow water recruits survived into summer 1998 (personal observation), an observation supported by the fact that no large *Sargassum* were present near the coastline in July 1997 (personal observation) or July 1999 (Fig. 2c) and that *Sargassum* covers at shallow depths were low throughout Limfjorden (Fig. 1a, Stæhr et al. 2000). Overall, *Sargassum* was the second most abundant species along the transect (mean of 4%, Table 1) only superseded by the encrusting *Ralfsia* (10%).

Distribution within the Sargassum-bed

Sargassum cover varied strongly both within and between years in the main bed. Thus, cover increased from spring to August, but was dramatically reduced in September, following the shedding of laterals in late summer, and remained low in November and January (Figs. 3, 4). Also, the mean cover in July 1998 (34%) was almost twice the cover of July 1997 (18%), and three times the cover of summer 1999 (10%). Overall, *Sargassum* was the second most abundant alga with a mean cover of 15% (excluding January 1998 and July 1999

Table 1 Mean percent cover of the 15 most abundant taxa comparing three different mapping methods (dates, distances and depths pooled, standard deviations in brackets, $N_{MPAPAE} = 66$, $N_{beach-transect} = 59$, $N_{main\ bed} = 952$) and form-group classification (Sar = Sargassum, She = sheet-like, Fil = filamentous, Enc = encrusting, Thi = thick and leathery, Coa = coarsely branched)

| Species	Group	MPAPAE	Beach-transect	Main bed
Sargassum muticum	Sar	16.01 (26.40)	4.07 (6.52)	15.37 (17.33)
Enteromorpha spp.	She	9.05 (12.02)	0.12 (0.65)	0.00 (0.00)
Dictyota dichotoma	She	8.98 (21.20)	0.05 (0.19)	0.01 (0.13)
Ceramium spp.	Fil	7.09 (10.87)	0.60 (1.86)	0.24 (0.66)
Ralfsia verrucosa	Enc	5.02 (12.82)	10.74 (9.81)	16.66 (8.73)
Fucus serratus	Thi	4.55 (12.44)	0.14 (0.41)	0.73 (2.23)
Chondrus crispus	Coa	4.36 (10.11)	0.44 (1.21)	0.40 (0.99)
Red encrusting spp.	Enc	4.30 (7.99)	1.79 (2.50)	3.81 (3.50)
Callithamnion corymbosum	Fil	4.04 (14.29)	0.12 (0.14)	0.11 (0.19)
Polysiphonia spp.	Fil	3.80 (5.36)	0.40 (1.15)	1.28 (3.40)
Halidrys siliquosa	Thi	2.76 (9.62)	0.28 (0.75)	0.35 (1.73)
Corallina officinalis	Enc	2.39 (6.55)	0.31 (0.81)	0.54 (1.19)
Laminaria saccharina	Thi	2.10 (6.10)	0.00 (0.00)	0.00 (0.02)
Fucus vesiculosus	Thi	1.97 (5.90)	0.00 (0.00)	0.00 (0.00)
Chorda filum	Fil	1.83 (6.03)	0.00 (0.00)	0.10 (0.26)
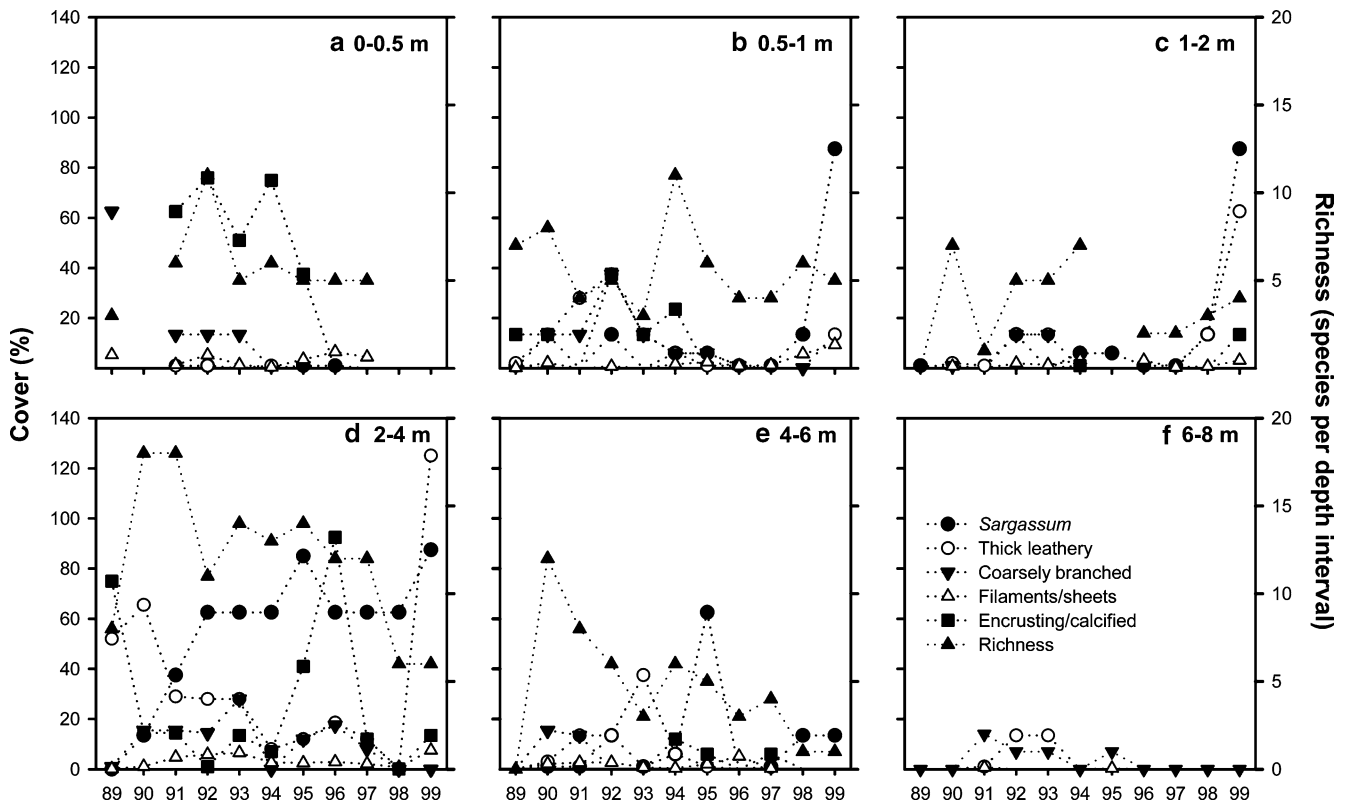
Fig. 1 Annual changes in percent cover of *Sargassum* and form-groups and species richness of macroalgae in Dråby Vig, Limfjorden

