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### Presence and development of populations of the introduced brown alga Sargassum muticum in the southwest Netherlands

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### Introduction

Sargassum muticum, an invasive brown alga of Japanese origin, has been found attached at two main localities in the southwest Netherlands: at Lake Grevelingen and the Eastern Scheldt (Fig. 1). Smaller populations occur on the Wadden Sea islands of Texel and Terschelling (Fig. 1, inset).

The southwest Netherlands comprises a number of islands making up the Dutch Delta region (i.e., the convergence of the rivers Rhine, Meuse and Scheldt). The area is of considerable ecological importance (reviewed by Saeijs & DeJong, 1981; Bannink et al., 1984; Nienhuis & Huis in'T Veld, 1984). Within this prescribed area the presence of S. muticum was thought to be a direct result of large quantities of fertile drift material originating from French and British populations (Fig. 1, inset and Critchley et al., 1983). Drift plants have been cast upon Dutch shores since 1977 (Prud'homme van Reine, 1977a, b) and have been clearly demonstrated to have preceded attached plants (Nienhuis, 1982; Prud'homme van Reine & Nienhuis, 1982).

The work presented here represents a continuous field study from November 1981 to November 1982, followed by periodic monitoring of distribution until 1985 and a resurvey of quadrats in May 1986.

### Description of sites studied

This paper is concerned with two main areas of S.

muticum colonization in the southwest Netherlands, Lake Grevelingen and the Eastern Scheldt (Fig. 1).

Lake Grevelingen: The Grevelingen estuary was once one of the distributaries of the large Rhine-Meuse river system. The estuary was closed off from all riverine and North Sea influences in 1964 and 1971 respectively. The area of the former estuary was reduced from 140 to 106 km<sup>2</sup> to become a non-tidal, shallow saline lake with an average depth of 5.3 m (64% of the lake <5 m; 46% of the lake < 2.5 m). Gradual eutrophication of the lake necessitated opening (via a sluice) a connection with the North Sea (Fig. 2; Saeijs & Stortelder, 1982). The sluice remained open briefly during the latter part of 1978 and for the whole of 1979. Subsequently, as a form of management, the sluice has been opened only during the winter months (October-March). The long-term management strategy for Lake Grevelingen remains undecided, and there is a possibility (albeit remote) that the water-body could become a freshwater impoundment (Bannink et al., 1984; Nienhuis & Huis in'T Veld, 1984).

Most of the perimeter of Lake Grevelingen was protected from erosion by artificial cladding (dike walls) of hard substrata (e.g., basalt, limestone, concrete aggregate and asphalt). Similarly, natural and man-made islands within the lake were protected from wave attack by the dumping of basalt boulders to form "rip-rap" dams (Nienhuis, 1982). All these structures provided many new substrata for biological colonization. However, certain areas of



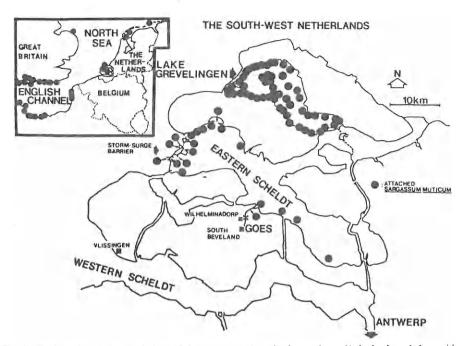


Fig. 1. The distribution of attached populations of Sargassum muticum in the southwest Netherlands and the positions in Lake Grevelingen and the Eastern Scheldt. Inset: Attached S. muticum along the European coasts of the English Channel and North Sea.

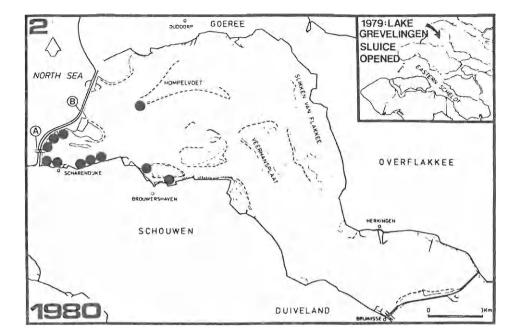
the lake (*i.e.*, Slikken van Flakkee, a former saltmarsh; Fig. 3) comprised bottom substrata of soft mud and silt and were largely devoid of rocks. In this shallow northeastern section of the lake the marine angiosperm *Zostera marina* was particularly common (Nienhuis, 1983).

