

NOTE

Zostera marina seagrass beds enhance the attachment of the invasive alga *Sargassum muticum* in soft sediments

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ABSTRACT: The first reports of *Sargassum muticum* occurring in British waters coincided with a warning that this invasive alga may replace seagrass beds, particularly those of *Zostera marina*. Initial fears were allayed when subsequent research suggested that both species required different attachment substrata, and, therefore, *S. muticum* would be unable to replace *Zostera* beds on soft sediments. Here, however, we present evidence supporting the original warning: contrary to previous research we found that *S. muticum* is able to successfully colonise soft sediments and, furthermore, that the presence of *Z. marina* may aid attachment. The majority of *S. muticum* plants within *Zostera* beds studied at Salcombe, SW England, were found attached within the soft sediment; outside of the seagrass bed, however, this occurred in greatly reduced numbers. Therefore, we suggest that the presence of *Z. marina* may actually enhance *S. muticum* colonization of soft sediments, trapping drifting fragments and allowing viable algae to settle on the seagrass matrix in an otherwise unfavorable environment. The consequences for the invasion of seagrass beds by *S. muticum* may therefore be more severe than previously thought.

KEY WORDS: *Sargassum muticum* · Seagrass · Invasive alga · *Zostera marina* · Soft sediment

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INTRODUCTION

In 1973, concerns were first raised about the possible ecological effects of the introduced Japanese seaweed *Sargassum muticum* (Yendo) Fensholt, when Druehl (1973) suggested that *S. muticum* may displace seagrass beds. His evidence was based on observations in British Columbia that the alga had become well established in sheltered low intertidal and shallow subtidal waters, a position usually occupied by the eelgrass *Zostera marina* L. *Zostera* spp. provide a large range of ecosystem services (Jackson et al. 2001); for example, they are an important nursery habitat for juvenile fish and have been shown to harbour a larger number of individuals and species than surrounding areas (Mattila et al. 1999, Polte et al. 2005, Pihl et al. 2006), so such replacement would have wide ecological consequences. North (1973) disputed the concerns of Druehl

(1973) after examining *S. muticum* patches in California, where he claimed that the alga requires a solid substrate for attachment. With *Z. marina* occurring solely on soft sediments, he concluded that, in California, the 2 species coexist without apparent competition, thus allaying fears that *S. muticum* may replace *Z. marina*. Subsequent studies on *S. muticum* also reported that the alga requires a hard substrate, e.g. bedrock, boulders, stones or solid man-made structures (Fletcher & Fletcher 1975, Norton 1977), while small stones (<10 cm in diameter), gravel and sand are considered unsuitable substrata (Thomsen et al. 2006). A study by den Hartog (1997) attempted to answer the question 'Is *Sargassum muticum* a threat to eelgrass beds?' He similarly concluded that due to the contrasting substratum preferences, the beds of the 2 species would remain well separated. He reported, however, that although *S. muticum* was not able to invade closed

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Z. marina beds on soft substrata, the alga was able to replace *Z. marina* in littoral pools with mixed substratum containing sand, gravel, stones, and shell grit.

During other seagrass ecology studies, we observed *Sargassum muticum* occurring within a *Zostera* bed (defined as a monospecific bed of the species *Z. marina*) in the Salcombe-Kingsbridge estuary (Devon, SW England), contrary to the conclusion of bed separation by den Hartog (1997). Therefore, the aim of this study was to investigate the attachment mechanism and growth of *S. muticum* within and outside seagrass beds at Salcombe to assess the significance of this observation. We investigated 2 questions: (1) can *Sargassum muticum* successfully attach on soft substrata, and (2) can *Z. marina* enhance this attachment?

MATERIALS AND METHODS

Study site. Sampling of *Sargassum muticum* plants occurred within Castle Bay (50° 23' N, 03° 77' W) of the Salcombe-Kingsbridge Estuary in Devon, SW England (Fig. 1). The system is termed a 'ria', a fairly sheltered

drowned river valley with minimal freshwater input producing salinities of around 34 to 35. The shores are gently sloping with a maximum width of 12.5 m. Tides are semi-diurnal with a mean tidal range of 4.6 and 2.0 m at spring and neap tides respectively. Total seagrass extent within the estuary is estimated at 6.3 ha, with 2 ha occurring within Castle Bay (Fig. 1); shoot density averages 240 shoots m⁻². *S. muticum* has been present in Devon since 1976 (Boalch & Potts 1977).