where *Sargassum* was the only species sampled, Table 1, Fig. 3), again only superseded by *Ralfsia* (17%, Table 1). In addition to seasonal variation, *Sargassum* abundance also varied spatially on small scales (Fig. 4). Thus, the maps in Fig. 4 show a slight gradient in cover values from west to east and consistent 'hot-spots' in specific positions. The line transects within the bed showed *Sargassum* abundance to be in close agreement with the main survey (September 1997 = 4.65%, SD = 0.72, July 1999 = 7.52% SD = 1.31, compared with 9 and 10% from the main survey). Within the bed, filamentous and sheet-like algae had a single peak in May (e.g., a bloom of *Ectocarpus siliquosa*), but had otherwise low abundances of primarily epiphytic red algae, i.e., *Ceramium* spp., *Polysiphonia* spp. and *Callithamnion corymbosum* (Table 1). Thick leathery canopy and coarsely branched algae also had low cover values (<2%) throughout the year. Taxonomic richness peaked in summer 1997 with ca. 8 taxa m^{-2}, but note that richness was somewhat lower in summer 1998 (5 taxa m^{-2}). Encrusting algae were inconspicuous, typically blending in with the rocks often being partly covered by a thin layer of sediment, and therefore difficult to quantify. The line transects showed 40% cover of encrusting algae (September 97, *Ralfsia* = 20.03%, SD = 6.88, *Hildenbrandia* = 12.97%, SD = 5.65, *Phymatolithon* = 8.33%, SD = 4.21), some-what higher than observed in the main survey. Clearly this group is the most important from a space-occupa-tion perspective, but would of course be much less important if compared for biomass. Densities of the

grazers, *Littorina* and *Psammechinus* varied from ca. 20–40 and 2–12 individuals m^{-2}, respectively. While *Littorina* showed a trend of the lowest densities in summer and highest in winter and spring, *Psammechinus* did not show any consistent seasonal patterns.

