Scottish Natural Heritage
Commissioned Report No. 324

Sargassum muticum in Scotland 2008: a review of information, issues and implications

COMMISSIONED REPORT

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Sargassum muticum in Scotland, 2008: A review of information, issues and implications

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SCOTTISH NATURAL HERITAGE

COMMISSIONED REPORT
Summary

Sargassum muticum in Scotland 2008: A review of information, issues and implications

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Sargassum muticum is an invasive, non-native species of brown algae. *S. muticum* was first recorded in the UK in 1973 on the Isle of Wight and has since spread along the south coast of England, around Wales and around Ireland.

The first reports of *S. muticum* in Scotland were in Loch Ryan in 2004 and by April 2007, populations had also been found at Great Cumbrae Island, the North Ayrshire coast, Arran and at Campbeltown Loch on the Mull of Kintyre. Drifting fragments of *S. muticum* had been recorded from Loch Fyne, Argyll and the Clyde Marina, Ardrossan, Ayrshire as well as on Arran and at Clonaig on the Mull of Kintyre. It had been thought that the Kintyre Peninsula would provide a temporary physical barrier to the continued spread of this invasive species up the west coast of Scotland. However, during early 2007, unattached drift *S. muticum* fragments were found in the Firth of Lorn at the Garvellachs and at Ganavan, near Oban.

S. muticum is a fast growing species and once established, colonies can form dense stands. In summer, the floating fronds spread out over the surface, creating a distinctive canopy. *S. muticum* quickly exploits any open spaces that become available and it is considered to be an ‘opportunistic gap-grabber or space-filler’. Concerns have been expressed about the potential for deleterious ecological change, where *S. muticum* displaces native species of algae or *Zostera* sp., or alters habitat characteristics. The introduction of *S. muticum* can have a number of other implications that relate to the amenity, recreational and commercial uses of coastal areas.

S. muticum has been identified for inclusion in Scottish Natural Heritage’s Species Action Framework as an active invasive with high potential for adverse impact on important biodiversity features. The ongoing dispersal of *S. muticum* along Scotland’s coastline has implications for the suite of nationally and internationally important marine protected areas established around the Scottish coast and for water bodies meeting environmental objectives of good ecological status under the Water Framework Directive.

A literature review of national and international research on *S. muticum* was undertaken. This report collates this information in a structured form that aims to provide context for the prediction of the potential spread of *S. muticum* in Scotland and to inform assessments of impacts and any future management plans and actions. The report provides background information on this species, its habitat preferences and environmental tolerances and the features and strategies that it employs to facilitate its dispersal. The anthropogenic vectors responsible for the global spread of *S. muticum* are described and an overview of its current global distribution is provided. The report presents an overview of the ecological, economic and natural heritage implications of *S. muticum* introductions, as well as management strategies and eradication techniques that have been employed, including a case study of Strangford Lough.

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1.0 INTRODUCTION

In 2007, Scottish Natural Heritage initiated a project to develop techniques for assessing the spread of a marine non-native species, *Sargassum muticum,* and to identify its impacts on biodiversity.

While *S. muticum* was not yet a major concern in Scottish waters, it was deemed to be suitable as a test case for developing methods for monitoring and controlling marine non-native species, which could then be applied to other invasive species that are potentially much more damaging. It also provides an opportunity to raise awareness of non-native species issues.

The objectives of this project are:
1. To predict the potential spread of *S. muticum* in Scotland and identify areas where it is most likely to become established
2. To assess the potential threat to relevant features of high biodiversity value, including designated sites
3. To conduct targeted field surveys at a representative sample of sites, to locate and/or assess established populations of *S. muticum*
4. To assess the effectiveness of manual clearing techniques as a potential measure to mitigate impacts in areas of high conservation value
5. If possible, to evaluate diversity and abundance of biota associated with established *S. muticum* populations

As part of this work, a review of previous research and practical work on *S. muticum* in the UK was required. This report is the product of this element of the project.

A literature review of national and international research on *S. muticum* was undertaken. This report collates this information in a structured form that aims to provide context for the prediction of the potential spread of *S. muticum* in Scotland and to inform assessments of impacts and any future management plans and actions. The report provides background information on this species, its habitat preferences and environmental tolerances and the features and strategies that it employs to facilitate its dispersal. The anthropogenic vectors responsible for the global spread of *S. muticum* are described and an overview of its current global distribution is provided. The report presents an overview of the ecological, economic and natural heritage implications of *S. muticum* introductions, as well as management strategies and eradication techniques that have been employed, including a case study of Strangford Lough. Finally, an overview of the current known distribution of *S. muticum* in Scotland is provided, along with research undertaken on *S. muticum* in Scotland to inform discussions of the projected expansion of the Scottish distribution.

2.0 DESCRIPTION OF *SARGASSUM MUTICUM* (YENDO) FENSHOLT

Kingdom	Plantae	
Phylum:	Phaeophyta	
Class:	Phaeophyceae	
Order:	Fucales	
Family	Sargassaceae	
Genus	Sargassum	
Species name:	*Sargassum muticum* (Yendo) Fensholt	
Common names:	Wire weed, strangle weed, Jap weed	
Names in other languages	Danish:	Butblæret sargassotang
	Dutch:	Japans bessenwier
	French:	Sargasse
	German:	Japanischer Beerentang
	Japanese:	Tama-hahaki-moku
	Norwegian:	Japansk drivtang
	Spanish and Portuguese:	Sargasso
	Swedish:	Sargassosnärja, Sargassosnärje, Japansk sargassotång

Seventy different species of the genus *S.* are found in the West Pacific region. The distribution of *S. muticum* extends from south east Asia, including Japan, along the Chinese and Russian Pacific coast. Within its natural range, *S. muticum* is one of the smaller *Sargassum* species, growing between 75 – 150 cm long.

S. muticum was first described from Japan by Yendo (1907) as *S. kjellmanianum* forma *muticus*. As a result of Fensholt's taxonomic work on *S. kjellmanianum* f. *muticus*, *S. muticum* was recognised as a separate species (Fensholt, 1955). Yoshida (1978) subsequently recognised *S. kjellmanianum* as conspecific with *S. miyabei,* with the latter having taxonomic priority. *S. kjellmanianum* is dioecious but Tseng and Chang (1954) recognised a monoecious form; *S. kjellmanianum* forma *longifolium.* As a result, Yoshida (1978) proposed that this form be re-named *S. muticum* forma *longifolium* (Critchley, 1983a).

S. muticum is a member of the fucoid family but is distinctively different to the wracks found around the UK coast, as illustrated in Figure 1. It is normally a pale brown colour but can be light orange or yellow where it is exposed to high light intensities and high surface water temperatures (Critchley *et al.,* 1990a).

The *S. muticum* plant, illustrated in Figures 2, 3 and 4, is attached to the substratum by a perennial, conical, discoid **holdfast** up to 5 cm in diameter. Occasionally smaller plants may be found attached to, or fused into, the holdfast of an adult plant. Germlings can settle simultaneously and their holdfasts can fuse, and one plant may become dominant and retard the development of the other plants by shading (Critchley, 1983b).

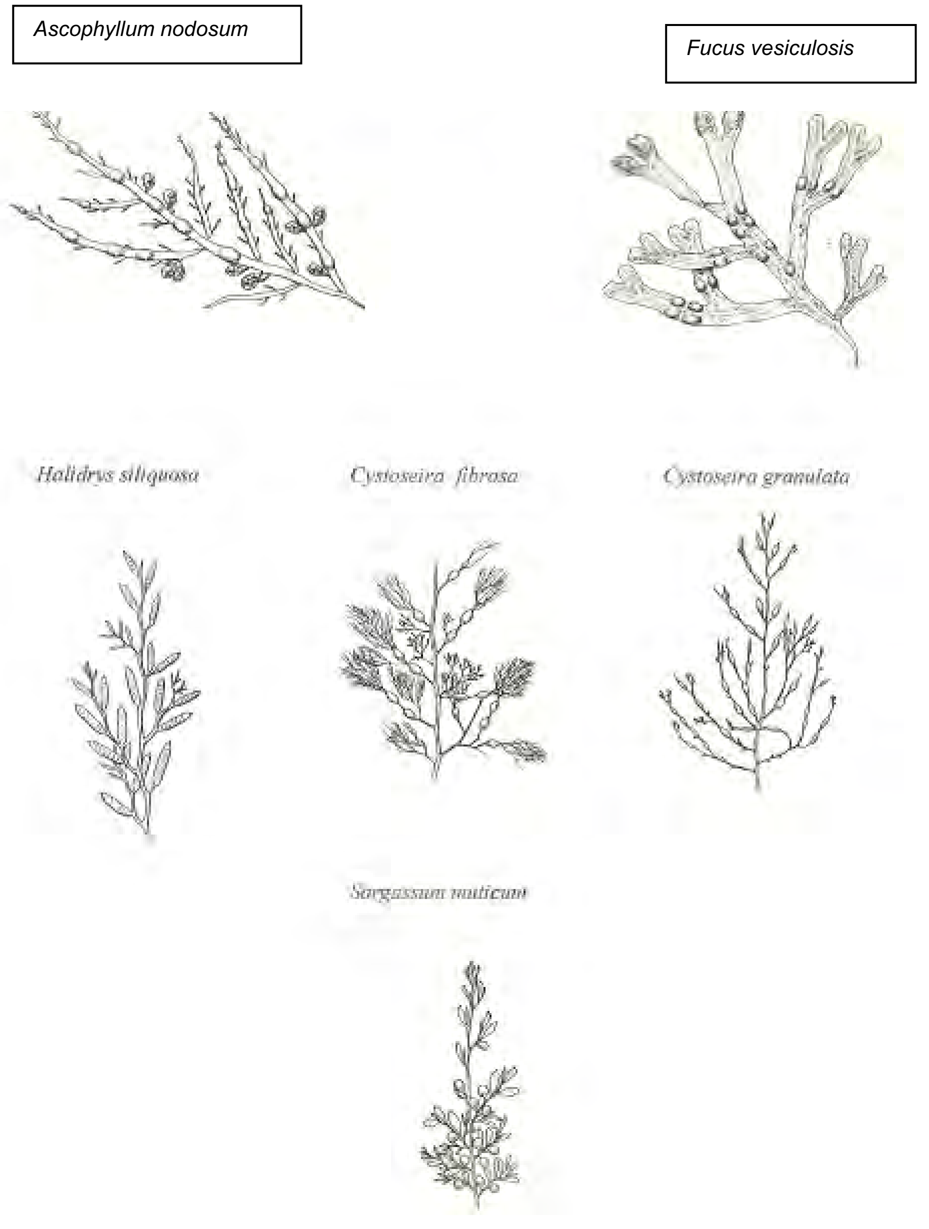
The holdfast gives rise to a short (up to 5 cm long and 10 mm in diameter) single, terete (cylindrical) **stalk or main axis**, which is under the control of an apical meristem, and is perennial. **Basal leaf-like laminae** and narrow **primary laterals (branches)** arise annually from this stumpy stalk. These are generally cast seasonally. Around the UK this typically occurs during the summer and autumn period. The regional variations in growth, reproduction and dormancy are discussed in Section 4.1.1. The number of laterals arising from the stalk increases with age and in older plants, the stalk may branch and may be gnarled by loss of laminae and laterals.

Large basal laminae (leaves) with an obvious midrib, can appear on the stalk, associated with the extension of the primary lateral. They are typically 1-5 cm long and 0.5-1.0 cm wide

(Wernberg- Møller *et al.,* 1998) but can grow up to 10 cm long and 2 cm wide (Critchley, 1983b). Leaves from sterile secondary and tertiary laterals, known as “winter” leaves, are up to 30 mm long and 15 mm wide. “Summer” leaves are generally linear-lanceolate and up to 15 mm long and 3-5 mm wide. Leaf shape may vary seasonally, in response to physical conditions, principally water temperature and light intensity (Critchley, 1983c).

Figure 1
Indigenous algae that may be confused with Sargassum muticum
(Jones and Farnham, 1973)

NOTE: In egg or knotted wrack, *Ascosphyllum nodosum*, the air bladders measure 2-3 cm while in bladder wrack, *Fucus vesiculosis*, the air bladders are around 1 cm. The shapes and sizes of the air bladders of sea oak or pod weed, *Halidrys siliquosa*, and some *Cystoseira* species can frequently lead to confusion with *S. muticum*.



Ascophyllum nodosum

Fucus vesiculosis

Halidrys siliquosa

Cystoseira fibrosa

Cystoseira granulata

Sargassum muticum

The primary laterals are 4-6 mm wide at the base and can develop a groove if twisted, They are tough and wiry, hence the common name of "wire weed". The longest lateral is known as the **dominant lateral (**main branch). The growth of the primary laterals is controlled by an apical meristem, which exerts apical dominance upon secondary lateral extensions.

The maximum size an adult plant can attain appears to be dependent on the geographical location. In Japan, *S. muticum* grows to between 75-150 cm (Yendo, 1907: Rueness, 1989) and other *Sargassum* species attain greater lengths and abundances (Yamada, 1955; Segawa, 1956). However, like many other "weeds", this alga grows considerably larger when transplanted outside its indigenous range. On the Pacific coast of North America, it may reach 7 m long (Jones and Farnham, 1973; Nicholson *et al.,* 1981). Plants up to 10-12 m have been collected from the Brittany coast of France (Critchley *et al.,* 1990b). In British waters the average size is between 2-4 m (Jephson and Gray, 1977; Critchley *et al.,* 1990b) but plants of 4-6 m have been recorded such as Strangford Lough, Northern Ireland (Davison, 1999; Strong, 2003) and the Isle of Cumbrae, Scotland (Wilson, 2006).

Secondary laterals arise from the primary laterals, tertiary laterals arise from the secondary laterals and fourth order laterals may arise from tertiary laterals, creating feathery fronds (Critchley, 1983b). The **secondary laterals** are 2-3 mm diameter at the base and usually grow to 30-40 cm, decreasing in size towards the tip of the frond. If the main axis is held horizontally by the holdfast and tip of the primary lateral, the numerous side branches and laminae hang down like "washing from a line" (Jones and Farnham, 1973). The branches tend to fragment easily, particularly at the tips and this tendency increases over the summer prior to their being shed from the basal stalk (Critchley, 1983b, Critchley *et al.,* 1990a, Nicholson *et al.,* 1981).

Strong (2003) undertook morphological studies in Strangford Lough, Northern Ireland, within the Dorn, a complex micro-tidal lagoonal system on the south eastern side of the Lough. On average, year one plants had two primary laterals with a mean length of 0.56 m, while year four plants have between six and seven laterals with a mean length of 0.97 m. He found that the numbers of tertiary laterals were proportional to secondary lateral length. Unlike other reported populations of *S. muticum*, the number of broken laterals in Strangford Lough was very low, which was probably a product of the extremely sheltered conditions within the Lough and especially at the collection site within the Dorn. The average length of a mature primary lateral was 0.63 m, with the longest lateral typically 0.8-1.0 m, very occasionally up to 6 m in length. The average lengths are more similar to *S. muticum* plants found on the north coast of Spain (Fernandez *et al.,* 1990) and native plants in Japan than other introduced populations. The mean length of primary laterals of *S. muticum* in the Solent, southern England (Critchley, 1981), Lagoon of Venice (Curiel *et al.,* 1998) and southern California (Norton, 1981a) was typically about one metre longer.

The loss of, or damage to, the primary lateral may result in the loss of apical dominance. This can stimulate the increased elongation of secondary laterals, particularly nearest the point of injury. Occasionally, a single secondary lateral may take over the role of primary lateral apex and maintain an apical dominance effect (Critchley, 1983b).

Each year the number of primary lateral branches produced may increase e.g. in the first year two are produced, in the second year up to five are produced and in the third year up to nine are produced (Jephson and Gray, 1977, Critchley 1981).

The most distinctive features of *S. muticum* are the numerous small stalked air bladders and reproductive receptacles. Cryptostomata are evident on the surface of the laminae and air vesicles.

The **air bladders or vesicles** provide the buoyancy that lifts the laterals to the surface and they arise in the axil of leafy lamina on all the laterals. They are small (2-6 mm), smooth-surfaced and are attached by 2-5 mm long stalks. They have spheroidal and pyriform (pear-shaped) forms. Towards the end of the autumn many air vesicles may be lost, often resulting in the plant losing buoyancy and sinking (Critchley, 1983c).

The **reproductive receptacles** develop in the axils of leafy (lanceolate) laminae of tertiary lateral branches and are attached by 2-10 mm long stalks. The reproductive receptacles are 0.5-2.0 cm long, 1-3 mm wide and the surface of the jelly-filled receptacles is generally rough or lumpy. They are dark brown when fertile (Wernberg-Møller *et al.,* 1998). Tiny cavities, known as **conceptacles**, that contain the reproductive gametes (gametangia), are arranged spirally upon the receptacle. As the receptacles mature, the conceptacles become visible as minute pale spots. As the receptacles are monoecious / androgynous, containing both male and female gametes within separate conceptacles, self-fertilisation can occur (Critchley, 1983c).

The size and shape of the laminae, air vesicles and receptacles can vary greatly. The extent of plasticity in terms of the variation in the taxonomic characteristics of leaf and air vesicle shape, that are used to identify *Sargassum* species indicates that further work is required regarding the taxonomy of the Sargassaceae, particularly in Japan (Critchley, 1983b; Critchley, 1983c).

Once *S. muticum* becomes well established, colonies of plants can form dense stands. The floating fronds spread out over the surface, creating a canopy. A canopy can create 100% cover and this can overshadow native algal species, by reducing the availability of photosynthetically active radiation (PAR). The shading effect can also cause a lowering of the water temperature below the canopy (Critchley, 1980; Critchley, 1983d).

Figure 2
The plant structure of Sargassum muticum
(Wernberg-Møller, *et al.,* 1998)

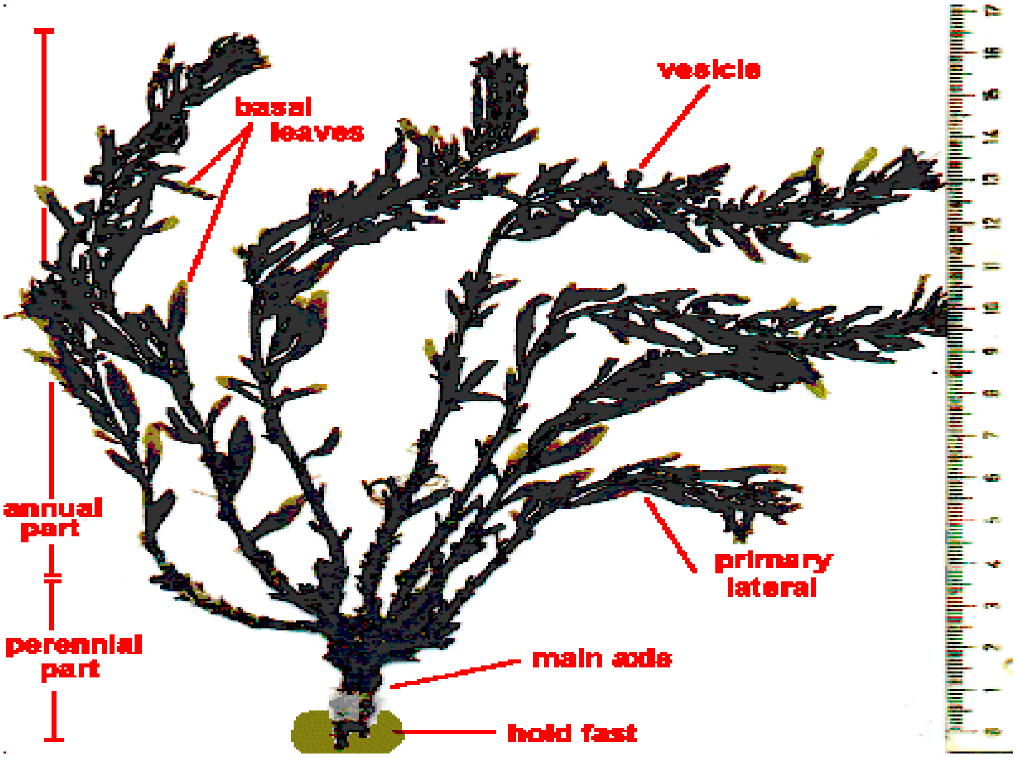
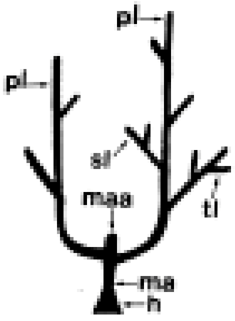


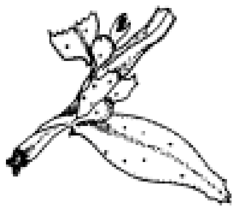
Figure 3
Illustration of a Sargassum muticum plant
(Daryl Birkett)

Figure 4
The morphology of Sargassum muticum
(Critchley, *et al.,* 1990b)

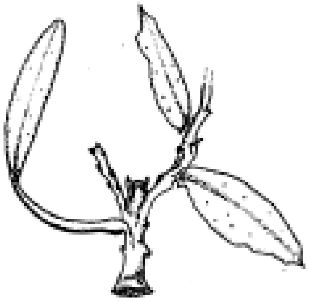


4a: Stylised plant

h: holdfast; ma: main axis; maa: main axis apex;
pl: primary lateral; sl: secondary lateral; tl: teritiary lateral



4b: The conical holdfast and main axis from which basal leaf-like laminae and primary laterals arise



4c: A twisted main axis can develop a groove. Air vesicles and secondary laterals arise in the axil of a lamina

4d: Receptacles and air vesicles arise in the axils of lanceolate lamina of a tertiary lateral

4e: Air vesicles vary in morphology; lower vesicle is spheroidal while upper vesicle is pyriform

3.0 HABITAT PREFERENCES AND ENVIRONMENTAL TOLERANCES OF *SARGASSUM MUTICUM*

The conditions in which a plant can grow will determine which areas it may inhabit if it is able to spatially disperse. These conditions are especially relevant when considering the possible spread of a non-native species that is capable of rapid dispersal and is potentially detrimental to the environments where it is introduced.

3.1 Zonation

The optimal tidal zone for *S. muticum* establishment is the extreme lower shore and sublittoral fringe and its low tolerance to desiccation prevents colonisation of regularly emersed littoral areas (Norton, 1977a; Roberts *et al.,* 2004). It colonises eulittoral tidal pools. Where the pools are small and very shallow, the plants are often small and reproduction may be impaired (Fletcher and Fletcher, 1975a). However, in more extensive areas of standing water on the mid to lower littoral shore, such as channels, pools and lagoons, *S. muticum* can become the dominant alga (Fletcher and Fletcher, 1975a; Norton, 1977b; Viejo, 1997; Connor *et al.,* 2004).

Norton (1977a) found that its upward extension into the littoral appears to be limited by its susceptibility to aerial exposure; desiccation and insolation in the summer and frosting in winter. Sublethal exposure retards the subsequent growth of the plants, thus diminishing their competitive ability. The degree of retardation increases with the severity and duration of exposure to the stress. High air temperatures will cause significant adverse effects, with a single hour of exposure to hot sun (26°C) being lethal to the entire plant. Exposure to air in hot sunshine can kill branches in one hour and in the shade, three hours exposure can kill the branches. This does not necessarily result in the death of the plant as the basal holdfast generally survives and can regenerate branches. However, even sublethal exposure can retard growth and reduce the plants' competitive ability (Norton, 1977a). Along the Pacific coast of North America*, S. muticum* in tidal pools were rarely found above 0.48 m above Mean Low Water (Norton, 1977b).

It rarely occurs deeper than a few metres subtidally, and its subtidal range is thought to be linked to water clarity and the availability of sufficient light for growth (Norton, 1977a; Thomsen *et al.,* 2006). Off the Pacific coast of North America*, S. muticum* is broadly restricted to the lower littoral and sublittoral fringe; generally 0.3-1.5 m but up to 3-4 m below Mean Lower Low Water (Norton, 1977b). However, it has been recorded at depths of 6-10 m in the Hood Canal, Washington, where there are no grazers and down to depths of 24 m in the clear water off Santa Catalina, southern California (Norton, 1977b).

To date, two UK biotopes have been identified that contain *S. muticum*:
IR.LIR.K.Sar: *S. muticum* on shallow, slightly tide-swept infralittoral mixed substrata with a depth band of 0-5m
LR.FLR.Rkp.FK.Sar: *S. muticum* in eulittoral rockpools.

A full description of these biotopes is available by accessing the Joint Nature Conservation Committee (JNCC) website.

3.2 Exposure tolerance

Wave exposure is an influential factor on coastal communities. *S. muticum* is thought to have a preference for sheltered sites but is found in a range of conditions and habitats (Fletcher and Fletcher, 1975a). High levels of wave action cause the plants to fragment and populations are unable to establish in more exposed locations (Viejo *et al.,* 1995). Thus, sheltered and moderately exposed sites offer optimal conditions for establishment (Critchley 1983a; Critchley *et al.,* 1983; Andrew and Viejo, 1998a; Andrew and Viejo, 1998b).

In its native Japan, *S. muticum* is confined to sheltered conditions (Norton, 1977a). Critchley *et al.* (1983) stated that for a *S. muticum* population to survive, it must be protected from excessive wave action, with the protection offered by a reef or a ledge being sufficient. They stated that populations could survive in moderately exposed shores.

In northern Spain, Fernandez *et al. (*1990) made similar observations, while Andrew and Viejo (1998a) stated that *S. muticum* is abundant on sheltered shores and in tide pools on exposed shores but rare or absent at low-intertidal levels on exposed shores. However, they observed that there was no significant difference in the recruitment of *S. muticum* to un-cleared plots between exposed and sheltered shores. They suggested that existing algal cover, irrespective of size or species, will deter colonisation by *S. muticum* and that recruitment was greatest on manually cleared, sheltered shores. They went on to (cautiously) conclude that it is unlikely that *S. muticum* will significantly disrupt the low intertidal areas of exposed shores. Further studies by Andrew and Viejo (1998b) stated that the survivorship of *S. muticum* was not influenced by wave exposure in the first four months of macroscopic growth but as the plants grow, survivorship would decrease as wave action would cause branches to detach, meaning that the plants may never be able to reproduce. Contrasting results were found by Espinoza (1990), who observed that *S. muticum* was able to colonise *and* reproduce on very exposed shores of the Mexican Pacific, although at a lesser rate than on sheltered shores. Whether this result is due to the warmer water conditions and year round fertility is unknown. It seems that, in general, *S. muticum* is able to colonise exposed shores but will be less able to establish a reproductive population, which will lower its invasive capabilities.

Strong (2003) working in Strangford Lough, Northern Ireland, examined *S. muticum* plants from two sites on a 'sheltered' and 'extremely sheltered' side of an island and recorded their morphology and reproductive status. The longest primary laterals of individuals on the 'sheltered' side of the island were 37% longer than those of the 'extremely sheltered' plants, and had 50% more main axial shoots than the 'extremely sheltered' plants. Despite this, the plant biomass between sites was not significantly different. By contrast, *S. muticum* collected on the 'extremely sheltered' shore were more reproductively mature than those individuals on the 'sheltered' shores. This resembled the situation for *S. muticum* in Aramar, on the north coast of Spain, where Andrew and Viejo (1998) found plants at exposed sites were longer than those in sheltered conditions. Strong (2003) postulated that this phenomenon of increasing plant length with increasing wave exposure might be particular to *S. muticum* among fucoids, whose thallus size generally decreases with increasing exposure. Strong (2003) went on to propose that intermediate levels of exposure might actually stimulate greater plant size within populations of *S. muticum*. As moderate exposure may reduce sedimentation and increase the turnover of water, hence thinning the boundary layer that would otherwise limit the diffusion of gases and nutrients to plants (Wheeler, 1982), the amelioration of gas and nutrient limitation and sedimentation might increase plant size.

3.3 Substrate preferences

S. muticum can establish on most substrates that provide an attachment point for the holdfast. Substrates include bedrock, pebbles or shell fragments scattered on a sediment surface (Fletcher and Fletcher 1975a; Norton, 1977; Critchley *et al.,* 1983; Connor *et al.,* 2004). It exhibits a preference for clean, hard, textured substrates and shells are particularly favourable, typically colonising previously un-exploited niches, such as fairly loose substrates of small stones and shells on mud or sand. (Critchley, 1983d). *S. muticum* does not respond well to continual abrasion but is far more resistant to decay as a result of burial in mud than *Laminaria digitata* (Morrell and Farnham, 1982).

S. muticum generally colonises open patches within an area of dense algae. In sheltered sites with dense algal cover, open patches tend to occur sporadically. These close within one to three months due to rapid re-colonisation by native species. This would appear to preclude colonisation by *S. muticum* germlings but this species quickly exploits any open spaces that become available and it is considered to be an 'opportunistic gap-grabber or space-filler' (Critchley, 1983d).

Britton-Simmons (2006) found that space pre-emption by crustose and turfy algae inhibited *S. muticum* recruitment and that light pre-emption, by canopy and understorey algae reduced *S. muticum* survivorship.

S. muticum can occasionally be found growing epiphytically on other algae such as fucoids or laminarians (Fletcher and Fletcher 1975a; Withers *et al.,* 1975; Critchley 1983a). It has been observed that this epiphytic mode of attachment can have a degree of longevity, with an individual *S. muticum* plant observed attached to a *F. serratus* frond for two years (Critchley, 1983a).

It also shows a preference for man-made structures, such as floating jetties and pontoons, which provide a relatively unfilled niche (Fletcher and Fletcher, 1975a). Bax *et al. (*2001) stated that boat marinas, in particular, could provide novel marine habitats which may be open to colonisation by introduced species that otherwise would not be able to compete with native species.

The unusual ability to colonise small fragments of hard substrate in an area of predominantly soft substrata has undoubtedly allowed this species to spread quickly, become extremely abundant and hence develop sufficient biomass to qualify as an ecosystem engineer and generate significant habitat modification (Strong *et al.,* 2006). The total area of marine sediments open to occupation by *S. muticum* in Europe and North America is vast, and cumulative habitat modification could be very significant (Strong *et al.,* 2006).

3.4 Growth conditions

S. muticum also exhibits considerable ecological resistance. *S. muticum* is tolerant of a wide range of temperatures, 5°C and 30˚C (Norton, 1977a). It can survive short periods of freezing temperatures (Norton, 1977a). High water temperatures are favourable for growth and this encourages southward spread while lower water temperatures tend to limit its spread north (Norton, 1977a). It is tolerant of a wide range of salinities, 6.8 ppt and 34.0 ppt, but at reduced salinities, growth rates are reduced (Norton, 1977a). The ideal growth conditions are thought to be a temperature of 25˚C and a salinity of 34 ppt (Eno and Clark, 1995).

3.4.1 Temperature

Water temperature also influences the local and geographical distribution of this species. *S. muticum* is tolerant of a wide range of temperature; the growth rate increases with temperature over the range 3°C to 30˚C (Norton 1977a; Hales and Fletcher, 1989a).

In its native Japan, *S. muticum* experiences an annual temperature range of between 5°C and 28°C. In southern California, it survives in shallow lagoons and tidal pools that reach temperatures of 30˚C and rarely fall below 14˚C (Norton, 1977a). In Alaska, *S. muticum* occurs where temperatures range between 3°C and 10°C (Hales and Fletcher, 1989a). The south of England experiences a range of between 3°C and 20°C (Hales and Fletcher, 1989a).

Experimental evidence suggests that the optimal temperature for growth and reproduction is about 25˚C (Norton, 1977b; Hales and Fletcher, 1989; Hales and Fletcher 1990). At this temperature, Norton (1977b) found the largest increase in length and width of the germlings. The number and length of rhizoids also increased with temperature. Norton also stated that, even at temperatures of 15°C, *S. muticum* could grow faster than the locally dominant fucoid, *F. distichus* at Friday Harbour, Washington, USA. Hales and Fletcher (1990) found that the receptacles of *S. muticum* could tolerate temperatures between 10°C and 30°C, with an optimum growth rate at 25°C.

However, Espinoza (1990) pointed out that there had been relatively slow movement of *S. muticum* into warmer Mexican waters, as the distance colonised between 1973 and 1988 in Mexico was half the distance colonised by *S. muticum* in 10 years along the west coast of North America. This is attributed to either coastal upwelling or permanent cold water eddies, which may have slowed the spread. Espinoza also stated the optimum temperature for growth in laboratory conditions can vary between 15°C and 20°C.

It is accepted that the temperature range in which *S. muticum* may grow is between 3°C and 30°C (Norton, 1977; Hales and Fletcher, 1989) but that a reduction in temperature from 17°C to 7°C will decrease germling growth (Steen, 2003).

S. muticum plants are susceptible to frosting (Norton, 1977a), with a single hour exposed to temperatures of -9°C being lethal to the entire plant. While *S. muticum* is susceptible to cold, its branches can survive at –1˚C (Norton, 1977a) and the perennating holdfast – main axis can survive even lower temperatures (Critchley *et al.,* 1987; Karlsson, 1988). Reproduction can still occur at 10˚C (Hales and Fletcher, 1990) and growth is still possible at 5˚C (Norton, 1977a) with *S. muticum* able to outgrow some native species at temperatures well below its own optimum (Norton, 1977b). It has successfully established in the cold waters of southern Alaska (Hales and Fletcher, 1989) and Scandinavia (Karlsson and Loo, 1999). In Sweden, the first populations observed in 1987 were noted to survive the winter, despite formation of ice on the nearby sea surface (Karlsson and Loo, 1999).

S. muticum is very susceptible to desiccation. Exposure to air in hot sunshine kills all the branches in one hour and in the shade, it is usually lethal after three hours. This does not necessarily result in the death of the plant as the basal holdfast generally survives, protected by the branches, and can regenerate branches (Norton, 1977a). After a sub-lethal exposure to desiccation, although plants were apparently undamaged, they subsequently grew less well than the controls, when cultured under conditions favouring rapid growth. The degree of retardation was found to be directly related to the duration of exposure, which in the case of Norton's (1977a) study was 15, 30, 60, 120 and 180 minutes (sun and shade treatments). Norton (1977a) found that a 15 minute exposure under sunny conditions was not enough to kill individuals of *S. muticum*, but resulted in growth rates that were half those of the control thalli. Strong (2003) undertook desiccation tolerance experiments in Strangford Lough and found that plants in the 15 minute aerial exposure treatment did not show signs of immediate mortality, but declined substantially over a seven week period.

The dense surface canopy that can be formed by the feathery fronds of *S. muticum* can cause the surface water temperature to elevate. Strong (2003) found that stands of *S. muticum* in Strangford Lough caused strong temperature stratification, including significant cooling of the water just above the sediment, as recorded in Lake Grevelingen, the Netherlands (Critchley *et al.,* 1990). A 2°C warming was apparent in the canopy of *L. saccharina* when compared to the ambient seawater in unvegetated areas, while warming within the canopy of *S. muticum* was much greater, with the water temperature elevated by

11°C above ambient (Strong, 2003). Unlike *L. saccharina* canopies, evidence of a significant cooling to 2°C below ambient was observed under the canopy of *S. muticum*. The extreme heating of the water associated with the surface canopy is typically restricted to a thin layer at the very surface of the water. Within the sheltered environment of Strangford Lough, the high density of *S. muticum* tends to prevent the water within the stands of vegetation being exchanged with non-canopy areas. In addition, the dark colour of the canopy absorbs much of the light, and on a sunny day the stagnant water can become extremely warm. Such temperature stratification did not occur in *L. saccharina* beds, perhaps due to the lower standing biomass and because the vegetation does not ‘interlock’ as it does for *S. muticum*. Strong (2003) proposed that warmer water temperatures could increase gamete production and extend the reproductive period of *S. muticum* so this effect may aid its reproductive success.

It appears that *S. muticum* grows comparatively slowly at the northern part of its range and can be very fast growing towards the southern part of its range. On the basis of distribution patterns, Van den Hoek (1982) distinguished 10 phyto-geographic distribution groups of wide applicability. *S. muticum* belongs to “Group 8”; north east American temperate / Japanese temperate for which the critical temperatures, determined experimentally, were found to be:

Northern lethal limit	-1˚C winter isotherm
Northern growth boundary	12˚C summer isotherm
Southern growth boundary	25˚C winter isotherm
Southern lethal limit	27˚C winter isotherm

The impact of climate change and a corresponding rise in the temperature of the world’s oceans may facilitate increases in the range of *S. muticum*, thereby reducing the limiting factor of lower temperatures on *S. muticum* at the current northern edges of its range (Wilson, 2006).

3.4.2 Salinity

Salinity influences the local and geographical distribution of this species. *S. muticum* prefers a salinity of 34 ppt, yet will grow in salinities ranging from 6.8 ppt to 34 ppt (Eno *et al.,* 1997).

It is tolerant of reduced salinity, although its growth rate and reproduction are impaired, with probable consequent reductions in competitive ability (Norton 1977a; Hales and Fletcher, 1989; Steen, 2004). *S. muticum* has been recorded growing at salinities of 24-25 ppt (Druehl, 1981), 30-31 ppt (Widdowson, 1965) and 27-35 ppt (Kjeldson and Phinney, 1972). Where the salinity of the surface layers is reduced by fresh water run-off, *S. muticum* can respond by growing in deeper water, as long as the water clarity is good (Norton, 1977a).

Studies on the effects of salinity at different life stages have been carried out. Hales and Fletcher (1989) and Norton (1977a) both carried out short term laboratory tests and reported that, in culture, germlings could tolerate minimum salinities of 6.8 ppt and 20 ppt, respectively. Laboratory analysis carried out by Steen (2004) concluded that salinities of between 10 ppt and 30 ppt had no effect on the survival of germlings after one week and that between 70% and 100% survived for up to five weeks after fertilisation.

The effect of salinity on the occurrence and survival of oogonia on receptacles was also measured. Oogonia appeared on all receptacles cultivated at between 10 ppt and 30 ppt, but on none cultivated at between 0 ppt and 5 ppt. Fertilisation and subsequent cell divisions only occurred, within 14 days, at salinities of between 20 ppt and 30 ppt and not below 15 ppt. Reproduction is stated as the most vulnerable life stage in the life history of *S. muticum*. This is also true for several other fucoid species; *Fucus ceranoides* (Brawley, 1992), *F. serratus* (Malm *et al.,* 2001) and *F. vesiculosus* (Serrao *et al.,* 1999).

Norton (1977a) found that, in culture, vegetative branches could tolerate minimum salinities down to 9 ppt but growth rates were much reduced. Transplanted mature plants (Steen, 2004) were also found to show a decrease in growth and reproductive rate at a station with salinities in the range of approximately 9.5 ppt to 17.4 ppt over a six month period, suggesting a shorter reproductive season and decreased recruitment potential. Field studies have also observed an absence of *S. muticum* in shallow Alaskan waters (6 m) at a salinity of 8.64 ppt, due to snow melt (Norton, 1977a). Steen suggested (2004) that the invasive capabilities decrease with reduced salinity, with a complete inability to invade areas with salinities lower than 15 ppt and potentially an inability to compete with other species at salinities lower than 25 ppt. Records of salinity can therefore be used to predict whether *S. muticum,* and other potentially invasive marine species, will be able to survive in a particular area.

Steen (2004) suggested that *S. muticum* colonisation is limited as salinity decreases, with a salinity lower than 15 ppt providing an effective barrier to this invasive species. However, since brackish ecosystems are often characterised by low biodiversity, it has been hypothesised that these areas will be more vulnerable to colonisation by *S. muticum* if it is able to withstand hyposaline conditions (Elmgren and Hill, 1997).

3.5 The competitive ability of *Sargassum muticum*

The status of *S. muticum* as a highly invasive species is not in doubt, although the biological traits that underpin this invasiveness are poorly understood. Recent research has concentrated more on the identification of traits common to invasive species. Once these traits are understood, predictions can be made about how invasive a species will be, once introduced, hence allowing a preventative approach to marine introductions (Carlton, 1996).

The interactions between an organism and its environment are either biotic or abiotic. Abiotic interactions encompass physiochemical environmental factors such as temperature, water motion, and nutrient concentrations. The main biotic interactions within subtidal macroalgal communities are competition, predation (including grazing) and symbiosis (mutualistic and parasitic relationships). Biotic interactions are often complex and highly variable (Connell, 1983).

Competition can occur when a resource common to two or more species is limited in supply (Connell, 1983). Competition has been demonstrated to be important in a variety of algal-dominated communities (Olson and Lubchenco, 1990). Most often, space and light are assumed to be the limiting factors for macroalgae within these habitats. Competition can be divided into exploitative competition and interference competition. Exploitative interactions deal with competitive consumption of a limiting nutrient required by more than one species or the pre-emptive colonisation of the substratum by one species to the detriment of another. Interference competition results from interactions between organisms that may not relate directly to any limiting resource, e.g. overgrowth and the use of allelochemicals (Denley and Dayton, 1985). Both exploitative competition and interference competition can be further divided into interactions that occur between species, which are called *inter*-specific, and those within a species, termed intra-specific. “Competition” is actually a product of both inter- and intra-specific competition and quantification of both is vital *(*Connell, 1983). The competitiveness of a species reflects its ability to inflict a cost on another species while suppressing the cost of intra-specific competition within its own population (Olson and Lubchenco, 1990).

One aspect of intra-specific competition is called the self-thinning law, which is well documented in macroalgae (Creed *et al.,* 1998). Creed *et al.* (1998) also found that plant density profoundly influenced the development of populations of *Laminaria digitata* and

Fucus serratus. Exploitation mechanisms include the consumption (depletion of resources) and pre-emption (passive prior occupation of limited substratum) of a limited resource. Uncolonised substratum is typically required for the settlement and attachment of most macroalgae. The pre-emptive covering of a substratum by turf-like algae often prevents other species establishing. The presence of a native sub-canopy or turf layer has also been found to form a physical barrier to the successful settlement and recruitment of *S. muticum* (Deysher and Norton, 1982). Interference competition in seaweeds typically occurs as the overgrowth of one species by another. Again, large size, rapid growth, and the ability to perennate help an alga to be successful (Olson and Lubchenco, 1990) in interference competition. It is often hard, if not impossible, to separate exploitative and interference competition, e.g. capture of light by one species interferes with another species by shading it (Olson and Lubchenco, 1990).

3.5.1 Competition within populations of Sargassum muticum

Arenas *et al.* (2002) investigated the intra-specific competition within a Spanish population of *S. muticum* and found notable morphological differences with increasing density, consistent with a self-thinning trajectory. At high densities, *S. muticum* thalli became longer, thinner and less branched, which was considered a mechanism to reduce overcrowding within the monospecific canopy. Arenas *et al.* (2002) also recorded an increased net mortality in the high-density *S. muticum* stands.

Strong (2003) investigated intra-specific competition within Strangford Lough, Northern Ireland and found that the growth of *Laminaria saccharina* and *S. muticum* decreased at higher monospecific plant densities and that the decline was particularly conspicuous for *S. muticum*, indicating that self-thinning tendencies are considerable in this species. Intra-specific competition had a significant impact on the growth of *S. muticum* when compared to the effect of inter-specific competition, indicating that this alga is more competitive in mixed canopies. The high level of intra-specific competition in this alga might be due to substantial amounts of self-shading. The results of Strong's study were similar to those of Arenas *et al.* (2002) who found strong intra-specific competition in Spanish populations of *S. muticum*. Growth decreased and mortality rates increased with greater thallus densities.

Strong (2003) hypothesised that the high intra-specific rates of competition in *S. muticum* compared to *L. saccharina* could be attributed to thallus morphology. The flat and simple blade morphology of *L. saccharina* maximises photosynthetic capture and the reduced quantity of structural tissue might allow a greater net conversion of the energy. By contrast, the bushy, multi-layered and complex morphology of *S. muticum* might reduce the surface area efficiently capturing energy. As *S. muticum* has a greater quantity of structural and reproductive tissue, this may also reduce the net productivity available for other metabolic processes. The morphological features of *S. muticum* would appear to be poorly suited to shady habitats or those with high plant densities, which may explain why intra-specific competition was greater and growth lower in high density plant frames than at lower densities. Strong (2003) also found that photosynthesis of *S. muticum* saturated at very high irradiances when compared to published values for *L. saccharina.*

Critchley *et al.,* (1990) demonstrated the severity of self-shading in a dense stand of *S. muticum*. He measured carbon fixation at different levels in a canopy. Just over 65% of the total carbon fixation occurred in the top 0.25 m of canopy, while below this, carbon fixation declined rapidly with canopy depth, indicating the impact of shading on primary production for the bottom half of the canopy. Thalli of *S. muticum* are reported to translocate manufactured chemicals and thereby alleviate any shortfall of photosynthate at the bottom of the canopy (Critchley *et al.,* 1990).

3.5.2 Competition with indigenous algae

Strong (2003) investigated the competition between *S. muticum* and *Laminaria saccharina.* He found that the timing of the reproductive phenology of *S. muticum* and *L. saccharina* was a critical factor. *L. saccharina* develops and releases spores in autumn and winter (White, 2000). Newly recruited sporophytes grow quickly in winter and spring, after which they are large enough to be considered part of the adult population. The majority of the reproductive and recruiting period for *L. saccharina* occurs when the canopy of *S. muticum* has declined (winter) or is at its lowest cover (spring). This would suggest that in Strangford Lough, the reproduction of *L. saccharina* was relatively unimpeded by the presence of a canopy of *S. muticum*. By the time the canopy of *S. muticum* has reached its maximum, the sporophytes of *L. saccharina* are typically large enough to be considered adults. Therefore, the competitive interactions are probably among the adult phases and are either direct, e.g. overgrowth, or indirect, e.g. opportunistic pre-emption of substrata. His investigations found that *L. saccharina* was unaffected by *S. muticum* under the experimental conditions applied over the six weeks. He concluded that rather than considering there to be competition between these species, facilitation may be a better concept, i.e. the growth rates of *S. muticum* are enhanced in mixed canopies. The lack of any impact of *S. muticum* on the growth of *L. saccharina* indicates that direct interactions between the two species in a mixed canopy are probably not responsible for any decline or substitution of *L. saccharina* by *S. muticum* seen in other parts of the introduced range. This supports Farnham's observations that *S. muticum* is better described as opportunistic, i.e. it is a species that colonises open habitat as it becomes available, rather than displacing native species in a mixed canopy it has invaded (Farnham, pers. comm.).

Once *S. muticum* is established, it can potentially compete effectively for light and space with native algae (Fletcher and Fletcher, 1975a; Nicholson *et al.*. 1981; Ambrose and Nelson, 1982; De Wreede, 1983; Viejo, 1997; Cosson, 1999; Staehr *et al.*. 2000; Bartsch and Tittley, 2004; Britton-Simmons, 2004; Sanchez *et al.,* 2005) by virtue of its pseudo-perennial lifestyle, rapid growth rate, large frond size and dense canopy (Wernberg *et al.,* 2000). Please refer to Section 7.4 for more information on competition with indigenous algae.

3.5.3 Competitive interaction between Sargassum muticum *as a macroalgal basiphyte and epiphytes*

Epiphytism is particularly prevalent in the marine environment because substratum for attachment is often limited and the aquatic environment allows nutrient uptake to be independent of substratum location. Therefore, all unprotected solid surfaces in the sea eventually become fouled (Wahl, 1989). Any epiphytic association may create both benefits and disadvantages for the basiphyte and the epiphyte. The most important disadvantage of heavy epiphytism for the basiphyte is shading. Fouling can increase the weight of the basiphyte and hence sink the plant away from the higher photic zone near the surface of the water. The potential impacts on the basiphyte from shading and competition for nutrients and gases have to be balanced against the cost of manufacturing antifoulant metabolites to suppress epiphytism. Many macrophytes, including *S. muticum,* suppress epiphytism through the production of antibiotic compounds that prevent the establishment of a biofilm (Conover and Sieburth, 1964).

Strong (2003) investigated the epiphytic fouling compared to the other common subtidal algae in the Dorn, Strangford Lough and found that *S. muticum* and *Cystoseira* sp. had the greatest amount of fouling. The annual development of *S. muticum* was closely followed by a heavy epiphyte load, although species that retain their vegetation between years such as *Halidrys siliquosa* were practically clean during this period. In the Dorn, there was relatively more fouling on *S. muticum* plants in soft sediment habitats. This has some similarity with the relationships between soft sediments, organic re-mineralisation and the abundance of ephemeral algae. Within the Dorn, Strong (2003) postulated that areas with greater quantities of soft sediment might augment the availability of nitrogen through re-mineralisation of sediment-bound organic matter. These local enrichments might stimulate a greater abundance of ectocarpoid biomass. Alternatively, he suggested, the sheltered nature of soft sediment habitats might mean that the reduced water motion 'washed' less of the loosely attached ectocarpoid biomass from the basiphyte.