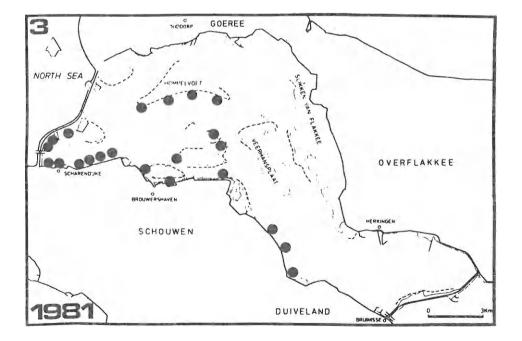
Observations of Sargassum muticum in Lake Grevelingen were based on sampling along the dike wall running from Scharendijke to Brouwershaven (Fig. 2). Within ca 10 m of the dike wall there is a gentle sublittoral gradient comprising scattered rocks and building material to a depth of ca 2 m. Mussels (Mytilus edulis) commonly form a dense cover (80-100%) of all substrata within the first meter of water. Beyond 10 m from the dike wall the profile deepens sharply and hard substrata are less common and tend to protrude from an underlying mud-clay bottom overlain by fine silt.

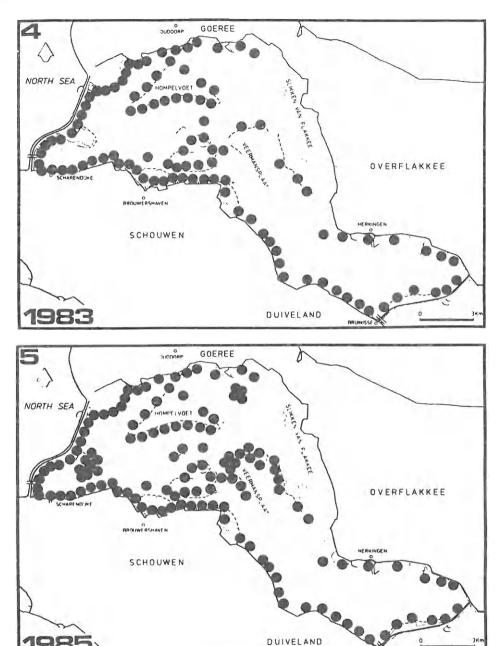
Lake Grevelingen contains a large natural-spatfall population of oysters (Ostrea edulis). In the main production areas of the lake some shallow beds are found at 4 m, but more commonly at >10 m depth (Critchley & Dijkema, 1984).

Eastern Scheldt: The Eastern Scheldt was to be the last remaining estuary destined for annexation from the North Sea as part of the Delta Plan (Saeijs & DeJong, 1981). However, in light of the problems of eutrophication experienced with closure of Lake Grevelingen (Bannink et al., 1984; Nienhuis & Huis in'T Veld, 1984) and under pressure from commercial interests (fishermen and shellfish farmers), the Dutch government decided not to dam off the mouth of the estuary. Yet the surrounding islands had to be made safe from flooding by the sea. The costly and technologically unique option taken was to construct a storm-surge barrier (SSB) in the mouth of the estuary spanning approximately 8 km (Fig. 1). The barrier comprises two man-made islands and a series of gates, so the estuary can be closed off from the North Sea should flood conditions threaten the southwest Netherlands. Construction of the barrier was not

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Figs. 2-5. Expansion of the population of attached Sargassum muticum in Lake Grevelingen, southwest Netherlands, 1980-1985. Figure 2, distribution 1980; A, sluice connection with North Sea; B, Grevelingen dam; inset: introduction of S. muticum to the lake via a sluice connection with the North Sea during 1979. Figure 3, 1981. Figure 4, 1983. Figure 5, 1985. Dotted lines within the lake are protective rip-rap dams. Solid dots represent attached Sargassum.

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itself without ecological consequences; as the SSB was completed only in 1986, its full effects on the estuary are still to be monitored. However, the presence of the construction caused reductions in tidal volume of 45% and mean tidal height of 35% (from that of the former open estuary). The area behind the SSB receives less tidal influence, and the residence time and clarity of the water have increased, but the influence of waves has not changed greatly.