Correlation analysis

Depth only varied from 2.7 to 3.4 m within the *Sargassum* bed, but the cover of *Sargassum* was never-theless significantly ($P < 0.039$) negatively ($r < -0.17$) correlated with depth in all months except July 1998 ($P = 0.808$, $r = 0.02$) where cover was high throughout the hectare. The cover of *Sargassum* was more strongly correlated to depth in summer than winter months (compare r values in Table 2). In general, r values were higher for substrata as compared to depth, and the cover of *Sargassum* was significantly correlated to both stones and boulders in all months. However, when *Sargassum* cover was positively correlated to boulders ($r > 0.26$), it was negatively ($r < -0.25$) correlated to stones. Species richness and filamentous algae showed similar correlation patterns, and *Sargassum* was posi-tively correlated to both variables in May, June, Sep-tember and November 1997. The particularly strong correlation between *Sargassum* and filamentous algae in May 1997 was probably caused by blooming *Ecto-carpus* covering *Sargassum* throughout the bed. Thick leathery and coarsely branched algae were only present

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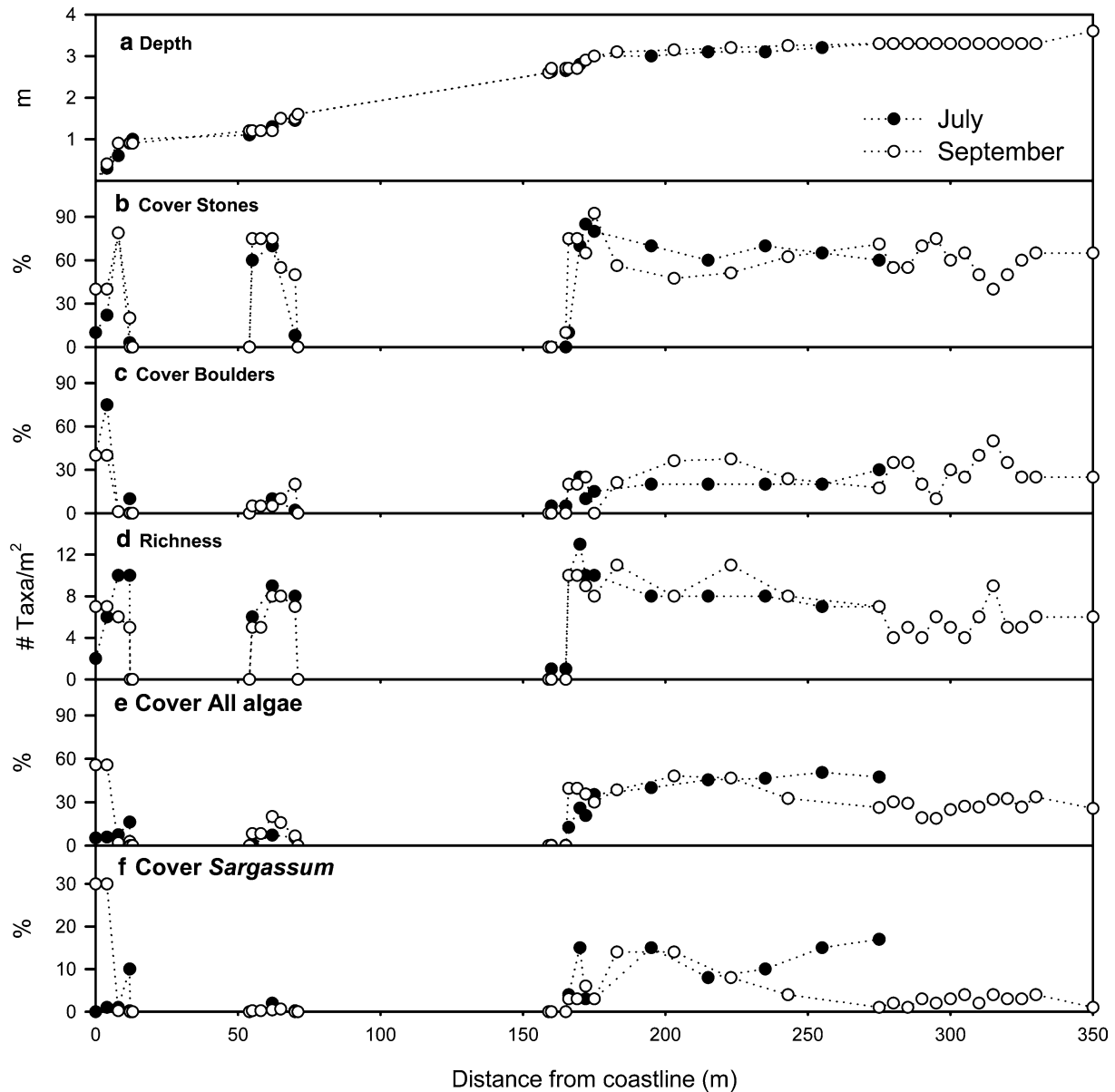
Fig. 2 Distribution of depth (**a**), stones and boulders (**b**), species richness (**c**), *Sargassum* (**d**), thick leathery and coarsely branched algae (**e**), and filamentous/sheet-like and encrusting/calcified algae (**f**) along a transect perpendicular to the beach to the main *Sargassum* bed, before (July) and after (September) *Sargassum* recruitment