However, Strong (2003) found that on plants collected from a hard substratum, the amount of fouling appears to be related to the structural form of the alga and the antifouling defence employed. The highly branched and complex algae, *S. muticum* and *Cystoseira* sp., appeared to have higher levels of epiphytism. The complex nature of these basiphytes appeared to retain loosely attached epiphytic biomass, especially the main ectocarpoid species, and may have prevented the sloughing of this fouling. Antibiotic compounds (polyhydroxyphenyl ethers) have been found in *S. muticum* and they are thought to suppress the initial phases of epiphytism, i.e. colonisation by bacteria (Glombitza *et al.,* 1982). Many fouling organisms require a surface pre-colonised with a biofilm for attachment and it is often assumed that the inhibition of the biofilm will lead to the reduced adhesion of other species (Hellio *et al.,* 2001). An analysis of 30 temperate macroalgae for antibacterial properties found that *S. muticum*, *Ascophyllum nodosum* and *Polysiphonia lanosa* were the most effective species against both gram-negative and gram-positive bacterial colonisation when compared to other temperate brown macroalgae (Hellio *et al.,* 2001). Although these compounds will not act directly on epiphytic algae, the inhibition of the biofilm may prevent further attachment and spread of epiphytes on *S. muticum*. Although this process might keep thalli of *S. muticum* epiphyte-free for most of the year, the antibiotic compounds are clearly not effective enough to suppress the spring bloom of ectocarpoid algae. However, the related lack of fouling on *H. siliquosa* may well be related to either a high metabolic contribution to antifouling compounds or to high surface cell shedding. The slow growth of *H. siliquosa* would suggest that it may partition more to such defences than other native species and 'skin' shedding is probably the most important protection from epiphyte for the macroalgae that employ this system (Norton, pers. comm. in Strong, 2003).

Strong (2003) also found that the extent and the timing of the fouling suggested that epiphytism played an important role in the mortality of epiphytised *S. muticum* in Strangford Lough. It appeared that ectocarpoid fouling had a detrimental and direct effect on the basiphyte, i.e. ectocarpoids shaded *S. muticum*. Separating the epiphyte and basiphyte increased the growth of *S. muticum*, which probably indicates that this was interference competition, with overgrowth causing shading being a direct impact mechanism.

Although Strangford Lough is not considered to be eutrophic, nutrients are more available in the spring, so the decline of the epiphytes after the spring suggests that nutrients might be involved. Furthermore, the soft sediment habitats in which *S. muticum* grows may contribute to the greater epiphyte biomass observed there compared to hard substrata. The larger, local supply of nutrients may help stimulate the epiphytism. Furthermore, the higher quantities of sediment are more likely to be caught in the epiphyte matrix and hence further reduce the penetration of light to *S. muticum*.

3.6 Susceptibility to herbivorous grazing

Herbivore effects on plant distribution, biomass and diversity can be dramatic. Herbivory can affect the competitive balance among seaweeds and several studies have shown that algal species diversity is highest with intermediate levels of grazing pressure (Menge, 2000). Macroalgal herbivores are often categorised into one of three groups: fish with large foraging ranges and low densities, urchins with intermediate ranges and densities and finally, mesograzers with small foraging ranges but high densities.

The mesograzers are the least studied group of herbivores, although the role of these smaller grazers in structuring marine plant communities is becoming increasingly recognised (Hay *et al.,* 1987). This group includes amphipods, copepods and polychaetes (Brostoff, 1988). The mesograzers appear to influence the macroalgal community in one of three ways: by enhancing algal spore dispersal, by grazing of both basiphyte and epiphytic algae, and through the consumption of algal propagules (Hay *et al.,* 1987).

Gray (1978) examined grazing as a possible source of biological control of *S. muticum* in the Solent. Molluscs only grazed small germling stages or the thallus parts of *S. muticum* already damaged by desiccation. However, the epiphytic amphipods (*Gammarus* spp.) were found to graze on the new growth of the alga, although the grazing pressure was not considered great enough to justify its application in biological control. Two other abundant epiphytic Crustacea, *Euryome aspera* and *Macropodia rostrata,* are known to include algae in their diet and occurred on *S. muticum*. However, Gray (1978) stated that neither of these species appeared to be important consumers of the *S. muticum* in the Solent.

Norton and Benson (1983) found that the herbivorous crustacea, *Caprella laeviuscula* and *Ampithoe mea* readily consumed *S. muticum* in laboratory trials. When the grazing pressure of *Ampithoe mea* was combined with that of the abundant epiphytic mollusc, *Lacuna variegata*, grazing removed more tissue than the reproductive *S. muticum* could replace because of its reduced growth rates. The mobile epifauna inhabiting *S. muticum* in the El Truhan Inlet, northern Spain, was characterised by large abundances of herbivorous amphipods, especially the families Ampithoidae and Ischyroceridae and the genus *Dexamine* (Viejo, 1999). The abundance of *Dexamine* spp*.* peaked in the summer months at approximately 750 individuals per 100 g of alga. The isopod *Dynamene bidentata* was the most abundant epifaunal species on *S. muticum* in rockpools and extensively colonised plants in the shallow subtidal; in the laboratory this species readily consumed *S. muticum* (Viejo, 1999).

Within Strangford Lough, Strong (2003) found that *S. muticum* provides a substratum for an abundant, although species poor, epiphytic faunal assemblage. The herbivorous amphipod, *Dexamine spinosa*, typically occurs at very high densities, i.e. approximately 360 individuals per 100 g (fresh weight) of basiphyte biomass, which is an order of magnitude higher than that around any native macroalgae in Strangford Lough. Although *S. muticum* is the preferred basiphyte, the dietary preferences of *D. spinosa* were not known. Grazing investigations undertaken by Strong (2003) found that on epiphyte-free basiphytes, the grazing preference of the abundant amphipod, *Dexamine spinosa*, was found to be *S. muticum* > *Laminaria saccharina / Halidrys siliquosa* > *Fucus serratus*. However, he pointed out that these results must be approached with a certain level of caution as the control samples of *S. muticum* declined by 30% (surface area) and 70% (wet weight). One could conclude that plants of *S. muticum* therefore provide both habitat and grazing material for this abundant epiphytic amphipod, *D. spinosa*. However, the 35% decline in the surface area for the control samples of *S. muticum* may indicate that the experimental samples were beginning to decay, explaining why grazing was observed to be particularly intense on *S. muticum*. One could hypothesis that the grazers present may have selected the ailing *S. muticum* due to greater palatability, increasing the apparent grazing pressure for this macroalga, compared to the other three species studied.

Mesograzer feeding preference between macroalgae has been shown to vary for several reasons but commonly, the preferences are set by either the concentration and potency of chemical defences found in the algal thallus, or the nutritional requirements of the mesograzer species. *S. muticum* is known to contain tannin-like substances (Conover and Sieburth, 1964). Despite the presence of these defences in *S. muticum*, this and several other studies have documented grazing of this species by herbivorous amphipods (Gray, 1978; Norton and Benson, 1983; Viejo, 1999). Although most mesograzers consume the epiphyte in preference to the basiphyte, many species will also consume the basiphyte (Bulthuis and Woelkerling, 1983; Cattaneo, 1983; Duffy and Hay, 2000). The finding in Strangford Lough (Strong, 2003) that *D. spinosa* was able to consume both basiphyte and epiphyte biomass reflects the findings of studies on other epiphytic amphipods (Karez *et al.,* 2000). While Fong *et al.,* (2000) discovered that the presence of mesograzers ameliorated the negative impact of epiphytism, Strong (2003) found that the presence of *D. spinosa* on fouled *S. muticum* appeared to contribute to the decline of both algal components; the basiphyte and epiphyte. Strong (2003) concluded that the 'double-impact' of epiphytism and amphipods on *S. muticum* was great and resulted in the rapid decline of the basiphyte as the individual impacts of epiphytic algae and amphipods typically lowered the growth of *S. muticum*, but never resulted in an actual decrease in its biomass. The severity of the decline of epiphytised *S. muticum* with amphipods might suggest some form of impact interaction and enhancement. Karez *et al.* (2000) documented enhanced negative effects of the interaction between epiphytism and mesograzing, which they termed 'co-consumption'. During experimentation, Karez *et al.* (2000) found the epiphytic isopod *Idotea granulosa* to consume significantly more *Fucus vesiculosus* and epiphyte biomass when it was offered as a basiphyte-epiphyte system than when presented as an unfouled basiphyte.

Although a variety of grazers can feed on *S. muticum,* there is little evidence to indicate that they are a controlling factor in its abundance or distribution. Norton (1977a) speculated that the shallow depth distribution of *S. muticum* off the coast of Washington state, USA might be due to increased sea urchin grazing pressure at deeper locations. More recent work (Britton-Simmons, 2004) indicates that the dominant grazer, the sea urchin *Strongylocentrotus droebachiensis*, tended to avoid *S. muticum* and did not appear to control plant abundance. Similarly, studies in Scandinavia indicate that while some grazers, specifically the sea urchin *Psammechinus miliaris* and the common periwinkle *Littorina littorea*, actively feed on *S. muticum* there was no evidence to indicate that their grazing controlled its abundance (Pedersen *et al.,* 2005; Thomsen *et al.,* 2006). However, observations on the coast of British Columbia, Canada suggest that in certain circumstances, grazing by the sea urchin, *S. droebachiensis*, can control *S. muticum* abundance (De Wreede, 1983). In the Solent, the most effective grazer of *S. muticum* was found to be the sea hare, *Aplysia punctata,* but these sea slugs showed a feeding preference for other algae and were not sufficiently numerous to control algal populations (Critchley *et al.,* 1986).

3.7 Overview of habitats where *Sargassum muticum* is currently found

3.7.1 Habitats of Sargassum muticum *on the west Pacific coasts of Japan and China*

S. muticum on the southern coast of Honshu is found growing on rocks in the upper sublittoral, along with other *Sargassum* species. Although widespread, the relative abundance of *S. muticum* is low compared to that of other macroalgae in Japan. When other *Sargassum* species are present e.g. *S. kjellmanianum*, *S. muticum* exhibits a distribution lower on the shore than the other species (Critchley, 1981).

3.7.2 Habitats of Sargassum muticum *on the east Pacific coast of North America*

3.7.2.1 Bath Island, British Columbia

S. muticum plants can be found on the low intertidal shore and in rockpools on more exposed coastlines (De Wreede, 1978). *S. muticum* was limited to a band 1-3 m wide in the immediate sublittoral of the shore. The lowest limit of *S. muticum* at Bath Island was determined by a combination of factors, including increased grazing by sea urchins, a marked decrease in the incident light during the winter months and the presence of native macroalgae (De Wreede, 1978).

In British Columbia and northern Washington, *S. muticum* inhabits a narrow vertical zone around extreme low water of spring tides, down to a depth of only 2–4 m and a plant of 2 m long was quite a large specimen (Norton, 1981a).

3.7.2.2 San Juan Islands, Washington

Norton (1977b) found that the well-established populations of *S. muticum* were generally restricted to the lower littoral and sublittoral fringe. Most of the rocky shores are relatively sheltered except for the wash from large ferries. Typically, the populations were found on rocky outcrops or promontories in relatively sheltered situations, attached to bedrock or stable boulders. *S. muticum* only occurred on small pebbles if they were wedged in some way or not easily dislodged even when the plant was lifted. Populations were also found in very sheltered bays or lagoons and in tidal pools on more exposed shores. Water currents sweep around the promontories at velocities approaching 4-5 km per hour. The diurnal tide range is 2.3 m but extreme tides can reach 4 m in range. Air temperatures can rise to 26°C – 33°C in summer and can fall to –3°C to –16°C in the winter. The sea water temperature is on average 7°C – 11°C with a maximum of 16°C and a minimum of 5°C. Due to the input from the Fraser River, the salinity varies between 28.5 ppt and 29.1 ppt but can fall to 18.3 ppt after snow melt in the spring. The water tends to be turbid due to high plankton productivity and suspended matter from the freshwater input. Underwater visibility is often less than 1 m (Norton, 1977b). Norton (1977b) observed that *S. muticum* seemed to be less aggressive in the San Juan Islands than in other, more recently invaded areas. However, he felt that this was probably a result of the restraining influence of the local conditions rather than a diminution of aggressiveness resulting from long establishment.

3.7.2.3 Santa Catalina, southern California

Most of the *S. muticum* plants were found to be stunted on the lower shore (0-2.9 m below MLW). The greatest number of large-sized plants occurred at a depth of 12-13 m. The growth rates of the alga reduced with depth, although elongation still occurred below 13m (Smith, 1973 in Aguilar-Rosas and Galindo, 1990). The clarity of the water around Santa Catalina Island was probably responsible for the increased penetration of the alga into the sublittoral, relative to other Californian sites.

Norton (1981a) found that here, the *S. muticum* zone could penetrate to a depth of 24 m and plants could grow, on average, to 3–4 m long. Nicholson *et al. (*1981) found that a number of factors appeared to limit the distribution of *S. muticum* in the sublittoral zone. These included the presence of *Macrocystis* sp. beds, the lack of hard substrate and possibly increasing water pressure with depth, that may have caused the walls of the air vesicles to collapse, reducing the plants' buoyancy. Aerial exposure, primarily desiccation, limited its distribution in the littoral zone.

3.7.2.4 Baja California, Mexico

S. muticum plants were confined to intertidal pools on a gravel substratum at semi-exposed sites and to rocky areas with high wave exposure (Aguilar-Rosas and Galindo, 1990).

3.7.3 Habitats of Sargassum muticum *on the western coast of Europe*

Within its present European distribution, *S. muticum* may be found attached to a very wide range of substrata from stable bedrock, to loose shells or broken stones or even to stones or shells embedded in mud. It occurs over a wide range of ecological conditions, from sheltered to moderately exposed shores. However, the permanent population nearly always remains wet during periods of low water. Often the population is protected from excessive wave action by some form of barrier, such as a ledge or reef. It is also found just below the waterline of floating pontoons and other buoyant structures and its growth can cause significant drag (Critchley *et al.,* 1983).

3.7.3.1 France

The area at St Vaast-la-Hougue, France, is a sheltered, flat beach of stones covered in muddy sand with strong currents. *S. muticum* was found to grow in channels on the lower shore and in the pools formed between the stone walls of the oyster parks (Gray and Jones, 1977).

3.7.3.2 The Netherlands

Individuals of *S. muticum* extensively colonised the lagoons and subtidal shore on rocky outcrops in otherwise soft sediment habitat (Critchley *et al.,* 1987). There were few native macroalgae that also occupied this habitat.

In the south west Netherlands, Critchley *et al.* (1990) found that *S. muticum* experienced its greatest development within Lake Grevelingen, a large (108 km^2) non-tidal, saline water impoundment, enclosed as part of the Dutch “Delta Works” to protect islands from flooding. *S. muticum* gained access during the opening of a sluice gate connecting to the North Sea in 1979. The population development and impacts were monitored and it was found that the alga was very successful, establishing an extensive population. The buoyant primary laterals form a 100% canopy over the lake’s surface from November until mid-August, when the primary laterals are cast off as part of the natural senescence cycle. The persistence of the canopy is due to the extreme shelter and non-tidal environment at this site. The dense canopy was found to severely restrict light penetration, with the *S. muticum* absorbing 97% of the photosynthetically active radiation (PAR). The canopy also elevated the surface water temperature, with the shading effect causing the water temperature below the canopy to be appreciably cooler. The temperature difference between the surface and 0.5 m depth was 9.2°C. Indigenous algae, particularly sub-canopy algae, decreased in size and frequency but the diversity had not yet been affected by the sub-optimal conditions created by *S. muticum.* In Lake Veere, the water is brackish (23 ppt) and eutrophic and *Ulva* species were dominant but *S. muticum* was able to grow and reproduce.

3.7.3.3 Limfjorden, Denmark

S. muticum plants are on a mixed substratum of scattered stones and boulders on a sand and mud base. *S. muticum* ranges in depth from 0-6 m (Staehr *et al.,* 1998; Staehr *et al.,* 2000).

3.7.3.4 Lagoon of Venice, Italy

Individuals colonise the infralittoral zone to a depth of 3 m. Plants are found attached to stones, wood, mooring lines and wharves (Curiel *et al.,* 1998).

3.7.3.5 Aramar Beach, Spain

Colonisation has occurred in the low intertidal and subtidal fringe. The individuals of *S. muticum* typically occupy boulders and stones overlaid with sand (Arenas and Fernandez, 1998). Areas with exposed bedrock are well colonised with native macroalgae that appear to exclude *S. muticum*.

3.7.4 *Habitats of* Sargassum muticum *in the British Isles*

3.7.4.1 The Isle of Wight

S. muticum occupies a range of habitats in pools between the mid tide level and low tide level and in the shallow sublittoral. The plants occur attached to solid substrata such as rocks, pebbles and mollusc shells and are occasionally found epiphytically on brown macroalgae such as *Fucus* sp., *Cystoseira* sp. and *Laminaria* sp.. The continual movement of the sand on these shores often embeds the holdfast and lower part of the primary lateral, which subsequently can blacken and decay and may absciss more easily. In these sandy areas, some specimens attach to the old shells of *Ostrea edulis, Crepidula fornicata* and *Buccinum undatum* (Fletcher and Fletcher, 1975a; Withers *et al.,* 1975).

At Bembridge, Isle of Wight, *S. muticum* appears to particularly favour the areas of low reef dissected by pools and channels which constitute the low tide level fringes of the lagoon system. Here they grow in apparent competition with a number of other algae. With 2-3 fronds per plant, that can grow to around 3 m in length, dense swards developed which covered several square metres, blanketing the indigenous algae. Scattered plants growing in shallow pools and lagoons higher up the shore were the least successful, being smaller, infertile and yellow in colour (Fletcher and Fletcher, 1975a). Plants were also found growing at depths up to 8 m despite the turbidity of the water (Gray and Jones, 1977).

At Warden Point, Isle of Wight, the preferred habitat of *S. muticum* was found to be mutually exclusive to *F. serratus* and *A. nodosum* due to different tolerances to desiccation and to *L. digitata* which formed a physical barrier to settlement and whose fronds caused abrasion. However, *S. muticum* did not colonise apparently suitable, free substrate in the sublittoral zone below the kelp forest (Critchley, 1983d).

3.7.4.2 Hampshire

In Portsmouth Harbour, *S. muticum* particularly favours numerous floating jetties and pontoons, attached directly or indirectly to slipper limpets, *Crepidula fornicata*. It became dominant in this previously relatively unfilled niche (Fletcher and Fletcher, 1975a; Withers *et al.,* 1975).

At Langstone and Chichester Harbour, the mudflats are dissected by a complex system of drainage channels, the bottoms of which are covered with stones and shells, including live *O. edulis* and *C. fornicata* chains. The indigenous macroalgae, *L. saccharina, H. siliquosa* and *Cytoseira nodicaulis* and other less common species formed a very open community with lots of substrate available for colonisation. *S. muticum* was found to slowly form virtually monospecific stands, dominating some of the drainage channels between 1975-77 and then to rapidly expand the canopy between 1977-79. However, by 1980-81, the rate of increase began to decline. The areas covered are listed in Table 1. *S. muticum* was unable to encroach upon the mudflats due to the lack of suitable substrate and the inability to withstand desiccation. Some transient populations survived, in stunted forms, in bait pits that were dug by fishermen (Critchley, 1983e; Fletcher and Fletcher, 1975a; Withers *et al.,* 1975).

Table 1
Area covered by S. muticum in Langstone Harbour, 1979 and 1981
(Critchley, 1983e)

Langstone Harbour	**Area covered by *S. muticum***	**% of total harbour area**	**% of low water channel area**	**% of algal cover**
1979	7.87 hectares	0.55	0.73	0.60
1981	14.2 hectares	0.75	2.90	1.90

In the Solent, *S. muticum* plants are found subtidally on bedrock and broken rock or shell fragments embedded into the soft sediment substratum. Attached plants were occasionally observed in water up to 10 m in depth (Critchley, 1983e).

3.7.4.3 Devon

The colonisation by *S. muticum* appears to be confined to the intertidal rockpools on semi-exposed coasts, e.g. Wembury. Peripatetic (stone-walked) individuals of *S. muticum* have also been found in subtidal seagrass beds in the Yealm estuary and Looe, Cornwall (Strong, 2003).

The habitats where *S. muticum* is found in Strangford Lough, Northern Ireland are described in Section 9 and in Scotland are described in Section 10.

4.0 ADAPTATIONS OF *SARGASSUM MUTICUM* THAT FACILITATE ITS DISPERSAL AND GLOBAL EXTENSION OF ITS RANGE

4.1 Growth features

Growth is affected by many factors, both abiotic and biotic, but principally seawater temperature, light quality and annual cycles of day-length.

*S. muticum g*ermlings have an extremely rapid growth rate when compared to native marine algae in the UK. Hales and Fletcher (1990) observed maximum growth rates ranging from 0.2-0.36 mm per day under favourable conditions. This is several times faster than other indigenous algae found around the British Isles. For example, the growth rate of *Ascophyllum nodosum* germlings is 0.02 mm per day, of *Halidrys siliquosa* germlings is 0.03 mm per day and of *Fucus vesiculosus* germlings is 0.035 mm per day (Hales and Fletcher, 1990).

Steen and Rueness, (2004) found that at 17°C, *S. muticum* germlings were also more than seven times larger and more robust than *F. serratus* and *F. evanescens,* which grows in approximately the same vertical zone. This may lead to an advantage during the early stages of substrate competition, although at 7°C, *S. muticum* was outgrown by both fucoids. Norton (1977a) found that, following settlement, the growth rate of germlings was significant, particularly at higher water temperatures. At 25˚C, germlings grew into 10 mm long plants in only three weeks and at 15˚C, they grew three times faster than the locally dominant fucoid, *Fucus distichus*.

In developed plants, growth rates of 4 cm per day have been recorded on the Pacific coast of North America and in the Solent, UK (Nicholson *et al.,* 1981; Critchley, 1981). Strong (2003) found that *S. muticum* typically grew by 20 mm per day during late spring and early summer in Strangford Lough, Northern Ireland. Summer growth rates of the populations of two Isle of Wight sites, St Helens and Bembridge were similar, at. 21 mm and 24 mm per day (Lewey and Farnham, 1981).

S. muticum has an annual cycle of growth, reproduction and dormancy, known as a pseudoperennial lifecycle. However, the timing of this annual cycle appears to be very flexible and differs in each region where it has been introduced (Jephson and Gray, 1977; Norton and Deysher, 1989). The yearly lifecycle of an individual *S. muticum* plant was described by Wernberg-Møller *et al.* (1998) "In spring, an individual *S. muticum* plant comprises the perennial holdfast and the main axis. New annual growth is in the form of primary laterals, which are represented as short and crisp basal leaves. The number of air vesicles and secondary laterals increase on the primary laterals as the season progresses. The colour of the plant becomes lighter and by the middle of the season, basal leaves are gone or strongly reduced. Tertiary laterals appear and the number of air vesicles is large. This results in a slim erect stature. It is at this point that the biomass of the plant is at its greatest. Receptacles form but are not yet fertile. The colour of the plant is now light yellow. In late summer, fertile receptacles dominate, appearing dark brown. Almost all the air vesicles have gone and the structure has almost collapsed due to the laterals disintegrating. Towards the end of the season, new primary laterals start to bud from the old perennial axis." Therefore a possible explanation for the successful expansion of *S. muticum* can be attributed to it possessing "both *r*- and K-selected species characteristics. It has a high growth rate (r) (Norton, 1976), large propagule production (r) (Norton, 1976), high thallus differentiation (K) and a long lifespan (K)" (Critchley, 1981; Wernberg-Møller *et al.,* 1998).

Gorham and Lewey (1984) investigated the seasonal growth of *S. muticum* and concluded that rapid early growth was not supported by reserves of stored polysaccharides since the amounts present were insufficient. Surprisingly, these reserves increased during the period of most rapid growth. Lewey and Gorham (1984) found that plants had the highest content of photosynthetic pigments in winter, suggesting that these pigment reserves allow very high rates of photosynthesis in spring, supporting rapid growth. In the summer, the quantities of pigments decline as a result of dilution due both to the rapid growth and to photo-degradation which prevents photo-oxidation.

Gorham and Lewey (1984) found that both juveniles and young adults of *S. muticum* had high concentrations of photosynthetic pigments. As growth continued, new pigments were manufactured, but not at a rate sufficient to maintain the concentration, thus the overall effect was the dilution of the pigments with age. Gorham and Lewey suggested that the high pigment content in younger individuals of *S. muticum* was responsible for the rapid growth of thalli early in the year. Arenas *et al.* (1995) and Rico and Fernandez (1997) also state that *S. muticum* showed the highest pigment concentrations and values for photosynthesis between March and May in the young, non-reproductive thalli, with a significant decrease in both parameters in June in the older, reproductive plants. However, this decline was considered to be a product of phosphorus limitation of nitrogen assimilation, rather than pigment dilution, by Rico and Fernandez (1997) and Arenas *et al.* (1995). Seasonality of photosynthesis has also been recorded in other *Sargassum* species (Kilar *et al.,* 1989).

Hales and Fletcher (1989) investigated the optimum irradiance for growth and found that the initial growth of germlings of *S. muticum* was inhibited at a photon flux density of 88 μE m^{-2} s^{-1} and terminated at a photon flux density of 175 μE m^{-2} s^{-1}. However, the ability to tolerate and utilise these high photon flux densities increased as early development proceeded. During the first two weeks of culture at 175 μE m^{-2} s^{-1} the mean germling length increased by 0.3 mm, yet during the second two weeks of culture the mean length increased by 4.9 mm. Hales and Fletcher (1989) stated that the optimum irradiance for growth may increase as young plants of *S. muticum* continue to develop. In comparison with other species, the optimum irradiance for *S. muticum* germlings was much higher than for the germlings of many other native species, e.g. young *Laminaria* spp., *Himanthalia elongata* and several subtidal red algae (Hales and Fletcher, 1989).

Strong (2003) working in the Dorn, Strangford Lough, investigated the irradiance absorption of *S. muticum* canopies. He found that the canopy of *S. muticum* had a strong shading effect, as previously observed (Critchley *et al.,* 1990; Curiel *et al.,* 1998) and that this was significantly greater than the native *L. saccharina*. In an unvegetated habitat, 89% of sub-surface irradiance penetrated to the substratum at low tide (depth 0.35 m), whereas under algal canopies this value was less than 5%. Canopies of *S. muticum* absorbed 97.2% of the sub-surface irradiance, compared to 95.6% for *Laminaria saccharina* canopies. In a native algal canopy, less than 5% of the light reaches the sub-canopy, so the extra 2% absorption by *S. muticum* potentially represents an approximate 40% loss of the available light for the sub-canopy macroalgae. Young thalli of *S. muticum* can probably tolerate and ultimately exploit higher irradiances than *L. saccharina*, supporting the rapid rates of growth seen during the spring (Strong, 2003).

S. muticum is high-light dependent in the sense that growth is sustained by higher photosynthetic rates during a short but favourable spring period with high light and nutrient conditions (Rico and Fernandez, 1997). Accordingly it can be said that *S. muticum* exhibits a responder-type reaction both in physiology and in phenology, with a marked physiological slowdown during the summer when resources are diverted to reproduction, which is followed by senescence, decaying and dying back to the basal portion (Strong, 2003).

Kane and Chamberlain (1979) found that *S. muticum*'s growth does not appear to be limited by the availability of nutrients or available nitrogen. Gorham (1979) found that growth was not limited by the amount of endogenous plant growth hormones.

Thomas and Tregunna (1968) documented the use of bicarbonate by *S. muticum* and suggested it supported fast rates of growth. The reaction is catalysed by extracellular carbonic anhydrase, which converts HCO_3^- to OH^- and CO_2; CO_2 is then taken up through the plasmalemma. Recent studies have also found this process in other brown algae such as *Fucus serratus* and *Laminaria saccharina* (Haglund *et al.,* 1992).

4.1.1 Regional variations in the annual cycle of growth, reproduction and dormancy

In Japan, under the constraints of its native environment, S. *muticum* accomplishes its growth and reproduction by the middle of the summer. It then enters a distinct dormant phase between mid-summer and late autumn, when the alga dies back to the perennial holdfast. The growth cycle then recommences in the late autumn (Yendo, 1907: Rueness, 1989).

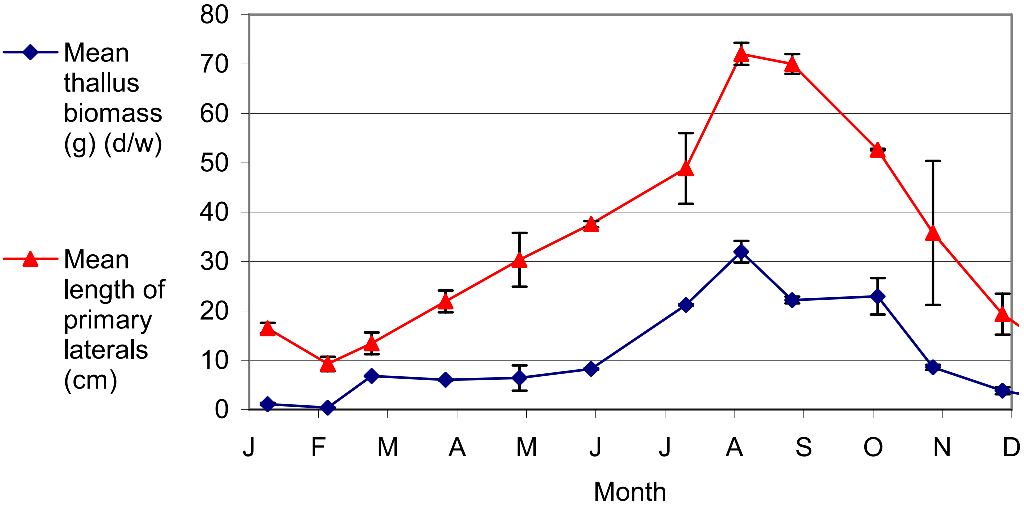
As *S. muticum* populations spread down the Pacific coast of North America, the occurrence and duration of dormancy appeared to decline as the water temperature increased in the more southern locations (Jephson and Gray, 1977). In the warmer southern waters off the Pacific coast of North America, during the autumn, newly recruited juvenile plants and new branches developing from the perennial main stalk begin to grow. The plants undergo a period of rapid vegetative growth over the late winter and spring, producing the fronds of primary, secondary, tertiary and even fourth order laterals. Nicholson *et al.* (1981) found that at Santa Catalina, southern California the intense growth period was between February and May and that fertile plants could be found at any time of the year. The density of the plants varied between five and 27 plants per square metre and it was calculated that a square meter with 15 plants could produce a total of 108g of tissue a day (Nicholson *et al.,* 1981). The growth rate then declines rapidly, by up to 80%; as the plants become fertilised reproductive growth inhibits vegetative growth. After the period of sexual reproduction, the fronds become senescent and die back. Many air vesicles may be lost, resulting in the plant losing buoyancy and sinking. Gradually the fronds are shed, leaving only the perennial holdfast, main stalk and some ‘winter leaves’ (Deysher, 1984; Norton and Deysher, 1989; Gorham and Lewey, 1984; Norton, 1977). In Mexican waters, fronds and fertile plants may be present throughout the year (Espinoza, 1990).

In Europe, dormancy is not apparent in more southerly populations. *S. muticum* undergoes maximum vegetative development from winter to early summer; October to July. Vegetative growth is reduced as reproductive receptacles develop between April and October. Many of these fertile laterals absciss during the summer months and being buoyant, drift away (Farnham *et al.,* 1981). During the year, mature primary laterals can reach lengths of 5 m but normally grow to lengths of 1-3 m. Due to the numerous air vesicles, the plants float close to the surface and are generally conspicuous from April to October (Critchley 1983e; Gorham and Lewey, 1984).

In the Solent, southern England, no dormant period has been observed. New growth starts before the last season’s lateral branches have degenerated. The growth rate of the primary laterals is on average 1-2 cm per day but can reach 4 cm per day between May and June. Reproductive maturity occurs between July and September when vegetative growth is reduced (Jephson and Gray, 1977; Lewey and Farnham, 1981). The plants begin to break up from early August, with a rapid drop-off in mass between October and November (Critchley, 1983d).

In Strangford Lough, Northern Ireland, Strong (2003) found that the mean number of main axial shoots increased from three in February to a peak of eight in October. The mean number of primary laterals per plant decreased slightly during the year to a low in September to November. A brief period of dormancy, when the plants die back to the perennial holdfast, was observed between December and February. He found that the mean plant biomass of *S. muticum* increased from February to a peak of 30 g in August, after which plant biomass declined rapidly to a low at the end of December. The mean primary lateral length followed a similar pattern, with elongation starting in February and increasing to a maximum of 0.70 m in August, after which the laterals were cast from the holdfast and the mean length was reduced to just 0.10 m in February. The change in mean length of the primary laterals suggests that *S. muticum* typically grew by 20 mm per day during late spring and early summer. The initial development and the timing of the peak in plant biomass (dry weight) and mean primary lateral length were similar in each of the three years, 2000 to 2002, illustrated in Figure 5.

Figure 5
Annual variation in the mean thallus biomass (dry weight) and mean primary lateral length for Sargassum muticum collected from the Dorn, Strangford Lough: 2000-2002
(Strong, 2003)



Strong (2003) found that *S. muticum* in Strangford Lough exhibited a seasonal periodicity in lateral elongation, fertility and biomass. Growth of *S. muticum* began in February and ended in September. The majority of plants started receptacle development in June and released zygotes during August. Reproductive development slowed the elongation of the laterals. A brief period of dormancy, when the plants died back to the perennial holdfast, was observed between December to February.

There is a marked tendency for populations of *S. muticum* at higher latitudes to develop sexually later in the year. Norton and Deysher (1980) examined the reproductive development of *S. muticum* at three different latitudes on the Pacific coast of North America. At 33°5'N (La Jolla), 34°25'N (Santa Barbara) and 48°33'N (Friday Harbor), *S. muticum* populations reached peak fertility in April, July and August respectively, thus suggesting a latitude dependency. Transplants of *S. muticum* to other parts of its introduced range on the Pacific coast of North America by Norton and Deysher (1989) confirmed that the timing of reproduction was under local environmental control rather than being due to the occurrence of different physiological ecotypes at different latitudes. Studies from Baja California (Mexico), Aramar Beach (Spain), Portsmouth (UK) and Strangford Lough (Northern Ireland), confirm this latitudinal shift. However, this generalisation does not necessarily apply to every population of *S. muticum*. At Baja California (c. 32°N), the most southern population of *S. muticum*, the peak of reproductive development is considerably later than expected, despite fertile plants being found at any time of the year. This can be attributed to the cold water upwelling at Baja (Aguilar-Rosas and Galindo, 1990).

Initiation of growth of *S. muticum* in winter raises the possibility that it is under short-day photoperiodic control (Strong, 2003). The later development of sexual maturity of *S. muticum* with increasing latitude could be a result of response to photoperiod, temperature, or an interaction between these factors. Photoperiodic responses to daylength are important in the reproductive timing of many species of algae but research does not appear to have been undertaken on photoperiodic responses and the initiation of reproduction in *S. muticum*.

4.1.2 Age determination in Sargassum muticum

Each year the number of lateral branches may increase e.g. in the first year two are produced, in the second year up to five are produced and in the third year up to nine are produced (Jephson and Gray, 1977, Critchley, 1981). Counting the number of stumps that remain after primary laterals have abscissed can provide an indication of age. Seasonal activity of the meristoderm, found at the periphery of the main axis, is responsible for annual growth rings observed in transverse sections. However, branching of the main axis in the third year appears to inhibit further meristoderm activity. Each main axis then undergoes independent, monopodial development, which results in large variations in the numbers of initials and developed laterals. This makes age determination of older *S. muticum* unreliable (Critchley, 1981). For example, the holdfasts of plants growing around San Juan Islands in California can produce up to 18 primary lateral branches in early spring, with each growing up to 3 metres in length (Britton-Simmons, 2004).

Population studies on the basis of this ageing scheme indicate that *S. muticum* has a maximum life-span of around three to four years, but heavy losses due to physical damage and detachment result in the average age of populations being 1-2 years (Critchley, 1981).

Strong (2003) produced an age-specific morphological for *S. muticum*, illustrated in Figure 6. This shows that year one plants can have up to three primary laterals and up to eight axial shoots. Year two plants can have up to five primary laterals and up to 15 axial shoots. Year three plants can have up to 12 primary laterals and up to 18 axial shoots. If the number of main axes exceeds approximately 18, then the monopodial holdfast branches dichotomously. Strong concluded that plants older than four years are impossible to age.

Davison (1999) found that in Strangford Lough, although the evidence suggested that *S. muticum* had originated on the tidally exposed oyster trestles before spreading to the Calf Rock, the number of basal branches of the Calf Rock population was higher each year surveyed (1995 – 1997) than for oyster trestle population. However, this may have been an indication that Calf Rock population was more ‘natural’ and consequently, more successful and subject to less environmental stress (aerial exposure) than the oyster trestle population. It was also found that the number of lateral branches declined between 1995 and 1997, which may have reflected the thinning effect of the 1995 and 1996 containment operations (Davison, 1999).

In a study by Wilson (2006) on the Isle of Cumbrae, west Scotland, he found that the method of counting basal branches to map the spread of *S. muticum* in terms of population age structure was flawed due to exposure affecting the plant mortality rate.

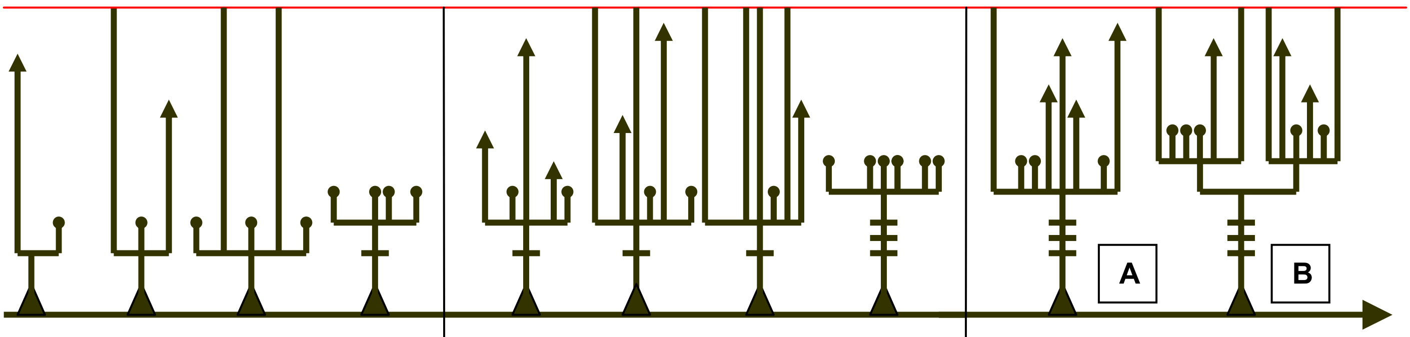
4.1.3 Life table analysis of Sargassum muticum

Strong (2003) reported that in Strangford Lough, the greatest amount of *S. muticum* mortality occurred between the settlement and recruitment of juvenile plants into the Year One age class. Approximately two thirds of the individuals in the Year One age class join Year Two.

Only a third of the individuals progressed from Year Two to Year Three, and a third of these went from Year Three to Year Four. Consequently, adult mortality in *S. muticum* population was lowest for Year One plants and increased for plants in the third and fourth year class. Total fertility per thallus increased with age, although the greater abundance of young plants meant their reproductive contribution was more important at the population level (Strong, 2003).

Excluding the juvenile phase, the increasing mortality of *S. muticum* with age is probably related to thallus size and the loose substratum common in Strangford Lough (Strong, 2003). As individuals become older, they increase the number and length of primary laterals, which in turn increases drag. Proportionally, holdfasts do not develop as much with age, and combined with an unstable substratum, large adult plants are more likely to shear off or stonewalk than smaller plants. Critchley (1981) also found the population of *S. muticum* on a mobile, soft sediment substratum in Bembridge, Isle of Wight, to be dominated by Year One and Year Two plants, whereas a population attached to bedrock was well represented in all four year classes, especially the older Year Three and Year Four classes. The contrast in age structure found between hard and soft substratum areas by Critchley (1981) indicates that attachment strength ultimately influences the age distribution and that older, larger plants are more likely to be lost in the absence of bedrock substratum (Strong, 2003).

Figure 6
An age-specific morphological of Sargassum muticum
(Strong, 2003)



Year One thalli

Settled zygotes from the previous year will start main axial growth 6-8 weeks after settlement. Primary lateral growth will start in February.

Throughout the first year, the main axis will continue to develop to a maximum of 8 axial shoots, with 2-3 forming primary laterals. The second lateral will not form until the first primary lateral has reached at least 0.5 m.

At the end of the first year, the primary laterals are cast and leave scars or stumps on the holdfast.

The population within Strangford Lough has a brief dormant period, between December and February.

Year Two thalli

In February, the primary laterals start growing again. One primary lateral will grow quickly, but several others will also start growing after a lag period. Year two plants grow 4-5 primary laterals within that year.

The main axial shoots will continue to develop and plants can finish the year with 12-15 axes and the holdfast begins to look crowded with axial shoots.

The attachment disc increases slightly in diameter, but tends to look proportionally smaller than the rest of the holdfast.

Very occasionally, one of the primary laterals is not cast and can re-initiate growth the next season.

Year Three (A) and Year Four + (B) thalli

By mid-February, growth is initiated and numerous primary laterals begin growing simultaneously. By August, third year plants in Strangford Lough can have up to 10-12 primary laterals that are over 0.50 m.

Older plants can have longer primary laterals, with some individuals reaching 6 metres.

If the number of main axial shoots exceeds about 18 (year four plants), then the monopodial holdfast will branch dichotomously.

Plants older than four years are impossible to age.

4.2 Regeneration features

The perennial holdfast, main stalk and basal leaves have the ability to regenerate rapidly when fronds are lost by natural senescence, physical damage or grazing, particularly in warmer waters.

The development of the secondary lateral appears to be dependent on the state of the primary lateral. If the primary lateral branch of a plant is damaged in any way, the secondary lateral can effectively replace it and mature more rapidly than normal to compensate (Fletcher and Fletcher, 1975b; Jephson and Gray, 1977). Herbivorous grazing damage has been observed to initiate the rapid maturation of the secondary lateral (Withers *et al.,* 1975).

Abscised laterals can continue to grow and become fertile while free-floating (Fletcher, 1975; Tsukidate, 1984).

If receptacles are damaged, they can regenerate under a wide range of temperatures and day lengths but regeneration is inhibited in winter conditions. Regeneration is a particularly rapid process with mature, zygote bearing receptacles (Hales and Fletcher, 1992).

4.3 Reproductive features and strategies

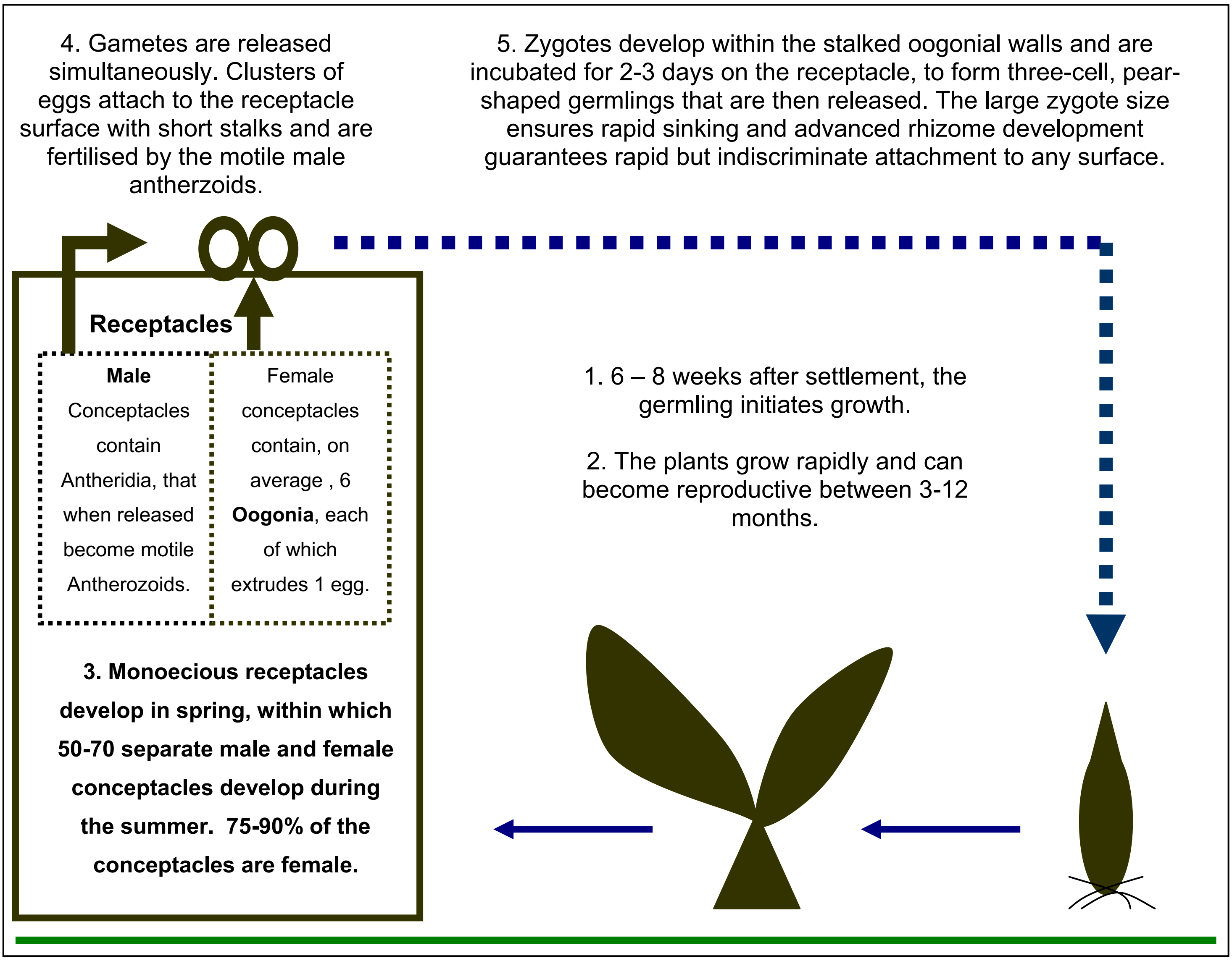
A fertile *S. muticum* plant bears hundreds of small hermaphrodite receptacles that expel gametes in a number of discreet pulses. The fertilised eggs cling to the outside of the receptacle for one to several days so that by the time the propagules are liberated into the sea, they are not just zygotes but quite advanced small germlings with developing rhyzoids. Abscissed branches that are fertile, or become fertile, while floating for up to three months, allow long distance dispersal of germlings. The life cycle is illustrated in Figure 7.

In *S. muticum* sexual reproduction is characterised by the production of numerous small receptacles in various stages of maturity. The receptacles are borne alternately along the axils of leafy (lanceolate) laminae of tertiary laterals, in the middle region of the plant. Strong (2003) found that in Strangford Lough, Northern Ireland, the number of receptacles was proportional to the length of the tertiary laterals.

Receptacles are lumpy, jelly-filled structures borne on a short stalk and have a stalked air vesicle at their base. Initially they are quite swollen but later, they become more linear. They are terete in section and reach lengths of 15-22 mm. The maturest receptacles are found at the branch tips (Fletcher and Fletcher, 1975a; Nicholson *et al.,* 1981).

The receptacles of *S. muticum* are monoecious, containing both male (antherida) and female (oogonia) gametes within separate conceptacles, allowing self-fertilisation to occur (Critchley, 1983c). Each receptacle contains 50 to 70 single-sex conceptacles (Norton and Deysher, 1989). The conceptacles are tiny cavities that contain the reproductive gametes (gametangia) and are arranged spirally upon the receptacle. As the receptacles mature, the conceptacles are visible as minute pale spots. The more abundant female conceptacles are usually almost entirely filled by rounded oogonia, between which lie dark, branched sterile hairs (paraphyses). The female conceptacles can contain between three and 22 oogonia but they generally contain six and each oogonia produces a single egg (Norton and Deysher, 1989). With 75-90% of the conceptacles being female, each receptacle can produce more than 300 eggs. In the male conceptacles, the colourless, branched hairs are smaller and give rise to oval antheridia at their tips (Fletcher and Fletcher, 1975a; Norton and Deysher, 1989).

Figure 7
The life cycle of Sargassum muticum
(Strong, 2003)



4. Gametes are released simultaneously. Clusters of eggs attach to the receptacle surface with short stalks and are fertilised by the motile male antherzoids.

5. Zygotes develop within the stalked oogonial walls and are incubated for 2-3 days on the receptacle, to form three-cell, pear-shaped germlings that are then released. The large zygote size ensures rapid sinking and advanced rhizome development guarantees rapid but indiscriminate attachment to any surface.

Male Conceptacles contain Antheridia, that when released become motile Antherozoids.

Female conceptacles contain, on average , 6 **Oogonia**, each of which extrudes 1 egg.

1. 6 – 8 weeks after settlement, the germling initiates growth.

2. The plants grow rapidly and can become reproductive between 3-12 months.

3. Monoecious receptacles develop in spring, within which 50-70 separate male and female conceptacles develop during the summer. 75-90% of the conceptacles are female.

Photographs of the reproductive stages of *S. muticum* from Strangford Lough are presented in Figures 8 – 12.