Much of the initial construction and reclamation work was undertaken by the dumping of  $1 \times 1$  m concrete blocks as a basis for further building. The structure of the perimeter walls of the SSB islands are very similar to those in Lake Grevelingen. Hence, as a result of the construction work there is an enormous amount of hard substrate available for colonization by benthic organisms, in an area previously unsuitable (*i.e.*, large sand bars).

#### Materials and methods

Field work was undertaken on foot and by boat, in order to determine the distribution and extent of *Sargassuin muticum* populations in the southwest Netherlands. In Lake Grevelingen, algal community structure was investigated by assessing percentage cover and attached basal frequency of dominant macroalgae in sample plots of 0.5-25 m<sup>2</sup> (Critchley, 1981a). Nomenclature of the identified algae follows Parke & Dixon (1976). Microalgae were not taken into account.

Material for phenological investigation was collected monthly (ca 30 plants taken randomly) and measured for mass, development of main axis shoots (MAS), length of longest primary laterals and reproductive condition of the receptacles (nomenclature after Jensen, 1974; see also Chamberlain et al., 1977; Jephson & Gray, 1977; Critchley, 1981a, 1983).

### Results

Expansion of Sargassum muticum populations in Lake Grevelingen

Figures 2-5 depict the spread in Lake Grevelingen of S. muticum since its first discovery in 1980 (Nienhuis, 1982); the distribution increased eastwards up to 1982-84 (Fig. 4) when virtually all of the available hard substrata were colonized to some extent. Areas in the region of Slikken van Flakkee remained largely uncolonized due to lack of suitable substrata. After 1983, the rate of Sargassum expansion had declined, but there was consolidation of existing populations to form extensive beds.

In the shallow areas of the lake where rocky outcrops were abundantly covered by *Mytilus*, their shells were often densely colonized by *S. muticum*. The depth distribution of the alga in Lake Grevelingen was generally restricted to 2 m by the availability of hard substrata. But where suitable substrata existed, plants were found at 9 m (Den Osse, midpoint between Scharendijke and Brouwershaven, Fig. 2). At depths below 2 m, *Sargassum* was not common and was much reduced in size. The alga has not been found attached to *Ostrea edulis* in the main production areas of the lake, though plants attached to oysters are found in the shallows (<2 m).

The colonization of Lake Grevelingen by S. muticum has not been a straightforward invasion with success of all progeny. The southwest Netherlands suffered from a series of severe winters during 1981-86. Figure 6A (December, 1981) illustrates the freezing conditions of the 1981-82 winter, when large areas of the lake froze, wind-driven ice floes scoured the dike walls and denuded a zone 0.5-1 m from the dike wall. Figure 6B (June, 1982) illustrates the resilience of S. muticum to such severe conditions. Nearest the dike wall, in a water depth of less than 30 cm, all organisms were removed by the ice-abrasion. In a depth of 30-50 cm, Sargassum primary laterals were frozen into the ice and perished, but the perennating holdfast-main axis was largely unaffected, and elongation of secondary laterals (Chamberlain et al., 1977) and regeneration of main axis shoots

soon took place. Sargassum plants at depths of >50 cm were unaffected by the freezing of the lake. Figures 5 and 6B show that S. muticum formed a canopy up to 10 m wide in summer 1982 around much of the perimeter of Lake Grevelingen and the internal islands (with the exception of Slikken van Flakkee). The canopy began to form in March (Fig. 7) with plants 20-30 cm long standing upright in shallow water. The canopy increased in extent throughout the growth season as more of the frond's length floated at the surface in shallow water and plants at greater depths grew to break the surface. During May-June 1982 the Sargassum canopy in Lake Grevelingen was particularly dense, and the ambient sunlight was reduced to  $1-2 \mu E \cdot m^{-2} \cdot s^{-1}$  within 30 cm beneath a full

canopy. Furthermore, a distinct temperature discontinuity existed between a thin lamina (1-2 cm)of water associated with the top of the canopy and water below or outside. The temperature difference on days of high insolation and heating of the upper water was up to 10 °C. This phenomenon of "extraheated" water was most noticeable in the tideless Lake Grevelingen on windless days (Critchley & De Visscher, unpubl.).

Loss of fronds due to natural senescence and wind-action resulted in the canopy breaking up from mid-June, yet persisting in patches until August. However, cover began to re-form from November (Fig. 7) by plants in the shallowest water reaching the surface (depths of 20-30 cm).