Sampling procedure. During a low tide in March 2006, the attachment substratum of *Sargassum muticum* plants growing in Castle Bay was investigated. The location of each plant was recorded (within or outside the *Zostera* bed, with outside the *Zostera* bed being termed 'Sargassum bed'). In order to record the attachment substratum of plants growing within the soft sediment accurately, specimens were dug up, the sediment rinsed away carefully, and the buried section examined. The attachment substratum was classified as either hard (i.e. visible stones, pebbles) or soft (i.e. sand/mud with no evidence of holdfasts attached to hard objects). Eight samples of sediment were taken from within each bed type to assess overall differences in the sediment structure between

Zostera and *Sargassum* beds, in particular, the availability of pebbles for settlement. Sediment analysis was undertaken using a Malvern Long-bed Mastersizer X laser particle sizer. The total length of the plant, from the bottom of the holdfast (if present) to the top of the longest primary lateral of each specimen was then recorded. When holdfasts were absent from plants buried in soft sediment, length was measured from the base of the plant.

Statistical analysis. Chi-square analysis was performed to identify any relationship between the location of *Sargassum muticum* plants and their attachment substratum. Due to very small n-values for *S. muticum* plants growing on hard substrata within seagrass beds, a formal balanced 2-way ANOVA was not suitable. Differences between the length of *S. muticum* plants at each location and on each sub-

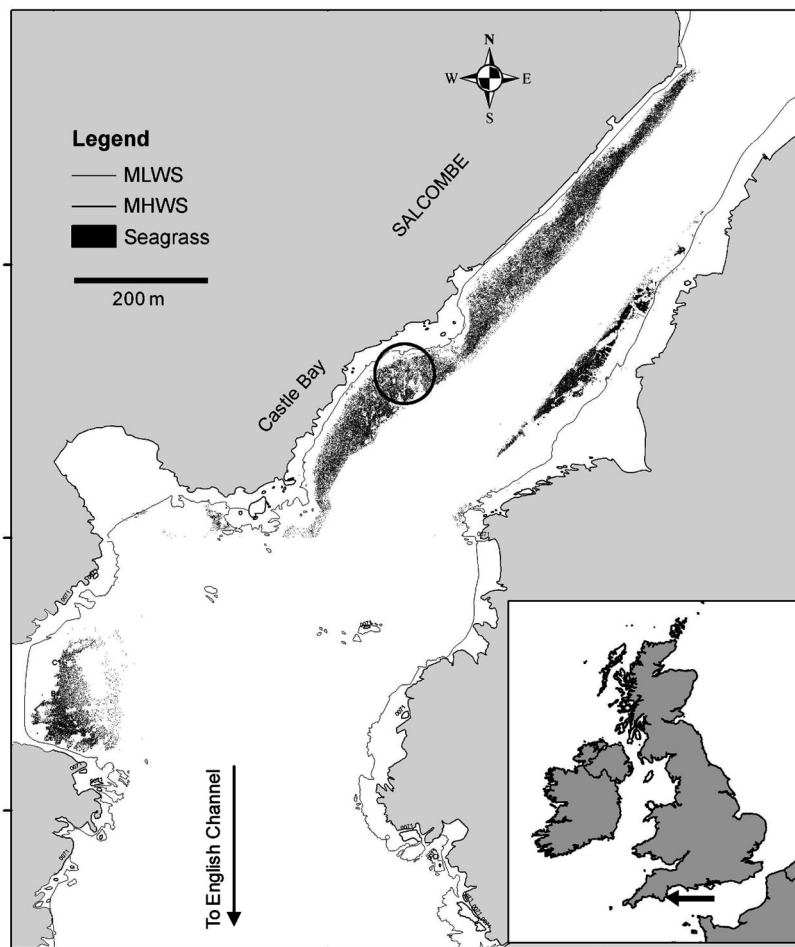


Fig. 1. Salcombe-Kingsbridge Estuary, Devon, England. Circle indicates the precise sampling location and the shaded area the location of seagrass beds. MLWS: mean low water springs; MHWS: mean high water springs

stratum were therefore compared using *t*-tests in order to maximize *n*-values within each category, but correcting the alpha level to 0.025 to account for multiple tests. Prior to analysis, data were tested for normality and homogeneity of variance using Anderson-Darling and Bartlett's tests respectively. In all cases, the assumptions of normality and homogeneity were met, thus allowing the use of parametric tests. For testing differences in sediment particle size, non-parametric Mann-Whitney *U*-tests were used to accommodate the percentage data.

RESULTS

There was no significant difference between available sediments within *Sargassum* and *Zostera* beds (Mann-Whitney *U*-test: $Z = -1.846$, $p > 0.05$) in terms of the percentage of pebbles available in each area for *S. muticum* attachment (*Sargassum*: 1.92 to 66.51%; *Zostera*: 0.16 to 66.07%). Median particle sizes were different, however ($Z = -2.216$, $p < 0.05$), due to larger amounts of finer particles in the seagrass bed, as would be expected.