The conceptacles nearest the tip darken as they mature towards oogonia release. The oogonia are initially released from those conceptacles nearest the tip, for fertilisation on the receptacle surface (Critchley, 1983b).

Large numbers of ova are squeezed out through the conceptacle ostiole and adhere to the receptacle surface with mucilaginous stalks, retained as a visible whitish mass for approximately 24 hours. 13-17 oogonia form a cluster around the ostiole through which they have been extruded. The antheridia are squeezed out through their conceptacle ostiole in relatively large numbers but are pushed beyond the attached oogonia and out into the water current. The walls of the antheridia then gelatinise releasing large numbers of active antherozoids, which are colourless and pear-shaped with two flagella (Fletcher and Fletcher, 1975a). The mature eggs, attached to the outer receptacle wall by their short stalks, are then fertilised by the motile male antherozoids.

Strong (2003) calculated that the average, sexually mature individual of *S. muticum* in Strangford Lough produced 7.45 million ova, or 36,369 eggs per gram of adult biomass. Estimates for the total oogonial output suggest that the number of eggs released per plant increased with plant age for *S. muticum*. The mean egg production standardised to plant biomass (wet weight) showed that one year old plants proportionally produced more eggs per gram of adult biomass. However, he found that for two, three and four year old plants, the egg production per gram of adult biomass increased by between 18-25% each year, as shown in Table 2.

Table 2
Estimated total number of oogonia produced per year from thalli of* Sargassum muticum *in each of the four age classes
(Strong, 2003)

Age class	**Mean number of eggs produced per plant per year***	**Mean number of eggs produced per gram of plant (fresh weight)**
Year 1	5,384,073	61,182
Year 2	7,455,715	36,369
Year 3	14,910,736	45,598
Year 4+	36,685,819	52,861

*****Percentage female conceptacles per receptacle 80% (Fensholt, 1955; Norton, unpublished)

Norton and Deysher (1989) found that a plant in its first season, weighing only 15g, could release well over 500,000 eggs. Norton and Deysher (1989) calculated total egg output for *S. muticum* in Friday Harbor, Washington to be, on average, 34,400 eggs per gram of tissue. The Strangford Lough average of 50 conceptacles per receptacle (Strong, 2003) is similar to the equivalent mean of 60 at Friday Harbor recorded by Norton and Deysher (1989). By contrast, Fensholt (1955) and Scagel (1956) observed less than half that number of conceptacles per receptacle in British Columbia.

A marked periodicity has been observed in the extrusion of oogonia onto the receptacle surface. It occurs, on average, every 13 days and corresponds with the period shortly after spring tides. Oogonia release occurs synchronously from a number of conceptacles, usually confined to the area behind the apical zone. Freshly released oogonia were usually surrounded by large numbers of actively motile antherozoids suggesting that they had a similar release period (Fletcher, 1980a).

The simultaneous release of large quantities of male and female gametes from all the mature receptacles within a population of *S. muticum* ensures high rates of successful fertilisation. The active ejection and wider dissemination of the male antherozoids also increases the chances of cross-fertilisation while reducing the chances of self-fertilisation where antherozoids fertilise oogonia from the same receptacles (Fletcher and Fletcher, 1975a; Fletcher, 1980a).

Following fertilisation, the zygotes develop within their oogonial walls and are retained or “incubated” on the receptacle surface, attached by mucilaginous stalks, for a period of two to three days. During this time the zygote cell divides to form a three-cell, pear-shaped germling. The two larger, upper cells divide to produce the young plant body while the smaller, lower cell divides into rhizoid “initial” cells. A characteristic “fuzzy” band appears around the apex of the receptacle as the zygotes develop into multi-cellular germling plants on the receptacle surface. This stage is generally reached simultaneously by all the germlings (Fletcher and Fletcher, 1975; Fletcher, 1980a).

At this stage, the slightest agitation of the plant will result in the release of large numbers of germling plants into the water. The release mechanism appears to involve the gelatinisation and collapse of the protective oogonial walls. Once released the germlings settle rapidly onto the substrate and the sticky terminal regions of the rhizoid initial cells ensure an immediate and tenacious attachment (Fletcher, 1980a).

The retention of the oogonia and zygotes on the receptacle surface is typical of many *Sargassum* species and offers numerous advantages to the immediate release of oogonia into the water that is employed by other fucoids in the British Isles.

Retention greatly increases the chances of either cross- or self-fertilisation. The mucilaginous stalk, which retains the oogonia and developing zygotes, offers protection from damage and ensures uniform conditions during the critical stages of growth. If the environmental conditions are unsuitable, the zygote germination process and release will be delayed (Fletcher and Fletcher, 1975a). The release of developed germlings enhances survival under adverse environmental conditions and aids rapid sinking and settlement (Fletcher, 1980a).

Most macroalgae can be divided into two modes of propagule dissemination, i.e. either 'broadcasters' or 'brooders'. In brooding, fertilisation occurs internally after sperm travel through the water column, whereas broadcasters exhibit external fertilisation after the release of both sperm and eggs. The mode of reproduction for *S. muticum* fails to fit in with either brooder or broadcaster category, as both eggs and sperm are released from the adult plant, but the eggs are temporally retained on the outside of the receptacles where self fertilisation typically occurs. This mechanism probably ensures that most of the eggs are fertilised before detaching from the adult plant. It thereby both reduces the wastage of eggs that might occur in a broadcaster mode of reproduction, and also decreases the uncertainty of successful sperm dissemination in a brooder mode. For most of the fucoids (broadcasters), fertilisation values are 70-100%, rather higher than the 30-80% for red algae (brooders). The fertilisation values for *S. muticum* appear to be very high, if not 100%, which might represent a successful trait that adds to the invasiveness of *S. muticum* (Strong, 2003).

Finally, the retention of the zygotes on the receptacle surface provides the opportunity for long distance dispersal. The casting and decay of all the fertile branches is an inevitable consequence of reproduction in *S. muticum*. However, the branch axis usually rots long before the receptacles. These abscised fertile branches may bear ripe and maturing receptacles so that germlings may continue to be released days or weeks after leaving the parent plant. In addition, abscised vegetative branches can continue to grow while free-floating and may also become sexually mature (Fletcher and Fletcher, 1975a; Fletcher, 1980a; Norton, 1981).

Warmer water temperatures can increase gamete production and extend the reproductive period. The dense surface canopy that can be formed by the feathery fronds of *S. muticum* can cause the surface water temperature to elevate (Critchley *et al.,* 1990a).

Strong (2003) found that the production of receptacles represented a total standing reproductive contribution of 55% of the total biomass of a plant of *S. muticum* from Strangford Lough, which was similar to the value obtained by Norton and Deysher (1989) on the Pacific coast of America. However, this contrasts with the results of Arenas and Fernandez (1998), who found that individuals of *S. muticum* on Spanish coastlines had a mean allocation of 24% in May and 20% in August. The maximum values recorded by Arenas and Fernandez (1998) were 55% in 1991 and 50% in 1992, much closer to the observed contribution in Strangford Lough. Variation in local physical conditions might explain why reproductive allocations differ for *S. muticum* between study sites. The overall size distribution of thalli in the Spanish population was skewed towards small plants, possibly due to the greater wave exposure at the site. The 55% contribution of *S. muticum* in Strangford Lough to receptacles is not an exceptional allocation for high-fecundity brown algae. Other fucoid examples that show similarity to the values obtained for *S. muticum* include *Ascophyllum nodosum*, which invests approximately 53% of its annual production of fresh weight to reproduction, while *Fucus spiralis* allocates 62%, *Fucus vesiculosus* 62% and *Fucus distichus* 64% (Mathieson and Guo, 1992).

Within three months of arriving at the new site, *S. muticum* plants may become fertile, providing a significant advantage over many of the native fucoids, which may have to wait until their second year to become fertile (Norton, 1976). However, a period of two to three years is generally required for the development of a breeding stock that allows the rapid extension of a population (Critchley *et al.,* 1983). As the plants become older, the number of fronds increase so that the reproductive output of each plant and the stand or population increases rapidly (Critchley, 1983d).

Figure 8
Sargassum muticum from Strangford Lough, 1995
Sexual development stage I: vegetative tissue only
(Davison and Davison, 1995)

Figure 9
Sargassum muticum from Strangford Lough, 1995
Sexual development stage III: Well developed receptacles and conceptacles becoming obvious
(Davison and Davison, 1995)

Figure 10
***Sargassum muticum* from Strangford Lough, 1995**
Sexual development stage IIIa: Well developed receptacles and maturing conceptacles, no zygotes obvious on the surface
(Davison and Davison, 1995)

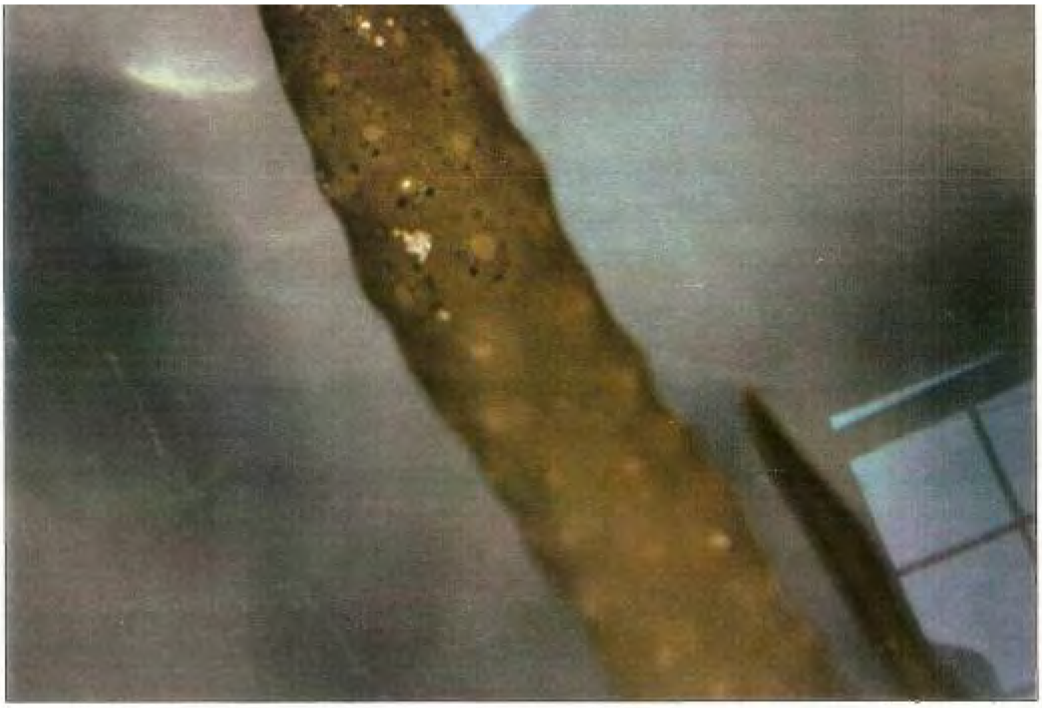


Figure 11
Sargassum muticum from Strangford Lough, 1995
Sexual development stage IV: Mature receptacles and conceptacles, zygotes obvious on the surface
(Davison and Davison, 1995)

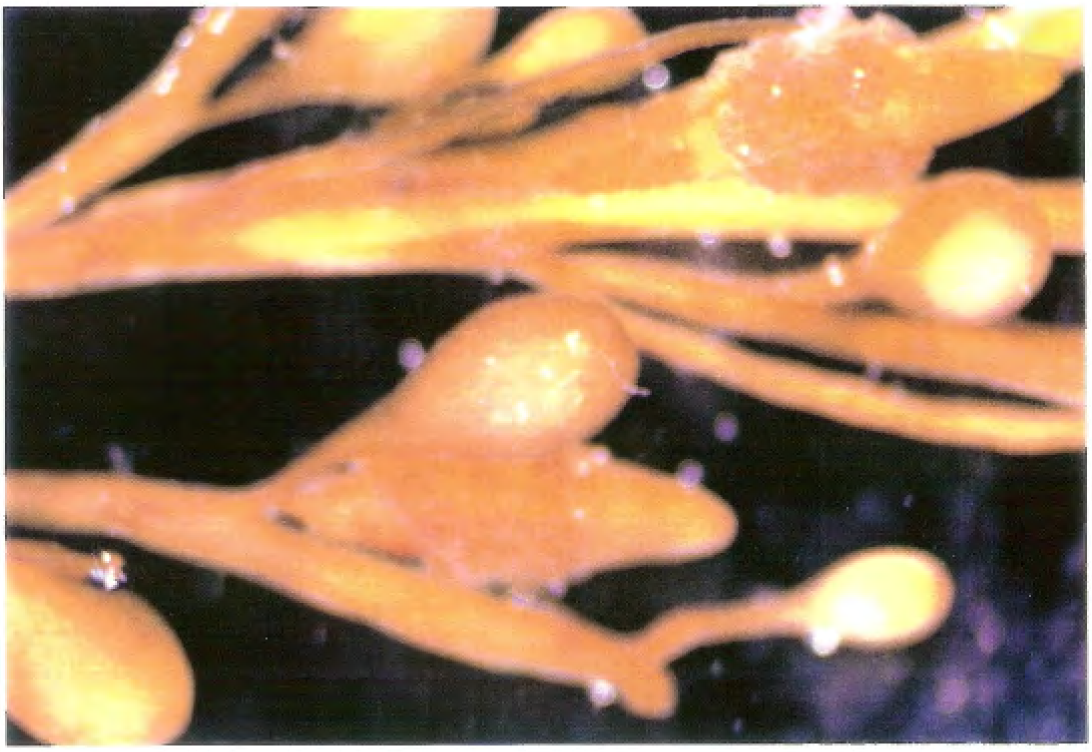
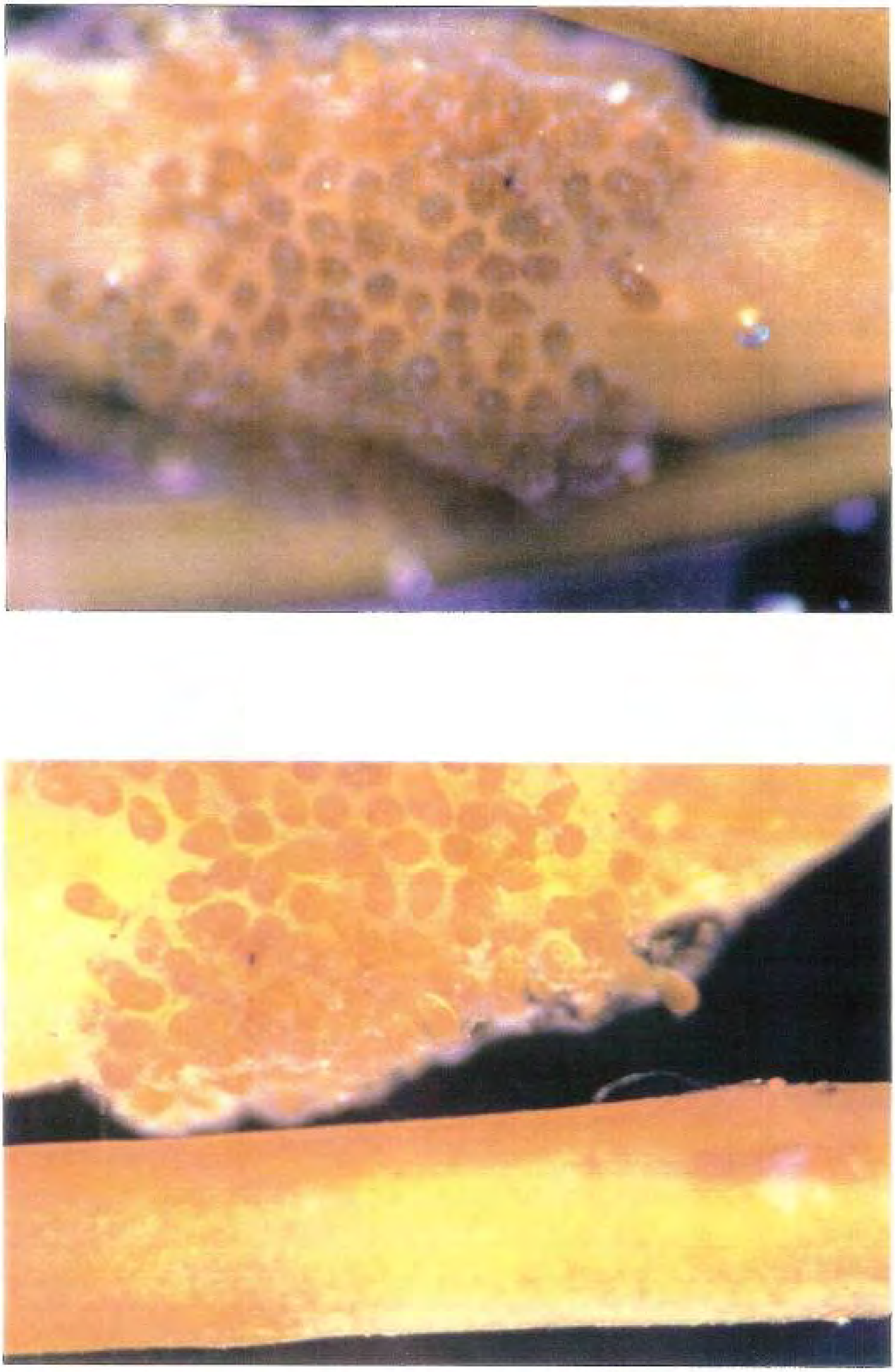


Figure 12
Sargassum muticum from Strangford Lough, 1995
Sexual development stage IV: Zygotes obvious on the surface
(Davison and Davison, 1995)



4.3.1 Variations in reproductive periods

There is a marked tendency for populations of *S. muticum* to develop later in the year at higher latitudes, but the timing at each site is related to temperature and day length. The reproductive periods of *S. muticum* at different latitudes are illustrated in Figure 13.

Davison (1999) found that in Strangford Lough, Northern Ireland, the maximum fertility in *S. muticum* appeared to occur during August in 1995 and 1996 but that it moved back to July in 1997. It would appear that while the environmental conditions experienced by both the original populations were not ideal, primarily due to aerial exposure, and may have caused some retardation of plant development, the majority of plants did reach sexual maturity during the summer months. However, it appeared that both of these original populations may have responded to the annual containment operations by becoming fertile earlier (Davison, 1999).

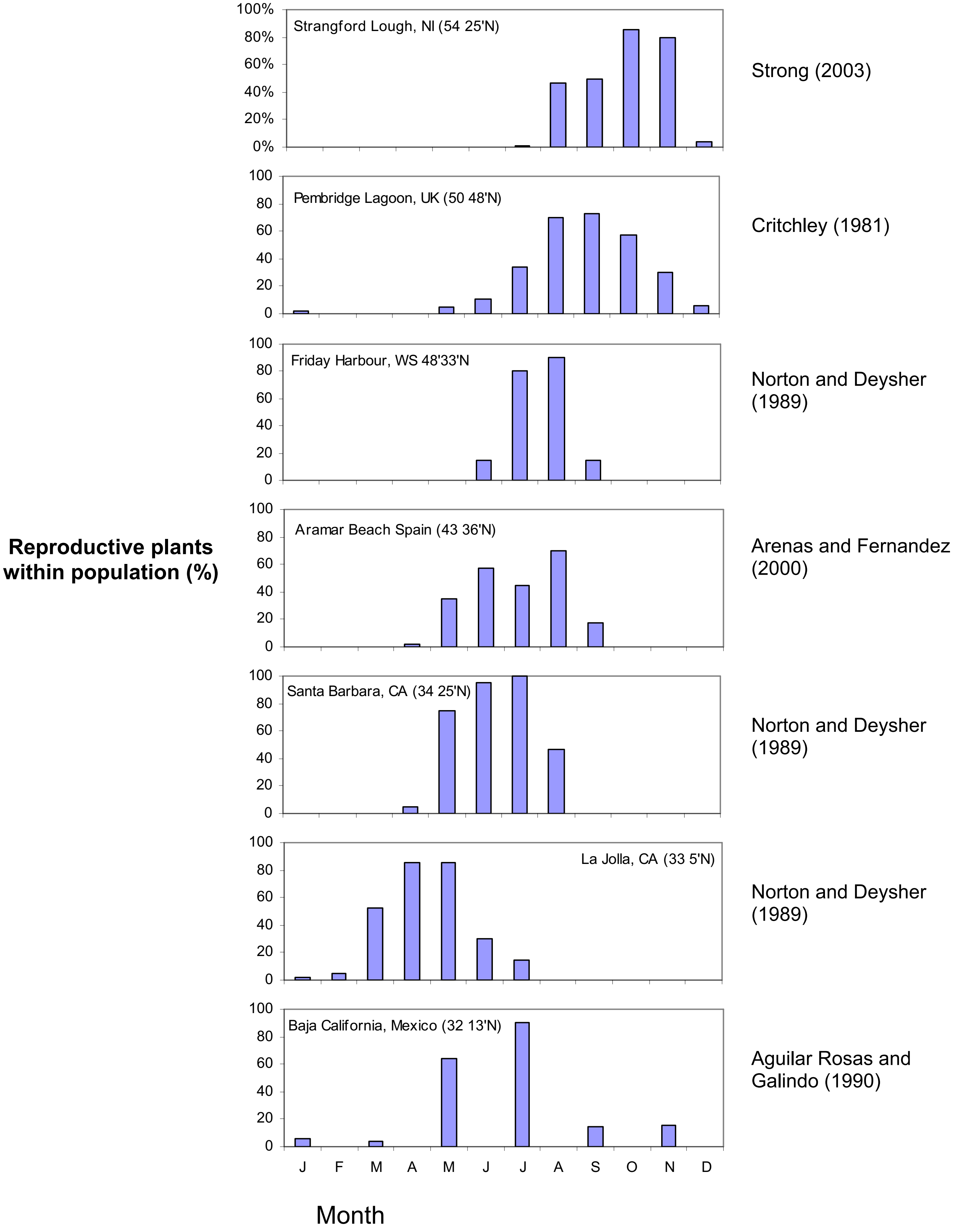
Strong (2003) found that in the populations that developed later throughout the Lough, the onset of reproductive development was fairly consistent between 2000 and 2002 and typically occured between May and June. For all three years, the stage four plants, i.e. those with fully developed receptacles and releasing zygotes, only started to appear in August and peaked in abundance in October, before becoming senescent (stage five) in November. Reproductive plants were very rare in December, i.e. less than 5%.

Fletcher and Fletcher (1975a) investigated the reproductive activity of *S. muticum* at Bembridge, Isle of Wight and found that the reproductive period lasted for five months. Maximum fertility was observed to occur during June and July. By September, receptacles were degenerating and the fronds were heavily colonised by epiphytes, primarily *Polysiphonia urceolata,* but limited reproductive activity was observed to continue into November. Critchley (1983e) found that the reproductive period at Langstone and Chichester Harbours occurred between early June and late September.

It would appear that increasing latitude and stronger seasonality further north in Pacific North America delay sexual development and make developmental stages more discrete (Strong, 2003). On the Pacific coast of the North America, the fertile period for the northerly populations begins much later in the year and is of shorter durations than the more southerly populations. For the Washington populations, it lasted for the four months of June to September, when the average sea surface temperature is around 10˚C. For the southern Californian populations, the fertile period began around January when the average sea surface temperature is 14˚C and finished in July, when the average sea surface temperature is 20˚C. The extended fertile period of the southerly populations may reflect a heterogeneous population, with a staggered succession of fertile plants. Alternatively, or in addition, the fertile period of each individual plant may be prolonged by producing a succession of receptacles on each fertile branch. Additionally, warmer water may encourage the production of a larger crop of gametes and may extend the reproductive life of plants by postponing the abscission of fertile branches that inevitably follows the decline of fertility (Norton and Deysher, 1989; Nicholson *et al.,* 1981).

However, at Baja California in Mexico, the most southerly latitude for *S. muticum*, the peak of reproductive development occurs in July, considerably later than would be expected. Aguilar-Rosas and Galindo (1990) suggested that this is related to cold water upwelling at Baja California. However, fertile plants can be found at any time of the year.

Figure 13
Reproductive periods of Sargassum muticum at different latitudes



4.4 Settlement features and strategies

The release of well-developed *S. muticum* germling plants enhances their chances of survival. They sink more rapidly than most algal propagules and the germling's pear-shape ensures that on settlement, the rhizoid initial cells are placed directly onto the substrate and can secure an immediate adhesion, with the microalgal and bacterial film on the substrate aiding the adhesion. This ensures that holdfast and shoot development can continue without any time lag. In comparison, indigenous algae use settlement mechanisms like sticky outer walls and do not begin to develop rhizoids until they are attached to the substrate. *S. muticum* germling plants exhibit a preference for highly textured or rugose surfaces and shells are particularly favourable.

In brown algae, the attachment rhizoids are typically not developed until several days after fertilisation and so it is usual for the zygote to develop an early adhesion mechanism such as a sticky outer wall to facilitate attachment to the substrate until the rhizoids develop. As *S. muticum* apparently lacks such a mechanism, this species consequently "incubates" the zygotes on the parent receptacle until the germlings develop and are released with protruding rhizoids (Norton, 1981c).

Zygotes that are released from the receptacle before the rhizoid initial cells have developed cannot attach to the substrate. The production of rhizoid initial cells is dependent on the completion of the zygote germination process, which may be delayed if environmental conditions are unsuitable.

As a consequence of their large size (150-200 μm long) and density, *S. muticum* germlings sink very rapidly, averaging a velocity of around 0.6 mm per second, which is faster than many other algal propagules (Norton and Fetter, 1981; Deysher and Norton, 1982). This allows settlement even in rapidly flowing water. Purely on the basis of sedimentation rates, a *S. muticum* zygote released from one metre above the substrate would take 19-24 minutes to sink to the substrate. Obviously, the sinking velocity is of little relevance in comparison to currents and turbulence. Generally, turbulent deposition is the most important force directing propagules to the substrate (Norton, 1992). However, *S. muticum* usually inhabits relatively sheltered waters and form dense stands that further reduce water movement and this can aid germlings sinking down to the substrate (Fletcher, 1980a; Norton, 1981a; Deysher and Norton, 1982).

Germlings attach almost immediately on contact with the substrate. The germling's pear-shape ensures that, on settlement, the rhizoid initial cells are placed directly onto the substrate and are therefore able to secure an immediate adhesion. This ensures that rhizoid and erect shoot production can continue without any time lag (Fletcher, 1980a). The tenacity of adhesion increases with time as the rhizoid mass develops and the quantity of adhesive increases, accumulating at the rhizoid tips. The germling's ability to effectively adhere to a substrate surface develops within 2-18 days after germling liberation but progressively declines thereafter and is lost completely within 49 days, as the quantity of the adhesive (acid mucopolysaccharides) being produced declines (Norton, 1980; Norton, 1983; Deysher and Norton, 1982).

Once secure attachment is achieved, it is not weakened even by the death of the germling. A film of bacteria and microalgae on the surface of the substratum enhances the tenacity of the adhesion, as the mucilage they produce is similar to the germling's adhesive so bonding occurs very readily. In fact *S. muticum* may be able to take advantage of the ready-made adhesion between the bacterial film and the substrate. (Norton, 1983)

It has been found that germlings that do not attach within 48 hours of release from the receptacle do not subsequently attach, even when suitable substrate is available (Deysher and Norton, 1982). Germlings retained on the surface of the receptacle beyond the normal incubation period seem unable to liberate themselves. Even when forcibly released or released through receptacle decay, they are unable to attach to the substratum (Deysher and Norton, 1982).

S. muticum germlings will attach to the first solid surface encountered, even when this is unsuitable for their subsequent development, such as other algae (Deysher and Norton, 1982). The surface texture or rugosity of the substrate plays a vital role in germling survival. Settlement success increases with the rugosity of the substrate. Smooth substrata are the least favourable for germling adhesion. On rough substrata the peaks and exposed surfaces are less favourable than the troughs or sheltered surfaces. Optimum rugosity is provided by substrates where the depths of the troughs or depressions are greater than the height of the germling (Norton, 1980; Norton, 1983).

The presence of existing algal populations on rock surfaces has been shown to inhibit the settlement and successful establishment of *S. muticum* germlings (Deysher and Norton, 1982; De Wreede, 1983; De Wreede and Vandermeulen, 1988; Britton-Simmons, 2006). In such environments the establishment of *S. muticum* may be reliant on disturbance events that create patches of open substrate that enable the settlement of the germlings (Harries *et al.,* 2007a).

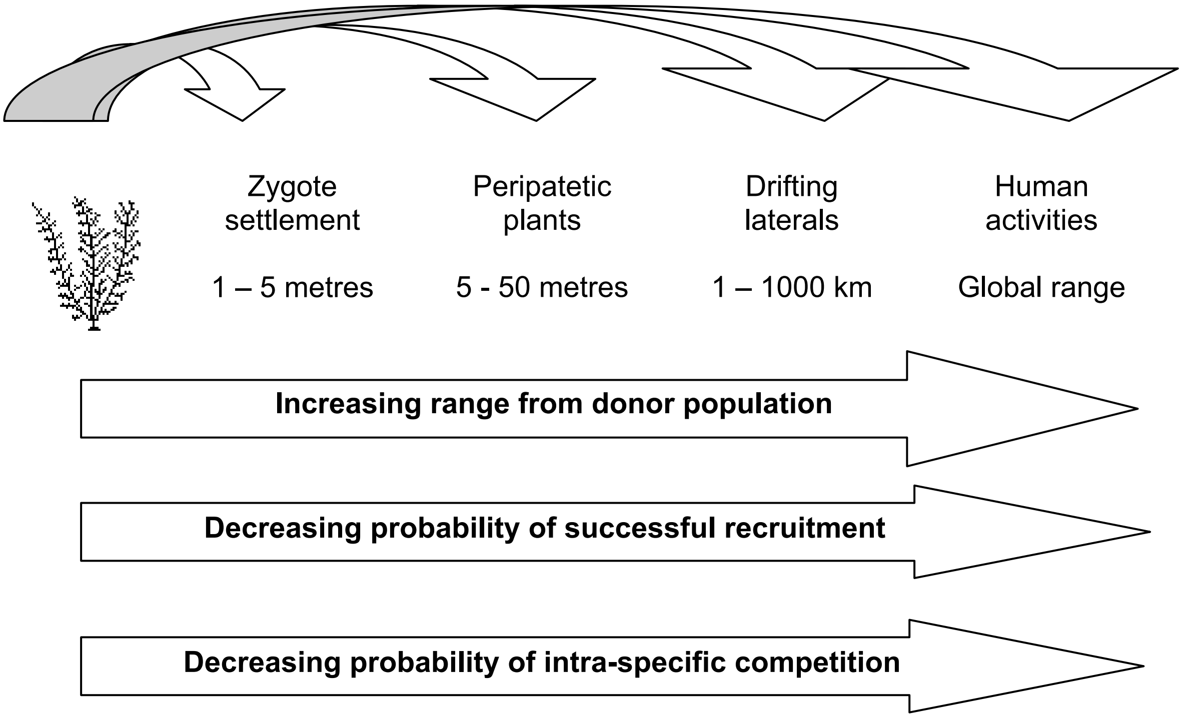
Paula and Eston (1987) observed that re-colonisation by *Sargassum* sp., after the manual scraping of substrata, was extremely rapid, regardless of the time of year. Therefore, a well established community of native macroalgae will be more resistant to colonisation by *S. muticum* than a damaged or stressed community.

Propagules of *Sargassum* sp. have very high mortality rates, with only 0.0045% surviving to become viable recruits and only 0.0001% surviving for longer than 12 months (Kendrick and Walker, 1995). Critchley (1981) found that the survival of *S. muticum* propagules in the Solent by February was below 0.01% and Strong (2003) found that the survival of propagules in Strangford Lough up to February was 0.008%. Strong's (2003) settlement panel experiments found that the greatest loss of propagules occurred in the first month, with only 1% of the settled propagules reaching the second month. Survival was the same for propagules under and outside the canopy for the four month period and was approximately 0.008% of the initial density of zygotes.

4.5 Dispersal and colonisation strategies

Despite the passive nature of dispersal in macroalgae, it has long been recognised that the invasive abilities of *S. muticum* lie, in part, in its dispersal mechanisms (Norton, 1976). Two factors need to be considered for each dispersal mechanism: the range of dispersal and the success rate of establishment in that range. The benefits and disadvantages of short and long distance dispersal are diametrically opposed to one another (Deysher and Norton, 1982). Short distance dispersal maintains the propagules in a habitat that has been hospitable for the adult and is therefore favourable for the progeny. However, the propagule must withstand the high *intra*-specific competition imposed by other individuals of *S. muticum*. In contrast, long-range dispersal involves high wastage as propagules are often transported to unsuitable habitat. However, propagules successfully settling in new habitats are free from crowding by other thalli of *S. muticum*. By utilising sexual reproduction to generate germlings with a short dispersal range and floating plants for long distance dispersal, *S. muticum* appears to have the best of both worlds (Deysher and Norton, 1982). The dispersal mechanisms employed by *S. muticum* are illustrated in Figure 14.

Figure 14
The dispersal mechanisms of Sargassum muticum and their potential range
(Strong, 2003)



S. muticum can be dispersed in four ways. In the first method, *S. muticum* release swarms of germlings in pulses, at intervals of up to 13 days, throughout its fertile period (Fletcher, 1980a; Norton, 1981c). This greatly increases the chances of at least one release coinciding with the conditions favourable for settlement. Furthermore, each batch of germlings may be released under different tidal conditions allowing a more even, multi-directional dispersal. Multiple batch release of this type is considered to be particularly beneficial to organisms like *S. muticum* whose germlings have a short planktonic existence (Deysher and Norton, 1982). Drifting germlings can be found in the plankton up to 1.3 km from the nearest fertile plant but most that settle successfully tend to do so within 3 m. This represents a mechanism for short-range dispersal *(*Deysher and Norton, 1982; Norton, 1981b; Norton, 1981c). Germlings released around the parent plants encourage the development of dense stands and consolidate the population. The expansion of a *S. muticum* population can reach a very rapid phase where plant numbers may increase linearly, as long as the availability of suitable substratum is not a limiting factor.

In the second method, stone-walking plants expand the linear extent of the population and are effective in colonising new areas locally.

In the third method, drifting fragments of fertile *S. muticum* material are an effective means of long-distance dispersal. The appearance of drifting plants in an area has often been followed by the appearance of an established attached population some two to three years later (Deysher and Norton, 1982; Critchley *et al.,* 1983).

The fourth method by which *S. muticum* is dispersed is as a result of human activities, primarily associated with the commercial introduction of Pacific oysters (*Crassostrea gigas*).

4.5.1 Local dispersal and colonisation strategies

The direction of germling dispersal and hence geographical spread is influenced by local topography and prevailing currents at the time of reproduction. The release of swarms of germlings intermittently, at intervals of up to 13 days, increases the probability that a release will coincide with favourable conditions (i.e. spring tides) for dispersal and settlement (Fletcher, 1980; Norton, 1981). This may also allow spread of *S. muticum* in multiple directions as tidal and current conditions change over time (Deysher and Norton, 1982).

The majority of *S. muticum* germlings settle within a short distance of the parent plant; less than one metre (Kendrick and Walker, 1995) or one to three metres (Norton, 1980). Few settle further than 30 m away as the distance over which germlings can successfully settle, drifting as part of the plankton, is limited by their short-lived ability to attach. Generally, the rapid dilution of the germling swarm means that this is a short-range dispersal mechanism that contributes to the development and consolidation of dense *S. muticum* stands.

Strong (2003) investigated dispersal of zygotes released by *S. muticum* in Strangford Lough, Northern Ireland. The vast majority of zygotes released from thalli of *S. muticum* settled within 0.5 m of the adult plant. The short range of the dispersal was probably related to the low water velocity in the sheltered habitats of Strangford Lough. Critchley (1981) reported that the maximum dispersal distance of *S. muticum* at Warden Point (Solent) was 3 m. Deysher and Norton (1982) recorded that the majority of settlement occurred within one metre of an adult plant, although not insignificant settlement was also evident up to three metres away.

Following initial attachment, the germlings develop rapidly, with the development of the erect shoot axis and the basal production of 6-8 primary rhizoids. When the primary branch is just over one mm long, a small basal bud is produced which develops into the leaf-like lamina. More laminae are produced while numerous secondary rhizoids are produced to form the holdfast (Fletcher and Fletcher, 1975a).

Successful colonisers require not only the close proximity of a fertile plant but also the availability of cleared suitable substrate. A clean, hard, textured surface is preferred; rock, shell or even metal. However, several experiments have shown that the presence of any existing canopy or algal turf can restrict or totally inhibit colonisation by acting as a physical barrier between the settling germlings and the substrate, rather than as a result of any form of chemical inhibition (Deysher and Norton, 1982).

S. muticum generally colonises open patches within an area of dense algae (Critchley *et al.,* 1983). In sheltered sites with dense algal cover, open patches tend to occur sporadically. These close within one to three months due to rapid re-colonisation by native species. This would appear to preclude colonisation by *S. muticum* germlings but this species quickly exploits any open spaces that become available and it is considered to be an 'opportunistic gap-grabber or space-filler'. It will also colonise previously un-exploited niches, such as fairly loose substrates of small stones and shells on mud or sand.

It has been observed that areas of apparently suitable substrate may remain un-colonised for a number of years, presumably for a variety of reasons relating to *S. muticum*'s dispersal mechanisms and factors that affect successful settlement and growth (Critchley, 1983d).

S. muticum has a second method of local dispersal, **peripatetic colonisation**, where buoyant, 'stone-walking / wandering / rafting' plants are dispersed by local currents. (Nicholson *et al.,* 1981, Critchley 1983a, Strong *et al.,* 2006, Thomsen *et al.,* 2006). This is caused by *S. muticum*'s settlement strategy, where germlings will attach to the first solid surface encountered, even when this may be mobile and therefore apparently unsuitable for their subsequent development. As *S. muticum* germling plants exhibit a preference for highly textured or rugose surfaces, sedentary molluscs are particularly favourable. As the plant grows, its increasing buoyancy can result in the plant and its attachment substrate of shell or stone being lifted and carried along by the current until it slackens. This can be an effective method of spreading the population along a stretch of shore (Farnham, pers. comm.; Franklin, 1979). At Bembridge, Isle of Wight, plants have been observed to move from the eulittoral to the sublittoral in this way (Jephson and Gray, 1977). At Langstone Harbour, first year plants were observed to "walk" and were mainly found at the outer limit of the populations (Critchley, 1983e). At Santa Catalina Island, California, plants attached to "fist-sized" rocks have been observed to move this way and to accumulate at depths of 15 m or more, with the air vesicles observed to have "imploded" (Nicholson *et al.,* 1981).

Strong (2003) investigated the importance of peripatetic colonisation of new habitat, within the Dorn, a complex micro-tidal lagoonal system on the south eastern side of the Lough, that was colonised by *S. muticum* in 1996 (Davison, 1999). The density of *S. muticum,* before clearance in June 2000, was 14.48 plants per metre. After two months, an average of 6.2 peripatetic plants per metre had moved into the cleared site, replacing nearly half of the individuals removed. All of the newly arrived thalli within the cleared area were reproductive. The majority of plants remained stationary but of those that did move, the average distances travelled at the two study sites was 4.2 m and 2.2 m. The maximum dispersal recorded at both sites was 34m. All of the peripatetic movement was in one direction along the shore, corresponding to the residual tidal currents in the Dorn. At the end of September 2000, the number of accumulated peripatetic thalli declined rapidly and field observations indicated that stormy weather was causing individuals to be stranded higher up the shore. The amount of loose rock on a soft sediment base in Strangford Lough may mean that this mechanism is an effective dispersal mechanism locally, but may not be as prevalent in other parts of *S. muticum*'s introduced range.

4.5.2 Long-distance dispersal and colonisation strategies

The advantage of successful dispersal it that it provides a wide geographical distribution that should ensure a degree of evolutionary "insurance", ensuring that local catastrophes will not eliminate a species over its entire range and that localised losses can be replaced from populations surviving elsewhere (Norton, 1992). Most seaweeds rely chiefly on small propagules for reproduction, proliferation and dissemination. These propagules are immobile or have "puny" powers of locomotion. The fate of the propagules is determined largely by the water flow in which they find themselves. Propagules sink, swim or drift. Dispersal distance is greatly influenced by the hydrographic conditions at the time of the propagule release. In several species, dispersal is greatly increased by storms. The direction and distance of germling dispersal is related to local topography and the set of the local currents at the time of liberation (Deysher and Norton, 1982). The speed of spreading is related to the generation time of the species, as this determines the number of “strides” that can be taken in a given time (Norton, 1992).

In the third dispersal method, fronds regularly abscise off the plants and drift away, along with fronds severed as a result of physical damage and herbivorous grazing. While these fragments cannot re-attach, they can continue growing and remain viable for up to three months (Farnham *et al.,* 1981). Abscised fertile fragments tend to rot rapidly and as the air vesicles are amongst the first parts to decay, buoyancy is usually lost within 14 days, thus limiting the distance over which they can disperse. Developing germlings on receptacles may not be released naturally from abscissed fertile branches until the receptacle rots, by which time the germlings will probably have lost the ability to attach to a substrate (Deysher and Norton, 1982). However, free-floating branches can become fertile and self-fertilise *en route*, carrying viable germlings to new sites (Fletcher and Fletcher, 1975; Norton, 1977b).

Drifting fragments of potentially fertile material are an effective means of long-distance dispersal and the discovery of new *S. muticum* populations is often preceded by the observation of drifting fragments of *S. muticum (*Rueness, 1989). It has been observed that frequently the development of new *S. muticum* populations is preceded by the appearance of drifting fragments or mats of *S. muticum* (Anon., 1978; Norton 1976; Rueness, 1989). These floating fronds may form large mats (Critchley *et al.,* 1983). Wind is thought to play the main role in determining the direction of drifting fragments of *S. muticum* (Deysher and Norton, 1982). Off the Californian coast, wind can disperse *S. muticum* plants at approximately 50 times the rate of water currents (Deysher and Norton, 1982). Tagged specimens of *S. muticum* have drifted 600 – 900 km, at an average speed of 18 km per day (Segawa *et al.,* 1959).

The appearance of drifting plants in an area has often been followed by the appearance of an established attached population some two to three years later (Deysher and Norton, 1982; Critchley *et al.,* 1983). Dispersal by drift is thought to have been largely responsible for the spread of *S. muticum* 3,000 km along the Pacific coast of North America (Norton, 1978) and along the Scandinavian coasts of Denmark, Norway (Staehr *et al.,* 2000) and Sweden (Karlsson and Loo, 1999).

When the ability of *S. muticum* to make a huge single jump of 1,100 km along the Pacific coast of North America was investigated, it was concluded that it was not as a result of an accidental introduction. It was also concluded that drifting germlings or abscised fertile branches were not responsible as they were produced too late in the year to take advantage of the inshore currents which are only seasonally favourable for southward dispersal *(*Deysher and Norton, 1982). It was concluded that floating vegetative branches which abscissed or were severed by herbivorous grazers earlier in the season and became fertile en route, provided the perfect mechanism for long-distance dispersal, being carried by currents, tidal streams and wind-generated surface drift (Norton, 1981a).

Davison (1999) observing *S. muticum* dispersal within Strangford Lough, Northern Ireland, found that the direction of the wind and its strength was of far greater significance than water currents, with the dispersal of *S. muticum* being consistent with prevailing wind conditions in the Lough.

The fourth method by which *S. muticum* is dispersed is as a result of human activities, primarily associated with the commercial introduction of Pacific oysters (*C. gigas*). Please refer to Section 5.0 for further information on oyster movements as a dispersal vector.

4.6 Overview of the features and strategies that make *Sargassum muticum* such a successful invasive coloniser

S. muticum occurs where it is not indigenous, having been accidentally introduced to the Pacific coast of North America, the coastline of Western Europe and the Mediterranean Sea and exhibits many features of an invasive alga (Norton, 1976).

S. muticum also exhibits considerable ecological resistance, being tolerant of a wide range of temperature (5°C – 30˚C) and salinity. The perennial holdfast may regenerate shoots when fronds are lost by natural senescence, desiccation, wave action, ice-scouring or grazing. This combination of opportunistic features and perennial persistence is unusual in a canopy-forming macroalgae (Norton, 1976; Rueness, 1989). However, its vertical distribution is limited by poor tolerance to aerial exposure and desiccation (Norton, 1977b; Farnham, pers. comm.).

S. muticum has an annual cycle of growth, reproduction and dormancy. Outwith its native range, when operating as an invasive coloniser, this annual cycle has changed, with the growth period extending and the dormant period reducing or not occurring. In southerly locations where *S. muticum* has been introduced, fertile plants can be found throughout the year. In warmer waters, the growth rate increases, larger quantities of gametes are produced and the reproductive season is extended (Norton and Deysher, 1989). "The apparent extended growth period of *S. muticum* away from the constraints of original Japanese environment and the degree of flexibility within the growth cycle may explain its success in colonising the Pacific coast of North America and western Europe" (Jephson and Gray, 1977).

As a coloniser, *S. muticum* has several reproductive assets. It is monoecious, has the ability to self-fertilise and can expel gametes in a number of discreet pulses. The fertilised eggs are incubated on the outside of the receptacle for one to several days so that by the time the propagules are liberated into the sea, they are not just zygotes but quite advanced small germlings with developing rhizoids.

S. muticum has several settlement adaptations that assist its effectiveness as a coloniser. The pulsed release of germling swarms throughout the fertile period, greatly increase the chances of at least one release coinciding with the conditions favourable for settlement. Each batch of germlings may be released under different tidal conditions allowing a more even, multi-directional dispersal. As the germlings have a short planktonic existence, most successfully settlement tends to occur within 3 m of the parent plant, representing a mechanism for short-range dispersal

The release of well-developed *S. muticum* germling plants enhances their chances of survival. They sink more rapidly than most algal propagules and the germling's pear-shape ensures that on settlement, the rhizoid initial cells are placed directly onto the substrate and can secure an immediate adhesion, with the microalgal and bacterial film on the substrate aiding adhesion. This ensures that holdfast and shoot development can continue without any time lag. In comparison, indigenous algae use settlement mechanisms like sticky outer walls and do not begin to develop rhizoids until they are attached to the substrate.

At water temperatures of 15˚C and above, the growth rate of both the developing germlings and the vegetative adult plants exceeds that of any of its competitors (Nicholson *et al.,* 1981). Rapid growth gives rise to bushy plants, several metres long, which can blanket the shore and overshadow most rival species (Norton, 1976).

As a result, one plant or reproductive fragment can release numerous progeny and give rise to a whole population (Norton, 1976). Within three months of first appearing on the shore, the plants can become fertile – unlike many of their competitors that do not become fertile until their second year. However, it does seem that a period of two to three years is required for the development of a sufficient breeding stock to allow a rapid extension of a population. (Critchley *et al.,* 1983) As colonists increase in age, the number of fronds that arise from the main axis increases so that the reproductive output of each population or stand rapidly increases.

After a massive production of gametes, germlings released around the parent plants encourage the development of dense stands and consolidate the population. Stone-walking plants expand the linear extent of the population and are effective in colonising new areas locally. The expansion of a population reaches a very rapid phase where numbers may increase linearly, as long as suitable substratum availability is not limiting (Critchley, 1983d).

Reproductive branches of *S. muticum* can absciss and float away, buoyed by the numerous air vesicles, while still carrying viable germlings and developing gametes. Vegetative branches, severed as a result of physical damage and herbivorous grazing, can continue to grow for up to three months while free-floating and can become fertile and shed germlings. The numerous air bladders make drifting fragments an effective means of long-distance dispersal and prevailing winds can disperse the fronds over significant distances, including over 1,100 km along the Pacific coast of North America (Deysher and Norton, 1982).

The potential evolutionary advantages of finding a new and more suitable habitats elsewhere is counter-balanced by the greater risks if the journey is prolonged. *S. muticum* benefits from both strategies. It has propagules for local colonisation, encouraging dense populations in newly colonised areas and drifting fragments that offer the possibility of long distance dispersal.

The main barrier to colonisation by *S. muticum* is the presence of an algal cover. The wide variety of algae that can prevent colonisation indicates that this is not due to chemical inhibition. It is probable that they exclude *S. muticum* simply because their canopy or turf forms a physical barrier and *S. muticum* will stick almost immediately to the first solid surface encountered, even when it is unsuitable for their subsequent development (Deysher and Norton, 1982).

Open patches occur naturally in sheltered sites only sporadically. They tend to close within one to three months as a result of rapid algal re-growth. Consequently, this would seem to preclude colonisation by *S. muticum.* However, the rapid development of dense populations and the displacement of some natural communities in recently invaded areas attests the opportunistic ability of this species to exploit space when it does become available (Deysher and Norton, 1982). Farnham (pers. comm.) describes it as a “space-filler” or “gap-grabber”, as it colonises previously un-exploited niches, such as fairly loose substrate (small stones and shells).

In its native Japan, it is an innocuous plant but where it has been introduced, it is an aggressive coloniser and opportunist. *S. muticum*’s colonising abilities and opportunistic nature, particularly the possession of monoecious (self-fertilising) reproductive structures, may explain why it is this *Sargassum* species, a relatively minor component of the Japanese Sargassaceae, that has been exported so successfully (Critchley, 1983a).