Throughout the year, S. muticum plants (>30 cm) attached to Mytilus edulis shells were washed out onto the dike walls. Once plants reached ca 30 cm, wind-generated waves created sufficient drag on the thallus to tear the attached mussels away from the substrata, by ripping their byssus threads free. This represented a significant transport of biological material from both algal and mussel populations. Those mussels cast onto the dike wall perished and formed extensive shell banks.

## Expansion of Sargassum muticum populations in the Eastern Scheldt

As a result of construction of the SSB, together

with major recontouring of the estuary and islands, it was not possible to provide a detailed sequential account of the expansion of *Sargassum* populations in the Eastern Scheldt.

Until 1982 the alga remained largely confined to the SSB and adjacent shores of the estuary. Figure I details the distribution of *S. muticum* in the estuary up to May 1986. The largest populations of *S. muticum* were still associated with the SSB work islands. *Sargassum* was spreading in an easterly direction with new records of attached plants from both the northern and southern shores of the estuary in 1984 and 1985.

The vertical and horizontal distribution of S. *muticum* in the Eastern Scheldt was similar to Lake Grevelingen, again determined by availability of hard substrata. Generally the plant was limited to a depth of ca 2 m, but some plants were found at 10 m. A canopy of Sargassum fronds was formed only in the Eastern Scheldt, at low water, between May and August 1982 (Fig. 7). Owing to tidal influence of the Eastern Scheldt, the Sargassum populations were not subject to ice-scouring during the severe winters.

### Phenology of Sargassum muticum in Lake Grevelingen and the Eastern Scheldt, 1982

Owing to the severe winter conditions, it was not possible to collect material during December 1981 (see Fig. 6A). The elongation of the longest primary laterals of Sargassum collected from Lake Grevelingen and the Eastern Scheldt is described in Fig. 7. From January 1982, attached plants collected from the Eastern Scheldt were consistently longer than those collected from Lake Grevelingen. Relatively little growth occurred from January to March in either population, but during April rapid elongation was evident. Maximum lengths were attained in Lake Grevelingen (ca 300 cm) in July and in the Eastern Scheldt (ca 350 cm) in August. Included in the Lake Grevelingen collections were detached Sargassum plants cast upon the strand line (i.e., detached by storms). The drift S. muticum plants began to appear in April 1982 and were longer than those which remained attached (Fig. 7). The majority of cast S. muticum were at-

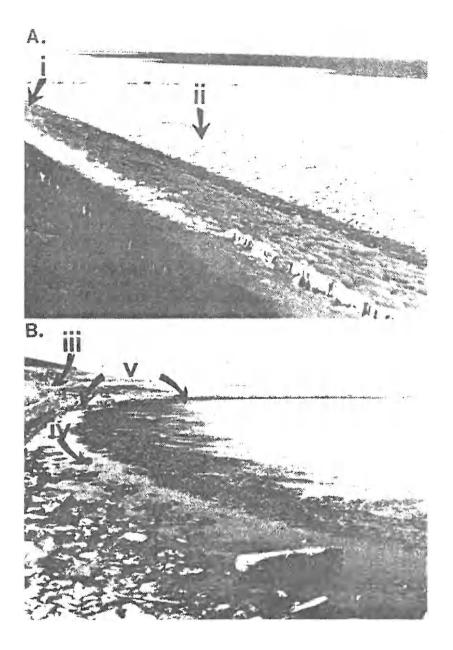


Fig. 6. A: freezing conditions during the 1981-82 winter: (i) dike wall, (ii) ice floes pushed towards dike wall causing abrasion. B: in June 1982, (iii) dike wall, (iv) area denuded by ice action, (v) Sargassum canopy formed.