in low abundances and had no correlation with *Sargassum*, except for thick leathery algae in August and coarsely branched algae in May. However, these variables deviated strongly from normality and thus had biased coefficients. Encrusting algae were, as filamentous algae, positively correlated with *Sargassum* in May, September and November, probably due to inter-dependency of boulders. Finally, there were no significant correlations between grazers and *Sargassum*.

Discussion

The introduction of *S. muticum* has altered subtidal habitats in Scandinavia (Karlsson 1988; Rueness 1989;

Karlsson and Loo 1999), but no Scandinavian studies have quantified both spatial and seasonal dynamics within a typical *Sargassaum* bed. We document that the abundance of *Sargassum* and other macroalgae vary considerably both within and among years within a relatively uniform *Sargassum* bed, and that the abundance of *Sargassum* correlates to small-scale differences in depth and substratum conditions.

Effects of season

Sargassum cover varied significantly over even short time periods because of high recruitment in autumn, rapid growth in late spring to mid-summer, and

Fig. 3 Seasonal changes in the cover of *Sargassum*, form-groups and species richness within the *Sargassum* bed from May 1997 to January 1998, with additional data in summer 1998 and 1999 ($N = 136$, ±SE). October and December data were not sampled, but extrapolated from previous and following month to provide a better presentation of the seasonal patterns
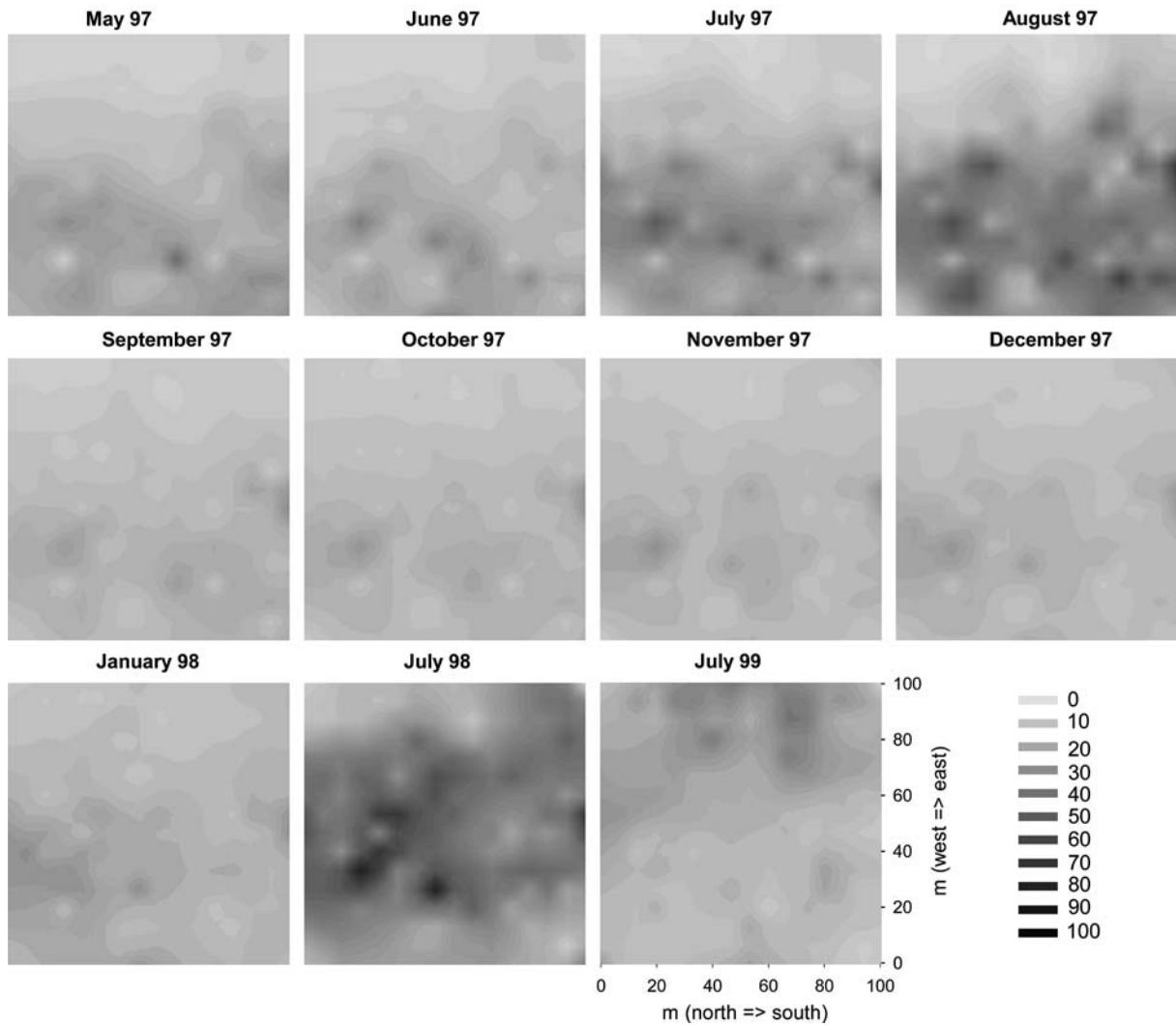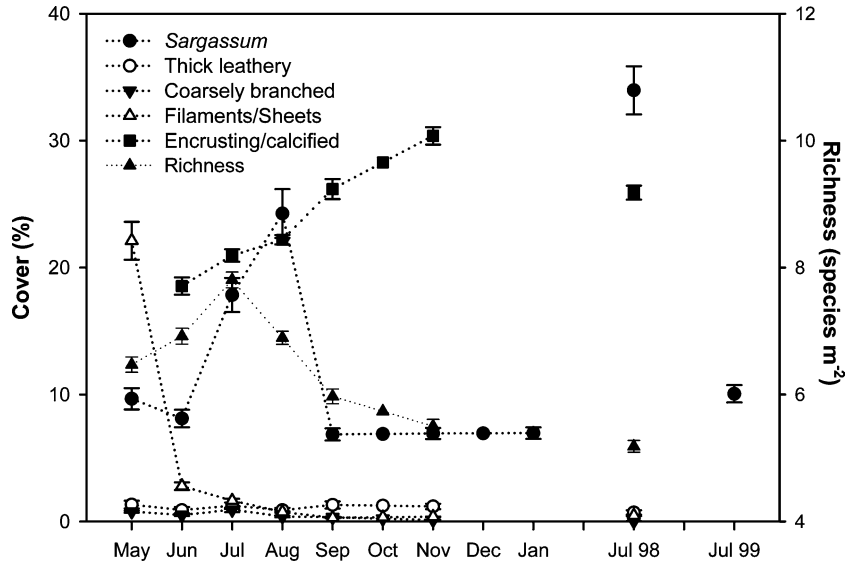
Fig. 4 Distribution of *Sargassum* within the bed, interpolated from 136 fix-points (inverse distance, exponent 2, nearest neighbor). October and December maps were calculated from averages from previous and following month