5.0 VECTORS IN THE SPREAD OF *SARGASSUM MUTICUM*

Determining which marine species have been introduced by the activities of man is fraught with problems, particularly when considering that the movement of species by artificial means such as boats, has been an ongoing process that began long before taxonomic records were kept. The date of first collection, the confirmation of identification and the establishment of these species is rarely coincident with the date of introduction so introduction dates are often approximate (Eno, 1995). For most introductions resulting from human activity, the method or vector is usually determined from circumstantial evidence as it is unusual for the vector to be caught '*in flagrante*' (Farnham, 1992).

The definition of an introduced species that has been adopted by the JNCC is from Carlton (1987) which states that "*introduced species are those taxa transported by human activity to regions where they did not exist in historical time*". It includes established non-native species and non-established or alien species. ("Historical time" is taken as being since the beginning of the Neolithic Age: c. 3500 BC.)

Non-native species are defined as *a species which has been introduced directly or indirectly by human agency (deliberate or otherwise), to an area where it has not occurred in historical times and which is separate from and lies outside the area where natural range extension could be expected. The species has become established in the wild and has self-maintaining populations; the term also includes hybrid taxa derived from such introductions* (Eno, 1995).

Non-established introductions or aliens are defined as *species which are introduced through the agency of man but which have not become established and are incapable of establishing self-sustaining or self-propagating populations without the interference of man* (Eno, 1995).

Currently 15 algae and 28 invertebrates are listed by the JNCC as non-native marine species in British waters. Once a non-native marine species is introduced, its ability to establish successfully and the rate of spread varies. Once established, many increase their distribution by marginal dispersal *(*Eno, 1995; Farnham, 1992).

Large expanses of water present a barrier to the natural movement of many species, particularly littoral species. Temperature and the type of available substratum are additional barriers that limit the biogeographic distribution of species. However, these barriers can be bridged through a variety of methods that generally involve man (Eno, 1995).

Long-distance introduction of marine organisms has been well known for more than a century. The rate of introduction of non-native marine species has risen dramatically over the past century through an increase in trans-oceanic shipping and modern aquaculture practices (Carlton, 2000).

The most obvious vector is international shipping, either as a result of the transport of fouling organisms attached to the hull, in the ship's seawater intake pipes, by the discharge of ballast, particularly ballast water, or on wet fishing nets. In the first case, the organisms involved are usually fouling species. Well-known examples are the Australasian barnacle *Elminius modestus* and the tunicate *Styela clava*. The transport of algae attached to ships has also been suggested (Farnham, 1980). Carlton (1985) considered that ballast water probably provides the greatest flow of neritic species globally in modern times and it has been implicated in the introduction of the planktonic diatom *Biddulphia sinensis.*

Many species have been deliberately introduced for commercial purposes by man, with associated unintentional introductions an inevitable consequence. Escapes from aquariums, release of species intentionally or unintentionally by research scientists, discarding or release back into the sea of bait and edible species can be included in this category.

Unintentional introductions are commonly sessile or fouling species, boring and vagile species (Eno, 1995).

5.1 Oyster cultivation

The most common method of introducing non-native marine algae has been unintentional, associated with the deliberate commercial introductions, principally oysters, *Crassostrea gigas*, from Japan and North America (Eno, 1995). *S. muticum* germlings may be attached on or inside oyster shells, or this alga may have been used as a packing material in the past (Critchley and Dijkema, 1984; Farnham, pers. comm.). Oysters can be sent live anywhere in the world in one to two days, which greatly increases the risks of accidental introduction of disease, pests and fouling species. Consequently, unless strict quarantine procedures are employed. *S. muticum* can be introduced inadvertently or unintentionally with oysters (Duggan, 1979).

Critchley and Dijkema (1984) stated that "In recent years the international business of oyster movement and relaying has been responsible for the introduction and spread of numerous marine organisms, with deleterious consequences, both ecological and financial" Elton warned in 1958 that "the greatest agency of all that spreads marine animals to new quarters of the world must be the business of oyster culture".

Table 3 and Table 4 list the algae and fauna that have been inadvertently introduced to the UK and Europe as a result of oyster translocations.

Table 3
Other algae inadvertently introduced to the U.K. and/or Europe as a result of oyster transplantation
(Eno, 1995)

Algal species	**Algal type**	**Introduction site**	**Introduction date**
Undaria pinnatifida	Brown	l'Etang de Thau	1971
		South English coast	1995
Laminaria japonica	Brown	l'Etang de Thau	~ 1971
Codium fragile subsp *tomentosoides*	Green	Europe to Devon	1939
Colpomenia peregrina	Brown	Cornwall and Dorset	1907
Polysiphonia harveyi	Red	South English coast	~ 1908
Antithamnionella spirographidis	Red	Plymouth	1934
Grateloupia filicina var *luxurians*	Red	The Solent	~ 1947
Asparagopsis armata	Red	Europe to UK	1949

Table 4
Other fauna inadvertently introduced to the UK and/or Europe as a result of oyster translocation

(Eno, 1995)

Faunal species	Common name
Bonamia ostreae	Microcel-X disease
Marteilia refrigens	“Aber “ gill disease of mussels which affected oysters
Mytillicola orientalis	Crustacean parasite
Urosalpinx cinerea	American oyster drill or tingle
Ocenebra japonica	Oyster drill
Pupura clavigera	Oyster drill
Crepidula fornicata	Slipper limpet
Petricola pholadiformis	American piddock or False angel wing
Haliplanella lineata	Anemone
Hydroides dianthus	Serpulid worm
Clymenella torquata	Polychaete worm
Eusarsiella zostericola	Ostracod
	Bryozoan species

Druehl (1973) predicted the occurrence of *S. muticum* in Europe as a result of the importation of Pacific oysters, one month before the first population was found in 1973. Critchley and Dijkema (1984) stated that “man is undoubtedly the most potent vector of long distance dispersal of *S. muticum* as it is very likely that transplanted oysters facilitated the extension of the geographic distribution of *S. muticum*.”

The earliest records of *S. muticum* introductions due to oyster transportation from Japan are from British Columbia in 1944, due to the importation of *C. gigas* oysters from Japan, which began early in the nineteenth the century (Norton, 1978; Britton-Simmons, 2004). Introduction to Europe was also facilitated by oyster transportation from either Japan or British Columbia in the late 1960’s (Critchley and Dijkema, 1984; Rueness, 1989). Critchley *et al.* (1990) concluded that the first site to be colonised in Europe was in northern France, near oyster beds at St. Vaast La Hougue, most likely due to importation of oysters from both British Columbia and Japan in 1966 (Jones and Farnham, 1973). The introduction of *S. muticum* from the UK to the Netherlands was also blamed on oyster translocation (Critchley and Dijkema, 1984). Internal relocation of *C. gigas* and *Ostrea edulis* between European oyster growing areas has been found to facilitate *S. muticum*’s spread (Critchley and Dijkema, 1984; Gruet, 1984; Lambe, 1979; Duggan, 1979). The importation of *C. gigas* to the Mediterranean directly from Japan has resulted in the introduction of *S. muticum* and other Japanese algae to the Mediterranean (Boalch, 1985; Gerbal *et al.,* 1985; Riouall, 1985; Ben Maiz *et al.,* 1987; Knoepffler-Peguy *et al.,* 1985; Rueness, 1989). Oyster movements have also be implicated in the *S. muticum* introductions to Denmark (Staehr *et al.,* 2000), Norway and Sweden in the early 1980’s (Karlsson and Loo, 1999; Stæhr *et al.,* 2000) and Strangford Lough in Northern Ireland (Boaden, 1995; Davison and Davison 1995; Davison, 1999) and the Republic of Ireland (Loughnane and Stengel, 2002).

The relaxation of trade barriers within Europe and to other areas of the world means that the movement of potential vector species, such as oysters, has become less controlled and restricted.

5.2 Commercial and recreational vessels

Two of the main vectors for the transport of non-native species throughout the world are via the ballast water of ships or through the fouling of ships' hulls. Ballast water may be responsible for up to 25% of non-native species introductions to the UK (Eno *et al.,* 1997). The possibility that *S. muticum* may have been spread through ballast water seems unlikely as any planktonic germlings would presumably settle in the hull, due to their rapid attachment strategy, or have lost the ability to attach and settle by the time the ballast water has been discharged (Norton, 1980). However, over short routes (for example, ferry routes), this remains a possibility, if plant fragments are transported within the ballast water.

Hull fouling is a significant vector for the introduction of non-native species (Eno *et al.,* 1997; Cohen and Carlton, 1998; Hewitt *et al.,* 1999; Gollasch, 2002) and non-native species were identified in 98% of samples taken from commercial ship hulls in the North Sea (Gollasch, 2002). Hull fouling has been well-studied on commercial tankers and container ships (e.g. Godwin, 2001; Gollasch, 2002; Coutts and Taylor, 2004). Dispersal of *S. muticum* via hulls seems unlikely as germlings cannot re-attach if dislodged from the hull (Deysher and Norton, 1982; Farnham, pers. comm.). The translocation of larger plants attached to boat hulls is similarly considered to be unlikely because they would become abraded or detached by the vessel's movement through the water long before they were large enough to become fertile (Deysher and Norton, 1982).

Recreational vessels were considered less likely to support extensive fouling accumulations due to their frequent cleaning regime, their relatively fast speed, and the fact that those on long voyages were unlikely to reside for long periods of time (more than 30 days) in any single port (Carlton and Hodder, 1995). However, recreational boating can be responsible for the spread of non-native species, especially on a local scale (Johnson and Carlton, 1996; Johnson *et al.,* 2001; Bax *et al.,* 2002; Ashton *et al.,* 2006b). Fertile *S. muticum* plant fragments may become entangled in anchor chains and steering gear and subsequently be carried to new locations short distances away and be capable of releasing viable germlings (Boalch and Potts, 1977; Critchley and Morrell, 1982; Critchley and Thorp, 1985; Farnham, pers. comm.). This has been observed in yachts arriving in the Channel Isles (Critchley and Morrell 1982; Critchley *et al.,* 1983) and in the Mediterranean where the spread of *S. muticum* has been partly attributed to transfer by pleasure boats and fishing boats (Knoepffler-Peguy *et al.,* 1985). More recently, yachts travelling around Ireland, and travelling there from France and the UK, have been blamed for dispersal of *S. muticum* due to the high occurrence of established *S. muticum* populations near boat moorings and pontoons (Kraan, 2004). Minchin *et al. (*2006) lists several cases where small craft have been recorded or implicated in the introduction of non-native species in the northern hemisphere. The dispersal of *S. muticum* on the west coast of Scotland attached or entangled with boats cannot be discounted and unattached plants have been reported in the Clyde Marina, Ardrossan in 2006, 2007 and 2008 (Ashton *et al.,* 2006a; E. Cook pers. comm.).

The proliferation of marinas for recreational vessels over recent decades is a world-wide phenomenon (Minchin *et al.,* 2006). Recreational vessels have become increasingly implicated in the spread of marine non-native species, including non-native marine algae such as *Undaria pinnatifida (*Hay, 1990) and *Codium fragile* spp. *tomentosoides* (Bird *et al.,* 1993; Fletcher and Farrell, 1998). There have been no systematic surveys along coastal areas of individual countries in the northern hemisphere to assess the importance of recreational boating in the distribution of marine non-natives.

Sea-planes on the Pacific coast of America and Canada have been observed carrying *S. muticum* fragments draped over the pontoons but as *S. muticum* is very susceptible to desiccation, it is unlikely to survive (Deysher and Norton, 1982).

6.0 AN OVERVIEW OF THE CURRENT GLOBAL DISTRIBUTION *OF SARGASSUM MUTICUM*

S. muticum is a non-native species originally from Japan that has been accidentally introduced to other parts of the world. Like many introduced species, once it is removed from the constraints of its native environment, it becomes an aggressive coloniser and grows bigger. Within its natural range, *S. muticum* is one of the smaller *Sargassum* species, growing between 75 – 150 cm long (Yendo, 1907: Rueness, 1989). It was initially introduced to the Pacific coast of North America, where it has been recorded growing to 7 m long (Jones and Farnham, 1973; Nicholson *et al.,* 1981). It was then introduced to Western Europe and the UK. Plants up to 12 m long have been collected from the Brittany coast of France and plants up to 6 m long have been recorded in Britain (Jephson and Gray, 1977; Critchley *et al.,* 1990b; Davison, 1999).

S. muticum has successfully invaded twelve European coastal countries and produced a nearly continuous distribution from Sweden to Portugal, including the British Isles, and into the Mediterranean Sea (Wallentinus, 1999). The process of colonisation also continues along the Pacific North American coast and into the southern hemisphere.

S. muticum is extending its range along the coasts of two continents, a phenomenon known only to have been achieved and surpassed by *Codium fragile* subspecies *tomentosoides* (Critchley, 1983a).

(Eno, 1995) listed terms that can be used to describe the rate of spread of a non-native species:

- very slow: no spread beyond a few kms from point of introduction
- slow: spread within country within 20 years and neighbouring countries within 40 years
- moderate: spread to neighbouring countries within 20 years
- rapid: spread to neighbouring countries within five years and considerable distances within the British Isles within 50 years
- very rapid: spread considerable distance within the British Isles in 30 years

It appears that *S. muticum* spreads comparatively slowly at the northern part of its range and can be very fast growing in the southern part of its range.

6.1 The dispersal rates of *Sargassum muticum*

The documented rates of *S. muticum* dispersal are often rapid, but they are variable and may be dependent on the geography of the coastline, the availability of suitable substrate and the prevailing wind and current directions. Wind is thought to be the main factor driving *S. muticum* drift and has considerably more influence than water currents (Deysher and Norton, 1982).

S. muticum spread particularly rapidly south along the Pacific coast of North America at an average rate of 60-100 km per year (Farnham *et al.,* 1981; Lewey and Farnham 1981). Strong (2003) reported that in France, the area of shoreline colonised expanded by 144 km per year. On the south coast of England and north coast of France populations of *S. muticum* became established along hundreds of kilometres of coastline within a ten year period (Critchley *et al.,* 1983). It has been estimated that the average dispersal rate along the English south coast was 30 km per year, mostly by drifting plants that were, or could become, fertile (Farnham *et al.,* 1981). Dispersal rates for *S. muticum* on the west coast of the UK, have averaged approximately 44 km per year since the population was recorded on the north coast of Cornwall in the early 1990s (Harries *et al.,* 2007b). In the Mediterranean, *S. muticum* was confined to a sheltered lagoon for four years before wider dispersal occurred, largely due to a lack of available suitable substrate (Knoepffler-Peguy *et al.*, 1985).

Dispersal around the coasts of Wales and Ireland appears to have been rapid, with several widely separate populations having become established within less than ten years of the first recorded occurrence of *S. muticum* (Kraan 2004; ICES WGITMO, 2006). The Strangford Lough populations dispersed at a rate of 5 km per year over six years (Roberts *et al.,* 2004). Expansions of specific populations have been estimated at 2-3 km per year in two bays on the Irish coast (Kraan, 2004).

Wallentinus (1999) reported a dispersal rate of 10 km per year in Limfjorden, Denmark but Staehr *et al.* (2000) reported that dispersal occurred at a rate of 15-17 km per year in Limfjorden. Rapid colonisation occurred on the west coast of Sweden, with populations becoming established along hundreds of kilometres of coastline within a ten year period (Karlsson and Loo, 1999). Wallentinus (1999) reported a dispersal rate of approximately 50 km per year in Sweden.

Dispersal on the north coast of Spain was at a similarly rapid rate, with populations increasing from three to covering the majority of the coast within six years (Fernandez, 1999). This rate is thought to be due to the abundance of available suitable substrate (Fernandez, 1999).

Wallentinus (1999) reported global range extensions in *S. muticum* of 10 to 45 km per year.

Invasive organisms may loose some of their “vigour” following an aggressive introduction. This may be true of *S. muticum* since new populations are often established from restricted gene-pools by self-fertilisation from small, floating fragments (Critchley *et al.,* 1990). Many terrestrial weeds are also imported aliens and often their initial aggression subsequently declines. *S. muticum*’s behaviour may follow a similar pattern but Norton (1976) feels that “as it spreads into warmer waters, it will become increasingly difficult for competing species to evolve methods of coping with its aggressiveness”. It is felt that there may be no absolute limit to *S. muticum*’s spread around the British Isles (Farnham, pers. comm.).

6.2 The distribution of *Sargassum muticum* in the western Pacific

Relatively little is known of *S. muticum*’s original distribution in Japan and adjacent west Pacific region where 70 different species of *Sargassum* are found. This is due to early taxonomic confusion and the fact that it is only a minor component of the *Sargassum* group. As a result of taxonomic clarification, its “indigenous” range has increased significantly.

It is found around the coast of Japan and populations occur on the Chinese and Russian Pacific coast. *S. muticum*’s distribution around Japan appears to be dependent upon the Kuroshio and Tsushima warm water currents. It may also be found in Korea, China and the Philippines, although there is some confusion between *S. muticum* and *S. miyabei* (Critchley, 1983a).

6.3 The distribution of *Sargassum muticum* along the eastern Pacific coast of North America

In the 1950’s, while Fensholt was carrying out taxonomic identification work that led to *S. muticum’s* classification as a distinct species, she established that this Japanese alga had been introduced into the eastern Pacific (Fensholt, 1955; Critchley, 1983a). It appears to have been introduced accidentally in the 1940’s as a contaminant on oyster spat of *Crassostrea gigas* imported from Japan (Scagel, 1956). Certainly *S. muticum* samples were first collected from oyster growing areas in British Columbia, Washington and Oregon where there had been repeated importations of *C. gigas* (Norton, 1981a).

Wallentinus (1999) reported that *S. muticum* was first recorded in 1944 around the Strait of Georgia, British Columbia, assumed to have been introduced as a contaminant with imported Pacific oysters (*C. gigas*) from Japan. It was then observed in Oregon in 1947 and in Washington in 1953 and both areas were involved with the importation of *C. gigas* from Japan. In 1963 *S. muticum* was first found in north California in Humboldt County. Eleven years later, the alga was also recorded in Baja California, Mexico (Espinoza, 1990). The southerly spread of *S. muticum* has been associated with the south-flowing California Current. In the 1990s, *S. muticum* was found in south east Alaska and as far south as the San Ignacio Lagoon (Mexico) where it is now one of the dominant algae.

S. muticum has spread progressively from these sites over almost the entire Pacific coast of North America from Alaska to Mexico. Despite *S. muticum*'s apparent requirement for sheltered habitats, it has colonised a predominantly exposed coast at a rapid and apparently accelerating rate. It seems to have taken 20 years to reach northern California from southern Oregon but it spread down the entire California coast to Mexico in around ten years, including a single jump of 1,100 km (Norton, 1981a).

It appears to be a more aggressive coloniser and successful competitor in warmer waters. In British Columbia and northern Washington, *S. muticum* inhabits a narrow vertical zone around extreme low water of spring tides, down to a depth of only 2m. A plant of 2m long is quite a large specimen. In southern California, the *S. muticum* zone can penetrate to a depth of 24m and plants grow on average to 3-4 m long (Norton, 1981a).

S. muticum may have reached its geographic limits along the Pacific coast of North America, between Alaska and Mexico. (Aguilar Rosas *et al.,* 1984; Espinoza, 1990) However, there are considerable areas between these boundaries that could still be colonised (Critchley, 1983a).

In January 1973, Druehl predicted that *S. muticum* would become established in the eastern Atlantic as the result of the introduction of Japanese oysters, *C. gigas*, from British Columbia to France in the spring of 1972.

6.4 The distribution of *Sargassum muticum* along the European coastline

The initial site of entry of *S. muticum* to western Europe is subject to controversy. However, the consensus of opinion and circumstantial evidence suggests that *S. muticum* was first introduced into western European waters in late 1960's (Jones and Farnham, 1973; Farnham, 1980) or in the early 1970's (Druehl, 1973) associated with the culture of Japanese oysters, *C. gigas*, imported from Canada or the USA.

S. muticum was first recorded in western Europe in 1971 as drift material when fragments of unattached, fertile branches were found on Southsea beach, near Portsmouth. The first officially recorded attached population of *S. muticum* in the UK and Europe was at Bembridge, Isle of Wight on 17 February, 1973 by Dr Farnham and Dr Fletcher of Southampton University. Initially 30 plants, up to 1 m long, were found on the Bembridge Ledges and then a large population, with plants up to 4 m long, was discovered covering 7 m^2 of the main lagoon (Critchley *et al.,* 1983). It is thought that floating fragments of *S. muticum* spread from France, where imported *C. gigas* oyster beds are present.

The *S. muticum* populations initially found on mainland western Europe were on the coasts of France and the Netherlands, generally associated with important oyster growing areas. The first population identified in France was at the Normandy oyster beds of St. Vaast-la-

Hougue where unquarantined *C. gigas* spat had been imported from Japan, South Korea, British Columbia, Italy and England (Anon, 1973a; Critchley, 1981; Critchley and Dijkema, 1984; Critchley *et al.,* 1990b; Druehl, 1973; Farnham, 1980; Farnham *et al.,* 1973; Gray, 1978; Gray and Jones, 1977; Gruet, 1976; Gruet, 1977).

S. muticum spread along the English south coast and was found in Plymouth (1977), Eastbourne (1978) and Cornwall (1991). Drifting *S. muticum* plants spread north and east to the Netherlands (1980), Denmark (1984), Sweden (1987) and Norway (1988) and Germany (1998) (Wallentinus, 1999). By 1983, it occupied suitable habitats along approximately 360 km of the southern coast of Britain, approximately 720 km of the northern French coast and it had well established populations in the Netherlands and the western Mediterranean Sea (Critchley *et al.,* 1983). *S. muticum* was found in Ireland, in Strangford Lough, Northern Ireland in 1994, and is considered to have been introduced with *C. gigas* in 1987 (Boaden, 1995) and has since spread to Belfast Lough (T. Mackie, pers. comm.). From the French Atlantic coast, *S. muticum* spread south to Spain (1985) and northern Portugal *(*1991) (Wallentinus, 1999). Imported *C. gigas* for aquaculture in Etang de Thau (1980) and to the Venice Lagoon (1992) accounts for the Mediterranean populations of *S. muticum* (Wallentinus, 1999). It was found in south Wales in 1998 and in north Wales in 2001. Since 2000, new populations of *S. muticum* have found in the Republic of Ireland in Counties Donegal, Cork, Galway, Kerry, Sligo and Wexford (Kraan, 2004).

There are currently no reported populations of *S. muticum* in the southern hemisphere, although many other *Sargassum* species can be found. As the introduction of this alga has been closely associated with the transportation of oysters, which predominantly takes place in the northern hemisphere, all of the associated introductions have occurred in this area.

The first most extensive stands of *S. muticum* were found at sites where attached plants were able to develop over a period of several years, such as the Solent Harbours, Bembridge on the Isle of Wight and on the Cherbourg Peninsula, northern France. In such areas, *S. muticum* can form large populations covering many hundreds of hectares. Many of these sites, which were well established on discovery, are considered to have been present for at least one to two years. As large amounts of *S. muticum* drift material had not previously been recorded, it is felt unlikely that the *S. muticum* plants discovered in 1973 originated from one “massive inoculum”. It is more likely that a limited number of sites were established, perhaps in the Solent harbours of Portsmouth or Langstone, with subsequent spread from these points (Critchley *et al.,* 1983). Critchley (unpublished data) illustrated distribution routes using drift bottles and indicated that either Bembridge or Langstone harbour were potential source (original) populations. Similarly, fronds could have crossed the Channel from previously unidentified or unrecorded populations in France (Critchley, 1983d). It is thought that *S. muticum* reached the Channel Islands drifting from France and via shipping; e.g. in 1979 a yacht from Portsmouth sailed into Alderney Harbour with a large, fertile frond hanging from the steering gear (Critchley and Morrell, 1982).

The first population identified in France was at St Vaast-la-Hougue, which is an important oyster growing region. Gray and Jones (1977) stated that spat on collectors has been imported and re-laid there without quarantine from Japan, South Korea, British Columbia, Italy and England (including the Solent) and *S. muticum* may have arrived with the oysters, from *S. muticum* drift material or with recreational boats. The area at St Vaast-la-Hougue is a sheltered, flat beach of stones covered in muddy sand with strong currents. *S. muticum* was found to grow in channels on the lower shore and in the pools formed between the stone walls of the oyster parks (Gray and Jones, 1977).

The increase in French distribution to Etel Bay on the Cote Sauvage, southern Brittany and in the Mediterranean at l’Etange de Thau is associated with oyster culture (Gruet *et al.,* 1976). Gruet *et al. (*1976) suggested that the internal movement of oysters for culture within

France will further enhance the spread of this alga. Furthermore, two other Pacific brown algae; *Laminaria japonica* and *Undaria pinnatifida* are growing within oyster beds of the l'Etange de Thau lagoons and were almost undoubtedly introduced along with imported spat of *C. gigas* (Critchley *et al.,* 1983).

Research in the Netherlands found that oysters imported from the eastern Solent area of England, contained live attached *S. muticum* juveniles as well as attached and detached adult holdfasts (Critchley and Dijkema, 1984). The alga had remained viable as the moisture content in the plastic fertiliser sacks used for the two-day transportation was high. However, it is believed that the Dutch populations originally developed from fertile *S. muticum* drift material that was observed along the coast prior to populations being identified (Critchley and Dijkema, 1984).

Critchley and Dijkema (1984) stated that "the commercial shipment and laying of oysters, either directly from Japan or indirectly form British Columbia where *S. muticum* occurs (Scagel, 1956; Critchley, 1983a) constituted a primary vector for the introduction and subsequent spread of *S. muticum* within European waters. However, the almost simultaneous appearance of *S. muticum* in some Dutch waters where no oysters had been re-laid (i.e. Lake Grevelingen and the mouth of the Eastern Scheldt) and the (present) absence of this alga from subtidal oyster beds in the Netherlands indicates that these established populations were a direct result of zygote release from fertile drift material." They went on to predict that the establishment of *S. muticum* in Yerseke Bank, the main oyster cultivation area in the south west Netherlands.

In the south west Netherlands, Critchley *et al.,* (1990) found that *S. muticum* experienced its greatest development within Lake Grevelingen, a large (108 km^2) non-tidal, saline water impoundment, enclosed as part of the Dutch "Delta Works" to protect islands from flooding. *S. muticum* gained access during the opening of a sluice gate connecting to the North Sea in 1979. The population development and impact were monitored and it was found that the alga was very successful, establishing an extensive population. The buoyant primary laterals comprise the majority of the biomass and form a 100% canopy over the lake's surface from November until mid-August when the primary laterals are cast off as part of the natural senescence cycle. The persistence of the canopy is due to the extreme shelter and non-tidal environment at this site. The dense canopy was found to severely restrict light penetration, with the *S. muticum* absorbing 97% of the photosynthetically active radiation (PAR). The canopy also elevated the surface water temperature with the shading effect causing the water temperature below the canopy to be appreciably cooler. At 0.5 m depth, the temperature difference was 9.2˚C. Indigenous algae, particularly sub-canopy algae, decreased in size and frequency but the diversity had not yet been affected by the sub-optimal conditions created by *S. muticum.* In Lake Veere, where the water is brackish (23 ppt) and eutrophic *Ulva* species are dominant, *S. muticum* is able to grow and reproduce.

Two dispersal agents have successfully effected the subsequent spread of this alga within Europe. The first agent is man; introducing "infected" oysters or transplanting "infected" oysters around the coast. Oysters may be "infected" by carrying a germling or juvenile plant on or inside the shell, having fragments or holdfasts of *S. muticum* mixed in with the oysters or even being packed in *S. muticum*. The second agent is wind generated surface currents, which transport drifting branches, which either are, or can become, fertile. Drifting fragments of *S. muticum* are often found prior to the discovery of attached plants (Critchley *et al.,* 1983).

The introduction of *S. muticum* to the English coastline has attracted interest from many bodies concerned with the marine environment as well as the general public. The consequent monitoring and research programmes have led to this being one of the best documented case-histories of an introduction of a non-indigenous marine organism to

European waters (Franklin, 1979). The chronology of European records, drift and attached populations, for *S. muticum*, between 1973-1981, is listed in Table 5 and is illustrated in Figures 15 to 18 (Critchley *et al.,* 1983; Rueness, 1989). The known distribution of *Sargassum muticum* around the UK and Ireland in 2004 is illustrated in Figure 19 (Harries *et al.,* 2007b).

Table 5
Chronology of European records, drift and attached populations, for Sargassum muticum, 1973-1981

(Critchley *et al.,* 1983)

Illustrated on maps, Figures 15 – 18

Year Population or Drift	Western European locations				
	U.K.	**France**	**Channel Islands**	**Belgium**	**Netherlands**
1971					
Drift	Southsea beach, Portsmouth				
1973					
Population 1	Bembridge, Isle of Wight				
Population 2	St Helen’s, Isle of Wight				
Population 3	Shanklin, Isle of Wight				
Population 4	Seaview, Isle of Wight				
Population 5	Portsmouth Harbour				
1974					
Drift		Atlantic coast			
Population 6	Langstone Harbour				
Population 7	Southsea				
Population 8	Puckpool				
Drift	Littlehampton				
1975	No reports				
1976					
Drift		Pointe du Hoc			
Population 9	Warden Point, Isle of Wight				
Population 10	Chapman’s Pool				
Population 11	River Yealm, near Plymouth				
Drift	East of the Solent – Newhaven				
Drift	Kimmeridge				
Drift	The Solent				
Drift		Ambleteuse			
Population 12		St Vaast-la-Hougue			
1977					
Population 13	Brighton				
Population 14	Batten Bay				
Population 15		Grandcamp			
Population 16		St Honorine			
Population 17		Luc-sur-Mer			
Population 18		Barfleur			

Table 5 continued
Chronology of European records, drift and attached populations, for Sargassum muticum, 1973-1981
(Critchley et al., 1983)
Illustrated on maps, Figures 15 – 18

Year Population or Drift	Western European locations				
	U.K.	**France**	**Channel Islands**	**Belgium**	**Netherlands**
1977 cont.					
Population 19		Pointe du Hoc			
Population 20		Boulogne			
Population 21		Granville			
Drift		South coast		Belgium	
Drift					
Drift				Off coast	160 km of coast
1978					
Population 22	Chichester Harbour				
Population 23	Poole Harbour				
Population 24	Renney Rocks				
Population 25	Eastbourne				
Drift				Off coast	
Population 26		Wimereux			
Population 27		Antifer			
Population 28		Le Harve			
Population 29		Herquemoulin			
Population 30		St Briac			
Population 31		St Enogat			
Population 32		Ile d'Haumet			
Population 33		Dielette			
Population 34		Omonville-la Rouge			
Population 35		Ile aux Oiseaux			
Population 36		L'Archipel des Chausey			
Population 37		Saccaviron			
1979					
Population 38	Seaford				
Population 39	Broad Bench				
Population 40	Studland Bay				
Population 41	River Hamble				
Population 42	Pagham Harbour				
Population 43	Bognor Regis				
Population 44	Worthing				
Population 45		Cap Gris Nez			
Population 46		Arromanches			
Drift	Isle of Wight				
Drift	Bournemouth				
Drift	Hastings				
Drift					Netherlands
Drift			Alderney		
1980					
Population 47	River Beaulieu				

Table 5 continued

Chronology of European records, drift and attached populations, for Sargassum muticum, 1973-1981

(Critchley *et al.,* 1983)

Illustrated on maps, Figures 15 – 18

Year Population or Drift	**Western European locations**				
	U.K.	**France**	**Channel Islands**	**Belgium**	**Netherlands**
1980 cont.					
Population 48	Wembury				
Population 49			St Helier		
Population 50			L'Etacq		
Population 51			Le Hocq		
Population 52			Guernsey		
Population 53			Les Echrehou		
Population 54		Guen Beach			
Population 55		Penvenan			
Population 56		Plouezec			
Population 57		Roscoff			
Drift		Trieux Estuary			
Drift					Netherlands
1981					
Population 58		Ile de Brehat			
Population 59		Ploumanac'h			
Population 60		L'Arcouest			
Population 61					Texel Island
Population 62					Lake Grevelingen
Population 63					Eastern Scheldt
Population 64	Salcombe				
Population 65			Alderney		
Population 66			Berchou		
Population 67			L'Oeillere		
Population 68			La Corbiere		
Population 69			Portlet Bay		
Population 70			La Rocque		
Population 71		Etel Bay			
Population 72		l'Etang de Thau, Mediterranean			
Population 73	Sheringham, Norfolk **(No longer present)**				
Drift	Cornish Coast				

Figure 15
Map illustrating the chronology of European records, drift and attached populations, for Sargassum muticum: 1973 – 1976
(Critchley *et al.,* 1983)

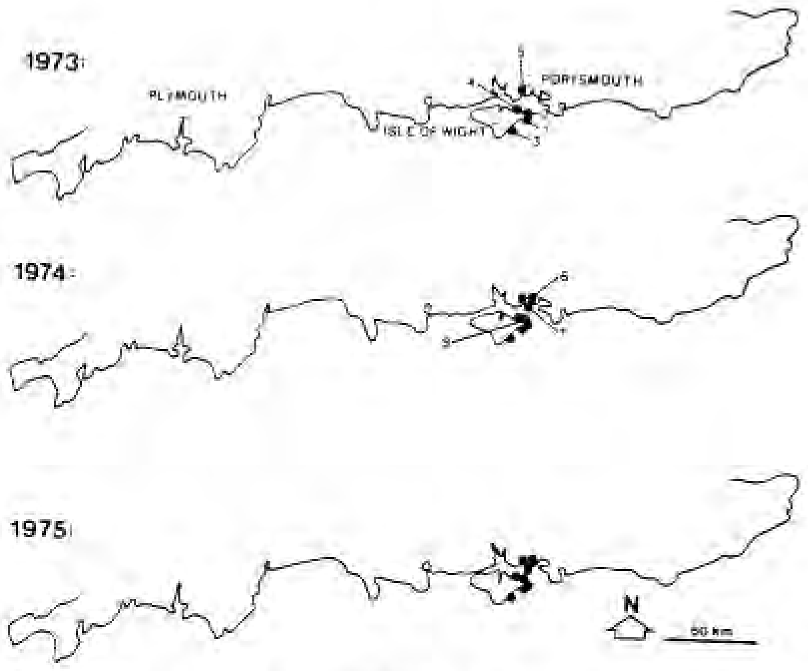


Fig. 1. New reported sitings, 1973–75. (1) Bembridge, (2) St Helens, (3) Shanklin, (4) Seaview, (5) Portsmouth Harbour, (6) Langstone Harbour, (7) Southsea, (8) Puckpool. No new reports in 1975.

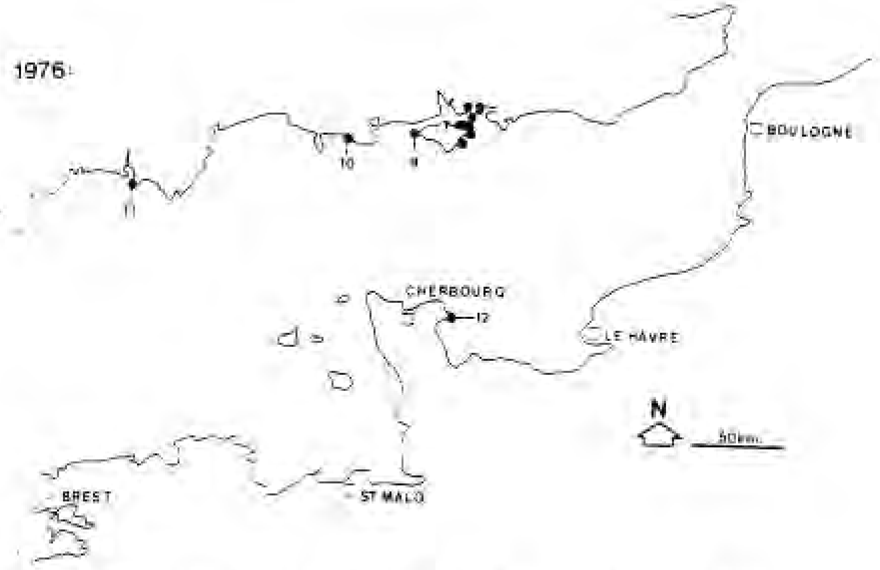


Fig. 2. New reported sitings, 1976. (9) Warden Point, (10) Chapman's Pool, (11) River Yealm, (12) St Vaast.

Figure 16
Map illustrating the chronology of European records, drift and attached populations, for Sargassum muticum: 1977 – 1978
(Critchley *et al.,* 1983)

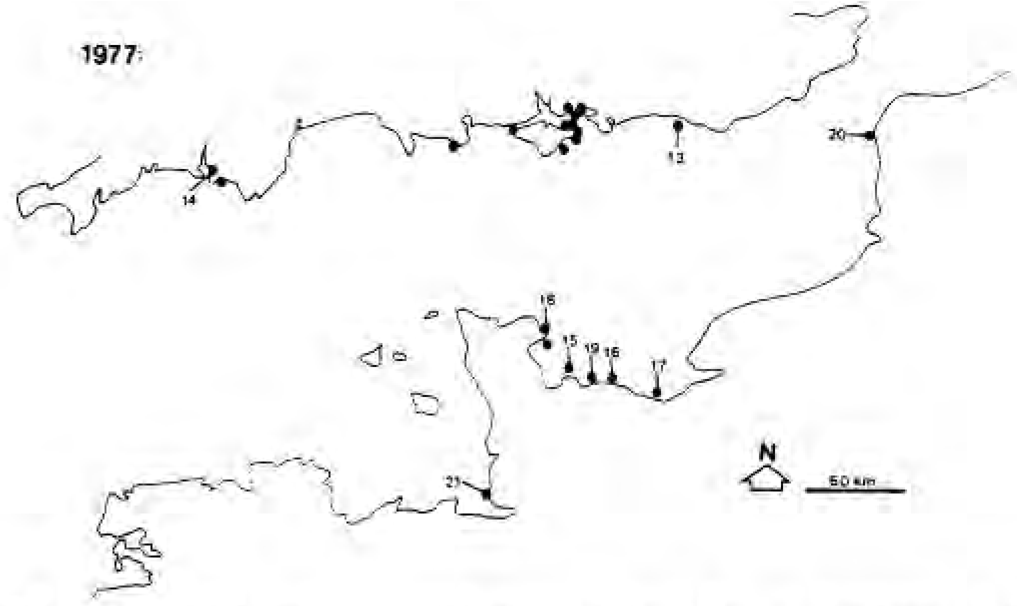


Fig. 3. New reported sitings, 1977. (13) Brighton, (14) Batten Bay, (15) Grandcamp, (16 Ste Honorine, (17) Luc-sur-Mer, (18) Barfleur, (19) Pointe du Hoc, (20) Boulogne, (21) Granville

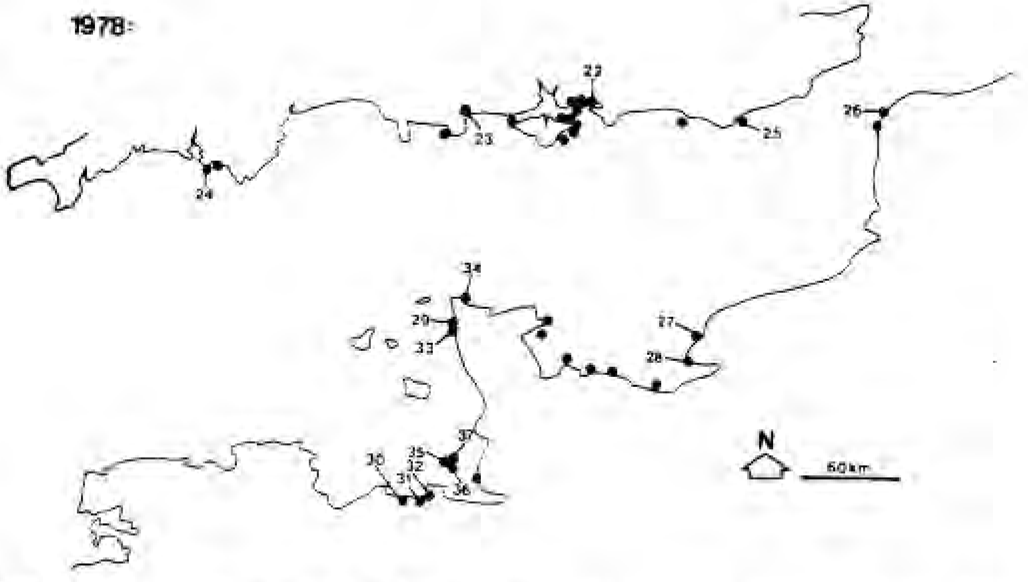


Fig. 4. New reported sitings, 1978. (22) Chichester Harbour, (23) Poole Harbour, (24) Renney Rocks, (25) Eastbourne, (26) Wimereux, (27) Antifer, (28) Le Havre, (29) Herquemoulin, (30) St Briac, (31) [illegible] Enogat (Dinard), (32) Ile d'Haumet (St Malo), (33) Dielette, (34) Omonville-la Rouge, (35) Ile aux Oiseaux (Iles Chausey), (36) L'Archipel des Chausey, (37) Saccaviron (Iles Chausey).

Figure 17

Map illustrating the chronology of European records, drift and attached populations, for Sargassum muticum: 1979 – 1980

(Critchley *et al.,* 1983)

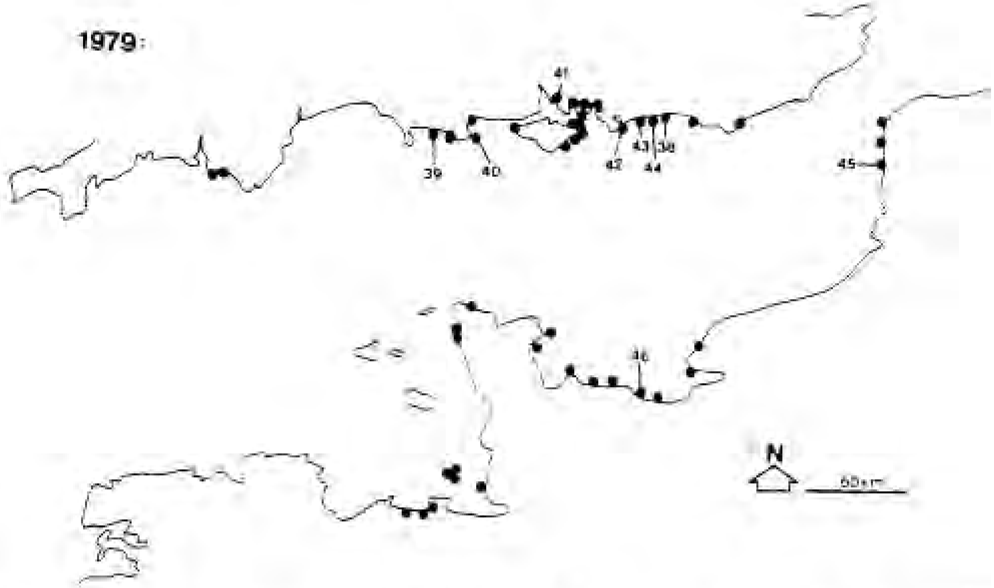
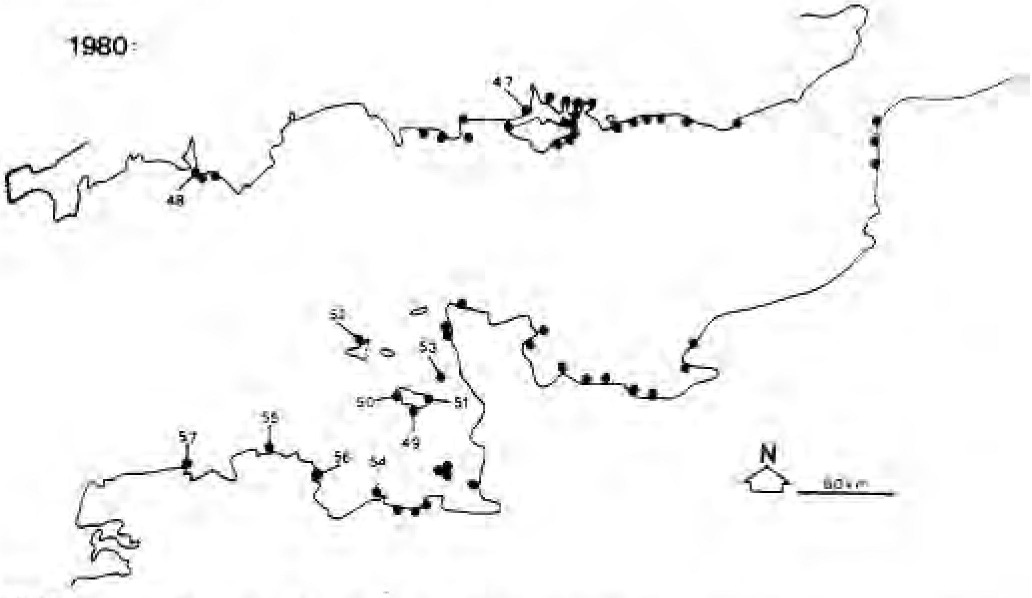


Fig. 5. New reported sitings, 1979. (38) Seaford, (39) Broad Bench, (40) Studland Bay, (41 R
Hamble, (42) Pagham Harbour, (43) Bognor Regis, (44) Worthing, (45) Cap Gris Nez, (4
Arromanches.



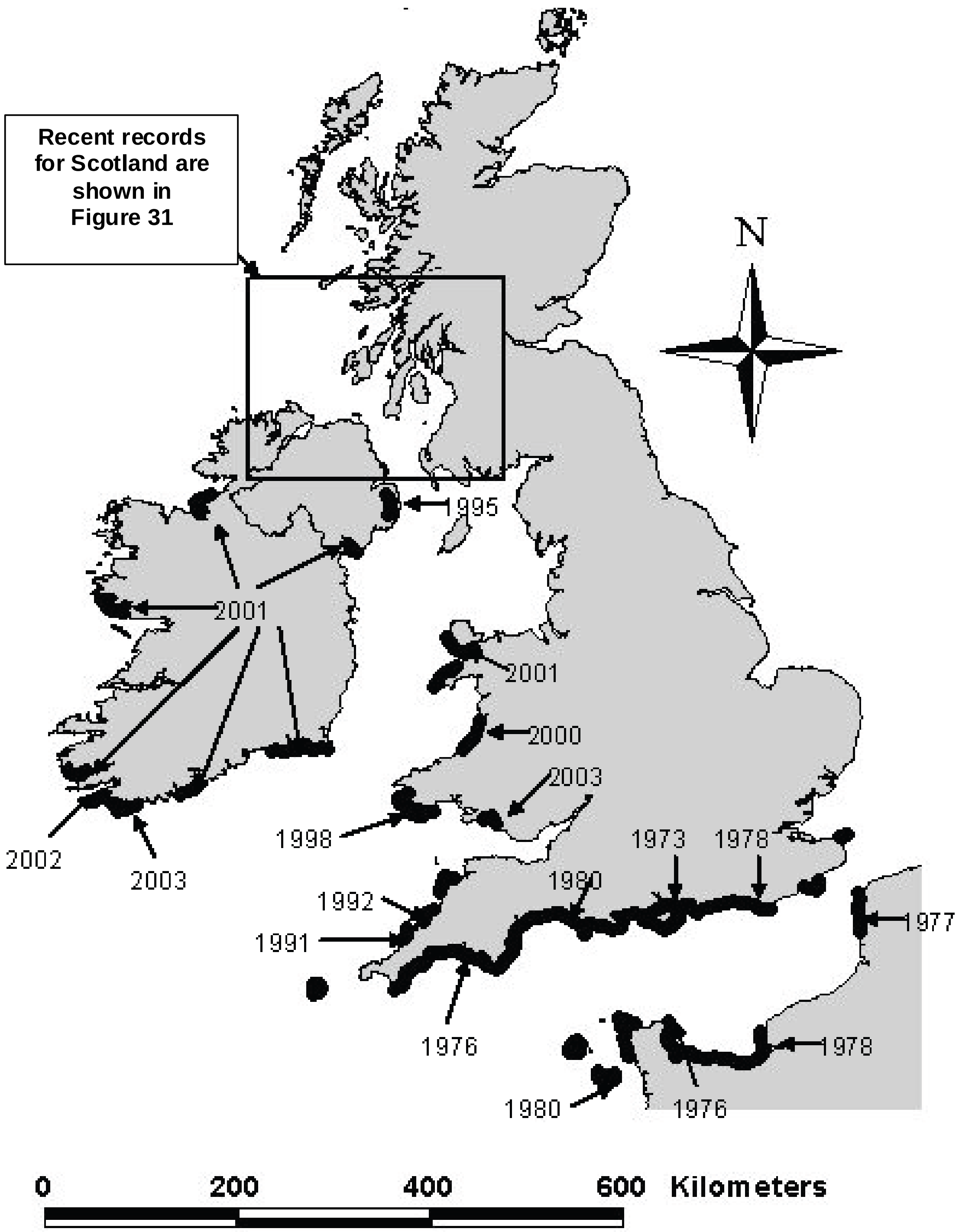
6. New reported sitings, 1980. (47) River Beaulieu, (48) Wembury, (49) St Helier, (50) L'Etacq, (51) Le Hocq, (52) Guernsey, (53) Les Echrehou, (54) Guen Beach (Cape d'Erquy), (55) Penvenan, (56) Plouezec, (57) Roscoff.