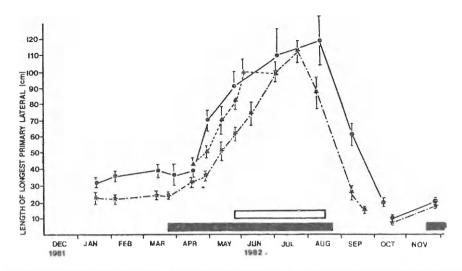


Fig. 7. Elongation of longest primary laterals of Sargassum mulicum (mean  $\pm 1$  S.E.) from populations within Lake Grevelingen and the Eastern Scheldt, 1982. ( $\star \_\_\_ \star$ ), Lake Grevelingen: attached, ( $\star \_\_\_ \star$ ) Lake Grevelingen: drift, ( $\bullet \_ \bullet$ ) Eastern Scheldt. Arrows indicate production of receptacles for reproduction. Solid bar, period of canopy presence of Lake Grevelingen; open bar, period of canopy presence in the Eastern Scheldt.

tached to less-stable substrata (e.g., small pebbles and in particular living *Mytilus*).

Fertile plants (possessing mature receptacles) were recorded from Lake Grevelingen in April (detached plants) and May (attached population); thus the most advanced and longest plants had become detached. Fertile plants were first found in the Eastern Scheldt in May. Plants from both localities continued to release germling plants until necrosis of the primary laterals in September and October (Fig. 7).

Figure 8 illustrates the frequency of MAS development in populations of *S. muticum* collected from two localities in February 1982. Lake Grevelingen populations were restricted to one group where 2-8 MAS had developed, whilst in the Eastern Scheldt three groups were determined: 2-7, 9-13 and 15-16 MAS.

### Sargassum muticum and indigenous algae in the southwest Netherlands

Interactions between the indigenous marine flora

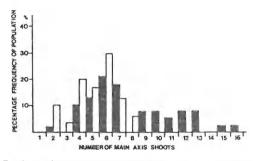


Fig. 8. Development of main axis shoots (MAS) of Sargassum muticum collected from the Eastern Scheldt (closed bars) and Lake Grevelingen (open bars), February 1982.

of the southwest Netherlands and S. muticum will be the subject of a separate publication (Critchley & Nienhuis, unpubl.). However, it is possible to comment generally on the presence of S. muticum.

Quadrat analysis of algal communities (see also Nienhuis, 1982) in the region of Scharendijke, Lake Grevelingen (Fig. 2) indicated that few algae could survive beneath a persistent dense Sargassum canopy. The most frequently occurring algae in such areas were Chondrus crispus, Dumontia incrassata and Polysiphonia spp. (P. elongata, P. nigrescens, P. urceolata and P. violacea). In areas where the canopy was less dense or broken Codium fragile, Bryopsis spp., Ulva spp., Petalonia fascia, Scytosiphon lomentaria and Ceramium rubrum were more common.

A resurvey of Nienhuis's (1982) permanent quadrat in May 1986 showed that there had been a reduction in the occurrence of such taxa as *Chondrus crispus, Ceramium rubrum, Dumontia incrassata, Polysiphonia* spp., and in particular, *Codium fragile* was rare or absent from some areas. No large *Codium* plants were present; only germling plants (< 5 cm) could be found associated with the bases of some *S. muticum* stands.

In the Eastern Scheldt S. muticum is associated with few macroalgae, as much of the substrate is "virgin", only recently being available to colonization by opportunistic species. Subtidally, at the SSB, S. muticum was the dominant alga with only scant coverings of Enteromorpha spp. (E. prolifera and E. intestinalis), Ulva spp., Dictyota dichotoma, Petalonia fascia, Scytosiphon lomentaria and Ceramium rubrum.

### Discussion

The populations of Sargassum in the southwest Netherlands arose from drift material abundant in the North Sea during the late 1970s (Prud'homme van Reine & Nienhuis, 1982). There was only one opportunity for the alga to gain access to Lake Grevelingen (*i.e.*, the summer of 1979), when the sluice connection with the North Sea remained open for the whole year. Brief openings of the sluice in winter 1978 and winter flushings (October to March) as part of the management regime of the lake occurred at times when no viable drift Sargassum was afloat (Farnham *et al.*, 1981; Prud'homme van Reine & Nienhuis, 1982).

In spite of freezing during winters, expansion of *S. muticum* populations has been most rapid in Lake Grevelingen, where the alga increased by dissemination of fertile drift material confined to a relatively small area. Drift *Sargassum* cannot reattach, but when fertile the monoecious and self-

compatible plants have the ability to release numerous progeny before being cast upon the shore (Norton, 1976). Since 1983, the Grevelingen population has not expanded greatly, but has experienced a period of consolidation and recuperation from icedamage. Conversely, in the Eastern Scheldt, *S. muticum* was still in an expansive phase, with new sites established as more virgin substrata were laid open to colonization. Completion of the SSB and its concomitant changes in the estuary made conditions more favorable for *S. muticum*.