Table 2 Correlation matrix for the cover of *Sargassum* versus depth, stones, boulders, richness, thick leathery, coarsely branched, filaments/sheets, encrusting/calcified algae and grazers

	May 97	Jun 97	Jul 97	Aug 97	Sep 97	Nov 97	Jan 98	Jul 98	Jul 99
Depth									
r	−0.41	−0.33	−0.32	−0.36	−0.35	−0.21	−0.18	0.02	0.36
P	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.014**	**0.038**	0.808	**0.000**
Stones									
r	−0.38	−0.27	−0.50	−0.47	−0.50	−0.55	−0.29	−0.63	−0.26
P	**0.000**	**0.002**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.001**
Boulders									
r	0.42	0.32	0.50	0.44	0.42	0.51	0.26	0.62	0.26
P	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.001**
Richness									
r	0.46	0.28	0.07	0.04	0.37	0.28		−0.14	
P	**0.000**	**0.001**	0.443	0.688	**0.000**	**0.001**		0.116	
Filaments/sheets									
r	0.83	0.43	0.40	-0.07	0.32	0.45		−0.14	
P	**0.000**	**0.000**	**0.000**	0.409	**0.000**	**0.000**		0.112	
Thick leathery									
r	0.16	0.05	0.19	0.03	0.03	-0.02		−0.03	
P	0.063	0.581	**0.028**	0.746	0.75	0.811		0.754	
Coarsely branched									
r	0.40	0.12	0.13	0.14	0.18	0.10		−0.00	
P	**0.000**	0.159	0.130	0.117	0.033	0.253		0.967	
Encrusting/calcified									
r	0.26	-0.06	0.03	-0.10	0.19	0.26		0.08	
P	**0.002**	0.516	0.726	0.261	**0.030**	**0.002**		0.386	
Grazers									
r	0.01	-0.28	0.01	-0.22	0.22	0.27	0.04	-0.14	−0.08
P	0.912	0.082	0.947	0.165	0.173	0.089	0.801	0.118	0.351
N	23	37	35	20	24	24	23	41	15

$N = 136$ except for grazers (bottom row). Significant factors are in bold

shedding of laterals in early fall. The summer peak thus co-varied with size and biomass of individual *Sargassum* (Wernberg et al. 2001) in concordance with laboratory (Norton 1977; Hales and Fletcher 1989) and field studies (Arenas et al. 1995) that demonstrate strong light and temperature dependent growth. This peak was mirrored by a peak in species richness of macroalgae, even though none of the other form-groups showed a similar seasonality in abundance. Ephemeral sheet-like and filamentous algae were dominated by a spring bloom of *Ectocarpus*, thick leathery and coarsely branched algae were uncommon but remained relatively stable throughout the year. Encrusting algae, although spatially dominant, probably did not change much through the season. Thus, *Sargassum* seems to emphasize and reinforce the seasonality of its new habitats.

Effects of depth

The distribution of *Sargassum* and other macroalgae was strongly depth-dependent, with a maximum distribution at intermediate depths of 2–4 m. Depth is often used as a surrogate for light conditions with macroalgal distribution and productivity ultimately being limited by a lack of light at depth (Markager and Sand-Jensen 1992; Stæhr et al. 2000). In Dråby Vig the lower limit of *Sargassum* was at 4–6 m, similar to most other algae, and within lower depth ranges observed in other turbid Danish systems (Sand-Jensen and Krause-Jensen 1997; Middelboe et al. 1998). However, the specific limit varied slightly between years, as exemplified by a peak at 4–6 m in 1995 (Fig. 1) and a lack of correlation between depth and *Sargassum* cover in July 1998 (Table 2). Such variation is probably caused by better-than-usual light conditions, and *Sargassum* may be better adapted to utilize enhanced light at depth compared to most other algae because of its rapid upward growth and large adult size. Thus, if good light conditions occur during 1–2 months in early summer, where growth reaches 2–3 cm day^{-1} (Arenas et al. 1995; Wernberg et al. 2001) *Sargassum* can gain a size advantage in excess of 1 m compared to other algae. At the other extreme, i.e., at shallow depth, *Sargassum* is

also subordinate, but lack of recruitment cannot explain this lack of dominance (Fig. 2d, Wernberg-Møller et al. 1998). The limiting processes are probably sand abrasion and burial which would be particularly stressful to small recruits (personal observation, Daly and Mathieson 1977). Furthermore, recruits that survive burial by growing into a large size are likely to be pruned (Andrew and Viejo 1998) or end up as beach cast by wave-induced drag (cf. next section).