Figure 18
Map illustrating the chronology of European attached populations, for Sargassum muticum: 1989
(Rueness, 1989)

The distribution of attached populations of *Sargassum muticum* along the European coasts. Arrows indicate some finds of drift specimens.

6.5 The known distribution of *Sargassum muticum* around the British Isles

Figure 19
Map illustrating the known distribution of Sargassum muticum around the UK and Ireland: 2004
(Harries *et al.,* 2007b)



6.5.1 The current known distribution of Sargassum muticum around England

The first record of drifting fronds of *S. muticum* off the UK coast was from Southsea beach, Portsmouth in 1971. The first attached specimens of *S. muticum* were discovered in February 1973 in eulittoral lagoons at Bembridge on the Isle of Wight (Farnham *et al.,* 1973). It is thought that floating fragments of *S. muticum* spread from France, where imported *C. gigas* oyster beds are present. Colonies were subsequently sighted at three further locations on the Isle of Wight and at Portsmouth harbour on the UK mainland, attached to floating pontoons (Critchley *et al.,* 1983). *S. muticum* colonies were confined to relatively local areas within the Solent region (the Isle of Wight and nearby mainland) until 1976, with a continued increase in population size at each locality and the summer appearance of large floating mats of drift *S. muticum*.

In 1976, a new colony was discovered on the western tip of the Isle of Wight, at Warden Point, 32 km from Bembridge, in lagoons similar to those at Bembridge. Between 1977 and 1980, the number of plants found at Warden Point increased significantly (Critchley, 1983a). In 1976, populations were found at Chapman's Pool, approximately 50 km west of Warden Point and then at Plymouth harbour, near the River Yealm, 230 km further west.

Between 1977 to 1981, *S. muticum* spread eastwards on the UK mainland, as far as Eastbourne, approximately 130 km away, with an isolated colony at Sheringham, North Norfolk (Critchley *et al.,* 1983). The Norfolk population has been the most northerly and the most easterly population recorded in England, but it has not survived (Eno, 1995; Farnham, pers. comm.).

Thereafter, the dispersal of *S. muticum* has been predominantly westwards, with discrete modes of dispersal. Surveys carried out in 1986 and 1993 (Eno *et al.,* 1997) confirm that *S. muticum* is now found along the entire Channel coast, from Cornwall to Kent, with dense aggregations forming in certain areas, for example Poole Harbour, during summer months (Dyrynda, 2001).

The first occurrence of north west movement was a sighting of drifting plants in south Wales in 1983, in the Bristol Channel (Davison and Davison, 1995). Attached plants were subsequently found on the north Cornish coast in 1992, at Lundy in the Bristol Channel in 1993 (Eno *et al.,* 1997) and at the entrance to Milford Haven, south Wales in 1998. There are also populations on the Scillies and Channel islands.

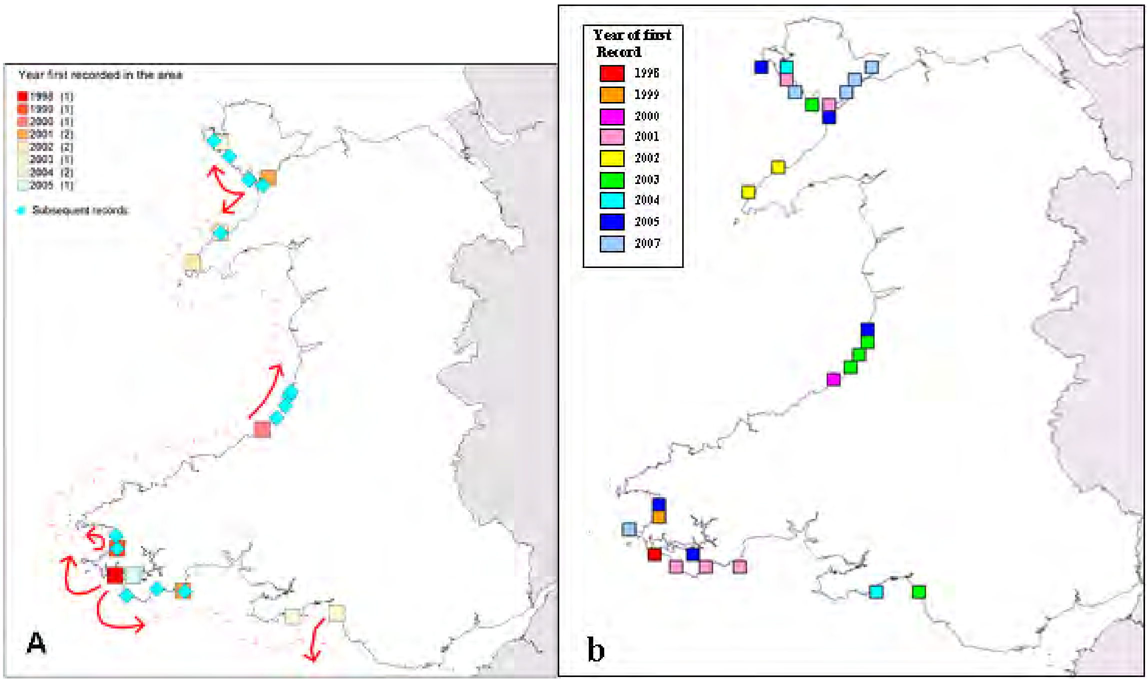
S. muticum was first recorded on Lundy in 1999. A previous record from 1993 is considered to be unlikely. The distribution has, until recently, been confined to the Landing Bay although plants were found in Devil's Kitchen in 2007. It was found in Lametry Beach in 2008, with a few scattered plants found elsewhere. Annual clearances are undertaken on Lundy, within the Landing Bay, from the region of the jetty, the Cove and Devil's Kitchen. As far as possible, whole *S. muticum* plants are removed, with a knife or paint scraper under the holdfast, often removing a sliver of slate. Dedicated teams undertook the clearances during 2005 and 2006 and the material removed was bagged and disposed of to landfill. Since 2006, the clearances have been opportunistic. The Lundy Warden reports that the clearances are challenging, with the methods being continually adjusted in an attempt to be more productive and not every year has been a huge success. There are some photographic records of pre- and post-clearance, but to date this is the only record of the effectiveness of this clearance programme (Nicola Saunders and Keith Hiscock, pers. comm.).

6.5.2 The current known distribution of Sargassum muticum *around Wales*

The chronology of Welsh *S. muticum* records, drift or attached populations, 1981 – 2007, is listed in Table 6 and illustrated in Figure 20.

In 1997 the Countryside Council of Wales (CCW) and Jones (pers. comm.) confirmed that no populations of *S. muticum* had been recorded on the Welsh coast but that drift *S. muticum* material had been observed in the Bristol Channel since 1983 and in the early 1990s off Pembrokeshire (Davison, 1999). It is likely that the sources of the drift *S. muticum* material came from the Scillies and Channel islands, where populations were first recorded in 1980, from the north Cornwall population, recorded in 1992, and from the Lundy Island population in the Bristol Channel, recorded in 1993 (Davison, 1999).

Figure 20
Maps illustrating the current known distribution of Sargassum muticum around the Welsh coast: 2008
(Brazier *et al.,* 2007) (Source: P. Hallas)



On 22nd June 1998, the CCW intertidal survey team found 12 well-established *S. muticum* plants, 3–75 cm long in West Angle Bay, at the entrance of Milford Haven, on the south west coast of Wales. Two of the plants were considered to be two years old but no *S. muticum* stands had yet developed. Staff at the Field Studies Council's Orielton Centre assessed the sexual status of some sample plants and they had not yet become fertile. By 1999, *S. muticum* was well established at this site.

On 9th and 30th July, 1998, all the *S. muticum* plants, including the holdfasts, found in deep pools on the mid and lower littoral of Skomer MNR were removed by CCW staff (Whin and Camplin, pers. comm.).

Since then, the distribution of *S. muticum* around the coast of Wales has expanded considerably, and currently ranges from Port Talbot in the south to Anglesey in the north (Hallas *et al.,* 2007). In 2006, the *S. muticum* range appeared to have remained stable in Wales, although an increase in the numbers of discrete populations around North Wales had been recorded (ICES WGITMO, 2007). It remains unclear whether the spread of *S. muticum* in Wales originated from the west Pembrokeshire population through natural means (germlings or drifting plant fragments) or whether separate introduction events have occurred as a result of human activities, such as aquaculture and shipping.

Over 75% of the Welsh coastline is designated as a Site of Special Scientific Interest (SSSI) and a significant area is also designated as Special Areas of Conservation (SAC). Consequently, the Countryside Commission for Wales (CCW) felt that a review of the invasion dynamics of *S. muticum* was necessary to be able to determine its potential impact upon the conservation status of these designated habitats. Consequently, CCW are funding a PhD student to investigate the molecular genetics of *S. muticum* in Wales to investigate the most likely route of introduction and whether the records are all from one introduction or several *(*Hallas, 2007). The phylogeography of the *S. muticum* populations in Wales will be assessed through the analysis of a combination of neutral genetic markers, including Amplified Fragment Length Polymorphisms (AFLPs) and direct sequence information from the mitochondrial genome (Meudt and Clarke, 2007). A hierarchical sampling design will enable the investigation of genetic variability and gene flow at a range of spatial scales, metres to kilometres, subsequently allowing the construction of dispersal models. This will then be integrated into existing Phase 1 Intertidal GIS maps compiled by CCW, providing a pictorial presentation of the population genetic structure of *S. muticum* in Wales, as well as generating predictions on the rate of spread along the Welsh coastline.

Table 6
Chronology of Welsh Sargassum muticum records, drift or attached populations: 1981 – 2007
(Source: Paul Hallas)

Location	Date	Record Type	Description
1. West Angle Bay, Pembrokeshire	January 1998	CCW Phase 1 biotope LR.FK.Sar	On bedrock at the north end of West Angle Bay beach.
2. Shag Rock, St Brides Bay	January 1999	CCW Phase 1 biotope LR.FK.Sar	Large deep LR.FK.Sar pool with *Sargassum muticum* (12m x 10m). Too deep to take species list
3. Shag Rock, St Brides Bay	January 1999	CCW Phase 1 Target Note	Shallow LR.SwSed pools with *Sargassum muticum* inside this hashed area within ELR.Bpat.Cht. Abundance of *Sargassum muticum* in pools varies between Occasional and Common.
4. Pen y Gloyn, Cardigan bay	April 2000	Anecdotal *(*Julian Woodman)	Hallas has not managed to track the original record for *Sargassum* in Cardigan Bay. His understanding was that it was on the rocky platform to the south of Aberaeron around SN448625, but this has never been confirmed.
5. West of Pen y holt Bay, Pembrokeshire	January 2001	CCW Phase 1 biotope LR.FK.Sar	Found at Pen-y-Holt Bay.
6. Star Cliff, Caldey Island	January 2001	CCW Phase 1 biotope LR.FK.Sar	Large pool at back of shore surrounded by ELR.Bpat.Cht.
7. Priory Bay, Caldey Island	January 2001	CCW Phase 1 biotope LR.FK.Sar	Atypical form of this biotopes. Pools are shallow in mid-eulittoral zone dominated by green algae but too species rich to be LR.G. Found in <1% of SLR.Fspi and MLR.FvesB.
8. Priory Bay, Caldey Island	January 2001	CCW Phase 1 biotope LR.FK.Sar	Atypical form of this biotopes. Pools are shallow in mid-eulittoral zone dominated by green algae but too species rich to be LR.G. Found in <1% of SLR.Fspi and MLR.FvesB.

Table 6 continued
Chronology of Welsh S. muticum records, drift or attached populations: 1981 – 2007
(Source: Paul Hallas)

Location	Date	Record Type	Description
9. Priory Bay, Caldey Island	January 2001	CCW Phase 1 biotope LR.FK.Sar	Atypical form of this biotopes. Pools are shallow in mid-eulittoral zone dominated by green algae but too species rich to be LR.G. Found in <1% of SLR.Fspi and MLR.FvesB.
10. Priory Bay, Caldey Island	January 2001	CCW Phase 1 biotope LR.FK.Sar	Atypical form of this biotopes. Pools are shallow in mid-eulittoral zone dominated by green algae but too species rich to be LR.G. Found in <1% of SLR.Fspi and MLR.FvesB.
11. Priory Bay, Caldey Island	January 2001	CCW Phase 1 biotope LR.FK.Sar	Atypical form of this biotopes. Pools are shallow in mid-eulittoral zone dominated by green algae but too species rich to be LR.G. Found in <1% of SLR.Fspi and MLR.FvesB.
12. Rhosneigr, West Anglesey	January 2001	Anecdotal (Ivor Rees)	Only two plants. Almost certainly rockpools.
13. Mermaid Inn, Menai Strait	May 2001	CCW Phase 1 Target Note	Large sand-bottomed deep pool (excised channel). LR.SwSed rockpool. *Sargassum muticum* and *Elminius modestus* frequent.
14. Freshwater East, Pembrokeshire	June 2001	CCW Phase 1 Target Note	*Sargassum muticum* washed up on the shore.
15. Porth Oer, North Lleyn	January 2002	Anecdotal (Nova Mieszkowska)	*Sargassum* found north side of the Llyn Peninsula earlier in 2002 – probably in rockpools.
16. Porth Dinllaen, North Lleyn	January 2002	Anecdotal (Nova Mieszkowska)	*Sargassum* found north side of the Llyn Peninsula earlier in 2002 – probably in rockpools.
17. Carreg Ti-Pw to Aberarth, Cardigan Bay	May 2003	CCW Phase 1 Site species list	Occurs on the site.
18. Morfa Bychan to Pantyrallad, Cardigan Bay	May 2003	CCW Phase 1 Site species list	Occurs on the site.
19. Newborough, West Anglesey	May 2003	Anecdotal (Ivor Rees)	Six attached plants on the Newborough / Llanddwyn shore. This was without searching so suspect there may be more. They were on the lower parts of the cobbles.
20. Pantyrallad to Carreg Ti-Pw, Cardigan Bay	August 2003	CCW Phase 1 Site species list	Occurs on the site.

Table 6 continued
Chronology of Welsh S. muticum records, drift or attached populations: 1981 – 2007
(Source: Paul Hallas)

Location	Date	Record Type	Description
21. Port Talbot Harbour, Glamorgan	September 2003	CCW Phase 1 Site species list	Occurs on the site.
22. Pwlldu Bay, Gower	April 2004	CCW Phase 1 Target Note	Large LR.SwSed pool with *Sargassum muticum* ® and Polysiphonia elongata. LR.SwSed make up 2% of ELR.Bpat.Cht.
23. Newborough , West Anglesey	April 2004	Anecdotal (Ivor Rees)	Occurs on mussel beds near the island.
24. Inland Sea, Anglesey	May 2004	Anecdotal (Monica Jones)	Large plants within the channel and smaller plants on mobile cobbles on the east shore
25. Pwll Crochan Flats, Milford Haven	March 2005	Anecdotal (John Moore)	Big plants attached to stones all along the lower shore
26. Newgale Sands, Pembrokeshire	April 2005	Anecdotal (Aethne Cooke)	Occurring within large tidal pool.
27. Trearddur Bay, West Anglesey	June 2005	Anecdotal (Monica Jones)	Large rockpool with one plant, approx. 1m in length.
28. Morfa Bychan, Ceredigion	July 2005	Anecdotal (Kathryn Birch and Anne Bunker)	*Sargassum* was found within LR.SwSed pools and within LR.Cor pools on the bedrock platform on both mid and upper shore.
29. Porth Dinllaen, North Lleyn	September 2005	Anecdotal Seasearch (Lucy Kay)	Three plants occurring sublitorally on mixed cobbles between 52 56.628N 004 33.714W and 52 56.809N 004 33.746W
30. Foryd Estuary, Menai Strait	September 2005	Anecdotal (Son Roberts)	Big plants attached to stones at very low water next to No. 10 buoy.
31. Porth Ysgaden	March 2007	Anecdotal Seasearch (photo, Lucy Kay)	Single, relatively small plant growing sublitorally attached to a stone in shallow water within the bay at Porth Ysgaden (probably not far seaward of LAT)
32. Pwlldu Bay, Gower	March 2007	Anecdotal (Paul Hallas)	Occurring in six rockpools at mid-shore level, approximately 40 plants in largest pool. Plants ≤ 70 cm, attached to bedrock, and some boulders in pools.
33. Port Dinorwic Marina	May 2007	Anecdotal (Bill Sanderson)	Single plant seen from boat in shallow water. Attached to bottom.
34. Martins Haven	June 2007	Anecdotal (Bill Sanderson)	Plant seen from boat in shallow water. Attached to bottom.
35. Broad Haven	June 2007	Anecdotal (Bill Sanderson)	*Sargassum muticum* washed up on the shore.

Table 6 continued
Chronology of Welsh S. muticum records, drift or attached populations: 1981 – 2007
(Source: Paul Hallas)

Location	Date	Record Type	Description
36. Church Island	August 2007	Anecdotal (Paul Brazier)	Two cobbles with very large *Sargassum* plants on the low shore, looked as though they have hopped along the Menai Strait.
37. Porth Aels, Aberffraw	July 2007	Anecdotal (Monica Jones)	Large rockpool with several large *Sargassum* plants
38. Beaumaris	December 2007	Anecdotal (Laura Grant)	15 individuals, from 27 cm to 373 cm long, found in a narrow band at low water springs. Attached to pebbles.
39. Borthwen	December 2007	Anecdotal (Laura Grant)	Found in lower shore rockpools and on pebbles on sand on the lower shore.
40. Moel-y-don, Menai Strait	December 2007	Anecdotal (Laura Grant)	Large individuals found at low water
41. Llanidan Menai Strait	December 2007	Anecdotal (Laura Grant, from previous observations by Ivor Rees)	Large individuals in a band at low water of spring tides.
42. Porth Cwyfan	December 2007	Anecdotal (Laura Grant, from previous observations by Ivor Rees)	Found abundantly in large shallow pools at low water springs to the south side of the church
43. Treath Penrhos, Holy Island	December 2007	Anecdotal (Laura Grant)	Two individuals found in a sandy pool attached to rocks on the mid to low shore
44. Trearddur Bay, West Anglesey	December 2007	Anecdotal (Laura Grant)	Very abundant at this site. Found in eight rockpools (although probably more) and in the lagoon at low water of spring tide.
45. Church Island	December 2007	Anecdotal (Laura Grant)	Abundant in the lagoon separated from the main channel of the Menai Strait
46. Newborough	December 2007	Anecdotal (Laura Grant)	Found at low water of spring tides. Attached to rocks and pebbles buried beneath sand
47. Llanddwyn Island	December 2007	Anecdotal (Laura Grant)	Found attached to a large rock in a sandy pool. Two individuals.
48. Tal y Foel (Mermaid Inn)	December 2007	Anecdotal (Laura Grant)	Very abundant, found in a band at low water. Large individuals.
49. Rhosneigr	December 2007	Anecdotal (Laura Grant)	Very abundant at this site. Found in many rockpools and attached to pebbles in the rock protected lagoons.

6.5.3 The current known distribution of Sargassum muticum *around Ireland*

In 1994, *S. muticum* was discovered in Strangford Lough, Northern Ireland, growing over the bags of Pacific oyster trestles and were considered to have been introduced with *Crassostrea gigas* spat from the Channel Islands in 1987-8 (Boaden, 1995; Davison and Davison, 1995; Davison, 1999). The colonisation of Strangford Lough has been closely monitored as it is a Marine Nature Reserve and candidate Special Area of Conservation. A second population was found nearby in 1995, on the Calf Rock pladdy but no *S. muticum* was found at the other 44 particularly vulnerable sites within Strangford Lough surveyed that year. Containment operations were undertaken in late 1995; around 2.5 tonnes were removed, but plants still remained. Follow-up surveys of 13 of these other sites were undertaken in 1996, when no new populations were discovered. Further containment operations were carried out and no new populations were observed. In 1997, a third annual survey of both of the original populations showed that these had expanded in area and plant density. In 1998, after the discovery of *S. muticum* within the Dorn NNR, 27 of the 44 other particularly vulnerable sites were re-surveyed. *S. muticum* was found at 17 of these sites, in the form of dense stands, patchy stands, scattered clusters of plants, single plants or drift *S. muticum* material (Davison, 1999). New eradications took place during 1997 and the following years, but failed (Davison, 1997; Davison, 1998; Davison, 1999; ICES WGITMO, 2000).

It is considered that the Strangford Lough populations originated due to *C. gigas* oysters being transferred from Guernsey, the Channel Isles in 1987-8 (Boaden, 1995; Davison & Davison, 1995) but that the *S. muticum* did not develop a noticeable population until 1994, when these plants were first observed by Cuan Sea Fisheries. This was probably due to the conditions in the initial site not being favourable for rapid growth, as the elevated oyster trestles were subjected to twice-daily aerial exposure, lack of suitable substrate and competition with native algae (Davison and Davison, 1995; Davison, 1999). The distribution expanded from 0.61 km of shoreline in 1996 to a maximum of 47.88 km in 2000 and then declined to approximately 29 km in 2002 (Strong, 2003; Roberts *et al.,* 2004).

Although *S. muticum* began spreading within Strangford Lough around 1998, having been introduced in 1987-88, it wasn't recorded outside Strangford Lough until 2005, when it was found in Carlingford Lough (ICES WGITMO, 2006), where it is thought to have been introduced due to oyster movements (T. Mackie, pers. comm.). The Water Management Unit of the Northern Ireland Environment Agency has found *S. muticum* in Northern Irish waters from Carlingford Lough, along the east coast in all areas to outer Belfast Lough at Ballymacormick Point. It was recorded at Ballymacormick near Groomsport, County Down for the first time in 2007. South Down and Strangford have well established populations of *S. muticum* but so far there are only a few plants at sites in North Down. In the northwest, a couple of individual plants have been found in Portstewart Bay but not in the Foyle or elsewhere in Counties Derry and Antrim (Charmaine Blake, pers. comm.).

S. muticum was recorded for the first time in the Republic of Ireland in 2001, from Kilmore Quay (Kraan, 2004) and in Cashel Bay, County Galway (Loughnane and Stengel, 2002). It is now found around the Irish coast, with records from counties of Galway, Sligo, Kerry, Cork, Wexford and Louth. It was also recorded in County Donegal in 2006 (Kraan, in press). A map of the known distribution of *S. muticum* around the coast of Ireland, excluding the Donegal record, is provided in Figure 21.

Dispersal around the coast of Ireland appears to have been rapid, with several widely separate populations having become established within less than ten years of the first recorded occurrence of *S. muticum* (Kraan 2004; ICES WGITMO, 2006). Expansions of specific populations have been estimated at 2-3 km per year in two bays on the Irish coast (Kraan, 2004).

The vectors are likely to have been imported oysters, drifting *S. muticum* from England and Wales and visiting leisure crafts (ICES WGITMO, 2002). Around Ireland, there has been a high incidence of *S. muticum* establishment near moorings and pontoons which implies a dispersal role for small boats (Kraan, 2004).

Minchin (2007) undertook a rapid coastal survey for targeted alien species associated with 29 floating pontoons located around the whole coastline of Ireland between 2005 and 2006. Pontoons in marinas, jetties and fish farms were examined. *S. muticum* was found at the Portaferry marina in Strangford Lough, Ardglass marina and Carlingford marina. Frond fragments were found floating close to the marina pontoons.

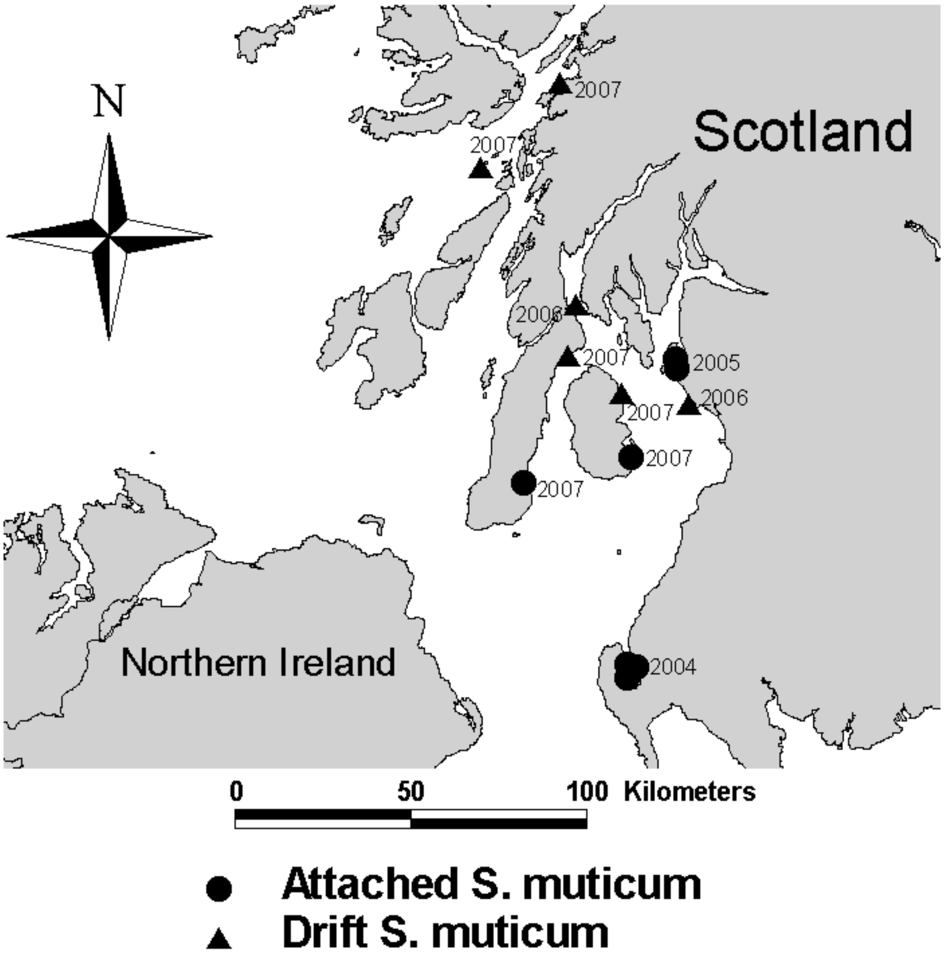
Figure 21
Map illustrating the known distribution of Sargassum muticum around the coast of Ireland: 2008
(Source EPA, 2008)

6.5.4 The current known distribution of Sargassum muticum *around Scotland*

The first reports of *S. muticum* in Scotland were in Loch Ryan in 2004 and by April 2007, populations had also been found at Great Cumbrae Island, the North Ayrshire coast, Arran and at Campbeltown Loch on the Mull of Kintyre. Drifting fragments of *S. muticum* had been recorded, from Loch Fyne, Argyll and the Clyde Marina, Ardrossan, Ayrshire as well as on Arran and at Claonaig on the Mull of Kintyre. It had been thought that the Kintyre Peninsula would provide a temporary physical barrier to the continued spread of this invasive species up the west coast of Scotland. However, during early 2007, unattached drift *S. muticum* fragments were found in the Firth of Lorn at the Garvellachs and at Ganavan, near Oban.

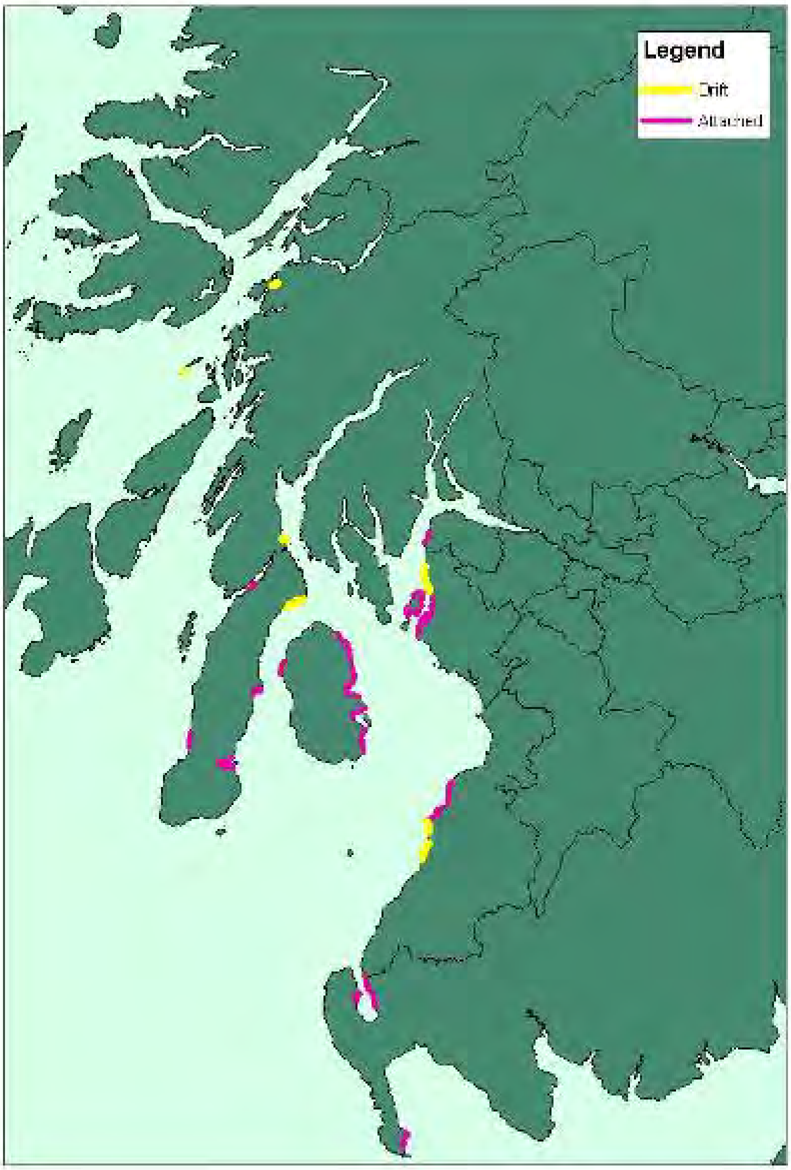
Detailed information on the known distribution of *S. muticum* around Scotland in 2007 is provided in Sections 10 and 11 of this report and illustrated in Figure 22.

Figure 22
Map illustrating the known distribution records of Sargassum muticum on the west coast of Scotland: 2004 - 2007
(Harries *et al.,* 2007b)



Alongside the production of this report, Royal Haskoning created a model of the northern Irish Sea and south western Scottish coast, to attempt to predict the future dispersal of *S. muticum* by identifying potential areas where the establishment of *S. muticum* was most likely (Royal Haskoning, 2008). This was used to identify high-risk sites where survey work was undertaken during July and August 2008. As a consequence of this fieldwork, the known distribution of *S. muticum* increased significantly and is illustrated in Figure 23. The results of this survey work will be detailed in a report by Royal Haskoning (in prep.).

Figure 23
Map illustrating the known distribution of the records of Sargassum muticum on the west coast of Scotland: 2008
(Royal Haskoning)



7.0 ECOLOGICAL, ECONOMIC AND NATURAL HERITAGE IMPLICATIONS OF *SARGASSUM MUTICUM* INTRODUCTION

Eno (1995) lists the main direct detrimental impacts caused by introduced species:

- A population explosion of the introduced species leading to competition for space with an eventual displacement or elimination of indigenous species.
- A concomitant introduction of new pests, diseases and parasites harmful to indigenous species.
- Habitat alteration including the provision of new niches and changes in water quality.
- Trophic alterations, including dietary competition and predation.
- Gene pool deterioration through hybridisation, particularly with genetically modified organisms.

In addition, there is an indirect detrimental impact:

- Methods used to control the introduced species may affect habitats and indigenous species.

Obviously some of these categories apply in the case of *S. muticum*.

An invasive species can be defined as “an introduced species that is ecologically and/or economically harmful, i.e. a pest” (Boudouresque and Verlaque, 2002). This definition implies that an invasive species always has a negative impact. It does not take into account species which naturally migrate, filling available niches as they colonise new areas, thereby increasing species diversity by new habitat creation.

In the UK, a large number of non-native species have been introduced, whether deliberately or accidentally. Of this number, few have established themselves and gone on to cause negative ecological impacts. Marine macroalgae constitute a large proportion of introduced non-native marine species and have the potential for significant environmental impact through the alteration of ecosystem structure and function (Schaffelke *et al.,* 2006).

Although only a very small fraction of transported and introduced species become invasive, the ability of these species to restructure and, hence, radically change the functioning of a recipient habitat is great (Crooks, 2002). The potential impact on the environment by invasive species regarded as ecosystem engineers, i.e. species with a disproportionate influence on ecosystem functionality that are considered pivotal in habitat creation, destruction and modification (Crooks, 2002), is particularly great. Invasive plant species that generate gross changes in the vegetation of an area are often regarded as highly influential ecosystem engineers. Terrestrial examples of the impacts of such species are plentiful whereas case studies in the marine environment are rarer and often confined to the intertidal zone, e.g. hybrids of the cordgrass *Spartina* spp. (Neira *et al.,* 2005) and the green seaweed *Codium fragile* (Levin and Hay, 1996; Levin *et al.,* 2002).

When an invasive species invades a new location, its chances of establishing a self-sustaining colony is low but its survival chances are greatly improved if the host community has been weakened by pollution, natural disaster, predation or anthropogenic activities. The potential effects of climate change and the general decline in UK biodiversity may increase the susceptibility of the marine ecosystem to invasive species (Manchester and Bullock, 2000).

As *S. muticum* typically develops extensive beds within its new habitats, considerable concern has been expressed and much research has been undertaken to determine the deleterious and beneficial aspects of this alga’s presence (Critchley *et al.,* 1990a). The main issue of concern regarding the development of established populations of *S. muticum* is the potential of deleterious ecological change where *S. muticum* displaces native species or alters habitat characteristics (Fletcher and Fletcher, 1975; Eno *et al.,* 1997; Harries *et al.,* 2007a). Most existing studies on the ecological impacts of *S. muticum* have concentrated on assessing competitive interactions with native macroalgae or assessing the community composition of the epibionts that colonise the *S. muticum* canopy (Harries *et al.,* 2007a).

In the subtidal zone, submerged aquatic vegetation constitutes a functionally important component of many marine soft-sediment environments and can profoundly influence animal assemblages by modification of physical, chemical and biological processes within these habitats (Everett, 1994). Little is known about the influence of macroalgae that inhabit similar soft-sediment habitats, despite some of these species being abundant and clearly identifiable as potential ecosystem engineers. In Europe, few attached perennial macroalgae are associated with soft sediments. However, the invasive *S. muticum*, is an exception. Although restricted to hard substrata in many parts of its introduced European range (Stæhr *et al.,* 2000), it also occupies extensive areas of subtidal soft sediments by growing in dense stands on embedded rock fragments and shells (Critchley, 1983; Critchley *et al.,* 1987). Once *S. muticum* has established a canopy over a previously unvegetated soft sediment substratum, there are three possible outcomes for the infaunal assemblages under this vegetation:

- The canopy could reduce the diversity of infaunal and epifaunal communities, in a similar way to ephemeral algal blooms of *Ulva* (including *Enteromorpha* spp.) that blanket soft substratum habitats (Soulsby *et al.,* 1982; Everett, 1994; Valiela *et al.,* 1997; Raffaelli, 2000)
- It might enhance infaunal diversity in a similar manner to other attached macroalgae (De Almeida and Ruta, 2000) and seagrasses
- It might have no detectable effects on the communities.

The effects of a particular invasion may change over time. Biological invasion theory suggests that changes in the abundance of invaders can occur i.e. they become ‘equilibrated’ (Williamson, 1996).

Strong (2003) proposed that in soft sediment habitats and on rock substratum, the dense canopy of *S. muticum* may well generate the following modifications:

- Thermal stratification
- Reduced water movement
- Reduced light penetration
- Increased sedimentation

Significant ecological consequences are often postulated but are generally difficult to detect (Harries *et al.,* 2007a). Ecological studies in Britain have been hampered by the conflicting aims of trying to study the plant while at the same time, often trying to eradicate it. Additionally, it is being studied in areas that it has only recently invaded and where it is still actively extending its range. In such circumstances, *S. muticum*’s initially aggressive behaviour may lead researchers to exaggerate the ultimate ecological impact on the native communities (Norton, 1977b).

Farnham (1992) concluded that in the years since its discovery in the UK, *S. muticum* had become dominant in many lower littoral areas with standing water and in the sublittoral fringe, covering a range of conditions and habitats and had spread extensively in European waters. He felt that *S. muticum* generally performed as an opportunistic “gap-grabber” or “space-filler”, without significantly out-competing or displacing indigenous algae as had originally been feared. Farnham (1992) said that it could even be argued that it had increased productivity and species diversity with its rich epibiota. E.B.G. Jones (pers. comm) agreed with Farnham’s conclusions and suggested that “the original fears regarding the ecological impact were too dramatic”.

7.1 The impacts of *Sargassum muticum* on the physical under-canopy environment

The rapid development of *S. muticum* populations can result in the formation of dense, virtually mono-specific, stands that develop a shading canopy, which may be present for a variable period of the year (Critchley, 1983d). The presence of a *S. muticum* canopy has the potential to modify the local environment in a number of ways.

Strong (2003) investigated the physical environment under the canopy of *S. muticum* in Strangford Lough, Northern Ireland. He found that levels of sedimentation were 2.3-4.0 times higher under a canopy of *S. muticum* when compared to an adjoining canopy of *Laminaria saccharina*. Sedimentation under *S. muticum* was 2.5-8.0 times higher than in unvegetated areas. Despite sedimentation being greater under *S. muticum*, sediment characteristics were the same under and outside the canopy and remained consistent over time. The organic content of sediment samples also remained consistent over time and no significant difference was found between canopy and non-canopy samples. Two out of the three sites sampled had similar chlorophyll levels in vegetated and unvegetated areas, although phaeopigments were significantly higher under *S. muticum* in two of the three sampled areas. Detritus from *S. muticum* may well be a substantial source of phaeopigments under the canopy. As the complexity, size and plant density of *S. muticum* is considerably greater than other native algae in Strangford Lough, the projected surface area is much greater, which, according to the conclusions of Garcia *et al.* (1999), would suggest why sedimentation within a patch of *S. muticum* is high.

Flow suppression was 84% within a typical canopy of *S. muticum* compared to 75% for *Laminaria saccharina*, although these values were not significantly different. Canopies of *S. muticum* are typically greater in biomass and density than *L. saccharina* (Strong, 2003). At higher plant densities of *S. muticum*, the laterals form a close and interlocking architecture, which appears to be particularly effective at baffling water movement. Seagrass communities have also been well studied with regard to the baffling of water motion and show similar levels of flow suppression to those observed in stands of *S. muticum* and *L. saccharina*. One of the other ecological implications of reduced flow is that water motion can also influence the boundary layer surrounding plants. Dissolved gases for photosynthesis, as well as nutrients, need to cross this layer of stagnant water by molecular diffusion, which can be limiting for some metabolic processes (Gambi *et al.,* 1990).

Strong (2003) found that the canopy of *S. muticum* absorbed 97.2% of the transmitted light and the *L. saccharina* canopy absorbed 95.6%. Since, under a native canopy less than 5% of the light reaches the sub-canopy, the extra 2% absorption by *S. muticum* represents an approximate 40% loss of available light for the sub-canopy community. However, this may not be consistent throughout the tidal cycle. Critchley *et al.,* (1990) observed a 97% reduction in the PAR within just 0.1 m of the canopy surface and Curiel *et al.* (1998) recorded a 90-95% absorption at a depth of 1.0-1.5 m below a canopy of *S. muticum*, whilst unvegetated areas at the same depth only experienced a 25% loss. In a previously unvegetated, soft sediment habitat, the level of shading under *S. muticum* represents a major modification of the physical environment, although if the chlorophyll *a* concentration can be used as an indication of microfloral biomass, then the shading appears to be unimportant (Strong, 2003).

Within Strangford Lough, Strong (2003) found that temperature stratification did not occur in *Laminaria* stands, but was evident in stands of *S. muticum*. In summer, the water temperature within the canopy of *S. muticum* was approximately double that of the ambient seawater. However, at the surface of the sediment, it was slightly cooler than the surrounding seawater. Within the sheltered environment of Strangford Lough, the high density of *S. muticum* tends to prevent the water in the middle from being exchanged. Also, the dark colour of the canopy absorbs much of the light and on a sunny day the stagnant canopy water can become extremely warm. Similar stratification does not appear to occur under other native species, probably as the standing biomass is typically less than that of *S. muticum* and the native species have less of an interlocking morphology that maintains water flow and exchange.

In Lake Grevelingen, Netherlands, Critchley *et al.* (1990) found that such dense canopy severely restricted light penetration, with the *S. muticum* absorbing 97% of the photosynthetically active radiation (PAR), as well as elevating the surface water temperature while the shading effect caused the water temperature below the canopy to be appreciably cooler. Under calm conditions, the temperature difference between 0.5 m depth and the water surface was 9.2°C, with the thin layer of water on top of the canopy reaching 2.7°C above the ambient air temperature (28°C). Critchley concluded that a canopy of *S. muticum* in shallow water not only elevated the surface water temperature, but the shading under the canopy also caused water 0.1 m below it to be appreciably cooler than water outside the canopy. No comparisons were made with other macroalgal species.

Strong (2003) suggested that the temperature stratification documented in canopies of *S. muticum* raises some interesting questions about the interaction of this warming and the physiology of this species. Norton (1977) found that the optimum temperature for *S. muticum* was 25°C, and that this species was also tolerant of temperatures up to 30°C. One could hypothesise that this localised warming within the canopy might actually benefit *S. muticum* and increase photosynthetic capabilities and ultimately growth. Furthermore, this warming may also have serious implications for the behaviour or survival of epiphytic fauna and the growth of epiphytic algae. He proposed that further experimentation on the longevity of this temperature stratification over the tidal cycle and its implication for physiology of the basiphyte, epiphyte and epiphytic fauna would be of great interest for understanding the ecology of *S. muticum*.

Strong (2003) found that under a canopy of *S. muticum,* sedimentation and shading increased and the water flow and temperature decreased. Despite the greater sedimentation, the particle size distribution remained the same. Strong (2003) concluded that, taken individually, none of these modifications appears great, but when the extent of the *S. muticum* population in Strangford Lough was considered, the combined impact may be significant.

Britton-Simmons (2004) measured a series of these variables (light levels, sedimentation, current speed, nutrient supply) and found that the only measurable change created by the *S. muticum* canopy was a reduction in light levels, but this research was undertaken on a more exposed site with primarily rock substrata.

7.2 Sargassum muticum beds as a habitat

In Japan, both *Sargassum* beds and floating mats of unattached branches are generally considered to be important as spawning, nursery and feeding grounds for a wide variety of fish, shellfish and other species. (Tsukidate, 1984). Although widely distributed in the western Pacific, *S. muticum* is regarded as being relatively insignificant ecologically (Critchley, 1983a). However, invasive species may perform ecologically quite differently in comparison to their behaviour in their native habitat (Farnham, 1992).

S. muticum is distinctive in that it is a large, habitat-forming species and this increases the probability of detectable ecological change (Rueness, 1989). *S. muticum* beds may contribute to increased productivity at affected sites, by colonising areas of mixed substrate where algal cover was formerly sparse (Jephson and Gray, 1977; Franklin, 1979; Viejo, 1999; Pedersen *et al.,* 2005; Sanchez *et al.,* 2005). The ecology of such areas typically changes noticeably, with the presence of a large standing stock of *S. muticum* and its associated epibionts, in areas where few macroalgae were found prior to its introduction (Farnham *et al.,* 1981; Critchley, 1983d; Critchley *et al.,* 1983; Critchley *et al.,* 1986). In areas of mixed substrate, *S. muticum* can increase habitat heterogeneity (Buschbaum *et al.,* 2006) and provide cover for mobile macrofauna, including young fish and small crustacea, such as prawns, and fish, including wrasse and gobies (Jephson and Gray, 1977; Critchley, 1983b).

Some authors have noted that the rapid growth and pseudoperennial lifecycle of *S. muticum* tends to result in a local increase in primary productivity (Sánchez *et al.,* 2005). Potential causes of the higher abundance of organisms associated with *S. muticum* may include the increase in habitat complexity and substrate extent provided by the large and structurally complex *S. muticum* fronds. In addition to a higher abundance of epibionts on the fronds, there was also a higher abundance of sessile epifauna which do not utilise the *S. muticum* fronds as a substrate. Reduced predation pressure within the dense *S. muticum* canopy may be implicated in accounting for the elevated abundance of epifauna. Another potentially significant factor affecting abundance is the increased detrital input likely to be associated with a dense canopy of *S. muticum* and increased turnover of organic matter and nutrients (Pedersen *et al.,* 2005).

Gastropod species can graze on *S. muticum* germlings (Franklin, 1979). A variety of grazers can feed on *S. muticum* fronds but there is little evidence to indicate that they are a controlling factor in its abundance or distribution. These include the sea urchins *Strongylocentrotus droebachiensis* (De Wreede, 1983; Britton-Simmons, 2004) and *Psammechinus miliaris (*Pedersen *et al.,* 2005; Thomsen *et al.,* 2006), the common periwinkle *Littorina littorea* (Thomsen *et al.,* 2006) and the sea hare, *Aplysia punctata* (Critchley *et al.,* 1986).

Due to the difficulties associated with quantifying the epifauna of rock surfaces very few studies have assessed the influence of a *S. muticum* canopy on this element of the ecosystem. Britton-Simmons (2004) studied a subtidal *S. muticum* habitat on bedrock in Washington State, USA. The study found no evidence of change in the abundance of detritivores or herbivorous molluscs and no change in the species richness of the invertebrate community in general. The abundance of grazing sea urchins, *Strongylocentrotus droebachiensis*, was found to be reduced within areas dominated by *S. muticum* and the experimental evidence of feeding preference tests demonstrated that *S. muticum* was less palatable to the urchins than native kelp species. Conversely, Pedersen *et al.* (2005) reported that the grazing urchin, *Psammechinus miliaris*, on the Scandinavian coast showed a feeding preference for *S. muticum* but did not indicate urchin abundances in these *S. muticum* beds. Thomsen *et al.* (2006) undertook an assessment of the grazers *Littorina* and *Psammechinus* on Scandinavian *S. muticum* beds and found no correlation between grazer density and *S. muticum*, concluding that grazers do not naturally control adult *S. muticum*.

Comparatively few studies have investigated ecological aspects of colonisation by *S. muticum* and, of those, the majority have investigated its occupation of hard substrata (e.g. Viejo, 1997, Stæhr *et al.,* 2000, Britton-Simmons, 2004).

Strong (2003) collected sediment cores under and outside canopies of *S. muticum* in Strangford Lough, where *S. muticum*, was first recorded in 1995, and Langstone Harbour, English Channel, where *S. muticum* was first found in 1974, to investigate modification of the infaunal assemblages. At both study sites, community analyses highlighted significant differences between the assemblages under the canopies and those in adjacent unvegetated areas. In Strangford Lough, the invertebrate community under the canopy contained a higher abundance of smaller, opportunistic, *r*-selected species than the invertebrate community outside the canopy. By contrast, the communities under and outside the canopy at Langstone Harbour were similar in species composition, diversity and dominance, but overall faunal abundance was greater under the canopy. In Strangford Lough, individuals of *Scoloplos armiger* and *Pygospio elegans* all occur in fine or muddy sands and were found in a greater abundance outside the canopy of *S. muticum*. *Dexamine spinosa*, an amphipod associated with vegetated areas, was found to be abundant under the *S. muticum*. Also, two species characteristic of organically enriched sediments, namely *Tubificoides pseudogaster* and *Capitellides giardi*, were also documented in greater numbers under the canopy. *Mytilus* sp. was also found in high abundances under the canopy. In Langstone Harbour, there was a greater abundance of *Cirriformia tentaculata*, *T. pseudogaster*, *Tubificoides benedini* and *Corophium* sp. in the canopy areas. The polychaete *Capitella capitata* was also more abundant under the canopy of *S. muticum*; this species has been shown to readily consume macroaglal detritus and to be capable of deriving a major portion of its nitrogen intake directly from the macroalgae. Sediment characteristics were not affected by *S. muticum* canopies, but the infaunal changes may be related to environmental modification; shading, flow suppression and temperature stratification were also investigated. The differences between these two sites indicate that localised conditions and/or the duration of colonisation of *S. muticum* are important in determining the nature of habitat modification (Strong, *et al.,* 2006). Please refer to Section 9.4.1. for further information on this research.