In total, 110 *Sargassum muticum* plants were sampled, of which 77 occurred outside the *Zostera* bed and 33 inside. Of the 77 within the *Sargassum* bed, 75% were attached to hard substrate; conversely, within the *Zostera* bed, 91% of the plants were attached to the soft substratum. Chi-square analysis of plant densities on the 2 substrata between bed types (Fig. 2a) proved significant ($\chi^2 = 41.02$, $p < 0.001$).

The mean length (\pm SE) of *Sargassum muticum* plants was 40.59 ± 2.69 cm in *Sargassum* beds and 37.43 ± 2.73 cm in *Zostera* beds, respectively (Fig. 2b), which proved to be non-significant (*t*-test: $t = 0.67$, $p = 0.416$), indicating that the location of the alga in relation to the *Zostera* bed had no significant effect on the length of the *S. muticum* plant. A significant difference was observed, however, when comparing the mean length of *S. muticum* plants on different substrata, with plants attached to hard substrata having a mean length of 41.93 ± 2.71 cm compared to 14.67 ± 3.28 cm when attached to soft substrate (*t*-test: $t = 6.41$, $p < 0.001$), thus indicating that the type of attachment substrate may influence the size of the plant.

DISCUSSION

The observations of *Sargassum muticum* growing in soft substrata presented here are, to the best of our knowledge, the only report to date of *S. muticum* growing in soft substrata without hard attachment. Virtually all other research indicates that *S. muticum*

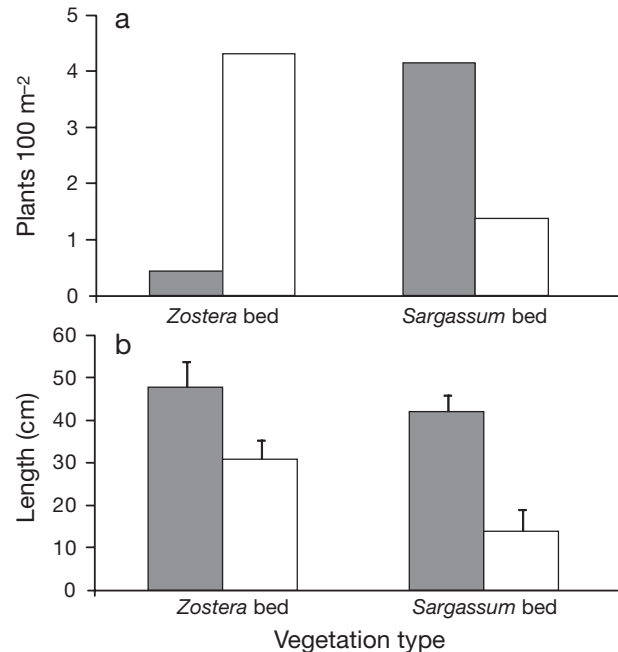


Fig. 2. *Sargassum muticum*. (a) Density of plants either attached to hard substrata or buried in soft substratum in both *Zostera* and *Sargassum* beds (chi-square: $\chi^2 = 41.02$, $p < 0.001$; $n = 110$). (b) Mean length (\pm SE) of plants in different substrata and vegetation types (see text for *n*-values and analyses). Grey bars: hard substratum, white bars: soft substratum

prefers a hard substrate (North 1973, Fletcher & Fletcher 1975, Norton 1977). Thomsen et al. (2006) even correlated the abundance of *S. muticum* with the presence of hard substrate >10 cm in diameter. The only report to state that *S. muticum* may grow in a mixed substratum was den Hartog (1997), who reported that *S. muticum* may occur in areas containing sand, gravel, and stones. However, if the plants were attached to stones in a mixed substratum, the attachment would be via the holdfast. In the soft substrate of Castle Bay, Salcombe, some *S. muticum* plants were devoid of a holdfast and in others the holdfast was not attached to any form of hard substrate (rock, stone, shell, etc.), but instead was buried, with the weight of sand around the holdfast and primary lateral providing the attachment. The plants attached to hard substrata via a holdfast were most likely either plants that had grown from a germling or plants transported to the Bay via 'stonewalking', where plants attached to small stones may become buoyant and dispersed by local currents (Critchley 1983b).

Norton (1983) investigated the resistance to dislodgement of *Sargassum muticum* germlings under different hydrographic conditions. He concluded that germling survival was positively correlated with substratum roughness up to an optimum rugosity where

the mean depth of depression was 420 μm and the vast majority of depressions were deeper than the height of the germlings. Germlings of *S. muticum* have an area of 400 μm^2 (Steen & Rueness 2004), and therefore will be unlikely to settle in Castle Bay as the average grain size within the *Zostera marina* beds is 159 μm ; any that may manage to settle will have insufficient support for further growth. Also, Morrell & Farnham (1982) reported that *S. muticum* is more susceptible to tissue loss due to sand abrasion than *Ulva* spp., again suggesting that *S. muticum* is unlikely to successfully settle in sandy substrates.