Effects of substratum

The distribution of *Sargassum* and other macroalgae was strongly dependent on the type of substratum, with a positive correlation to boulders but negative correlation to stones. The negative relationship between *Sargassum* and stones is probably due to the loss of large individuals, abundant in late spring and summer, that are carried away by waves and currents as they experience large drag, lift and buoyancy forces (Dromgoole 1982; Denny 1995; Kendrick and Brearley 1997). We often observed shoreward drifting *Sargassum* attached to stones, and this mode of transport has been suggested as an important medium-range dispersal mechanism (Den Hartog 1998; Stæhr et al. 2000; Wernberg et al. 2001). Given the lack of *Sargassum* at shallow depths (this study, Stæhr et al. 2000) shoreward transports probably end up as beach cast (personal observation, Ben-Avraham 1971; Critchley et al. 1987) and drift dispersal may therefore primarily be beneficial when long-shore currents deposit the alga-stone complex at intermediate depths.

Effects of other algae

There were no negative correlations between *Sargassum* and any other form-group within the main *Sargassum* bed, and none of the form-groups diminish consistently at 2–4-m depth during the invasion of *Sargassum* (1989–1999), indicating that no algae were out-competed by *Sargassum* at this site. The high amount of stones and boulders suggest that plenty of free space is available for propagule settlement, and that space-exclusion is unlikely. The main space-competitors are likely to be the encrusting algae that cover a large proportion of the hard substratum and that have been shown to limit *Sargassum* recruitment (Norton 1977). In contrast, species richness increased with the abundance of *Sargassum*, probably because it serves as a host to filamentous epiphytes. For example, in Mexico, 48 epiphytic algae were observed on *Sargassum* (Aquilar-Rosas and Galindo 1990), 52 in England (Withers et al. 1975) and 82 in Norway (Bjaerke and Frederiksen 2003). The comparatively species-poor epiphytic flora found in Limfjorden is most likely caused by harsh conditions at this turbid, low salinity locality (Wernberg et al. 2004). Nevertheless, the relatively high abundance of *Sargassum* (up to

25% cover and higher if only boulders are considered), its fast vertical growth and its high light interception (Critchley et al. 1987) are likely to have negative effects on non-epiphytic and smaller algae. This is particularly the case for thick leathery species that also depend on boulders for long-term stability (Sousa 1979), which also have high light requirements (Markager and Sand-Jensen 1992) and have comparatively low growth (Pedersen 1995; Pedersen and Borum 1997). However, as resource availability changes during the season, competition may change as well, for example as competition for light in spring-summer, for nutrients during mid-summer (Pedersen 1995; Wernberg et al. 2001) and for space (boulders) during and after propagule-release (Norton 1977) in late summer and fall.

Effects of grazers

Grazing gastropods and urchins were common throughout the bed in all seasons, typically with 20–40 individuals m^{-2}. However, the lack of correlation between grazers and *Sargassum* suggests that grazers do not control adult *Sargassum*. Instead, grazers are more likely to prefer filamentous and sheet-like epiphytes and diatoms, and could instead provide improved growth conditions by reducing shading (Anderson et al. 1998) and increasing nutrients by release of waste products (Giannotti and McGlathery 2001).

Conclusions

We have documented that both large- (> 6 m) and small-scale (< 1 m) depth differences determine the distribution of *Sargassum*, probably due to light stress at depth and physical disturbance and sediment stress at shallow depth. Substratum further influenced distributions as large boulders correlated positively with *Sargassum*. Other algal form-groups or grazers did not correlate negatively with *Sargassum* suggesting that *Sargassum* is not limited by competitors or herbivory. The introduction of *Sargassum* in Scandinavia has possibly caused a more pronounced seasonality in small-scale patterns of species richness and abundance, as compared to non-invaded algal habitats.

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