During July 2005 and 2006, comparative studies were conducted on intertidal algal and faunal communities associated with *S. muticum* and native algae on the Isle of Cumbrae, Scotland (Harries *et al.,* 2007a). Significant differences were detected in the structure and composition of the communities. Elevated faunal abundances were associated with *S. muticum* and evidence indicated that increased detrital input may have been a possible contributory factor. Differences in faunal community composition were most pronounced in the sessile epifauna below the *S. muticum* canopy. Faunal communities associated with *S. muticum* were less heterogeneous in composition than those associated with native algae at equivalent shore positions. Some of the compositional differences may be coincidental and attributable to factors favouring the establishment of *S. muticum* rather than to the direct influence of the *S. muticum* canopy (Harries *et al.,* 2007a). Harries *et al.* (2007b) concluded that dense canopies of *S. muticum* alter the community structure in the immediate surrounding area but they are unlikely to cause radical reductions in the abundance of native biota on a wide scale.

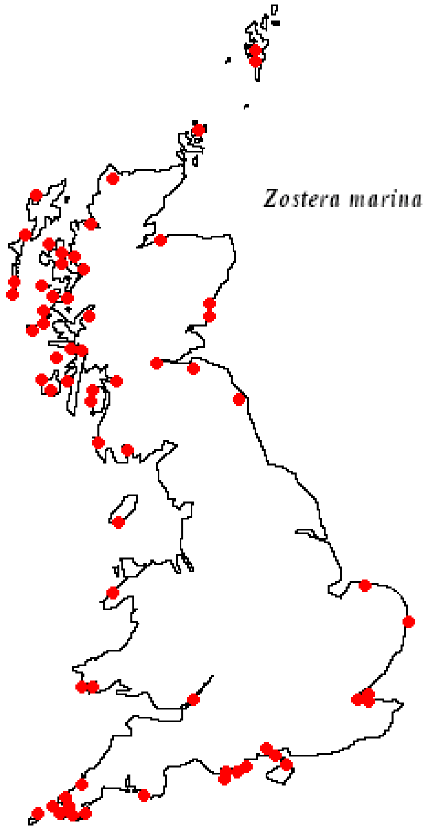
Such studies have lead to the conclusion that the presence of dense *S. muticum* may have a significant effect on local habitat dynamics and on physical factors that influence ecosystem functioning. Although often overlooked when considering the environmental impact of *S. muticum,* its extensive colonisation of unvegetated soft-sediment habitats has both generated a new epibenthic habitat and modified the resident infaunal assemblages. The resulting influence of this species differs between sites, ranging from a strong perturbation to a moderate enhancement of infaunal density, suggesting strong site-specific effects of *S. muticum* that make generalisations about the impact of this species difficult. Additionally, the long-term residence of *S. muticum* appears to change the nature of its influence (Strong *et al.,* 2006).

7.3 Competition with eel grass, *Zostera marina*

Seagrasses (*Zostera* sp.) are marine flowering plants found in shallow coastal areas, typically on sheltered sandy or muddy substrata to a maximum depth of about 10 m. A map of the known UK distribution of *Zostera marina* is provided in Figure 24.

In the subtidal zone, submerged aquatic vegetation constitutes a functionally important component of many marine soft-sediment environments (Everett, 1994). Seagrasses can profoundly influence animal assemblages by modification of the physical, chemical and biological processes within these habitats (Everett, 1994; Webster *et al.,* 1998; Attrill *et al.,* 2000; van Houte-Howes *et al.,* 2004). The physical presence of a plant canopy provides shelter and protection from predation for invertebrates and young fish (Summerson and Peterson, 1984; Boström and Bonsdorff, 1997; De Almeida and Ruta, 2000; Norkko *et al.,* 2000; Jackson *et al.,* 2001; Bloomfield and Gillanders, 2005). Seagrasses also influence localised water flow (Fonseca and Cahalan, 1992; van Keulen and Borowitzka, 2002), which changes the sedimentation rate and can enhance sediment organic-nutrient content and food availability for infaunal and epifaunal communities (Hull, 1987). Consequently, seagrass beds are typically characterised by high primary production, species diversity and faunal abundances (Webster *et al.,* 1998; Bloomfield and Gillanders, 2005). Seagrass beds thus constitute an important reservoir of coastal biodiversity. The beds also provide food for wildfowl and the juveniles of some commercially important fish species. The dense root networks of the plants stabilise the underlying substratum and so act to reduce coastal erosion. Seagrass beds are therefore of considerable economic and conservation importance (Davison and Hughes, 1998).

Figure 24
Map illustrating the known UK distribution of Zostera marina: 1994
(Davison and Hughes, 1998)



In the UK, three species of eelgrass typically occur; common eelgrass *Z. marina*; narrow-leaved eelgrass *Z. angustifolia* and dwarf eelgrass *Z. noltii*. All three species are generally found on sedimentary (muddy or sandy) substrata, in areas that are either sheltered or extremely sheltered from tides and currents. Fletcher and Fletcher (1975a) reported that *S. muticum* particularly favoured areas colonised by the ecologically important eelgrass, *Z. marina*, within the Bembridge lagoons on the Isle of Wight. However, unlike seagrasses, *S. muticum* favours solid substrata. Competition is therefore more likely in areas of mixed substrata, where both may exist (den Hartog, 1997). Den Hartog (1997) expressed concern that *S. muticum* may have a negative effect on eelgrass beds, if it colonised bare patches or around the edges. *S. muticum* has been reported to displace *Zostera* in some situations where *Zostera* occurs on mixed substrates that offer sufficient attachment points for an *S. muticum* canopy to develop (Den Hartog, 1997; Davison and Hughes, 1998).

Observations based on numerous surveys within Europe led den Hartog (1997) to state that *S. muticum* and *Zostera marina* usually do not occur in mixed stands. Despite this, it would appear that *S. muticum* will colonise substratum left by the retreat of a bed of *Z. marina* and this process prevents recolonisation by *Z. marina*. This substitution was seen in Roscoff when the Amoco Cadiz crude oil spill caused the local decline of *Z. marina,* and *S. muticum* colonised the exposed substratum (den Hartog, 1997). The ability of *S. muticum* to colonise substratum previously occupied by *Z. marina* was also highlighted on Isle de Re, in the Bay of Biscay. De Beauchamp mapped the eelgrass beds before the wasting disease in the 1930s. Subsequent mapping by Belsher (1984) and analysis by den Hartog (1997) revealed that the current *S. muticum* distribution almost exactly fitted the former eelgrass distribution and no *Z. marina* existed locally. In the Solent, Critchley (1981) also observed the die-back of *Z. marina* and subsequent colonisation of the exposed substratum by *S. muticum*. Although this is not direct competition, Critchley (1981) stated that the opportunistic invasive strategy by *S. muticum* might result in the further decline of eelgrass within the shallow eulittoral lagoons at Bembridge (UK).

Druehl (1973) reported that *S. muticum* was capable of replacing *Z. marina* in certain areas and Tubbs (1995) observed that *S. muticum* and *Z. angustifolia* competed for space in lower shore lagoons. However, there is evidence suggesting that both *S. muticum* and *Z. marina* may co-exist, without any evidence of conflict or displacement, in their differing habitats. In the San Juan Islands, Washington, *S. muticum* and *Z. marina* were found to co-exist in different habitats with no evidence of competition or displacement (Norton, 1977b). Similar results were observed in the Solent and Cornwall regions (Davison and Hughes, 1998) and in Sweden (Karlsson and Loo, 1999).

Strong (2003) found that several shallow *Zostera* sp. beds in Strangford Lough, Northern Ireland, contained peripatetic (stone-walked) individuals of *S. muticum*. However, transplants confirmed that *S. muticum* was unable to establish itself in these beds. No *S. muticum* was found in the deeper seagrass beds where light penetration might have limited its depth distribution. Please refer to Section 9.4.2 for more information on Strong's (2003) experimental transplant work with *S. muticum* in *Zostera* beds within Strangford Lough.

In the Republic of Ireland, *S. muticum* is growing in seagrass beds, apparently 'sharing' a habitat with *Zostera* sp., and no evidence of negative impacts has been found (Kraan, 2004). *S. muticum* has been found with *Z. marina* in the Yealm Estuary, Devon in 1997 and at Looe, Cornwall in 1996 (Strong, 2003). Strong reported that the Yealm Estuary had a deepwater *Z. marina* bed with a very low density of large peripatetic plants of *S. muticum*, whereas the shallow seagrass lagoon in Looe was 'infested' with the alga.

At Bembridge, Isle of Wight, over the winter of 1979-80, the *Z. marina* beds died back due to frost damage and *S. muticum* sporelings colonised the newly exposed rock. This did not represent direct competition since the *S. muticum* behaved as an opportunistic space-filler but its establishment may have prevented subsequent re-colonisation by the eel grass (Critchley, 1980; Farnham *et al.,* 1981).

After *S. muticum* has colonised an area, it appears to impede the re-establishment of a native population. This is thought to be the reason *Z. marina* was replaced in the Gulf of Biscay, France. The population of *Z. marina* died back due to a wasting disease in the 1930's (den Hartog, 1997). Today a population of *S. muticum* is found where previously *Z. marina* beds would have been found. *S. muticum* could not establish a population when the *Z. marina* beds filled all the available space, but due to an extreme weather event, it seized the opportunity presented and benefited at the expense of the *Z. marina*. Once colonised by *S. muticum*, it may be that *Zostera* sp. were unable to regenerate the beds previously occupied. Therefore, it seems that *S. muticum* interferes with the regeneration cycle of the *Zostera* sp. beds rather than acting as a direct competitor.

7.4 Competition with indigenous algae

Invasive species of macroalgae are a threat to other algae and to marine biodiversity as they have the potential to replace native species by out-competing them for light and substrate. The result of native species being replaced by non-native species has a direct impact on the biodiversity of an area. By replacing dominant macroalgae, an invasive species can cause a shift in marine communities and their trophic food webs (Walker and Kendrick, 1998).

S. muticum is an opportunistic alga that has high a reproductive output, rapid growth and an ability to "grab" any available free space. When *S. muticum* displaces other algae it is generally initially taking advantage of "free space" that has appeared as a result of natural or cyclical die-back of the indigenous dominant algae or uncolonised space that exists naturally between indigenous, established algae. Since most *S. muticum* germlings settle within a few metres of the parent plant, this tends to result in persistent and dense local populations that inhibit colonisation by other algal species (Arenas *et al.,* 2002). Once *S. muticum* is established, it can potentially compete effectively for light and space with native algae (Fletcher and Fletcher, 1975a; Norton, 1976; Nicholson *et al.* 1981; Ambrose and Nelson, 1982; De Wreede, 1983; Viejo, 1997; Cosson, 1999; Staehr *et al.* 2000; Bartsch and Tittley, 2004; Britton-Simmons, 2004; Sanchez *et al.* 2005) by virtue of its pseudo-perennial lifestyle, rapid growth rate, large frond size and dense canopy (Wernberg *et al.,* 2000). Wernberg *et al. (*2000) suggested that the competitive success of *S. muticum* is due the energetic efficiency of its pseudo-perennial life history, compared to the truly perennial life histories of many of its native competitors, combined with effective dispersal mechanisms and the low risk of displacement of the holdfast by winter storms, when on solid rock.

The reduction in the abundance of a dominant native algal species through competition with *S. muticum* can, in certain circumstances, result in an indirect positive effect on other algal species as they are no longer competing with the dominant native species (Sánchez *et al.,* 2005).

The outcomes of competitive interactions are also influenced by abiotic factors. *S. muticum* is known to have a broad tolerance range for salinity and temperature but it is likely that the competitive ability of *S. muticum* will be impaired at sites near the limits of its tolerance range (Norton, 1977). The low desiccation tolerance of *S. muticum* means that it is less likely to successfully displace native algae in intertidal sites, excluding tidal pools, and more likely to compete successfully in subtidal sites (Norton, 1977; Deysher and Norton, 1982; Britton-Simmons, 2004; Sánchez and Fernández, 2005). The competitive success of *S. muticum* can also be limited in conditions of high exposure (Viejo *et al.,* 1995; Sánchez *et al.,* 2005).

Concerns have been expressed that *S. muticum* may compete with and displace some indigenous brown alga; *Laminaria* species, *Cystoseira* species and *Halidrys siliquosa* as well as *Ceramium rubrum, Gracilaria verrucosa, Chondrus crispus, Scytosiphon lomentaria, Polysiphonia* sp.*, Ulva lactuca and Enteromorpha* sp. (Fletcher and Fletcher, 1975). In Britain, these species characterise large areas of the littoral and shallow sublittoral and are important in terms of food chains and as hosts for many epibiont species (Withers *et al.,* 1975; Anon, 1973b). *S. muticum* may be a successful invasive alga because it has the ability to compete with other species of alga at various tidal levels, include the shallow sub-littoral, lower intertidal and tidal pools.

The observed outcomes of competitive interactions are highly variable depending on the specific environmental conditions of the study site (Viejo, 1997; Andrew and Viejo, 1998; Sánchez *et al.,* 2005). The presence of any existing algal populations on rock surfaces has been shown to inhibit the settlement and successful establishment of *S. muticum* germlings (Deysher and Norton, 1982; De Wreede, 1983; De Wreede and Vandermeulen, 1988; Britton-Simmons, 2006). In such environments, the establishment of *S. muticum* may be reliant on disturbance events that create patches of open substrate, which enable the settlement of the germlings. However, the timing of disturbance events may be critical and in some circumstances, disturbance may allow the development of a persistent turf of native algae that prevents settlement by *S. muticum* (De Wreede, 1983).

Fletcher and Fletcher (1975a) reported that off the Pacific coast of North America "*S. muticum* was not held in check by the natural vegetation and considerably disturbed the ecology of the coastline. It became the dominant species at low-tide level in a number of regions and was considered to be pushing out indigenous species of *Cystoseira* and *Laminaria.*" At Santa Catalina, southern California, Nicholson *et al. (*1981) found that *S. muticum* colonised sites that opened up following a natural disappearance of the native giant kelp, *Macrocystis pyrifera,* following unusually high water temperatures. The giant kelp is the dominant macroalgae and is of significant ecological importance. Colonisation by *S. muticum* appeared to prevent giant kelp recruitment even though the *S. muticum* died back to the perennial holdfast in early summer and did not resume vegetative growth until the autumn. It is thought that the canopy of the dense beds of *S. muticum* created shading at a critical point in the giant kelp's life cycle which reduced and prevented giant kelp recruitment. There does appear to be intense competition between *S. muticum* and *M. pyrifera* as both species utilise the same habitat and both form canopies but it is likely that *S. muticum* can only displace *M. pyrifera* when it dies back (Ambrose and Nelson, 1982). This interpretation was supported by observations that *S. muticum* out-competed *M. pyrifera* in marinas where the water temperature rose to over 15˚C in summer causing the giant kelp to die back but that *M. pyrifera* re-established itself during the winter and early spring (Nicholson *et al.,* 1981).

Mixed stands of *S. muticum* and *Rhodomela larix* occur on Bath Island, British Columbia, Canada. De Wreede (1983) showed experimentally that within mixed canopies of reproductive plants, *S. muticum* was able to dominate newly cleared space and nearly exclude *R. larix*. The overall effect of the introduction of *S. muticum* was the reduction in cover of *R. larix* in the Straits of Georgia. The mechanisms of exclusion were not investigated, but appeared to be related to the lack of recruitment of *R. larix* under *S. muticum*, which again could be a result of sub-canopy shading.

Britton-Simmons (2004) studied the effects of *S. muticum* on benthic subtidal communities in Washington State, USA. Results indicated that native brown and red algae were found in higher abundance in areas where *S. muticum* had been removed and that competition for light with *S. muticum* led to a reduction of native canopy algae by approximately 75% and a reduction of native understory algae by approximately 50%. In this instance *S. muticum* had the ability to grow taller than all but one of the native algal species present. This was particularly important during the summer months, when *S. muticum* reaches its maximum growth, as this is also a critical period of growth and reproduction for many of the native algal species.

On the Isle of Wight, *S. muticum* growing in the Bembridge lagoons was found to be competing with a number of algal species; *Ceramium rubrum, Chondrus crispus*, *Cystoseira* spp*, Enteromorpha* spp, *Gracilaria verrucosa, Halidrys siliquosa, Laminaria* spp*, Polysiphonia* spp*, Scytosiphon lomentaria, Ulva lactuca* and *Zostera marina* (Fletcher and Fletcher, 1975a). However, *S. muticum* did not colonise the exposed ledges of *Fucus serratus* or the upper littoral region. *S. muticum* was attached to bedrock or large stones and boulders scattered over the lagoon bottom but these were frequently overlaid to varying depths by mobile sand and shingle. At Warden Point in 1980, the lower limit of *S. muticum* coincided with the upper limit of the *Laminaria digitata* forest. However, after 1980, the *Laminaria digitata* increased while the *S. muticum* died back, probably due to sand abrasion and shading caused by the *Laminaria* fronds (Critchley, 1983d).

Fletcher and Fletcher (1975a) found that in Portsmouth Harbour, *S. muticum* grew on the previously relatively unfilled niches of buoyant structures and out-competed *Ectocarpus* spp*, Enteromorpha* spp, *Giffordia* spp, *Petalonia fascia, Polysiphonia* spp*, Scytosiphon lomentaria, Ulva lactuca* and the occasional *Laminaria saccharina*.

Critchley (1981) stated that the survival of *Laminaria saccharina* and *Fucus serratus* germlings appeared to have been reduced in areas where *S. muticum* was present. Critchley *et al.* (1983) suggested that the growth of the native germlings beneath the canopy of *S. muticum* may have been retarded by reduced light penetration. The retarded germlings may have lost vigour or remained at a small enough size to be grazed by molluscs (Critchley, 1981).

Stands of *S. muticum* have also been implicated in the decline of *Halidrys siliquosa* in rockpools (George, Tittley and Wood as cited in Eno *et al.,* 1997) and the loss of large, shallow beds of *Scytosiphon* spp. in Washington (Scagel, 1956).

Givernaud *et al. (*1991) documented the replacement of *Laminaria saccharina* and *Zostera marina* by *S. muticum* at Grandcamp on the French Atlantic coast. In deep water pools and lower littoral lagoons or in the sublittoral fringe, *Halidrys siliquosa*, *Cystoseira* spp and *Laminaria saccharina* may be in competition and can be displaced by *S. muticum* as the dominant species (Critchley *et al.,* 1986; Farnham, pers. comm.).

The gradual decline of *Laminaria digitata* from the Calvados coastline (France, Normandy) occurred at the same time as the spread of *S. muticum* (Belsher *et al.,* 1984). The decline of *Laminaria digitata* and *L. saccharina* beds and their total replacement by *S. muticum* on the Calvados coastline (France) took less than five years (Givernaud *et al.,* 1991; Cosson, 1999). In 1983, large mixed populations of *L. digitata* and *L. saccharina* occurred in permanently flooded channels in the middle of a rocky bar between +1.5 m and –5.0 m (LAT). The biomass of *Laminaria* spp. was roughly estimated at 26,000 tonnes by Thouin *et al.* (1983, in Givernaud *et al.,* 1991). By 1988, *Laminaria* spp. had completely disappeared and there had been a parallel development of the *S. muticum* population at this site (Givernaud *et al.,* 1991, Cosson, 1999). *S. muticum* plants were first seen to colonise the unvegetated areas, i.e. the sandy beaches of the bay of Veys. As free space was generated by the declining *L. digitata*, *S. muticum* colonised this area. Plants of *S. muticum* now colonise 80% of all submerged substrata with a standing biomass of 2–4 kg (fresh weight) per metre. The loss of *L. digitata* had serious economic consequences for the commercial alginate industry. Belsher *et al.* (1984) suggested that *S. muticum* might be responsible for the decline of *L. digitata*, but the most likely explanation is interference competition. Critical points in the development of the life cycle of *L. digitata* occurred when the canopy of *S.*

muticum was at its greatest, which might have deprived the young plants of *Laminaria* spp. of light and hence reduced recruitment locally (Cosson, 1999).

Strong (2003) investigated the competition between *S. muticum* and *Laminaria saccharina.* He found that the timing of the reproductive phenology of *S. muticum* and *L. saccharina* was a critical factor. *L. saccharina* develops and releases spores in autumn and winter (White, 2003). Newly recruited sporophytes grow quickly in winter and spring, after which they are large enough to be considered part of the adult population. The majority of reproductive and recruiting period for *L. saccharina* occurs when the canopy of *S. muticum* has declined (winter) or is at its lowest cover (spring). This would suggest that in Strangford Lough, the reproduction of *L. saccharina* was relatively unimpeded by the presence of a canopy of *S. muticum*. By the time the canopy of *S. muticum* has reached its maximum, the sporophytes of *L. saccharina* are typically large enough to be considered adults. Therefore, the competitive interactions are probably among the adult phases and are either direct, e.g. overgrowth, or indirect, e.g. opportunistic pre-emption of substrata. His investigations found that *L. saccharina* was unaffected by *S. muticum* under the experimental conditions applied over the six weeks. He concluded that rather than considering there to be competition between these species, facilitation may be a better concept, i.e. the growth rates of *S. muticum* are enhanced in mixed canopies. The lack of any impact of *S. muticum* on the growth of *L. saccharina* indicates that direct interactions between the two species in a mixed canopy are probably not responsible for any decline or substitution of *L. saccharina* by *S. muticum* seen in other parts of the introduced range. This supports Farnham's observations that *S. muticum* is better described as opportunistic, i.e. it is a species that colonises open habitat as it becomes available, rather than displacing native species in a mixed canopy it has invaded (Farnham, pers. comm.).

Studies in the Dorn (Strong, 2003), a complex micro-tidal lagoonal system on the south eastern side of Strangford Lough, found that the distribution and abundance of both *Laminaria saccharina* and *S. muticum* increased between 2000 and 2002 but *L. saccharina* remained the most widespread canopy species. *S. muticum* doubled both the area occupied and the density of plants, whereas the distribution of *L. saccharina* increased by a third and the mean canopy cover enlarged by approximately 50%. Overlap between the two species increased in 2002, with *S. muticum* expanding from the unvegetated soft substratum areas into habitat characteristic of *L. saccharina*. At the end of the survey period, there was no evidence that the distribution of *L. saccharina* had diminished with the increased presence of *S. muticum*. This finding is in contrast to the findings of other studies that have documented the decline of leathery macrophytes during the invasion of *S. muticum* in Spain and Denmark (Viejo, 1997; Stæhr *et al.,* 2000).

Critchley *et al. (*1990) found that in Lake Grevelingen, south west Netherlands, the persistence of the *S. muticum* canopy was due to extreme shelter and a non-tidal environment. The dense surface canopy was found to severely restrict light penetration, with the *S. muticum* absorbing 97% of the photosynthetically active radiation (PAR). The canopy also elevated the surface water temperature with the shading effect causing the water temperature below the canopy to be appreciably cooler. Indigenous algae, particularly sub-canopy algae, had decreased in size and frequency but the diversity had not yet been affected by the sub-optimal conditions created by *S. muticum.* Field studies at Bembridge, Isle of Wight, indicate that in lagoons, the shading caused by a 100% cover of *S. muticum* at low water, reduced the size and number of the sub-canopy algae (Critchley, 1980; Critchley, 1983d).

In Denmark, *S. muticum* was first discovered in Limfjorden in 1984 (Christensen, 1984; Thomsen *et al.,* 2006) and since then it has established itself as the most abundant macroalga (Stæhr *et al.,* 2000). Stæhr *et al. (*2000) reviewed the impact of *S. muticum* colonisation on native macroalgal communities over a period from 1990 to 1997. They showed that an increase in cover of *S. muticum* led to a slight decrease in diversity, partly due to an increased dominance of *S. muticum* but also due to a decrease in dominance (and cover) by native species such as *L. saccharina*, *Codium fragile* and *F. vesiculosus*. Competition for light and hard substrate were considered to be the factors that caused the displacement of the native algae. Year-to-year change in the subtidal community structure was small and significant changes appeared only when community structure was compared over time scales of more than two to three years. Reduced heterogeneity has been recorded in Denmark (Staehr *et al.,* 2000), where the composition of the macroalgal community (excluding *S. muticum*) was found to become increasingly homogeneous in composition as dominance of *S. muticum* increased. A similar trend appears to be occurring on the Isle of Cumbrae, western Scotland (Harries *et al.,* 2007a).

A study by Thomsen *et al.* (2006), in Draby Vig Bay, Limfjorden, showed that *S. muticum* became the dominant macroalga in the early 1990s but was limited to the 2-4 metre depth interval. Over a period of 11 years of summer monitoring, no groups of alga were found to be detrimentally affected by the invasion of *S. muticum*, but kelp species, such as *Laminaria sp.*, did decrease in abundance in the 2-4 metre depth interval. This decrease in abundance was attributed partly to competition with *S. muticum* for boulders as both *S. muticum* and kelp species depend on boulders for long term stability (Sousa, 1979). This study showed that the dominance of a community by *S. muticum* maybe limited by seasonality. Therefore “as resource availability changes during the season, competition may change as well” (Thomsen *et al.,* 2006). *S. muticum* and *Laminaria sp.* have similar resource needs, but the rapid growth rate of *S. muticum* may result in it eventually out-competing the native macroalga; *Laminaria* sp. (Wilson, 2006).

On the north coast of Spain, when Viejo (1997) investigated the impacts of *S. muticum* colonisation on native macroalgal communities, there was evidence of an impact on the leathery macrophytes in rockpool assemblages, namely *Bifurcaria bifurcata, Cystoseira baccata, Cystoseira tamariscifolia* and *Saccorhiza polyschides*. Within one area of rockpools, the foliose algae also declined, although this was not a consistent trend found in all of the rockpools examined. The cause was considered to be shading by *S. muticum* and this affected the brown algae *Bifurcaria bifurcata,* which is unable to grow under low light conditions, and some foliose algae. The establishment of *S. muticum* seemed not to affect other functional groups such as the crustose and the articulate calcareous algae, probably due to their tolerance to low light conditions.

During July 2005 and July 2006, comparative studies were conducted on intertidal algal and faunal communities associated with *S. muticum* and native algae on the Isle of Cumbrae, Scotland. The abundance of the dominant native algae *Dictyota dichotoma* was found to be reduced in areas dominated by *S. muticum* and displacement may have occurred through competition for substrate or light (Harries *et al.,* 2007a). Wilson (2006) found that *S. muticum* and *Laminaria digitata* formed very distinct bands on the Isle of Cumbrae and that in only two years, *S. muticum* had established itself, forming an almost complete band, normally at the level of *L. digitata*. This may indicate that *S. muticum* displaced or out-competed *L. digitata* in only a short time frame at this site (Wilson, 2006).

S. muticum has been recorded growing epiphytically on a number of other algae; *Chondrus crispus, Cystoseira nodicaulis, Fucus vesiculosis, F. serratus, Halidrys siliquosa, Laminaria saccharina, Laurencia pinnatifida* and *Ulva lactuca* (Withers *et al.,* 1975).

Critchley (1983e) found that at Langstone and Chichester Harbours, annually *S. muticum* germlings opportunistically colonised stones and shells within pits left in the mud by bait diggers. However, the majority were carried away (stone-rafting) by the tide or were killed or severely stunted by desiccation. These settlements were not very successful, with only limited development of the plants. However, as the populations were replaced annually with new germlings, the settlement and development of other colonising algae was probably prevented. Additionally concern was expressed that the *S. muticum* beds may encourage siltation.

7.5 Epibionts on *Sargassum muticum*

Assessing the typical flora and fauna associated with *S. muticum* beds provides information on whether the species composition of an area has been altered by the introduction of *S. muticum*.

Epibiont species appear to show little host plant specificity and the epibiota of *S. muticum* tends to be similar to that of morphologically comparable native algal species occurring within the same habitat (Withers *et al.,* 1975; Jephson and Gray, 1977; Norton and Benson, 1983; Viejo, 1999; Wernberg *et al.,* 2004; Buschbaum *et al.,* 2006). The similarity of epibiont communities may be linked to the fact that most epibionts re-colonising the *S. muticum* re-growth each season are likely to be derived from the epibiont communities inhabiting the local native perennial algae (Buschbaum *et al.,* 2006). As a consequence of the pseudo-perennial lifecycle of *S. muticum*, the epibiont community must re-establish itself on a seasonal basis and in certain circumstances, this may result in an epibiont community of relatively low diversity and abundance (Norton and Benson, 1983). The diversity of the epibiont community can vary in relation to exposure levels (Aguilar-Rosas and Galindo, 1990).

Epiphytism occurs despite *S. muticum* possessing antibiotic and tannin-like substances, claimed to inhibit the development of surface microflora and discourage epiphytic fauna (Sieburth and Conover, 1964; Withers *et al.,* 1975). Jephson and Gray (1977) found that the tannin-like substance produced by *S. muticum* during the rapid growth phase may have an anti-algal effect. Generally, epiphyte settlement occurs in the basal regions and continues along the primary laterals, presumably because any antibiotic effect is reduced away from the active apices. Exceptions are the colonial diatom, *Amphipleura rutilans* and the nest-building amphipod, *Pleonexes gammaroides,* which were abundant during the early part of the cycle and colonised the length of the alga.

Thomsen *et al.* (2006) studying a Danish *S. muticum* bed found that “species richness increased with the abundance of *S. muticum*, probably because it serves as a host to filamentous epiphytes”. The species richness of the community was seasonal, peaking at the same time as the *S. muticum* reached its maximum size. However, epiphyte-grazing fauna such as gastropods and urchins were common throughout the bed in all seasons (Thomsen *et al.,* 2006).

Buschbaum *et al.* (2006) studied the impact of *S. muticum* on the epibiota diversity of one rocky and one sedimentary environment on two islands in the North Sea. The native macroalgae consisted of either *Fucus vesiculosus* or *Halidrys siliquosa*. On the rocky shore, *H. siliquosa* supported a very similar epibiota community to *S. muticum* but on the sedimentary shore, *F. vesiculosus* supported a less diverse community of epibiota than the *S. muticum*. They concluded that in a rocky shore environment, *S. muticum* has a negligible impact on epibiota diversity because it does not form new habitat, whereas on the sandy shore it enhances epibiota diversity by increasing the available habitat (Buschbaum *et al.,* 2006).

7.5.1 Epiflora / epiphytes (algal epibionts)

S. muticum hosts epiphytes (Fletcher and Fletcher, 1975; Critchley, 1983; Fernandez *et al.,* 1990). Epiphytic species on *S. muticum* are numerous and can be similar to those of indigenous macroalgae although the abundances may vary as the other macroalgae are truly perennial and are more stable hosts (Jephson and Gray, 1977; Withers *et al.,* 1975). During the period when *S. muticum* is experiencing rapid vegetative growth, the plants remain relatively free of epiphytes but they become increasing heavily colonised in summer with the onset of fertility and later senescence. Seasonal variations in the abundance and diversity of algal epiphytes have been observed with little carry over of epiphytes from one year to the next as most of the colonised tissue is lost over the winter. A few species maintain their presence over the winter attached around the perennial base of the plant.

Withers *et al. (*1975) studied the epibionts on *S. muticum* around the eastern Solent between May 1973 and July 1974, and identified 52 algae and nine fungal species, listed in Table 7. Algal epiphytes were most numerous and varied on the *S. muticum* growing in tidal lagoons on sheltered rocky shores. Withers *et al. (*1975), found that the algae *Polysiphonia urceolata*, *Ceramium rubrum* and the colonial diatom, *Amphipleura rutilans* aggregate, grew on *S. muticum* throughout the year. Other algal species showed marked seasonal variation, with the majority occurring in the summer, after the plant's fertile period. At Bembridge, Isle of Wight, the following algae were found to grow epiphytically on *S. muticum* after it had become fertile; *Achrochaetium* spp, *Ectocarpus* spp*, Enteromorpha* spp, *Erythrotrichia carnea, Giffordia* spp, *Myriactula rivulariae, Polysiphonia urceolata* and *Ulothrix* spp. (Fletcher and Fletcher, 1975a). Fungal studies isolated only saprophytic species, which are common on indigenous brown algae. Some other *Sargassum* species have host-specific parasitic fungi but these are relatively rare. However, the attempted eradication operations in the Solent area during the course of this research indicated that the climax community for *S. muticum* was probably not observed (Withers *et al.,* 1975).

Aguilar-Rosas and Galindo (1990), found a total of 48 epiphytic algal species and stated that *S. muticum*, in Baja California, supported a wide and diverse community of epiphytes. They also observed that the greatest abundance of epiphytes was found in more sheltered areas.

Jephson and Gray (1977) and Gray (1978) found that *S. muticum*'s epiphytes were similar to those found on *Halidrys siliquosa.*

Studies in the Dorn, Strangford Lough (Strong, 2003) found that plants of *S. muticum* supported a small biomass and low diversity of epiphytic algae, compared to two of the native algae. The mean number of epiphyte species per basiphyte was significantly lower on *S. muticum* when compared to the other species. The three other basiphytes typically had twice the number of epiphytic algae species per thallus. Individuals of *Laminaria* possessed the greatest epiphyte diversity per basiphyte. *Dictyota dichotoma* was found on all four species, yet differed in how prevalent it was on each macroalga. On *Laminaria* and *Cystoseira* sp., *D. dichotoma* was almost always present in the epiphyte community, although rarer on *S. muticum* and *Halidrys*. Epiphytic growths of ectocarpoid species were shown to be one of the characteristic species of *S. muticum*.

Halidrys siliquosa had a slightly lower epiphytic biomass than *S. muticum,* but had a higher species diversity. Most of the epiphytes on *S. muticum* were associated with the holdfast, whereas the native species i.e. *H. siliquosa, Laminaria saccharina* and *Cystoseira* sp. had more species on the distal portions. Comparisons of epiphyte diversity between *S. muticum* in Strangford Lough and at other locations (Withers *et al.,* 1975; Aguilar-Rosas and Galindo, 1980) revealed a highly impoverished epiphytic flora in Strangford Lough. The epiphyte diversity on *S. muticum* plants in the Solent, excluding those in Langstone Harbour, was two to six times higher. *S. muticum* plants in Mexico had more than twice the number of epiphyte species found in Strangford Lough (Strong, 2003).

Table 7

Epiflora (epiphytes) found on Sargassum muticum *in the eastern Solent area*

(Withers *et al.,* 1975)

Phylum	Species	Phylum	Species
Rhodophyceae 26 species	*Acrochaetium* sp.	Phaeophyceae 14 species	*Ectocarpus siliculosus*
	Rhodochorton floridulum		*Giffordia granulosa*
	Cystoclonium purpureum		*Pilayella littoralis*
	Plocamium cartilagineum		*Leathesia difformis*
	Corallina officinalis		*Myriactula rivulariae*
	Melobesia sp.		*Stilophora rhizodes*
	Dumontia incrassata		*Asperococcus fistulosus*
	Chylocladia verticillata		*Punctaria plantaginea*
	Lomentaria articulata		*Colpomenia peregrina*
	Lomentaria clavellosa		*Scytosiphon lomentaria*
	Rhodymenia (Palmaria) palmata		*Laminaria saccharina*
			Sphacelaria cirrosa
	Callithamnion sp.		*Dictyota dichotoma*
	Ceramium diaphanum		*Fucus serratus*
	Ceramium rubrum		
	Griffithsia corallinoides	Chlorophyceae 9 species	*Ulothrix* sp.
	Griffithsia flosculosa		*Enteromorpha* sp. (2)
	Heterosiphonia plumosa		*Ulva lactuca*
	Laurencia hybrida		*Urospora bangioides*
	Laurencia obtusa		*Chaetomorpha linum*
	Polysiphonia nigrescens		*Cladophora* sp.
	Polysiphonia urceolata		*Derbesia* sp.
	Rhodomela confervoides		*Bryopsis plumosa*
	Goniotrichum alsidii		*Codium fragile* sp. *tomentosoides*
	Erythrotrichia carnea		
	Porphyra sp. – 2		
	Bangia fuscopurpurea	Bacillariophyceae 1 species	*Amphipleura rutilans* aggregate

7.5.2 Epifauna (animal epibionts)

The Withers *et al.* (1975) study of *S. muticum* epibionts identified 80 animals, listed in Table 8. Epifauna were most conspicuous on permanently submerged plants growing around the edges of floating harbour installations, with up to 13 species on a single plant. Polychaetes, especially *Spirorbis inornatus*, were common along with various bryozoans and ascidians but hydroids were infrequent. Tube-building amphipods were found living and feeding directly on *S. muticum* plants growing in deeper water. Other herbivores included periwinkles, *Littorina* species and topshells, *Gibbula* species. However, their grazing did not appear to have a controlling effect, probably because they were relatively easily dislodged from the narrow leaflets and branches (Withers *et al.,* 1975).

Jephson and Gray (1977) working on the Isle of Wight, found that the epibiont communities on *S. muticum* were similar to those of the brown alga *Cystoseira nodicaulis*. The colonial ascidian, *Trididemnum tenerum* and the spirorbid worm, *Janua pagenstecheri* occurred on *S. muticum* throughout the year with the numbers increasing during the reproductive period. Interestingly, the spirorbids, *Janua braziliensis* and *Pileolaria rosepigmentata* were newly recorded in the British Isles in the same year (1975) and it is thought that both were introduced to Portsmouth via *S. muticum* (Eno and Clark, 1995).

Norton and Benson (1983) found that the epibionts on *S. muticum* in Friday Harbor, Washington were more limited in terms of diversity with 43 faunal species, although only 18 were commonly present and in great abundance. Additionally, most of the faunal species were vagile, apparently migrating from nearby eelgrass beds to colonise *S. muticum plants* whereas the "British" epifauna were sedentary and encrusting and mainly confined to the perennial base of the plant. The most common "American" epifauna were four amphipods; the nest-building *Ampithoe mea, Aoroides columbiae, Caprella laeviuscula* and *Ischyrocerus anguipes* and the gastropod, *Lacuna variegata*. They found that these animals were attracted by the diatoms, *Biddulphia aurita* and *Melosira dubia,* growing over the *S. muticum* and the greater the abundance of live diatoms, the greater the abundance of epifauna. The amphipods grazed on the diatoms and some also grazed on *S. muticum* tissue. Only *Lacuna variegata* grazed directly on *S. muticum*. They all moved over the plant and, unusually, the majority were found on the more distal region of the frond. In late summer, these grazers could remove more tissue than was being formed. However, *S. muticum* was in its slow-growth period at this time and shortly after, most of the epifauna were lost when the plants cast their branches. A number of the epifauna were carried away on drifting material. It was felt that this grazing did not have a controlling effect, as during the earlier maximum growth period, the plants were not heavily colonised.

Viejo (1999) found the community composition of the mobile epifauna on *S. muticum* in El Truhan Inlet, northern Spain, to be similar to that reported from Friday Harbor by Norton and Benson (1983). Individuals of *S. muticum* collected from the low shore were characterised by large abundances of amphipods, especially the families Ampithoidae and Ischyroceridae and the genus *Dexamine*. Viejo (1999) used quantitative methods to compare the epibiota of *S. muticum* with two native species; *F. vesiculosus* and *Cystoseira nodicaulis* on the north coast of Spain. Results showed that the composition of epifauna was similar between the three macroalgal species and that the invertebrates adapted to their macroalgae habitat, regardless of the species. The lack of specificity to a particular host alga was thought to be due to the fact that the epifauna fed on epiphytes (attached to the three species) rather than the host algae themselves. Another reason suggested is that both *S. muticum* and *C. nodicaulus* are structurally similar, both having complex morphologies. *S. muticum* was shown to have a higher abundance of epifauna in the low intertidal region than in rock-pools due to the fluctuations in physical conditions (temperature and salinity) in rock-pools making for harsher living conditions for any epibiota to survive. The impact on the epifauna is therefore dependent on the degree of specificity for the host plant and the similarity between the invasive and native macroalgae. Viejo concluded that *S. muticum* colonised areas with a low cover of macroalgae, thus providing an additional habitat for the local epifauna and that this would ultimately lead to an increase in the secondary production of the local benthic system.

Epibiont studies tend to reach two contrasting views about the epiphytic fauna diversity on *S. muticum*. Withers *et al.* (1975) and Aguilar-Rosas and Galindo (1980) concluded that *S. muticum* supported a diverse epiphytic community, whereas Norton and Benson (1983) and Viejo (1999) found it to be abundant, yet relatively species poor. These contrasting conclusions about *S. muticum* cannot be attributed to the period of time *S. muticum* has been present within these areas. Local physical and biological factors are important in determining the epiphytic diversity on *S. muticum*. Important physical factors are likely to include the amount of wave exposure, water turbidity and sedimentation onto the *S. muticum* thalli.

Studies in the Dorn, Strangford Lough, (Strong, 2003), found that the sessile fauna on thalli of *S. muticum* was best represented by *S. spirobis* and *Electra pilosa*. The epiphytic fauna of *Cystoseira* sp. was also characterised by *S. spirorbis,* with a high presence of *Halichondria panicea* and *Obelia* sp. The community associated with *Halidrys* was represented by both *Halichondria panicea* and *Alcyonidium* sp. With regard to the individual species present in the assemblages, individuals of *Halidrys* had the most distinct community, with *Cystoseira* sp., *Laminaria* and *S. muticum* showing greater levels of community similarity. The mean number of mobile epiphytic fauna species was not found to be significantly different between the four algae studied. The greatest variation was in the total community abundance, with *S. muticum* having a mean abundance of over 900 individuals, which made it significantly different to the other three basiphytes. The abundance of the epiphytic fauna communities on *Halidrys, Fucus* and *Laminaria* was similar and each basiphyte supported between 50-100 individuals. The species richness values for the community inhabiting *S. muticum* were significantly lower, per thallus, than for the other basiphytes; this was a product of the high community abundance not being distributed evenly among the resident species. Very high densities of *Dexamine spinosa* and *Caprella linearis* were found within the epiphytic assemblage on thalli of *S. muticum*. The abundance of *D. spinosa* varied greatly between species, with *Laminaria* having a mean of five individuals, *Fucus* 18, *Halidrys* 69 and *S. muticum* over 700 individuals per thallus. Higher abundances of *Littorina mariae* and *Isopoda* spp. were characteristic of *Fucus.* Basiphytes of *Laminaria* supported a broad community with many species contributing to similarity, although *Ophiothrix fragilis, Corophium volutator* and *Ischyrocarus anguipes* were particularly characteristic (Strong, 2003).

In Denmark, Wernberg *et al. (*2004) compared the epibiota supported by *S. muticum* and its closest native relative in the area, *Halidrys siliquosa*. They found very similar epibiota community structure and concluded that the introduction of *S. muticum* was unlikely to cause major changes to the local epibiota community structure but that the standing stock of epibiota is likely to have increased.

Work carried out by Giver (1999) to compare the associated epibiota between *S. muticum* and *L. saccharina* in Washington State, USA, found that *S. muticum* altered the ecology of coastal communities by allowing certain native epibiota, that prefer the shelter and food provided by *S. muticum*, to dominate over those that prefer *L. saccharina*. Giver concluded that *S. muticum* supports a more abundant and species rich epibiont community.

Britton-Simmons (2004) studied the effects of *S. muticum* on subtidal, benthic communities in the San Juan Islands, Washington State, USA and concluded that the replacement of native kelp communities with *S. muticum* had led to a reduction in the number of green urchins *Strongylocentrotus droebachiensis* in shallow subtidal communities. Green urchins are described as being an important member of these communities as they clear patches of rock, thus increasing a mosaic distribution and ultimately enhancing diversity. The loss of these herbivores was due to increased vulnerability to predation, due to the positive buoyancy of *S. muticum* fronds, which do not offer cover like native kelp does or due to an avoidance of areas where unpalatable *S. muticum* grows. This is one example of how *S. muticum* may negatively affect native communities, both directly and indirectly.

In Denmark, Pedersen *et al. (*2005) concluded that grazing of *S. muticum* was generally low, due to the high abundance of phenolic compounds that inhibited grazers. However, they also concluded that the sea urchin *Psammechinus miliaris* preferred to graze on *S. muticum*, rather than native *H. siliquosa*, but that grazing losses were still negligible.

Herbivores may contribute to the spread of *S. muticum* by gnawing through lower branches, allowing fertile fronds to drift away. If grazing damages the apices of plants, the remaining fronds rapidly become fertile and one may become apically dominant (Critchley, 1983b)

Table 8

Epifauna found on* Sargassum muticum *in the eastern Solent area

(Withers *et al.,* 1975)

Phylum	Species	Phylum	Species
Porifera	*Sycon ciliatum*	Crustacea	*Apherusa cirrus*
3 species	*Leucosolenia* sp.	Continued	*Nototropis swammerdami*
	Grantia compressa		*Gammerellus angulosus*
			Maera othonis
Coelenterata	*Tubularia* sp.		*Maera grossimana*
10 species	*Coryne* sp.		*Gammarus locusta*
	Sarsia sp.		*Hyale nilssoni*
	Clytia johnstoni		*Aora typica*
	Obelia geniculata		*Pleonexes gammaroides*
	Obelia dichotoma		*Sunamphithoe pelagica*
	Laomedea flexuosa		*Jassa falcata*
	Kirkenpaueria pinnata		*Jassa pusilla*
	Haliclystus auricula		*Corophium acutum*
	Anemonia sulcata		*Corophium* sp
			Phthisica marina
Nemertini	*Amphiporus lactifloreus*		*Elminius modestus*
2 species	*Tetrastemma* sp.		*Carcinus maenas*
Annelida	*Phyllodoce maculata*	Insecta	*Diptera* larvae
11 species	*Syllis* sp.	1 species	
	Platynereis dumerili		
	Polydora sp.	Pycogonida	*Anoplodactylus angulatus*
	Audouinia tentaculata		
	Capitella sp.	3 species	*Achelia longipes*
	Polymnia nebulosa		*Achelia echinata*
	Pomatoceros triqueter		
	Spirorbis inornatus	Bryozoa	*Pedicellina cernua*
	Janua sp.	10 species	*Barentsia gracilis*
	Pileolaria sp.		*Scruparia chelata*
			Electra pilosa
Mollusca	*Gibbula umbilicalis*		*Bugula stolonifera*
	Gibbula cineraria		*Celleporella hyalina*
7 species	*Littorina littoralis*		*Cryptosula pallasiana*
	Littorina littorea		*Alcyonidium* spp
	Hydrobia ulvae		*Bowerbankia gracilis*
	Rissoa parva		*Amathia lendigera*
	Facelina sp.		*Clavelina lepadiformis*
Crustacea	*Tanais* sp.	Tunicata	*Morchellium argus*
24 species	*Limnoria lignorum*	9 species	*Trididemnum tenerum*
	Dynamene bidentata		*Diplosoma listerianum*
	Sphaeroma sp.		*Ascidiella aspersa*
	Idotea balthica		*Polycarpa fibrosa*
	Idotea pelagica		*Botryllus schlosseri*
	Idotea granulosa		*Botrylloides leachi*
			Molgula spp.

7.6 Economic impacts

The introduction of *S. muticum* can have a number of other implications that relate to the amenity, recreational and commercial uses of coastal areas. When *S. muticum* sheds its branches at the end of the growing season, considerable volumes of drift *S. muticum* material can be released. Floating mats of drift *S. muticum* can affect water sports, including swimming, water skiing, wind surfing, sailing, as well as trapping marine debris and being cast ashore. They can foul fishing lines and nets and the steering gear of small boats and clog the intake pipes of boats, coastal industries and power stations. Dense growth in harbours and marinas may hinder their commercial and recreational use while growth just below the waterline of floating pontoons and other buoyant structures can cause significant drag. Dense growth on commercial shellfish beds may hinder shellfish growth and harvesting, while buoyant *S. muticum* plants can float off, carrying away the shellfish to which they are attached.

Franklin (1979) reported that the overall effect of the introduction of *S. muticum* on fisheries was difficult to gauge due to a number of conflicting factors but that *S. muticum* could cause the following problems:

- considerable mechanical nuisance in trawling and dredging operations
- beach-seine netting being made more arduous
- fixed nets becoming badly fouled.
- commercial shellfish beds being smothered
- buoyant plants floating off, carrying the shellfish to which they are attached away from commercial beds

However, fishermen continue to fish affected areas, even to concentrate their efforts in them and report greatly increased catches, especially of eels, mullet and bass. *S. muticum* appears to provide shelter for adult fish, allowing them to remain in estuaries over a large part of the tidal cycle, thus greatly increasing their availability for capture (Franklin, 1979). According to some fishermen, *S. muticum* increases prawn yields (Farnham, pers. comm.). In Japan, beds and floating mats of *Sargassum* species are regarded as important fisheries' assets to be encouraged. Interestingly, *Sargassum* species are being seeded to encourage beds to extend or develop and plants are being cut specifically to create floating mats (Tsukidate, 1984).

To attempt to assess the impact of *S. muticum* in areas of the UK where it has become well established, Strong (2003) created a questionnaire that was sent to 35 harbour authorities. All of the harbour authorities were on the south coast of England or the Channel Islands, representing a range of locations where *S. muticum* has been present for between five and 20 years. The questionnaire was split into three sections with a description, diagram and photograph of *S. muticum* in the introduction. The harbour authorities were initially asked about how much *S. muticum* occurred on different marine structures, e.g. marinas, buoys, slipways and seawater locks. The second section of the questionnaire asked participants to describe the impact of *S. muticum* on common maritime activities. This section also included issues with drifting accumulations of *S. muticum.* The final section asked how and when they removed *S. muticum* and whether this containment represented a significant increase in antifouling effort.