It is suggested here that *Sargassum* plants occupying the soft substrate had therefore not grown from germlings, but are vegetative material detached from older plants that may have become caught up in the seagrass bed. Norton (1981) showed that detached floating material is viable for up to 3 months, and that it may become fertile during this time. Sediment is deposited in macrophyte beds due to their capacity to reduce current velocities and attenuate wave energy (Grady 1981, Gambi et al. 1990). Therefore, if detached vegetative material from *S. muticum* plants washed up in a *Zostera* bed, then deposition of sediment onto the bed may bury the basal part of the plant within the rhizome mat, providing a secure attachment within the substratum. Morrell & Farnham (1982) reported *S. muticum* to be far more resistant to burial than *Laminaria digitata*, and it even decayed slower than control specimens submersed in filtered seawater and kept in the dark. They suggested that burial initiates some self-protective response from the plant. To date, 18 species belonging to the genus *Sargassum*, including *S. muticum* (Withers et al. 1975, Gorham & Lewey 1984), are known to produce tannins and other antibiotic substances (Conover & Sieburth 1964, Stiger et al. 2004). These substances inhibit microflora and epibionts (Sieburth & Conover 1965, Ryland 1974) and so could conceivably inhibit microbial degradation of the below-ground *Sargassum* biomass when parts of the plants become buried in the *Zostera* bed, providing the self-protective response that Morrell & Farnham (1982) suggested. This response, together with a secure attachment point, could provide *S. muticum* plants with a suitable habitat in which to grow. Although the base of the alga would be buried, the plant is not in danger of total burial, as growth rates of *S. muticum* primary laterals growing in the Solent (Southern England) averaged 1 to 2 cm d^{-1} and may increase up to 4 cm d^{-1} between May and June (Davidson 1999), indicating that the alga would grow faster than the sediment deposition rate. In addition, the axil of leaf lamina on all laterals contains air bladders, providing positive buoyancy and thus keeping the laterals from being buried.

Significant differences were found, however, between the lengths of *Sargassum muticum* plants growing in the different substrata, with plants attached to hard substrata being longer. One possible reason for this may be that larger plants become buoyant and break free from their attachment from within the rhizome mat or sediment of the *Zostera* bed. As discussed, the plants provide enough buoyancy that at times they are able to lift the hard substrate they are attached to, a phenomenon known as 'stonewalking' (see Critchley 1983b). Therefore, it is conceivable that larger, more buoyant plants may become detached during turbulent hydrographic conditions, thus leaving only the smaller, less buoyant plants buried in the soft sediment (Critchley 1983b).

No significant difference was found between the lengths of *Sargassum muticum* plants attached to similar substrata in different vegetation types, indicating that it is the substratum that dominates the growth of the plant and not the surrounding conditions. This is consistent with the work of North (1973), Norton (1977) and den Hartog (1997), who stated that the plant can coexist with *Zostera marina* without any apparent direct competition. However, this does not mean there is not any competition, and these results only show that at Castle Bay the mean length of *S. muticum* plants remained consistent regardless of the surrounding vegetation. As *S. muticum* is an opportunistic species and rapidly colonises any free space (Critchley 1983a), it is therefore potentially in indirect competition with *Z. marina*. After *S. muticum* settles in an area previously colonised by *Z. marina*, it can interfere with the regeneration of the bed; no germlings of *Z. marina* have been found in *S. muticum* stands (den Hartog 1997). This is similar to reports of competition between *S. muticum* and the giant kelp *Macrocystis pyrifera*, where once *S. muticum* has settled it prevents re-establishment of the indigenous *M. pyrifera* (Ambrose & Nelson 1982).

CONCLUSIONS

This study demonstrates that the presence of *Zostera* beds may enhance the settlement of *Sargassum muticum* plants, allowing the alga to settle in an otherwise sub-optimal substratum. Rather alarmingly, den Hartog (1997) forecast that 'in time one may expect that *S. muticum* will replace the eelgrass (*Z. marina*) bed'. His prediction, however, was based on a decline in the *Zostera* beds due to disease, environmental and anthropogenic effects rather than just interactions with *S. muticum*. If the presence of *S. muticum* attached within *Zostera* beds shown in the study is found to occur in other locations, it is possible that the predic-

tion made by den Hartog (1997) may occur more rapidly than previously thought. Further research is needed into this area before any conclusions can be drawn, with more sites sampled to see if *S. muticum*'s ability to settle in soft sediment is prevalent just within the Salcombe-Kingsbridge Estuary due to any topographic, hydrographic and climatic conditions, or whether this phenomenon occurs elsewhere.

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