Within Lake Grevelingen, competition between S. muticum and Zostera (as suggested by Druehl, 1974) was unlikely, principally due to differences in substrata requirements (see Nienhuis, 1983 for Zostera distribution and population fluctuations). Studies of Z. marina in Britain (Critchley, 1981a) showed that opportunistic germlings of S. muticum could settle amongst Zostera plants colonizing small pebbles and shells of the aggregate substrata. But juvenile plants rarely developed due to physical damage from abrasive Zostera leaves, and shading maintained the alga at a size (<1 cm) where it was susceptible to grazing. If any Sargassum individuals attained a length of more than 10 cm their attached substrata were usually below the mass required to keep the plants secured. With increasing length and buoyancy (due to numerous air vesicles) the plants became mobile and were carried from the Zostera beds by currents. Likewise, it is possible that large S. muticum plants might carry off attached oysters. The most extensive oyster populations of Lake Grevelingen were at a depth greater than 10 m, which was below the limiting depth for S. muticum in this habitat.

The phenology of S. mulicum in the southwest Netherlands (Figs. 7 and 8) closely followed that for the south coast of Britain (Jephson & Gray, 1977; Critchley, 1981a). The most well-developed main axes were found in the Eastern Scheldt populations with three distributions of development; plants from Lake Grevelingen were restricted to one. These distributions agreed with MAS development determined for 1-, 2- and 3-year age classes (Critchley, 1981a, b). Variations in the length and age construction of the populations studied was a reflection of substrate stability; in Lake Grevelingen many plants, in shallow water, were attached to mussels which, in turn, could be detached from their rocky substrata. Regular recolonization by S. muticum ensured maintenance of a low-age-group population. Conversely, in the Eastern Scheldt, S. muticum was attached to stable substrata, below the level of mussel colonization, which allowed the development of a more mature population. Figure 9 indicates the presence of three-year-old plants in the Eastern Scheldt, thereby dating establishment at 1979, the same time as suggested for Lake Grevelingen (Nienhuis, 1982). Notwithstanding these observations, investigations in Lake Grevelingen during 1986 showed a marked decline in the number of mussels, enabling Sargassum to attach to the dike wall, thereby increasing the longevity of individuals within the population.

Dense stands of Sargassum in the southwest Netherlands also caused problems for recreational and amenity usage of the waterways (see Critchley et al., 1986). The problems were particularly prevalent in Lake Grevelingen where the canopy is a persistent feature during the summer months at a time of greatest recreational demand, e.g., swimming, scuba-diving, sailboarding, fishing, etc. (Fig. 7).

### Conclusions

Sargassum muticum is a permanent member of the Netherlands marine flora. Its distribution will be restricted by the availability of suitable habitats (submerged, stable, hard substrata); therefore, much of the dutch coastline, comprising sand and particulate shores, will remain uncolonized.

The unique, non-tidal, saline Lake Grevelingen had approached its maximum capacity for Sargassum within ca four years of its introduction. The alga was limited by substrata availability. The Eastern Scheldt, however, was not such a closed system until completion of the SSB. We predict the rate of colonization in this body of water will increase rapidly due to the favorable environmental changes which occurred in the estuary as a result of the barrier.

With the rapid expansion of *S. muticum* in Lake Grevelingen, concern was expressed that the alga

might be deleterious to the populations of Zostera marina, Ostrea edulis and indigenous algae, and to amenity usage. The habitat preferences of Z. marina and the brown alga were largely mutually exclusive, whilst the major oyster beds (at a depth of >10 m) were too deep to be colonized by significant Sargassum populations. Light attenuation in the lake was a factor determining the lower limit of the alga.

Direct competition with S. muticum may not be sufficient to oust indigenous algae in the shortterm. But the opportunistic colonizing strategy of Sargassum takes advantage of natural catastrophes, in that blanket coverage of substrata by germlings and growth of a canopy can preclude reestablishment of some components of the natural fauna and flora.

The persistence of a Sargassum canopy within non-tidal environments requires further investigation of its effects on biotic physical conditions of shallow waters. The most extensive populations of S. muticum may require some form of control for both ecological and amenity-usage considerations.

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