Of the 35 harbours contacted, 27 returned questionnaires and only six harbour authorities did not have *S. muticum*. Rocky shores and revetments were the most commonly colonised marine structure by *S. muticum* (78%), followed by marina pontoons (53%). Half of the authorities also found some *S. muticum* attached to buoys, mariculture apparatus and inlet pipes, but the levels of colonisation reported were typically low. *S. muticum* was also found on boat hulls and slipways in a third of the harbours, although again, the quantities present were not great. Free-floating *S. muticum* was observed in 70% of the areas examined. The most common impact of *S. muticum* stemmed from the quantities of drift *S. muticum* material produced. The rapid fouling of pontoons, the entanglement of steering gear and the quantities of material stranded on beaches were also common problems in over half of the harbours questioned. There appears to be little impact of *S. muticum* on mariculture or recreational activities in the majority of harbour authorities surveyed, and the clogging of water inlets for both industrial plants and boats was also rare. Marina pontoons were more likely to be colonised by *S. muticum* when compared to other maritime structures. As these are common structures to all harbours, the authorities were asked to provide more detail on how *S. muticum* impacted on the use of pontoons. Reduced passage and the unsightliness of the fouling caused particular concern, with drag being less important. Harbour authorities were also asked about how much effort was required to control *S. muticum*. 54% of harbour authorities did not undertake extra containment for *S. muticum* and routine antifouling measures were sufficient. When extra antifouling effort was required for *S. muticum,* cleaning twice a year appeared to be the commonest method.

The survey of the harbour authorities demonstrated that *S. muticum* does not represent a significant impact for human utilisation of colonised shoreline. Equally, the effort required for the containment of the fouling was not great. Therefore, Strong (2003) concluded that the initial concerns regarding the impact of *S. muticum* on human activities were overstated.

7.7 Natural heritage implications

When it comes to policy for the conservation of the natural heritage there are additional grounds for concern. Non-native species in general are unwelcome in designated sites (whether under UK or European legislation) which have been selected due to the presence of special or characteristic biotopes. *S. muticum* is likely to form a visually distinct band on the lower shore/shallow subtidal, quite different in character to the native shoreline. The density and the area of the surface canopy of established stands of *S. muticum*, coupled with their unusual colour, means that they are distinctively different to the indigenous large brown seaweeds on the shore. The visual intrusions of large stands of *S. muticum* may have a detrimental impact on the aesthetic quality of Strangford Lough, as perceived by the public and Davison (1999) noted that dense stands had a very distinctive strong ‘tea’ smell from the tannins produced by the plants.

The impact of an invasive species therefore depends on the habitat it colonises. An assessment of the receiving habitat could identify any potential impacts in advance. The ecological value of a Special Area of Conservation (SAC) will be high, as will the economic value of a commercial interest such as a shellfish farm. The damage to a SAC could lead to loss of biodiversity and ultimately the removal of SAC status. A commercial shellfish farm could find that the fouling of its equipment and shellfish causes extra costs to be incurred. Both examples would consider the invasive species to be a ‘pest’ and would suffer a negative economic and/or ecological impact.

In the UK a large number of non-native species have been introduced, whether deliberately or accidentally. Of this number, few have established themselves and gone on to cause negative ecological impacts. But the potential effects of climate change and the general decline in UK biodiversity may increase the susceptibility of the marine ecosystem to invasive species (Manchester and Bullock, 2000).

Under the European Union’s Water Framework Directive, all countries were required to have undertaken a risk assessment on the characterisation, pressures and impact analysis for freshwater, transitional and coastal waters. The UK identified *S. muticum* as a species of high priority. The Scottish Environmental Protection Agency (SEPA) is recording and collecting any *S. muticum* found as part of routine monitoring, in compliance with the Water

Framework Directive’s requirement to report on the presence of alien species in water bodies.

8.0 MANAGEMENT STRATEGIES AND ERADICATION TECHNIQUES

8.1 General management issues and strategies regarding the introduction of species

Marine biological invasions are argued to be the second greatest threat to marine biodiversity after habitat destruction and as having “immense, insidious and usually irreversible” effects on biodiversity (IUCN, 2000). Invasive species represent a significant component of ecological change in coastal marine systems.

The vast majority of introductions are due to anthropogenic activities, particularly trade, transport and travel, all of which are increasing as globalisation increases (Perrings, 2004). The majority of introduced species go unnoticed and do not cause any adverse effects, but those that do become invasive can cause ecological and commercial damage. It is estimated that less than 10% of introduced species cause significant impacts (Williamson and Fitter, 1996). The introduction of non-native species threatens biodiversity and has accounted for more global extinctions in the last 400 years than any other factor (World Conservation Monitoring Centre, 1992).

Initial detection of non-native species relies upon the presence of the expertise to recognise the unusual nature of the species but invasive species are often only recognised when they assume epidemic proportions. In many cases, after the initial intense activity caused by its discovery wanes, little further interest is afforded the species, unless or until additional introductions or spread from an established population occurs. The time and effort allocated for monitoring invasive species varies so that data necessary for the formulation of management plans may be insufficient or patchy e.g. distribution data usually reflects where and when a species has been recorded rather than its present distribution (Eno, 1995).

The potential impacts of an introduction are hard to predict and control methods are generally ineffective. No non-native species has been successfully eradicated from British waters. The only way of preventing detrimental effects from occurring as a result of introductions is to ensure that non-native species do not gain entry (Eno, 1995).

Farnham (1992) listed a number of issues that are raised when a species is introduced:

- recognition
- site of introduction
- date of introduction
- country of origin
- method or agent of introduction
- further spread – rate and new sites
- ecological effects on indigenous species and communities
- detrimental effects on Man’s activities
- success – assessing overall impact and distribution
- predictability
- control methods

In terms of rate of spread and success, *S. muticum* could be considered to be the “most successful” example of an alien introduction (Farnham, 1992).

The risks involved in the introduction of non-native species into the natural environment are well known to scientists worldwide. Until relatively recently, there was limited public awareness of the potential detrimental effects of introductions. In contrast to the strict quarantine rules governing the import of domestic animals and plants, the introduction of wild species remained unregulated for a long time. In fact. introductions were often considered to be a way of enriching the local fauna and flora for the benefit of hunters, fishermen and other groups. In countries like Australia and New Zealand, acclimatisation societies flourished and hundreds of species were introduced. The damage that can be caused by ill-conceived introductions is now almost universally considered to be unacceptably harmful to biological diversity and legislation has gradually been enacted in many countries to bring such introductions under control. Australia and New Zealand now have the strictest introduction controls in the world (de Klemm, 1992).

Apart from standard quarantine regulations, few laws lay down specific rules for the prevention of accidental introductions (de Klemm, 1992). The implications of introductions caused by the introduction and movement of commercial shellfish are most significant in areas of high marine nature conservation interest. Preventing or minimising the introduction of non-native species needs to be addressed on both a global scale and on a regional basis (Eno, 1995).

The International Council for the Exploration of the Seas (ICES) recognised the risks associated with uncontrolled species introductions and transfers more than 40 years ago and has launched two working groups to address the issue. The ICES Working Group on Introductions and Transfers of Marine Organisms (WGITMO) deals with the movement of non-indigenous species for e.g. aquaculture purposes. The ICES / IOC / IMO Working Group on Ballast and Other Ship Vectors focuses on species movements associated with ships.

The ICES Code of Practice on the Introduction and Transfers of Marine Organisms was originally developed in 1973 but has been revised several times since. Wallentinus (1992) reported that this working group (WGITMO) "will objectively evaluate the risks and impacts on the marine environment of proposed introductions and to encourage the use of native species for mariculture wherever possible. The goal is to cease poorly-considered introductions and to urge member countries to guard against accidental introductions into their waters." He also reported that "lately there has been great concern that the new EC Fish Health Directive 91/67/EEC that permits the free transfers of shellfish between EEC countries might counteract the intention of the ICES Code by increasing the risk of accidental introductions of associated species, parasites and disease, since no permission of the receiving country is needed for the import." Similar concerns have been expressed by the JNCC (Eno, 1995) and the UK Conservancy Agencies who have all developed policies on introduced species.

Wallentinus (1992) reported that "despite the ICES Code of Practice, several new species have been introduced, especially by the import of Japanese oysters which has introduced around a dozen exotic macroalgal species to Europe. In many cases, these introduced algae have become dominant in the new areas, particularly the brown algae; *S. muticum, Laminaria japonica* and *Undaria pinnatifida.* Some have later spread to other areas by natural means, while in some cases they have been dispersed to other European coasts through illegal imports of oysters. There are also many examples of other animals, symbionts and parasites being spread to new areas by this vector".

Critchley and Dijkema (1984), pointed out that invasive biota show no regard for international boundaries. Several introductions have crossed the channel between Britain and the rest of Europe (Eno, 1995). Eno (1995) states that better measures for reviewing and licensing the introduction and movement of species which are not native may be required.

Knoepffler-Peguy *et al. (*1985) predicted that "with the gradual disappearance of European frontiers, the world-wide development of marine cultures and the multiplication of giant Sea Worlds, the transfer of live marine organisms will become routine and the risk of new introductions will considerably increase. Only international legislation, established by the countries of the littoral, will be able to control these problems."

The most successful introductions occur in areas with similar latitudes to the natural origin location (Carlton, 1985) and more broadly, similar environmental conditions.

It is also possible that a non-native species will benefit an area due to commercial enhancement (DEFRA, 2003). However, a general decline in UK biodiversity, along with the potential effects of future climate change, may increase the susceptibility of ecosystems to invasions (Manchester and Bullock, 2000).

8.2 UK management issues and concerns

Critchley *et al.* (1986) drew up a list of possible environmental problems and complaints caused by *S. muticum*:

- Dense *S. muticum* stands may affect the diversity of indigenous marine flora and fauna in the lower littoral and shallow sublittoral zones.
- Dense *S. muticum* stands may cause loss in amenity and recreational use of coastal areas e.g. swimming, water skiing, wind surfing, sailing and fishing.
- Physical hindrance of small boats with outboard engines of up to 20 m.p.h., entangling around steering gear.
- Clogging intake pipes of boats and coastal industrial or power station installations.
- Floating mats fouling commercial fishing lines and nets.
- Floating mats concentrating marine debris and creating an eyesore.
- Floating mats being cast ashore and creating amenity, removal and disposal problems e.g. on calm days in June and July 1976, floating mats up to 50 m^2 were common in the eastern Solent and several miles out to sea (Gray and Jones, 1977)..
- Dense growth on commercial shellfish beds, hindering shellfish growth and harvesting. Buoyant plants having the potential to float off, carrying away the shellfish to which they are attached (Franklin, 1979; Scagel, 1956). Note: Earlier this century, French oyster fishermen experienced similar problems from another brown alga introduced from the Pacific. *Colpomenia peregrina* became known as the "oyster thief" due to the fact that their air filled globous thallus had sufficient buoyancy to carry them, and the oysters to which they were attached, off in currents (Critchley and Dijkema, 1984).
- Growth just below the waterline of floating pontoons and other buoyant structures causing significant drag. (Critchley *et al.,* 1983).
- Dense *S. muticum* growth in harbour installations and marinas hindering their commercial and recreational use (Fletcher and Fletcher, 1975).

8.3 UK methods of monitoring *Sargassum muticum* populations

New populations are generally discovered as a result of research, volunteer, commercial or recreational activities in a coastal area. Researchers then generally extensively survey the affected area and adjacent areas to determine occurrence, frequency and distribution and to monitor the rate of development and/or spread of populations. The effectiveness of any eradication programme is monitored (Gray and Jones, 1977).

Surveying techniques include standard procedures such as random sampling, permanent transects and quadrats, tagged plants and manipulative experiments, such as the removal of all or selected species within permanent quadrats in affected areas and observing recovery or transplanting to define physical tolerances (Jephson and Jones, 1977; Farnham, pers. comm.).

In addition to field surveys, infra-red false colour (IRFC) photography has also been used to monitor *S. muticum* populations (Critchley, 1983e; Farnham *et al.,* 1981). Between 1975-81, aerial runs were made on calm days between June and August when *S. muticum* was most abundant and formed obvious canopies on the water's surface. Infra-red rays are absorbed in seawater within 1 m. Vegetation below this depth can only be detected as boundaries. Living vegetation is revealed as shades of red through to blue, with each plant species having its own, more or less, characteristic spectral reflection. Changes in plant vigour and substrata may interfere with interpretation of photographs but can be checked against ground surveys to produce accurate vegetation maps (Critchley, 1983e). Similar aerial surveys have been used to map marine macroalgae, including *S. muticum*, in the Straits of Georgia, British Columbia by Austin and Adams (1978).

8.4 Review of the development of management strategies on the south coast of England

On 4-5th May 1973, 18 marine biologists met at Portsmouth Polytechnic to discuss the implications of the appearance of *S. muticum* in British waters (Anon, 1973b; Farnham and Jones, 1974; Gray and Jones, 1977).

Arguments in favour of eradicating *S. muticum* were proposed, based on the following considerations. *S. muticum* was the most significant introduction into the British marine algal flora within recorded history. The likelihood of deleterious ecological effects within the habitats invaded and colonised by *S. muticum* was thought to be high. A loss in recreational amenities to users of shallow coastal waters was also expected.

It was accepted that while eradication might not be possible, it should be attempted and initiated promptly, as the possibility of success would be reduced with time. It was proposed that such a campaign, even if unsuccessful, would provide valuable experience for any comparable event in the future.

Other speakers argued against eradication, based on the desirability and the feasibility of eradicating *S. muticum.* They were not convinced that *S. muticum* constituted a proven ecological problem. It was argued that introductions of species are a natural part of the evolution of flora and fauna. It was also pointed out that much of the information, relating to the ecological effects caused by *S. muticum* on the Pacific coast of North America, was largely based upon unpublished and unsubstantiated observations. It was argued that the probability of success in completely destroying the populations of *S. muticum* in the British Isles was low (Jones and Farnham, 1973; Farnham and Jones, 1974; Gray and Jones, 1977).

However, the decision had to be made before *S. muticum* became a major pest. Otherwise eradication would be impossible, as first the British Colombians and then the Californians discovered. It was concluded that the presence of *S. muticum* in the Solent region represented an undesirable addition to the British marine flora and should therefore be eradicated. An extermination policy was decided upon after discussion of the available eradication methods. The main affected areas, although intertidal, were regarded as being unsuitable for mechanical clearance. The use of herbicides was felt to be neither desirable or practicable when dealing with seaweeds so it was decided that *S. muticum* should be removed by hand, a selective albeit time-consuming method using volunteers, and should be disposed of carefully in council refuse tips inland. Large numbers of volunteers would need to be recruited through appeals via the media and would require instruction on identification and the need to remove the whole plant to prevent regeneration. It was acknowledged that achieving total eradication would be very difficult and that if any plants were not removed, this seaweed would continue to spread (Jones and Farnham, 1973; Farnham and Jones, 1974; Gray and Jones, 1977; Critchley *et al.,* 1986).

8.5 Review of the implementation of the eradication programme

The first eradication programme began at Bembridge, a Site of Special Scientific Interest, on 9th May 1973 but could not be completed before *S. muticum* entered its fertile period. With new populations being discovered at Portsmouth Harbour and elsewhere, it was acknowledged that the eradication programme would have to be repeated annually to ensure that all populations and all newly settled germlings were eradicated. A major problem encountered was the difficulty of identifying *S. muticum* when germling plants were only a few centimetres long and having to search the shore fortnightly to identify and remove them. However, it was felt that the fortnightly searches were effective at keeping the situation under control (Anon, 1973c; Farnham and Jones, 1974).

To ensure that *S. muticum* did not become established, it was agreed that eradication needed to continue for two to three years. A Portsmouth *S. muticum* Working Party was formed, which appointed a full-time post of volunteer co-ordinator for the eradication programme. A "Wanted" poster was produced and distributed widely along the entire south coast and requested members of the public to search for *S. muticum*, report it to the working party and send samples for verification to Portsmouth Polytechnic. In 1974, Dorset County Council set up its own working party and initiated a volunteer monitoring scheme and in 1976, Devon County Council also set up a similar working party (Anon, 1973c; Farnham and Jones, 1974; Gray and Jones, 1977; Critchley *et al.,* 1986).

8.5.1 Hand-gathering

Hand-gathering was the eradication method employed on the Isle of Wight and Portsmouth Harbour between 1973-1976, with the quantities removed listed in Table 9 (Gray and Jones, 1977; Critchley *et al.,* 1986).

Table 9
Annual removal of Sargassum muticum by hand gathering, Isle of Wight and Portsmouth Harbour
(Gray and Jones, 1977)

Year	Number of volunteer trips	Tonnes of *S. muticum* removed (wet weight)
1973	250	3
1974	360	5
1975	400	26
1975	600	450

This method, using volunteers, was found to be extremely time-consuming, labour intensive, ineffective and impractical on extensive well-established populations since it needed to be repetitive. The efficiency of volunteers was low, especially when plants were small or weather conditions poor. The same area needed to be cleared several times, to remove small (less than 10 cm long) *S. muticum* plants growing under the canopy that were initially missed but grew vigorously after clearance and to remove newly settled germlings. Due to a lack of volunteers, clearance could not be continued throughout the winter months (Gray and Jones, 1977).

Gray and Jones (1977) concluded that it was impossible to keep an area clear of *S. muticum* by using volunteers and hand-gathering, as some plants would be missed and would reach reproductive maturity, efficiently re-colonising the cleared areas. After 1976, hand-gathering by teams of volunteers was only employed on newly settled areas or amenity areas where all the plants could be removed fairly easily.

However, as it was highly selective and caused the least ecological damage, it was considered to be best suited to removing small, recently established populations and could offer effective control within a sensitive, restricted area.

8.5.2 Mechanical control

Gray and Jones (1977) reported that a tractor towing an agricultural harrow had been used fairly successfully on smooth, flat, amenity beaches on the Isle of Wight in 1976 but that large quantities of benthic fauna and substrate were removed and hand-gathering was required afterwards. Franklin (1979) reported that a specially designed saw-toothed dredge was used on fairly smooth shores and sublittoral areas in 1979 and that oyster dredging appeared to be an effective clearance method.

In July 1976, a meeting of the Department of Environment Advisory Group considered methods of mechanical clearance and concluded that no suitable, commercially produced machinery was available. Most existing devices were intended for controlling macrophytes in freshwater bodies where herbicides and biological control could also be used. A detailed report was commissioned from the Design and Projects Division of Vickers Ltd Engineering Group. The available methods were reviewed, given the constraints of operating areas, manning costs, running costs, operating depth, length of weed removed and gathering and removal of weed. Devices were assessed for their suitability for use in the marine environment, including operating in open sea conditions. The device would need to be easily operated by relatively unskilled people in exposed, tidal waters between the months of March and July. Further considerations included transportability and manoeuvrability of the craft on land and at sea, operator protection and safety and versatility for other applications during the rest of the year. Vickers' concluded that none of the available devices satisfied all of the above criteria and recommended considering a device that would pull the alga rather than cut it (Critchley *et al.,* 1986).

The Department of Mechanical Engineering and Naval Architecture at Portsmouth Polytechnic undertook the design of developing a suitable device to effectively clear *S. muticum*. The principle design objectives were that the machinery would be simple and safe to handle from a conventional inshore fishing boat, that the "hardware" should be cheap and that it would minimise damage to the seabed and removal of other marine species.

A 10 m, purpose-built, research vessel, "Torika" (meaning harvester in Japanese), was used to carry out sea trials of machinery designed and constructed for the removal of *S. muticum* in the West Cut, a channel linking Langstone and Chichester Harbours. Three techniques were developed for the mechanical removal of *S. muticum* – trawling, cutting and suction. The application, effectiveness and costs of these techniques are outlined below. In all cases, the removal implement was mounted upon "shoes", operated from the boat by a central tow so that the head followed the contours of the seabed (Critchley *et al.,* 1986).

8.5.2.1 Trawling methods

A trawling technique was developed, based on a modified oyster trawl raised upon two 50 mm wide shoes, which operated 25-50 cm above the seabed and required three operators. A "bar weed head" was required in front of the trawl to engage the alga and a collecting net was mounted behind the trawl. The most effective weed collection heads were up to three metres long with round bar teeth in two staggered rows. It removed around 90% of the 1m long *S. muticum* plants and the collected seaweed could be removed from the trawl rapidly. Little damage to the seabed was caused but benthic fauna were removed as by-catch; mainly crabs, *Carcinas maenus*, elvers, *Anguilla anguilla*, and some oysters. The estimated costs listed in Table 10 varied with plant length, density, trawl size, tide, weather and crew efficiency (Critchley *et al.,* 1986; Hurley, 1981; Farnham *et al.,* 1981).

Table 10
Annual removal of Sargassum muticum by trawling, Isle of Wight and Portsmouth Harbour
(Critchley *et al.,* 1986)

Weight of weed removed per hour	1 tonne
Area cleared of weed (in 6 hours)	3000 m^2
Cost of removal, disposal not included	£20.00 per tonne wet weight
Cost of removal, including disposal	£22.38 per tonne wet weight (Hurley, 1981)

8.5.2.2 Cutting methods

This method was designed to minimise disturbance of the seabed and avoid removal of attachment substrata. The cutting technique required a boat-housed power source, a form of power transmission and a cutting device. Two metre blade cutters replaced the trawling head and cut 1m wide strips at about three knots, leaving behind *S. muticum* plants that were 0.5 m long. The main constraints on efficiency were the shape of the cutter and the clearance of weed from the cutter heads. The collection net behind the cutters required frequent emptying and this restricted continual operation (Critchley *et al.,* 1986; Hurley, 1981; Farnham *et al.,* 1981).

Cost of removal, including disposal	£24.08 per tonne wet weight (Hurley, 1981)

8.5.2.3 Suction methods

It was found that suction methods caused an unacceptable amount of ecological damage but it was considered that it could be used in marinas and channels dredged regularly. With algal fronds up to 1.5 m long, beds of medium density and attached to substrata less than 10 cm, a swathe 1.5 m wide could be cleared at two knots, with the suction head 1m above the seabed. It was ineffective in denser beds, with longer fronds or bigger substrates. The weed was collected in net cages which were buoyed and released when full, to be towed ashore. This method caused the *S. muticum* plants to fragment and the 50 mm mesh net did not retain these fragments. An air-driven cutter combined with an air-lift pump allowed continuous cutting and removal (Critchley *et al.,* 1986; Hurley, 1981; Farnham *et al.,* 1981).

Cost of removal, including disposal	£22.56 per tonne wet weight (Hurley, 1981)

8.5.2.4 Impacts of mechanical control

A variety of mechanical methods were developed and tested in the UK. Farnham *et al.* (1981) and Morrell and Farnham (1981) suggested that mechanical clearance must be considered to be an annual undertaking, with clearance operations taking place between April and June when the alga is at maximum length but not fully fertile. Monitoring of experimental areas demonstrated that mechanical clearance efficiently removed the length of the fronds and, therefore, the bulk of the biomass but could not remove the perennial bases, from which the plants regenerated annually. Consequently, during the following growth season, elongation of the fronds in cleared and non-cleared areas was similar

(Morrell and Farnham, 1981). It was found that surviving *S. muticum* plants responded to the physical damage by regenerating quickly, in response to damage to their apical meristems and by becoming fertile earlier (Jephson and Gray, 1977). Clearance of larger and older plants, encouraged the growth of juvenile plants and the settlement of germlings so that re-growth after clearance was actually denser than before the clearance (Critchley *et al.,* 1986). Finally, it was found that the natural clumped distribution of plants in undisturbed areas was lost after clearance, with the distribution being more evenly spread (Morrell and Farnham, 1981).

8.5.3 Herbicide control

A range of herbicides was tested and evaluated by Lewey (1976) and Lewey and Jones (1977). Problems were experienced with their application in the marine environment and high dosages were required to compensate for the dilution factor. Few were found to be effective, mainly because they could not penetrate *S. muticum*'s highly sulphonated cell walls. As the herbicides were non-selective and toxic to other algae and fauna and as large doses and extended contact times were required, this created application problems within the marine environment (Franklin, 1979; Gray and Jones, 1977; Critchley *et al.,* 1986).

8.5.4 Biological control

A number of molluscs and amphipods graze on *S. muticum* in the Pacific. Gray (1978) investigated grazing as a potential control method. Small germlings and plants already damaged by desiccation were susceptible to grazing by gammarids and the sea urchin, *Echinus esculentus*. In the turbid waters of the Solent, the most effective grazer was found to be the sea-hare, *Aplysia punctata*. However, these sea slugs were scarce in the Solent area and showed a preference for other algae. It was concluded that there were no indigenous marine herbivores that would restrict *S. muticum* growth or distribution. Additionally, the grazing activity of winkles, *Littorina littorea* and *L. littoralis,* may aid *S. muticum* spread by causing fertile or potentially fertile vegetative laterals of *S. muticum* to break off and drift away (Critchley *et al.,* 1986).

8.5.5 Control of S. muticum on commercial oysters

Lewey (1976) described a method of brine-dipping imported oysters as an effective method for preventing the survival of attached *S. muticum* on commercial oysters.

8.5.6 The impact of the Solent Management Strategy

In conclusion, all of these control methods were considered during the development of the management strategy for the Solent but it was found that each method could result in the release of *S. muticum* fragments and may inadvertently contribute to its dispersal. It was found that these forms of control measures could prevent populations ageing naturally by removing the large plants but this then resulted in a proportionally higher number of juvenile plants.

It was found that whichever eradication or control method was used, *S. muticum* always quickly re-grew and effective methods for its permanent removal were not identified due to *S. muticum*'s prolific gamete production and vegetative regeneration (Farnham *et al.,* 1981; Critchley *et al.,* 1986).

Fletcher and Fletcher (1975b) and Tsukidate (1984) investigated the regenerative ability of *S. muticum* and found that the cut surfaces of the basal main axis and holdfast could regenerate easily and that abscissed free-floating plant material could survive and continue to grow. For an eradication programme to be successful, the complete removal of the whole plant is essential to prevent sexual maturation and to prevent perennial vegetative re-growth.

Attached populations on the south English coast continued to increase in size, despite the 1973-76 clearance programme. This programme did not prevent the spread of the alga but may have slowed down its rate of dispersal and consolidation (Critchley, 1980; Critchley *et al.,* 1983; Farnham *et al.,* 1981; Gray and Jones, 1977; Morell and Farnham, 1981). The only recorded success was at Batten Bay when one plant and five sporelings were removed and did not return in 1979 (Critchley *et al.,* 1983). The other recorded success was when a single plant found in 1981 at Sheringham, Norfolk, the most north eastern UK record, was not found again (Farnham, pers. comm.).

Attempted eradication and the removal of *S. muticum,* results in the need to dispose of large amounts of biomass without utilisation. A number of researchers have investigated the extraction of commercially useful compounds or the production of biogas from this material (Critchley *et al.,* 1990a).

8.6 The Strangford Lough containment operation

The aim of the containment operations in 1995 to 1997 were to restrict and monitor the existing, discreet populations of *S. muticum* and prevent further spread within Strangford Lough.

The containment operations concentrated on two known populations at the Paddy's Point oyster trestles and at the Calf Rock pladdy were carried out by hand-gathering the weed. While hand-gathering is acknowledged to be time consuming and labour intensive, it is highly selective, unlike mechanical and herbicide control methods. The containment programme aimed to undertake a number of clearances, carried out in a methodical manner to ensure maximum efficiency and effectiveness. The recommended annual clearance months were June and early August to attempt to minimise the risk of fertile and potentially fertile plant fragments being dispersed as drift material. These dates were reviewed annually on the basis of monitoring and removal data.

The containment strategy was based on the following assumptions:

- that the fertile period is limited principally to the summer months and that fertile plants do not occur throughout the year
- that fronds that break off as a result of physical damage or grazing will not develop into fertile *S. muticum* drift material
- that there were no other *S. muticum* populations in Strangford Lough.

Hand gathering required the whole of each plant to be completely removed, either by removing the plant together with the substrate to which it is attached or by scraping the remains of the holdfast off a fixed substrate. All *S. muticum* plant material must also be removed from these sites with care to reduce the risk of inadvertent release of fertile plant fragments and should be disposed of carefully.

Attempting to remove entire *S. muticum* plants from the trestles at Paddy's Point and Calf Rock with complete holdfasts, was found to be very time consuming. Given the timing of these operations and the reproductive status of the plants, a decision was taken to remove as much of the *S. muticum* fronds as possible to reduce the "standing crop" of fertile plants available for dispersal to other areas of Strangford Lough. Where the plant was attached to a mussel or stone, complete removal of the entire plant was achieved.

The details of the containment operations are provided in Table 11.

Table 11

Total biomass of Sargassum muticum cleared from the oyster trestles and Calf Rock, 1995 – 1998

(Davison, 1999)

Year	Month	No. of staff	Total *S. muticum* material removed
1995	17, 18 and 31 August	18	2.2 tonnes
1996	21 August	7	1.1 tonnes
1997	7 and 8 August 19 September	32	8.3 tonnes
1998	15, 19 and 30 June 28 and 29 July	23 Unknown	14 tonnes
1998 The Dorn	18 and 20 May 31 July	10	1.4 cubic metres

In 1995 and 1996 the plant material was collected in large plastic bags which had some element of drainage to allow surplus water to drain before being placed in a boat. The material was then taken by boat to a waste skip at Cuan Sea Fisheries, Sketrick Island, and disposed of by a local contractor at a local approved landfill site.

It was felt that the majority of the standing crop was removed but it was acknowledged that residual holdfasts, small, juvenile plants and some plants in deeper water were missed. The stand at the eastern point of Calf Rock was not cleared in either year (Bradley, pers. comm.).

The 1996 survey indicated that the 1995 containment operation appeared to be relatively successful. However, the presence of small, apparently first year, plants indicated that some successful settlement of germlings had occurred before and potentially during the containment operation.

The 1997 survey indicated that the 1996 containment operation was far less successful. At both sites, the area covered and the number of plants had increased. In 1997, the plant density at the oyster trestles had returned to the level found in 1995 and, at Calf Rock, plant density was greater than in 1995. Plant density at Calf Rock was estimated to be double that found at the oyster trestles. This may have been a result of the containment operations as *S. muticum* plants can respond to control measures by regenerating quickly, becoming fertile earlier and rapidly re-colonising newly cleared areas. Although removing plants during August (the fertile period) may have contributed to the expansion of both populations by germling settlement, it attempted to reduce the risk of large quantities of fertile *S. muticum* drift material being released into Strangford Lough at the end of the growth season.

In 1997, some 8 tonnes of *S. muticum* material were removed from both Calf Rock and the oyster trestles involving 140 man hours. However, the containment operations took place in August and September 1997, by which time a proportion of the plants would have already released some fertile *S. muticum* drift material to be dispersed through the Lough. In 1998 after the discovery of a new population in the Dorn NNR a total of 14 tonnes of material were removed from Calf Rock along with 1.4 cubic metres from the Dorn. Assessing the impact of these intensive control operations was not within the scope of the 1998 survey. However field observation of the population at Calf Rock indicated that the stands here were extensive although the plants were generally small and heavily fouled. This may have been in response to the containment operation or simply reflecting the fact that both the Calf Rock and Paddy's Point populations were in sub optimal habitats and conditions. Only when the *S.*

muticum could colonise more ideal habitats, such as those at North Reagh and the Sheelaghs, could luxuriant canopies of 3-5m long plants develop.

The containment operation in Strangford Lough was not successful. It appears that, as in all other containment and eradication operations in the UK, the operations were not sufficiently intensive nor were they undertaken over an adequately extensive area to be effective. It is possible that had considerably more resources been made available, a more effective, methodical, and thorough eradication programme could have been undertaken. However, the allocation of human resources was significant.

As a result of the first meeting of the *S. muticum* Control Group in September 1998, the effectiveness of the containment strategy was reconsidered. Due to the expansion of the Calf Rock population across the bay to the western tip of North Reagh and the development of an extensive stand along the northern shore of North Reagh, it was agreed that containment of *S. muticum* in this area was no longer possible. It was accepted that the containment strategy had failed to restrict the *S. muticum* expansion since 18 new *S. muticum* populations had been identified in 1998. All the control options and methods were considered. However, it was recognised that despite best efforts, previous eradication campaigns for *S. muticum* have not been successful and it was acknowledged that the aim of limiting the spread of *S. muticum* was no longer achievable.

It was agreed that sites should be prioritised and that containment operations would only be undertaken at the most vulnerable sites. Due to its very high conservation status, an ongoing containment operation would be undertaken at the Dorn. The other high priority site was the large tidal pool, south of South Chapel Island, which would be an ideal habitat for *S. muticum*. No *S. muticum* plants were found in the pool in 1998 but it is under threat as a large *S. muticum* stand has developed off the east coast of Jackdaw Island and a cluster of three plants was found off the eastern shore of South Chapel Island. *Halidrys siliquosa* and *Cystoseira* sp. dominate the pool and if it was to be colonised by *S. muticum*, it could develop an abundant population, with the potential to seed Strangford Lough and the Irish Sea.

9.0 CASE STUDY: *SARGASSUM MUTICUM* IN STRANGFORD LOUGH, NORTHERN IRELAND

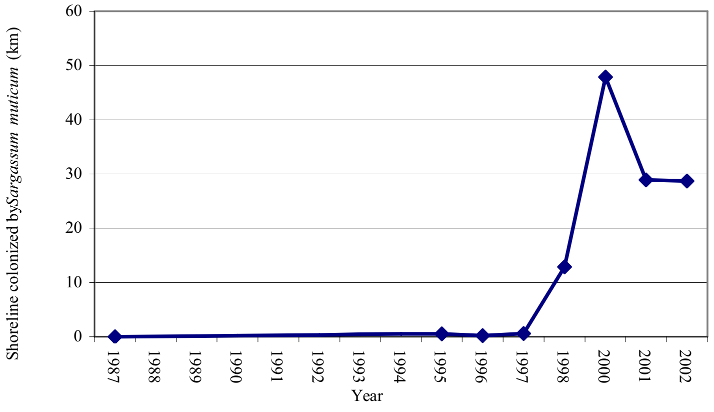
Strangford Lough is a large sea lough, with a narrow entrance and is situated on the East Coast of Northern Ireland. It is a Marine Nature Reserve and a Special Area of Conservation.

S. muticum was first observed in Strangford Lough in 1994 and formally identified and recorded in 1995. After notification, the Environment and Heritage Service (E.H.S.), Department of the Environment (N.I.) commissioned five distribution studies. Distribution surveys were undertaken in 1995 (Davison and Davison, 1995), 1996 (Davison, 1996), 1997 (Davison, 1997), 1998 (Davison, 1998; Davison, 1999) and 2000 (Birkett and Maggs, 2000). E.H.S. also undertook containment operations in 1995, 1996, 1997 and 1998 and removed 2.2 tonnes, 1.1 tonnes, 8.3 tonnes and 14.0 tonnes respectively (Davison, 1999).

The distribution of *S. muticum* expanded dramatically in 1998, colonising many of the islands in the northern half of the Lough. The area of shoreline colonised by *S. muticum* increased from 0.61 km in 1996 to 12.86 km in 1998 (Strong *et al.,* 2006). This increase was mainly due to a greater occupation of habitats with loose rock on a soft sediment base. Between 1998 and 2000, the distribution of *S. muticum* consolidated on the northern islands and the eastern side of the Lough was invaded. The distribution of *S. muticum* in 2000 represented a peak in colonisation with 47.88 km of shoreline occupied in Strangford Lough. From 1998 to 2000, although the colonised shoreline increased more than three-fold, the relative proportions of each substratum type remained the same, 97% of the occupied shoreline being mobile, soft substrata not previously occupied by macroalgae (Strong, 2003; Strong *et al.,* 2006).

The distribution of *S. muticum* declined substantially, by nearly 50%, in 2001 after a widespread mortality event, and is illustrated in Figure 25. The majority of mortalities were from predominantly soft sediment habitats where this alga grows on embedded small stones and shell material. Despite this, 93% of the shoreline occupied *S. muticum* was where the plants were attached to loose rock on soft sediment (Strong, 2003; Strong *et al.,* 2006). Mapping in 2002 found no restoration of the retracted distribution, although new, hard substratum habitats were colonised by *S. muticum*.

Figure 25
Kilometres of shoreline colonised by Sargassum muticum in Strangford Lough between 1987 and 2002
(Roberts *et al.,* 2004)



The colonisation of shoreline occupied by *S. muticum* over time in Strangford Lough appeared to have two distinct phases, prior to the mortality event in 2001, in a pattern which is common in many biological invasions. Rates of observed spread were less than 0.1 km per year between 1987-1997, which is often called the 'establishment phase'. After 1997, the colonisation rate accelerated greatly to 23 km per year which is termed the 'spread phase'. The rates and timing of the spread of *S. muticum* have probably been modified greatly by the containment operations of the E.H.S., undertaken between 1995 and 1999.

In Strangford Lough, there is an abundance of loose rock embedded in a soft substratum, which is unoccupied by native macroalgae. Areas unsaturated with species are thought to contain 'empty niches' (Cornell, 1999). The initial success of the invasion by *S. muticum* may have been due to its ability to colonise this plentiful substratum without having to compete with native species. In this habitat, the population size and extent of *S. muticum* appeared to expand without constraint, hence allowing the population to overcome quickly the problems of a small inoculation into the Lough. Once established, these areas provided the propagule pressure and drift *S. muticum* plants required to exploit transient openings in other habitats, including vegetated, hard substratum habitats.

9.1 Introduction and colonisation: 1994 - 1998

An "unusual" seaweed was noticed in 1994 by Dr J. Parsons, Director of Cuan Sea Fisheries, on oyster trestles at Paddy's Point, Strangford Lough, but was not identified. During a visit to these trestles by Dr P.J. Boaden and Dr Parsons on 15 March 1995, a specimen of this seaweed was collected and identified as *S. muticum.* The presence of *S. muticum*, the first occurrence of this species in Ireland, was reported to the D.o.E. (N.I.) on 16 March 1995. In early April 1995, students from Queen's University Belfast, surveyed the 24 long oyster trestles and mapped the presence and absence of *S. muticum*. Thereafter, five annual studies to investigate the distribution, status and management implications of the introduction of *S. muticum* to Strangford Lough were commissioned by Environment and Heritage Service (E.H.S.), Department of the Environment (N.I.).

The first study was undertaken between July and September 1995. Forty-four sites in Strangford Lough were surveyed for the presence of *S. muticum*. Two *S. muticum* populations were found, at the Paddy's Point oyster trestles and at the adjacent Calf Rock pladdy. Their locations are annotated on the map in Figure 26. A comprehensive literature review on *S. muticum* was also undertaken (Davison and Davison, 1995). The E.H.S. undertook a containment operation at both sites on 17th, 18th and 31st August 1995 and removed 2.27 tonnes of material.

Between 10th – 21st June 1996, the *S. muticum* populations of the Paddy's Point oyster trestles and Calf Rock pladdy were re-surveyed and re-mapped to monitor the development and status of the known populations of *S. muticum* and to assess the impact of the 1995 containment operation. Fourteen of the forty-four sites that had been surveyed in 1995 were re-surveyed to identify whether any new populations of *S. muticum* had developed in Strangford Lough (Davison, 1996). No new *S. muticum* populations were identified and the containment operation that had been undertaken in August 1995 appeared to have been relatively successful in terms of achieving reductions in the areas covered and the numbers of plants present. The E.H.S. undertook a second containment operation at both sites on 21st August 1996 and removed 1.10 tonnes of material.

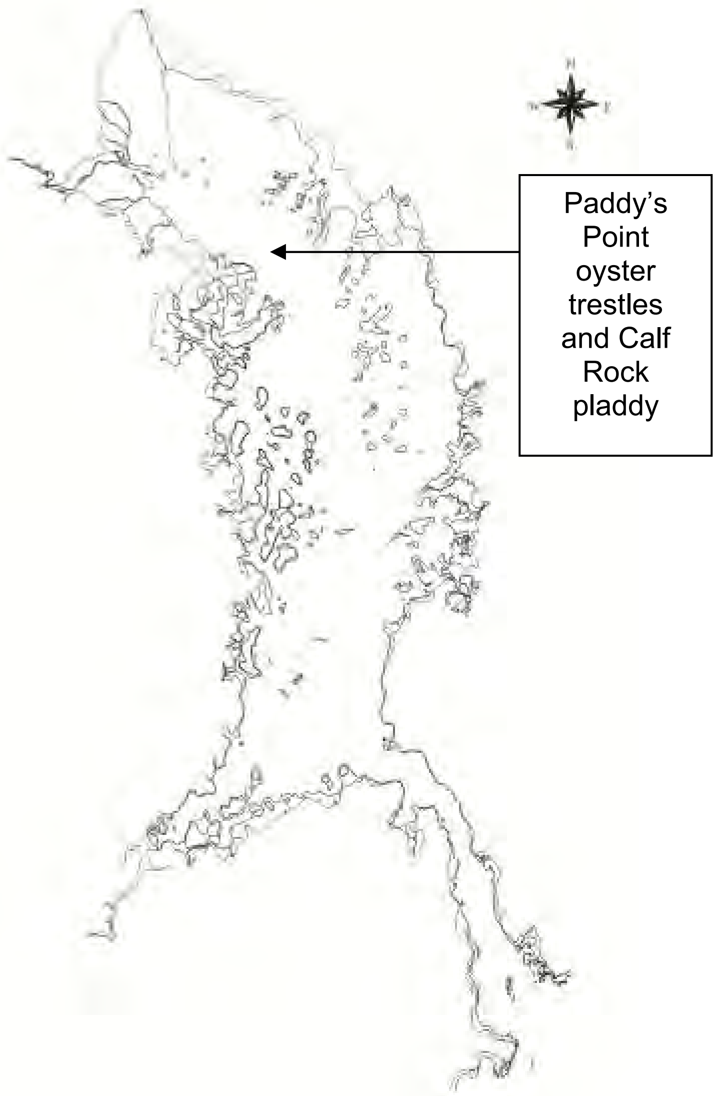
Between 4th – 10th July 1997, the *S. muticum* populations of the Paddy's Point oyster trestles and Calf Rock pladdy were re-surveyed and re-mapped to monitor the development and status of these *S. muticum* populations and to assess the impact of the 1996 containment operation. No other sites in Strangford Lough were surveyed and no new *S. muticum* populations were reported (Davison, 1997). It was found that the 1996 containment operation was not as successful as the 1995 operation, since both populations had expanded in terms of extent (area) and numbers of plants present. The E.H.S. undertook a third containment operation at both sites on 7th and 8th August and 19 September 1997 and removed 8 tonnes of material.

A third *S. muticum* population was identified in the Dorn and was reported to the E.H.S. on 7th May 1998. The E.H.S. undertook a containment operation at the Dorn on 18th and 20th May and 31st July 1998 and 1.4 cubic metres of material were removed. A containment operation was also undertaken at the Calf Rock on the 15th, 29th and 30th June and the 28th and 29th July and 14th August 1998 and 14 tonnes of material were removed. No containment operation was undertaken at the Paddy's Point oyster trestles.

Between 8 - 22 August 1998, the fourth study of *S. muticum i*n Strangford Lough was undertaken. Twenty-seven sites in Strangford Lough were surveyed for the presence of *S. muticum*. The majority of these sites had been surveyed previously in 1995 or in 1996 but some new sites were surveyed. At seventeen of these sites drift fronds, scattered plants or stands of *S. muticum* were found. The original *S. muticum* populations at the Paddy's Point oyster trestles and the Calf Rock pladdy and the recently identified *S. muticum* population in the Dorn were visited but not surveyed in detail (Davison, 1998).

Staff from Queen's University undertook a fifth distribution survey in 2000 and further survey work was undertaken by a PhD student between 2001 and 2003 (Birkett and Maggs, 2000; Strong, 2003; Strong *et al.*, 2006).

Figure 26
Map illustrating the known distribution of Sargassum muticum in Strangford Lough: 1995
(E.H.S. N.I.)

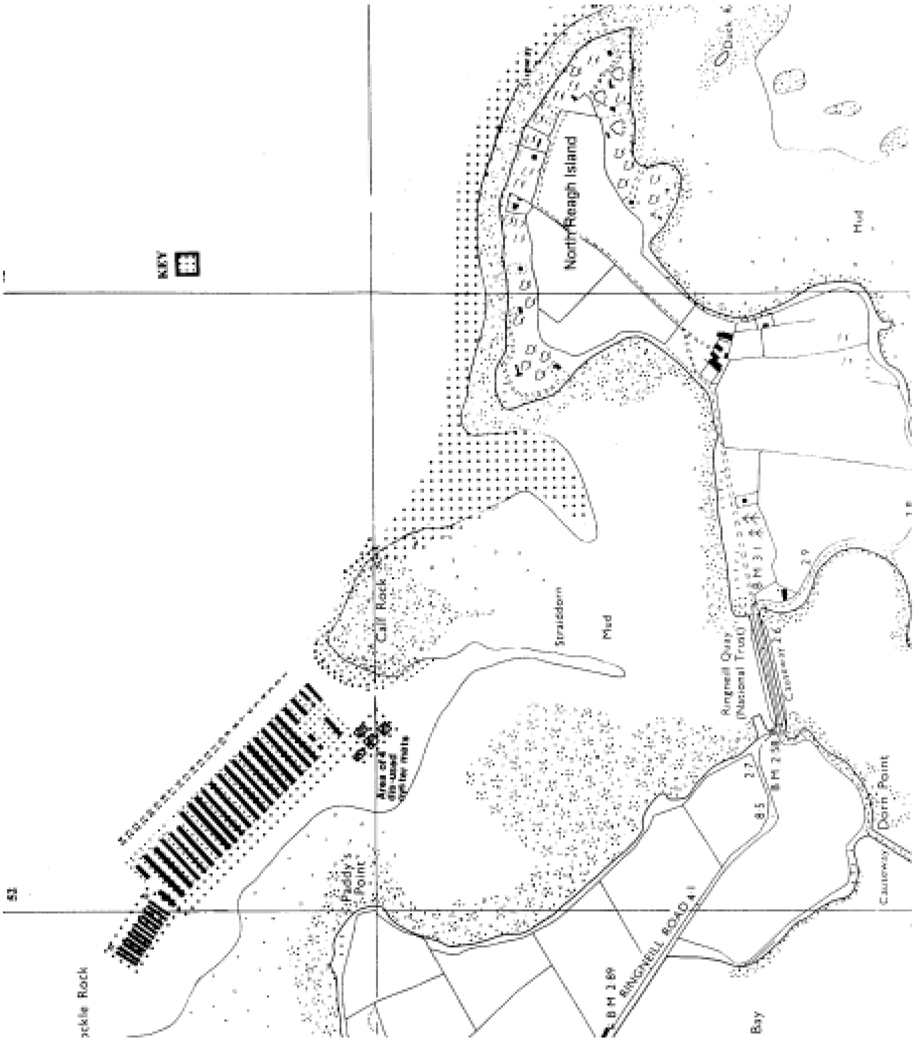


Paddy's Point oyster trestles and Calf Rock pladdy

Figure 27
The distribution of Sargassum muticum at Paddy’s Point, Calf Rock and North Reagh Island, Strangford Lough: 1998

(Davison, 1999)

The shading indicates the areas covered by *Sargassum muticum* on the Paddy’s Point oyster trestles (first population), the Calf Rock pladdy (second population) and North Reagh Island



9.1.1 Sargassum muticum population development, 1995 – 1997, at the Paddy's Point oyster trestles

The site of the first populations of *S. muticum* in Strangford Lough is shown in Figure 27. At Paddy's Point, 35 lines of metal trestles of varying lengths, are used to support "poches" (plastic mesh bags) containing oysters, mostly *C. gigas.* The 35 lines of trestles run from the lower shore (neap low tide level) into the shallow sublittoral (just below spring low tide level) with alleys between them. The lines of trestles are composed of groups of four individual trestles together (rows) and the numbers of rows vary. The longer lines of trestles, numbered 1 – 24, are referred to as the 'long trestles' while the shorter rows of trestles, numbered 25 – 35, are referred to as the 'short trestles'. The trestles keep the oysters above the substrate, which is fine muddy sand with occasional stones and shell. Algae of many species foul the trestles; the dominant species are brown algae. *Fucus serratus* is dominant on the trestles located in the lower littoral while *Laminaria saccharina* is the most common alga on the trestles located in the shallow sublittoral. Cuan Sea Fisheries use mat culture in their other sites at Ardmillan Bay and Castle Ward Bay. An area of matting is also present immediately adjacent to the first long trestle at Paddy's Point, marked with poles. It is understood that this area of matting was created in 1983 - 1984 but as the oysters were washed off by wave action, it has not been used since nor has it been removed (Parsons, pers. comm.).

In 1995, the closest populations of *S. muticum* were in West Angle Bay, at the entrance of Milford Haven, Wales (discovered on 22nd June 1998) and on the north coast of Cornwall, at Constantine Bay. It is extremely unlikely that *S. muticum* entered Strangford Lough via drift *S. muticum* material from Cornwall. If this had been the case, it is likely that other sites in the Irish Sea and Strangford Lough would have been colonised before the oyster trestles or Calf Rock. No other *S. muticum* populations were recorded elsewhere in the Lough until 1998.

In 1987-88, seed oysters were obtained from a hatchery in Guernsey, Channel Islands and were on-grown using the trestles at Paddy's Point until they were harvested between 1990 - 1991 (Parsons, pers. comm.). Until further evidence to the contrary is obtained, contaminated seed oysters from the Channel Islands were the most likely source of the *S. muticum* introduction to Strangford Lough. It is not known what impact the management regime of the oysters on the trestles in the years prior to and since 1995, has had on the development of this *S. muticum* population. It not known if activities such as regularly turning, removing or replacing the oyster bags or the management of fouling algae on the trestles have been undertaken. However, in 1996, it was confirmed that the short trestles would continue to be used for oyster cultivation by Cuan Sea Fisheries and that the oysters on the long trestles may be harvested and processed in the future (Parsons, pers. comm.).

S. muticum plants are found in the lower littoral zone and in the shallow sublittoral zone of the trestles, competing with the indigenous algae for the limited available space on the oyster bags and metal trestle frames and they tend to occupy a distinct band between the *F. serratus* and *Laminaria* species. *S. muticum* plants growing in the littoral zone are exposed twice daily at low water and are generally in poorer condition than those growing on the trestles located in the sublittoral fringe which are exposed less frequently. *S. muticum* has a poor tolerance to aerial exposure, particularly high air temperatures and intense sunshine, and even sublethal exposures can retard subsequent growth. The degree of retardation increases with the severity and duration of exposure and the competitive ability of many of these plants may have been diminished. In the gaps between the trestles, *S. muticum* has colonised the very limited supply of stones or shells occurring in the soft mud. As these plants were not subject to the same degree of aerial exposure as those growing on the trestles, they were generally in better condition.

In 1995, *S. muticum* was present on the short trestles but in 1996 no *S. muticum* plants were found on the short trestles. In 1997, *S. muticum* was found to be present in 41% of the total available area of the short trestles and inter-trestle gaps. On the long trestles, the densest area of *S. muticum* plants occurred between trestle numbers 11 - 17, on rows 11 - 40, approximately 30 - 80 m from the top (littoral zone) of the trestles. The development of this population appears to have radiated from this area.

In 1995, *S. muticum* was present in 39% of the total area of the trestles and inter-trestle gaps but in 1996 this had declined to 14.16% of the total area. In 1997, despite the 1996 containment operation, *S. muticum* was present in 45% of the total area, a 14% expansion since 1995. The main direction of expansion appeared to be towards the sublittoral ends of the trestles and towards trestle number one and the Calf Rock pladdy. The total numbers of *S. muticum* plants recorded at the oyster trestles was found to have increased by 80% from 374 in 1996 to 1,938 in 1997. Plant numbers were not recorded in 1995. In 1997, four areas of oyster matting, which had previously been clear of *S. muticum* plants, were found to have been colonised. The area of matting located lower down the shore formed a mini-tidal pool and contained 166 plants while the three slightly drier mats located above contained a total of 39 plants

9.1.2 The development of the Sargassum muticum *population at the Calf Rock pladdy*

Calf Rock is a low-lying island that is composed of glacial till material; boulders, stones and gravel. It is located several hundred metres to the south east of the oyster trestles and is surrounded by soft muddy sand.

Calf Rock supports a sheltered boulder shore community, with *F. serratus* and *Ascophyllum nodosum* abundant in the lower littoral zone and a dense but patchy kelp forest in the shallow sublittoral zone. The kelp zone is narrow; restricted by the lack of hard substrate in deeper water. In addition there are two areas of *Mytilus edulis* beds on stone and gravel at the western and eastern fringes of the pladdy.

The *S. muticum* population at this site could be considered to be more "natural" than the oyster trestle population and it is subject to less environmental stress (aerial exposure). The *S. muticum* plants occur in shallow sublittoral zone, with two distinct stands on the two mussel beds at the western and eastern fringes of the pladdy. These stands are linked by scattered clumps of individual plants that have colonised any available free space within the kelp forest that extends around the north fringe. Both stands can create a 100% canopy cover on the surface. It is likely that the stand at the eastern point developed after the western tip stand, as a result of marginal dispersal.

In 1996, the 1995 containment operation appeared to have been quite effective although the two main stands were still obvious. The average density had dropped from an average of 21.3 plants per m^2 in 1995 to an average of 14.66 plants per m^2 in 1996 but the number of small, possibly first year, plants had increased.

In 1997, the 1996 containment operation at Calf Rock appeared to have been less effective. 3,378 plants were found, an increase of 90% from the 1996 total of 332 plants. The density of the main stands was found to have increased to 27 plants per m^2, higher than in 1995. The population at the western point, which had been significantly reduced in 1996 after the 1995 containment operation, appeared to have consolidated and expanded in 1997. The canopy cover was generally 100% and covered a similar or greater area to that observed in 1995. A significant development in 1997, was that the number of plants had increased with numerous smaller plants contributing to the surface canopy, whereas in 1995 fewer, larger plants created similar coverage. The stand around the eastern tip of the pladdy had expanded significantly. More plants were found in deeper water, spreading towards the western tip of North Reagh Island as well as into the bay between. Areas of 100% surface canopy were observed to be developing which were not visible in 1996. This area was not cleared in 1995 or in 1996 (Bradley, pers. comm.) so these increases in area covered and plant density were due to natural expansion.

During the 1995 survey, some *S. muticum* plants were seen in the deeper water beyond the sublittoral ends of the trestles and off the Calf Rock pladdy. During the 1996 survey, two transects were observed from the boat, approximately 50 and 100 m off the Calf Rock and the trestles. The limited hard substrate that was present was fully colonised by kelps. Less than ten *S. muticum* plants were observed. The total number of such plants is unknown but it is clear that some of the most buoyant plants from both populations have been able to "stone-walk" a considerable distance. As a boat was not used in the 1997 survey, this work could not be repeated.

9.1.3 Drift Sargassum muticum *material*

All drift seaweed encountered during the course of the annual fieldwork was investigated for the presence of *S. muticum* drift. In 1995, some drift *S. muticum* material was observed at the oyster trestles but not on the shore above the trestles or at Calf Rock. However, a report of drift *S. muticum* material was received from Queen's University Marine Biology Station, wrapped around experimental equipment moored between Shark and Jackdaw islands, southern Strangford Lough. In 1996, less drift *S. muticum* material was observed at the oyster trestles and none was found on the shore above the trestles or at Calf Rock. During the ten days of fieldwork in 1996 no drift *S. muticum* material was observed either on the shore or within the Lough and no reports of drift *S. muticum* material were received from other sources during the course of the fieldwork. In 1997, at the original populations, the *S. muticum* plants were found to be breaking up easily, particularly at the oyster trestles, and drift *S. muticum* material was observed on all of the eight tidal cycles when fieldwork was undertaken. Drift *S. muticum* material was wrapped around the sublittoral ends of the oyster trestles, which had been previously observed in 1995. For the first time, drift *S. muticum* material was also found high on the shore above the trestles and on the rocks below the causeway adjacent to the quay. Drift *S. muticum* material was observed around the Lough during the fieldwork period and removed but no reports of drift *S. muticum* material were received from other sources during the course of the fieldwork. Please refer to the end of Section 9.0 for information on Strong's investigations of drift *S. muticum* material in Strangford Lough (Strong, 2003).

9.1.4 The identification of a third Sargassum muticum *population at the Dorn NNR*

The Dorn is complex micro-tidal lagoonal system that is linked to the main body of Strangford Lough by a series of sills and tidal rapids. It is the only lagoon system within Strangford Lough and is of at least national conservation importance, which is reflected in its designation as a National Nature Reserve. The main body of the Dorn lagoon system consists of sediment basins, linked by tidal channels. The species present reflect the ultra-sheltered conditions and are representative of lagoon communities identified by the MNCR. The tidal sills and rapids are very species rich, with an abundance of sponges, ascidians, hydroids and bryozoans and these high-energy communities complement the low-energy ultra-sheltered lagoon communities. A degree of 'emergence' has been observed in the tidal rapids, where sublittoral species occur in the littoral zone.

In early May 1998, a student from QUB MBS undertaking research in the Dorn found a number of *S. muticum* plants. A baseline survey was not undertaken prior to the E.H.S. containment operation, which was initiated in mid-May. However, it is understood that the plant lengths ranged between 2 cm – 1 m+ and that quadrat densities of 100 per m^2 were recorded

9.2 The distribution of S*argassum muticum* within Strangford Lough: 1995 – 2003

The circumstantial evidence indicates that *S. muticum* was probably introduced to Strangford Lough in 1987-88 with imported oysters from the Channel Isles (Parsons, pers. comm.), so it seems initially surprising that *S. muticum* had not significantly expanded its distribution within the Lough until 1998. Due to its location on oyster trestles exposed at low water, this original population was under considerable environmental stress caused by aerial exposure. Its expansion and consolidation was also limited by the lack of suitable substrate in the shallow sublittoral.

It has been observed elsewhere that *S. muticum* populations often require several years to develop a sufficient breeding stock (a monospecific stand) to allow rapid population expansion. It is reasonable to suggest that the growth of the original oyster trestle population was very slow and the plants themselves were subject to stress from both the sub-optimal environment and the management of the oyster farm. The population appears to have been able to survive and spread, although thinly without the characteristic plant density and surface canopies. This appears to be borne out in the distribution data of the plants on the trestles from 1995. The general lack of suitable substrate beneath or within a few metres of the trestles precluded the settlement of all but a very few of the germlings produced by the plants on the oyster trestles. The degree of environmental stress on the plants also resulted in the plants being rather small and in generally poorer condition to those luxuriant specimens observed in other locations, such as the Sheelaghs, in 1998. It is likely therefore that the trestle plants would produce little vigorous drift *S. muticum* material and hence no other populations developed in Strangford Lough in the late 1980's and early 1990's. This is consistent with what has been experienced in other introduction sites where the population was initially slow to establish, but then rapidly expanded, spawning other satellite populations in the area once a good foothold has been established (Critchley *et al.,* 1983).

In terms of colonisation chronology, it seems likely that between 1987-8 and 1995, one or a few plants probably stone walked the short distance from the trestles to the eastern end of Calf Rock. While the conditions at Calf Rock were not ideal, they were more favourable than on the oyster trestles. The *S. muticum* at this site was not subjected to the same degree of aerial exposure and more suitable substrate was available. A small stand of *S. muticum* developed on small stones and shells in the shallow subtidal, grabbing the gaps that no other algae was filling at the time. It was around this time, with the spread to Calf Rock and the establishment of a new, more 'normal' and more vigorous population, that the presence of the alien weed was reported to the D.o.E. (N.I.) E.H.S. in 1995. In 1995, the work to assess the spread of *S. muticum* and to attempt to contain it was initiated. Initially, the threat that this population posed in terms of the production and dispersal of fertile drift *S. muticum* material initially appeared to be potentially manageable. This population was more successful than the oyster trestle population and was able to develop dense stands of longer-lived plants that were in better condition and grew larger. Since 1995, the population consolidated and expanded, despite the annual containment operations. Although the 1998 containment operation removed the majority of the large *S. muticum* plants from this site, hundreds of small plants, heavily overgrown by ephemeral algae, were left behind.

It was possible that due to the factors outlined above, the development of both populations had been retarded so that this species' competitive ability had been diminished, until 1996 – 1997. The increases in area covered and the numbers of plants of both populations recorded in 1997, indicated that the reproductive germlings of both populations were viable and that significant expansion has taken place since 1996, particularly at the Calf Rock population, which consolidated and expanded eastwards. This could also be related to the fact that the 1995, 1996 and 1997 containment operations all took place in August, when the *S. muticum* plants in Strangford Lough appear to be most fertile. It is known that eradication may in some circumstances result in a younger, more vigorous population and may result in more sporelings being released earlier as an adaptation to the eradication attempts (Farnham and Jones, 1974; Critchley *et al.,* 1986). *S. muticum* populations tend to respond to clearance operations by regenerating quickly and rapidly re-colonising newly cleared areas. Clearing areas of adult plants may have aided the settlement of germling plants, released naturally and as a result of removal. In 1997, the plants were found to be breaking up easily and drift *S. muticum* material was observed on all of the eight tidal cycles when fieldwork was undertaken. For the first time drift *S. muticum* material was also found high on the shore above the trestles and on the rocks below the causeway, adjacent to the quay. In conclusion, while removing plants during August may have contributed to the expansion and consolidation of these populations by germling settlement, it attempted to reduce the risk of large quantities of fertile drift *S. muticum* material being released naturally to potentially seed new sites elsewhere in Strangford Lough. However, the discovery of *S. muticum* in the Dorn and at 17 other sites in Strangford Lough in 1998, indicates that these containment attempts were unsuccessful.

To the east of Calf Rock lies the rocky shore of North Reagh Island and the mussel beds and open algal cover of this island were judged to be very vulnerable to colonisation. By 1997 the shallow bay between Calf Rock and North Reagh was found to be colonised by small plants (25 cm – 75 cm long), either attached to the small stones in the muddy sand substrate or in the process of ‘stone walking’ away from Calf Rock attached to small shells and pebbles. By 1998 *S. muticum* was common in the bay and the whole of the outer coast of North Reagh was ringed by a luxuriant stand of *S. muticum*, forming a large resource of drift material for dispersion throughout the Lough.

The majority of the new *S. muticum* populations recorded in 1998 and shown in Figure 28, were from the north eastern part of the Lough with much less material found along the west coast and the most southerly records were close to the Narrows. However in making any general comments on the spread of *S. muticum* within Strangford Lough, it must be recognised that the 1998 survey visited only 27 sites along the 150 km coastline of Strangford Lough. It is possible that other populations existed within the Lough that were not detected by the 1998 survey.

The new populations within Strangford Lough are principally on the eastern islands where certain habitats were considered vulnerable:

- Permanent littoral pools e.g. adjacent to South Chapel Island, Audleystown.
- Isolated patches of hard substrate surrounded by soft sediments and typically colonised by *Cystoseira* species and *Halidrys siliquosa* e.g. Boretree islands.
- Open algal communities, which have large patches of shell and stone amongst dense populations of indigenous brown algae e.g. Jackdaw Island and Shark Island.
- Some firm sediment shores with large quantities of shell and stone e.g. Chapel Island.
- Mussel beds e.g. Boretree Islands and Gabbock Island.
- *Zostera* sp. beds that have a high proportion of shell material, such as cockle beds.

Generally, the tidal streams in the main body of Strangford Lough are slight and in a north-south direction but the complex of reefs and islands in the Lough complicate the flow greatly (Boyd, 1973). The Strangford Lough tidal model maps, indicate that outgoing tidal currents could rapidly carry drift *S. muticum* material released from the Calf Rock and North Reagh populations, into the main deep channel of the Lough where the current flow is strongest. Theoretically, drift *S. muticum* material could then be carried south, carried between the western islands and eastern pladdies towards the Narrows. On an incoming tide, drift *S. muticum* material could be carried north, either into the Comber Estuary or around the northern mudflats towards the north eastern islands of the Boretrees, Chapel, South and Gabbock. However, wind direction and strength is of much greater significance than the tidal currents in determining the direction and distance travelled by drift *S. muticum* material. In

Strangford Lough, the prevailing wind generally blows from the south west with the eastern shore of the Lough being more exposed to wave action. The wind would generally tend to carry drift *S. muticum* material north and east but extended periods of light northerly winds would aid southerly dispersal. This effect of wind and tide in an enclosed sea loch would also explain the two stands at Jackdaw Island and Chapel Island near the Strangford Lough Narrows, illustrated on Figure 28.

As the majority of the other populations (nine new records) were found in the north east part of the Lough, it is likely that the 1998 survey has revealed the early stages of the widespread colonisation of Strangford Lough. It is likely that fertile drift *S. muticum* material released from the Paddy's Point – Calf Rock area in 1996 and 1997 had been blown north east and then been carried along the eastern coast by tidal currents. The range and variety of sites that have been colonised suggests that over time, more sites will be found to have *S. muticum* populations or will be colonised by *S. muticum*.

The best-established stand found was at the Sheelah's and it is likely to be no more than two years old. All of the winkle pickers that were encountered during the fieldwork during 1998 were shown samples of *S. muticum* and asked if they had seen it anywhere in the Lough. Those winkle pickers who lived around the Lough were the most helpful and well informed. One of the local winkle pickers accurately described the stand off the Sheelah's and stated that the extensive surface canopy present in 1998 had not been visible in 1997.

The most northerly record within the Lough was from the Boretree Islands. In 1998 *S. muticum* was found as small, patchy stands, scattered clusters of plants, single plants or drift material at North Chapel Island, South Island, Gabbock Island, Downey's Rock, Long Skart Rock, Bird Rock, West Rock and Darkin Pladdy. All of these sites lie between the original populations of the Paddy's Point – Calf Rock area and the third recorded population in the Dorn NNR.

Much less *S. muticum* was found down the west coast of Strangford Lough. The north western part of Mahee Island appears to have been colonised recently as the number and sizes of the plants found were generally small. A stand is developing along the north western shore of Sketrick Island, immediately adjacent to Cuan Sea Fisheries oyster processing site and many of the plants are attached to *C. gigas* shells or abandoned oyster bags. This site is likely to have been colonised as a result of processing oysters from the Paddy's Point oyster trestles, with oysters acting as the vector rather than this population developing as a result of marginal drift. Only one plant was found off the north west tip of Drummond Island and only three plants were found off the north eastern shore of the Long Sheelah.

The most significant new records in 1998 were from the south of the Lough. One of the densest stands was found off Jackdaw Island, along with a cluster of plants off South Chapel Island. These are on either side of the large tidal pool that lies between the mainland and South Chapel Island. This has not yet been colonised by *S. muticum* but this pool is considered to be an ideal habitat. If colonised, it could form a seeding reservoir that could allow *S. muticum* to consolidate its colonisation of Strangford Lough and due to its proximity to the Narrows, would release significant quantities of drift *S. muticum* material that would be dispersed out into the Irish Sea.

At all the sites where dense stands, patchy stands or scattered clusters of *S. muticum* plants were found in 1998, they occurred in the shallow sublittoral fringe or on the lower littoral *(F. serratus* zone), where areas of tidal pooling occurred. The *S. muticum* plants had colonised any free substrate, available in gaps amongst the kelp or uncolonised substrates in areas of tidal pooling. The attachment substrates were pebbles, stones and shells (live and dead) and occasionally boulders.

The only site where plants were found exposed at low water on the lower littoral was at North Chapel Island, but all 15 plants were in very poor condition. At one site, South Island, only two drift *S. muticum* plants were found on exposed muddy sand. The only other record of a drift *S. muticum* plant was on the exposed mud between Bird Island and North Mahee. Some of the *S. muticum* plants were found growing epiphytically. At the Darkin pladdy, plants were found growing on kelp, *F. serratus* and *A. nodosum* and one of the plants found off South Chapel Island was growing on *F. serratus*.

Stands of *S. muticum* appeared to have developed or were beginning to develop most successfully off the shore that is the most sheltered from the prevailing wind and wave action. The eastern shores of the Sheelah's, Jackdaw Island, Long Skart Rock, Downey's Rock, the Boretrees, North Chapel Island, Bird Island off Mahee Island, South Chapel Island and Gabbock Island were all developing stands of *S. muticum*, although the extent of the stand and the plant density varied.

The sizes of the *S. muticum* plants found in 1998 varied between less than 5 cm to more than 4 m in length. While the plants in the Calf Rock to North Reagh area were heavily overgrown by brown ephemeral algae, few of the plants found elsewhere in the Lough had any epiphytes. The single *S. muticum* plant found off Bird Island had a *Leathesia difformis* epiphyte. The *S. muticum* plants found in the most extensive stands off the Sheelah's and off Jackdaw Island were very large, over 4 m long, and had luxuriant feathery fronds, forming extensive surface canopies.

By 1998, *S. muticum* appeared to be doing what it does best; grabbing and filling any gaps present amongst the kelp cover of the shallow sublittoral and uncolonised mobile substrate in areas of tidal pooling on the lower littoral. Dense stands had only developed along North Reagh and off the Sheelah's and Jackdaw Island. Elsewhere the stands were small and patchy or the *S. muticum* population was restricted to small clusters of plants or to scattered plants. This indicated that within Strangford Lough, *S. muticum* had entered the early stages of widespread colonisation, reflected by the development of numerous pioneer populations where germlings released by fertile drift material have found suitable substrates.

The sites within Strangford Lough that were considered to be most vulnerable to colonisation by *S. muticum* were prioritised for survey in 1995, 1996 and 1998. This selection and prioritisation process has been supported by the results of the 1998 survey. It is felt likely that the tidal pool at South Chapel Island will be colonised. Due to the ideal conditions within this large pool, the subsequent *S. muticum* population would contribute to the continued colonisation and consolidation of *S. muticum* within Strangford Lough, as well as potentially releasing significant quantities of drift *S. muticum* material that could be dispersed into the Irish Sea.

An additional high priority habitat was identified in 1998. Deep drainage channels in the northern mudflats, lined with shells, retain water at low tide and could be colonised by *S. muticum*. Due to their location, they are very difficult to access, either from the shore or by boat, and aerial photography may be the most effective survey method.

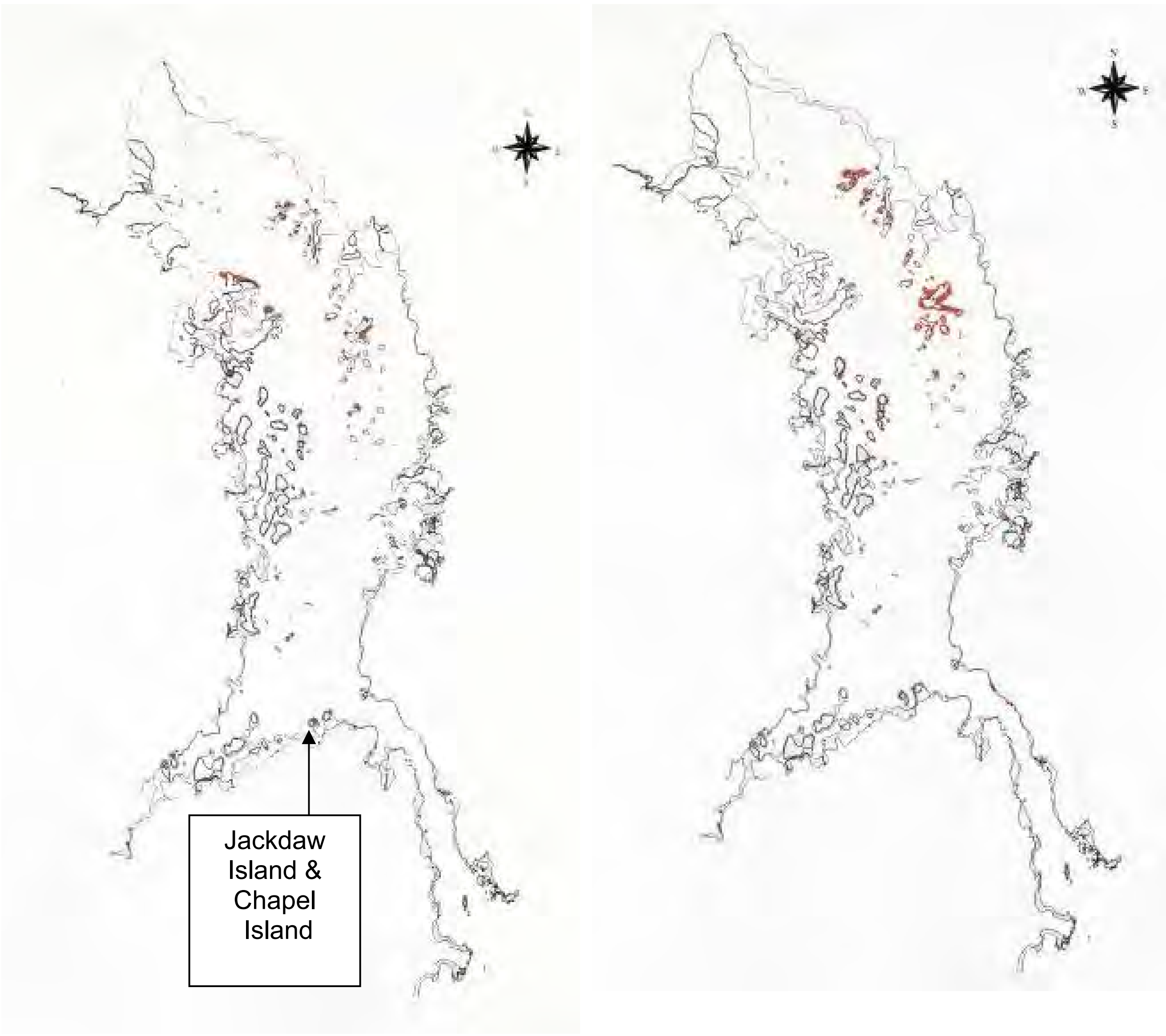
Strong (2003) found that in 2000, the most extensive and best colonised habitat for *S. muticum* in Strangford Lough was mud substratum with some loose rock and shell, with no native canopy-forming algae. The relative proportions of substrata use by *S. muticum* were approximately the same as the availability of these substrata within the Lough. This would suggest that unlike native macroalgae, *S. muticum* was able to colonise almost any available substratum in Strangford Lough to the same degree. As the soft sediment habitats in Strangford Lough are under-utilised by other macroalgae, they could be termed 'unsaturated' or containing 'empty niches'. The locations of *S. muticum* populations within Strangford Lough in 2002 are shown in Figure 28.

In the Dorn, within Strangford Lough, Strong (2003) found that peripatetic dispersal contributes significantly to the rapid consolidation and, hence, invasiveness of this species. In the sheltered confines of Strangford Lough, the average distance travelled, about three metres in two months, was not great, yet the quantity of peripatetic individuals was large enough to repopulate half of the original density in cleared sites after just two months. The maximum dispersal recorded at both sites was 34 m and all of the peripatetic movement was in one direction along the shore, corresponding to the residual tidal currents in the Dorn. Plants that stone-walked between July and September were reproductive and releasing propagules, so even if they were lost from favourable habitat after storm events, the released germlings could ensure that the site would still be invaded. The amount of loose rock on a soft sediment base in Strangford Lough may mean that this mechanism is an effective dispersal mechanism locally, but may not be as prevalent in other parts of *S. muticum*'s introduced range. Strong (2003) hypothesised that over greater periods of time, localised accumulation and depletion of the loose rock by peripatetic *S. muticum* might occur in certain areas of Strangford Lough and that the long-term change in substrata might have repercussions for the distribution of both native and introduced macroalgae.

During June-August 2002, Strong (2003) recorded 70-170 floating and reproductive fronds of *S. muticum* leaving Strangford Lough with each tidal cycle. It was assumed that the material caught in the net at the side of the Narrows was representative of the material leaving the Lough through the mid-channel. An additional assumption was that the majority of material leaving the Lough was not returned by the flood tide. From June, the number of floating units of *S. muticum* increased to a peak in August when rough weather appeared to generate substantial amounts of drifting material. Using surface floats, the dispersal of drifting material was estimated for Strangford Lough. Floats released from the west shore of the Lough travelled northeast with the prevailing wind direction. Releases on the east shore moved predominantly north and some south. This pattern would suggest that the surface wind patterns, rather than local currents or tidal action, are more influential for drift *S. muticum* material. The dispersal of drifting *S. muticum* in the English Channel has also been found to follow the direction of the prevailing wind rather than the water currents (Critchley, 1981).

Strong *et al.* (2006) reported that the total shoreline colonised by *S. muticum* lengthened from 0.61 km in 1996 to 12.86 km in 1998. This increase was mainly due to a greater occupation of habitats with loose rock on a soft sediment base. From 1998 to 2000, although the colonised shoreline increased more than three-fold, the relative proportions of each substratum type remained the same, 97% of the occupied shoreline being mobile, soft substrata. By 2000, *S. muticum* had colonised nearly 50 km of shoreline, most of it consisting of small loose rock on a muddy sand base not previously occupied by macroalgae. Between 2000 and 2002, the length of shoreline occupied decreased by nearly 50%, mostly due to loss of plants from soft rather than hard substrata. Despite this, 93% of the shoreline occupied was still loose rock on soft sediment (Strong *et al.,* 2006).

Figure 28
Maps illustrating the sites in Strangford Lough where Sargassum muticum populations, plants or drift material, were recorded: 1998 and 2002
(E.H.S. N.I.)



1998 **2002**

9.2.1 The mass mortality of Sargassum muticum *in Strangford Lough, 2001*

In June 2001, a mass mortality of *S. muticum* occurred in Strangford Lough, which reduced the distribution of this species considerably as illustrated in Figure 29. The first indication that a mortality event had occurred was when plants were found undergoing rapid decomposition in the second week of July but, judging by the degree of decomposition, Strong (2003) estimated that the actual 'source' of the mortality was sometime in June. In July, all of the plants in the affected areas had lost their laminae, bladders and receptacles and the laterals had lost all buoyancy and disintegrated when handled. By 2002 there had been no recovery of the population in the affected areas, suggesting that both the annual parts of the thalli and perennial holdfasts had died during this event. By the end of July 2001, all of the plants at the affected sites had died and no healthy plants were left. One-third of Strangford Lough's *S. muticum* population was lost within two months. The mass mortality of *S. muticum* was mostly confined to soft substratum habitats. In 2002, *S. muticum* did not re-colonise these areas. Stands of *S. muticum* on hard substrata appeared unaffected.

The mass mortality event that occurred in 2001 happened during a period of particularly low tides. In mixed canopies, individuals of *S. muticum* died, but *Laminaria saccharina* was unaffected, which might suggest that, if a low tide and lethal exposure were responsible for the event, there is differential desiccation tolerance between these species.

Strong produced a comprehensive list of all the possible causes of large-scale mortality for *S. muticum* in Strangford Lough, collated in Table 12. The causes that were not considered likely to have caused the mass mortality are collated in Table 13.

Table 12
Potential causes of mass mortality of Sargassum muticum in Strangford Lough, 2001
(Strong, 2003)

Physical **Extreme environmental conditions**	**Chemical**	**Biological**
Strong winds, causing • Sheer stress and rough sea damage • High turbidity reducing light transmission • High turbidity causing excessive sedimentation on *S. muticum* • Large re-suspension of sediments causing low dissolved O_2 levels High freshwater input on a very low tide High air temperature on a very low tide High irradiance levels on a very low tide Aerial exposure and desiccation on a very low tide	Pollution event, e.g. herbicide and fertiliser run-off from agricultural land	Grazing Heavy epiphyte load Disease Limiting resource, e.g. self shading, nutrient depletion

Table 13
The causes that were not considered likely to have caused the mass mortality of Sargassum muticum in Strangford Lough, 2001
(Strong, 2003)

Other potential causes of the mass mortality	Reasons why these causes could be rejected
Pollution event, e.g. herbicide and fertiliser run-off from agricultural land	The mortality event occurred throughout the Lough, which suggests that a pollution event was unlikely. The Environment and Heritage Service of Northern Ireland stated that they were unaware of any pollution events in Strangford Lough or of any containment undertaken on *S. muticum* during 2001. The probability of a pollution event affecting the whole Lough and only affecting *S. muticum* are very small and hence this mechanism is an unlikely source of the mortality.
Sheer stress and rough sea damage, caused by strong winds	According to the meteorological data, no high winds occurred of the required severity to damage the plants in very rough seas.
High freshwater input on a very low tide	Three peaks of precipitation occurred during the mortality period, but the quantities of rain were not particularly excessive for June. In areas like Paddy's Point and Pig Island, *S. muticum* declined in both shallow and deep water areas, which suggests that low salinity events were unlikely to be the causal mechanism. Furthermore, *S. muticum* is tolerant of a wide range of salinities, with growth being sustained at salinities of 20 ppt (Norton, 1977). The extent of salinity tolerance was also established for *S. muticum* collected from Strangford Lough (unpublished Strong, 2002). Only individuals exposed to a salinity of 10 ppt showed a significant decline in photosynthetic efficiently 24 hours after the treatment. This would seem to make a low salinity event an unlikely mechanism for the mortality of *S. muticum*.
High air temperature on a very low tide and / or High irradiance levels on a very low tide	High light levels and extensive photo-oxidative damage also seem to be unlikely due to the complete loss of all the individuals at affected sites. One might expect small, sub-canopy individuals of *S. muticum* to be protected from this stress and to resume growth after the event, however, no such plants were found. In areas that maintained S. *muticum*, both the canopy and sub-canopy individuals of this alga were found to be healthy. Equally, thalli of *S. muticum* are common rockpool species on the Portuguese coastline where light levels must be considerably higher than the irradiances experienced in Strangford Lough. Furthermore, Strong's photosynthesis and irradiance studies found a high saturation irradiance for *S. muticum* collected from Strangford Lough.

Table 13 continued
The causes that were not considered likely to have caused the mass mortality of Sargassum muticum in Strangford Lough, 2001
(Strong, 2003)

Other potential causes of the mass mortality	Reasons why these causes could be rejected
Grazing	Although grazing on *S. muticum* by the epiphytic fauna can be intense, it is highly unlikely that this could be the mechanism by which a third of the population could be lost within two months. Equally, there were areas (e.g. the Dorn) where high mortality occurred close to areas where the *S. muticum* remained healthy. It seems unlikely that mesoherbivore grazing could generate such patterns of survival in the basiphyte population. However, larger grazers have been known to cause the mass mortality of macroalgal populations. Sea urchin grazing almost entirely eradicated the population of *S. muticum* in British Columbia (De Wreede, 1980). When the grazing pressure by urchins declined, the population of *S. muticum* was able to re-establish. However, urchins do not occur at great enough densities to impact the population of *S. muticum* in Strangford Lough. Equally, the population density of other possible grazer species was not observed to be any higher than normal for that time of year in the Lough.
Heavy epiphyte load and associated hypoxic conditions	Excessive epiphytism on *S. muticum* can cause the adult plant to die back prematurely. High levels of mortality in the *S. muticum* population were observed during a spring bloom of ectocarpoid species in the Dorn. However, areas where plants were lost, i.e. Paddy's Point, the Dorn and Kircubbin, were not heavily fouled in June. Environmental probes, only available in August, were deployed for a week and consequently, the results obtained could only be used as an indication of the variability experienced in different habitats of *S. muticum* and not as a record of the physical conditions that may have occurred during the mortality period. Dissolved oxygen concentrations were found to fluctuate to a greater extent in a canopy of *S. muticum* and in soft sediment habitats, compared to unvegetated and hard substratum areas. Temperature followed a similar pattern of variability, but to a lesser extent. None of the fluctuations were anywhere near low enough to produce hypoxic conditions. Even low density stands and isolated individuals of *S. muticum* were lost indicating that low dissolved oxygen levels were probably not related to the decline. Microalgal blooms may have been important in localised hypoxic events within the Lough, although none were reported for the period of mortality or for a significant time before the event.

Table 13 continued
The causes that were not considered likely to have caused the mass mortality of Sargassum muticum in Strangford Lough, 2001

(Strong 2003)

Other potential causes of the mass mortality	Reasons why these causes could be rejected
Disease	Examining the extent, specificity and rapidity of the mortalities, a pathogen would appear to be an appropriate mechanism to consider. As no samples of *S. muticum* were collected at the time, the possibility of the occurrence of a disease can neither be accepted nor excluded. However, the proximity of areas with healthy and dying individuals of *S. muticum* in the Dorn suggests that a disease is less likely, when compared to a habitat-specific factor like sedimentation. It could also be argued that a combination of poor environmental conditions may have weakened the plants and made them more likely to succumb to infection, as is the case with the slime mould, *Labyrinthula* sp., responsible for the wasting disease in *Zostera marina* (Muehlstein *et al.,* 1988). It is thought by some to be only mildly infectious and that it is only when the *Zostera marina* is stressed by poor environmental conditions, that *Labyrinthula* sp. becomes pathogenic (Burdick *et al.,* 1993). A similar process could be occurring in the population of *S. muticum*. Factors specific to soft sediment habitats, e.g. high sedimentation and variable physical conditions, might be stressing, and thereby suppressing the immunity of this alga to a pathogen present in the Lough.
Limiting resource, e.g. self shading, nutrient depletion	The possibility of a limiting resource causing the mass mortality was difficult to substantiate. Many of the areas maintaining healthy *S. muticum* were characterised by faster flowing water that might prevent limitation. Strangford Lough is shallow and well mixed between tidal cycles, so resources are not likely to be limited to the extent necessary to cause extensive mortalities.

As a result of Strong's initial investigations, he narrowed this list down to aerial exposure and sedimentation.

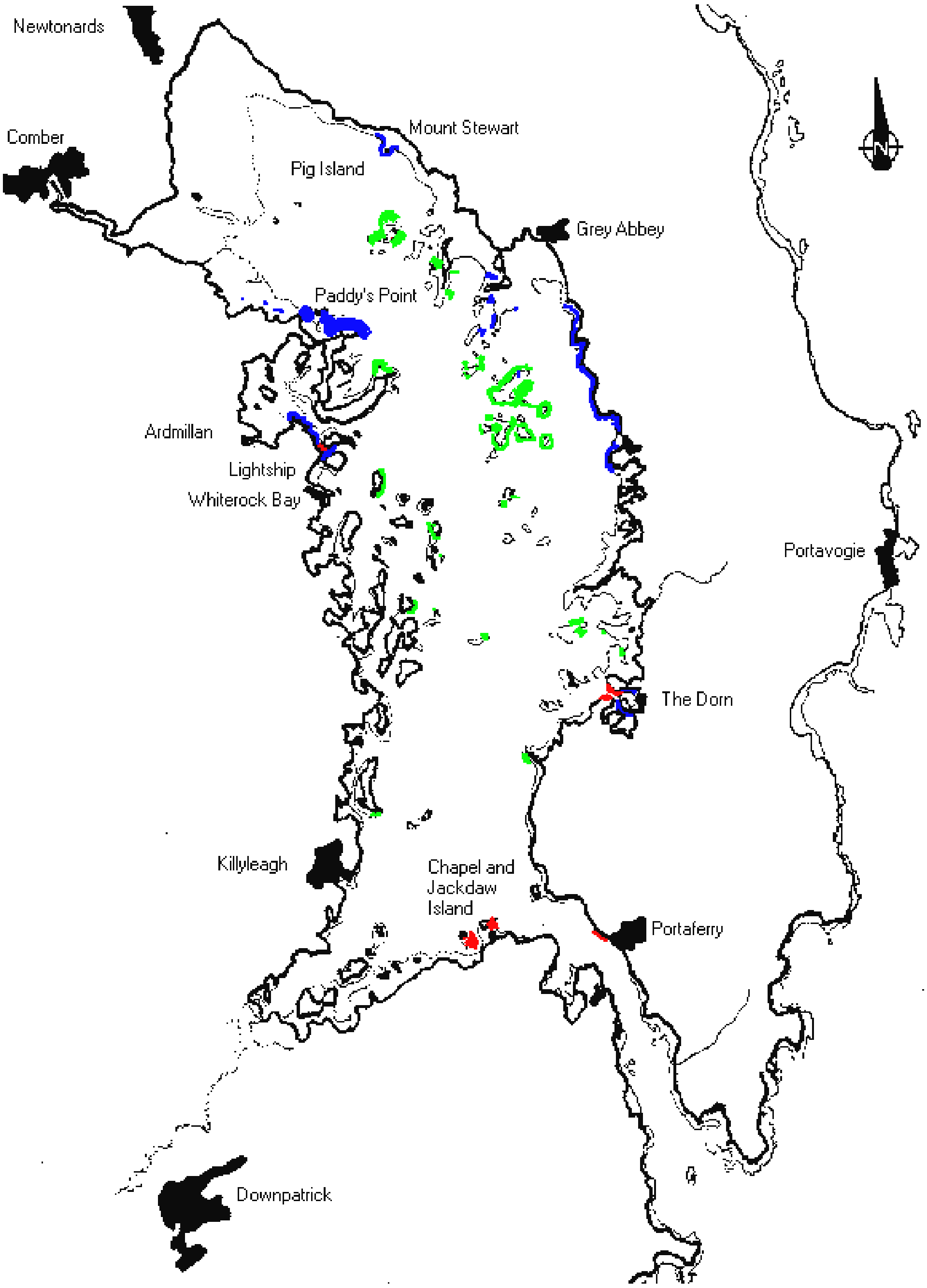
His field experiments to investigate the roles of desiccation intolerance and sedimentation effects (2003), suggested that sedimentation was the more likely causal factor, due to the extent of the mortalities in soft sediment habitats and the fact that *S. muticum* was lost in the Dorn, where low tides are moderated. The fact that *S. muticum* transplants into the historic range failed, i.e. where *S. muticum* was previously distributed in 2000, indicated that the conditions that initially caused the loss of *S. muticum* in these areas still persisted. This evidence weakened the possibilities of disease or a limiting resource being responsible for the decline. The similarity of the decline of *S. muticum* in Strangford Lough and the loss of other submerged aquatic vegetation, e.g. *Z. marina*, through sedimentation and the persistence of this factor in preventing re-colonisation adds weight to its likelihood as the causal factor of this mass mortality.

The fact that the mortalities were localised in soft sediment and sheltered habitats, and that in 2002 there was no apparent recovery of the population of *S. muticum* in these areas might suggest that other mortality events are unlikely in Strangford Lough. Should the factors that currently prevent the re-colonisation of *S. muticum* in soft sediment areas subside, then it would be expected that these areas would be re-occupied quickly, however, the long-term viability of these re-colonised sites would be questionable. Only through the identification of the fundamental factor that caused the die-back, could predictions be made about the longevity of the occupation of these sites. If exposure on a low tide was the sole factor responsible for the decline, then predictions about the frequency of mortalities could probably be made. Alternatively, if changing environmental conditions, e.g. shifting wind patterns or summer irradiance levels, were the underlying factors responsible, then predictions about the timing of future mortalities are likely to be impossible. Current research on environmental change in Northern Ireland has predicted a greater storm frequency, as well as an increase in the average wind strength and a slight shift in the prevailing direction. These factors are currently thought to be contributing to a decline of the *Ascophyllum nodosum* in Strangford Lough (Davies pers. comm.) and may also be responsible for the recent mortalities in the population of *S. muticum*.

Figure 29
Map illustrating the areas of Strangford Lough where mortalities of Sargassum muticum occurred: 2001
(Strong, 2003)

KEY

Blue:	Shoreline where *S. muticum* was present in 2000 and absent after the mass mortality in 2001
Red:	Remained healthy in 2001
Green:	Not checked in 2001 but presumed to have also suffered mortalities



9.3 Modelling the spread of *Sargassum muticum* in Strangford Lough

Strong (2003) used a random stratified diffusion model to generate predicted rates of spread for the population of *S. muticum* in Strangford Lough. As two very different dispersal coefficients were obtained for drift dispersal of *S. muticum*, i.e. 0.96 km^2 per year (east shore; low dispersal) and 2.90 km^2 per year (west shore; high cross-lough dispersal), they were used separately in different variations of the model. The probabilities for the production of drift thalli was then estimated by 'fitting' the exponential phase of the predicted curve to the observed rates and the two values (0.01% and 0.001%) produced were used for the probability of drift *S. muticum* material establishing new populations (Strong, 2003).

Both predicted and observed values produced an accelerating rate of spread, although the establishment phase appeared to be much longer than in the observed dataset. The average observed rate of spread for *S. muticum* was approximately 4 km per year. However, at the drift plant establishment probability of 0.001%, the model predicted average rates of spread of 2.6 km per year (low dispersal) and 3.3 km per year (high dispersal). At the higher probability of drift plant establishment, the model predicted rates were 3.7 km per year (low dispersal) and 7.3 km per year (high dispersal). Although the overall observed rate of spread was similar to some of the predictions, the model appeared to over-perform during the establishment phase. Furthermore, only the predictions using the high drift dispersal and higher probability of successful establishment had similar rates of spread during the spread phase.

The random stratified diffusion model predicted that the rate of spread for *S. muticum* in Strangford Lough would accelerate exponentially and an exponential process was evident in the observed rates of spread. However, the mean predicted rate of spread was 13 km per year for the last fifteen years, which was much greater than the observed rate of spread of 4 km per year. There are several possible reasons why many of the model outcomes have overestimated the rate of spread. Firstly, the original populations were in sites where the aerial exposure and lack of hard substrate on a soft mud substrate severely limited their ability to consolidate and to develop a breeding stock capable of releasing sufficient quantities of fertile *S. muticum* drift to colonise new sites. Another significant factor was the extensive containment operation undertaken between 1995 and 1999. Consequently, although *S. muticum* was introduced in 1987-88, the first evidence of colonisation elsewhere in the Lough was when the third population was recorded in the Dorn in 1998, ten years later.

Sources of error in the model included the estimation of drift dispersal and the probability of successful colonisation from fertile floating material. The probabilities used for the colonisation of drift plants may have overestimated the success of this process. The drift diffusion coefficient was only an approximation of this highly stochastic and variable process. The inclusion of a stochastic function with the drift dispersal in the model might better simulate the actual dispersal process.

Both the observed and predicted rates of spread for *S. muticum* in Strangford Lough appear to be significantly lower than observed rates of spread in other parts of the introduced range. Please refer to Section 6.1 for details of global dispersal rates for *S. muticum.*

Although the model failed to simulate the observed rates of spread, the sensitivity testing has provided some insights into the importance of the different dispersal mechanisms. Dispersal by settlement and peripatetic plants was unimportant in generating the predicted rates of spread at the 'Lough' scale. These processes are bound to be important in consolidating new habitat and for localised perimeter expansion of the primary population, but contribute little to overall expansion of the population. The sensitivity test indicated that the dispersal of drift plants was the most important factor in determining the predicted rates of spread. The rare, but long distance, leaps in distribution undertaken by drift plants were found to be of overriding importance in deciding the outcome of the model.

Strong (2003) proposed that to improve the model predictions for Strangford Lough, variation in habitat quality could be taken into account with a patchy or heterogeneous model. Strong also proposed a stochastic function for the dispersal of the drifting plants would also make the simulation more realistic. The dispersal coefficients for *S. muticum* plants would have to be re-assessed for generating rates of spread in other geographic areas.

9.4 Research work undertaken on *Sargassum muticum* in Strangford Lough: 2000 - 2003

The main objective of Strong's Ph.D. study (2000-2003) was to test the hypothesis that the canopy of invasive *S. muticum* over soft sediment would affect infaunal communities in the same manner as macroalgal blooms, reducing diversity and abundance. The other results of his research are included within the relevant sections throughout this report.

9.4.1 Impacts of Sargassum muticum *on infaunal communities*

Strong *et al.* (2006) reported on this element of Strong's Ph.D. research. Two populations were studied within Strangford Lough, which had developed approximately five to six years previously and within Langstone Harbour, southern England, which had been colonised 26 years previously in 1974. Any effects of *S. muticum* canopies on the physical environment were determined in comparison to native macroalgal canopies, i.e. stands of *Laminaria saccharina* that can form over soft sediments when embedded stones are present.

In Strangford Lough, there were no differences in either the mean number of species or the abundance of individuals sampled from under and outside the canopies. Both surface detritus feeders and surface deposit feeders were equally abundant under the vegetation. In contrast, in unvegetated areas, the assemblages had a greater proportion of surface deposit feeders. Infaunal samples from under the canopy contained significantly more individuals. Surface deposit feeders were the dominant trophic guild in both vegetated and unvegetated samples. However, the infaunal community under a canopy of *S. muticum* was of a lower diversity and was characterised by a greater abundance of numerically dominant small organisms than the non-canopy community. Many of the abundant species under the canopy, such as *Tubificoides pseudogaster* and *Capitellides giardi*, were opportunistic *r*-selected species (Pearson and Rosenberg, 1978). The greater dominance of surface detritus feeders under these conditions was consistent with the localised primary production. Many of the abundant species under the canopy in Strangford Lough were those typically associated with organically enriched sediments or with other subtidal native algae.

The species that were abundant at sites outside the canopy were all larger-bodied and typical of a muddy sand substratum. The larger body size in the non-canopy community was an indicator of a stable habitat, in which disturbance is infrequent and the infauna are skewed towards *K*-selected strategies. Species such as the polychaetes *Scoloplos armiger* and *Ophelia rathkei* were more abundant outside the canopy. *K*-selected species were rarely numerically dominant, but were foremost in terms of biomass (Clarke and Warwick, 1994). When a community is perturbed, *K*-selected species are less favoured and opportunistic *r*-selected species quickly proliferate (Clarke and Warwick, 1994), so the enhancement of *r*-selected species below the canopy suggests that this assemblage was under some form of 'stress'. These results therefore support the hypothesis that a newly established canopy of the invasive macroalga *S. muticum* will reduce the diversity and abundance of infaunal communities under this vegetation.

In Langstone Harbour, the differences observed between assemblages under and outside the canopy were fundamentally distinct from those found in Strangford Lough. Under the canopy, species composition remained the same as outside the canopy. However, abundance increased substantially, which did not change the assemblage diversity, dominance, community trophic status or evenness between canopy and unvegetated areas.

Comparable studies that examine the interaction of macroalgae and infauna are few. The results obtained from Langstone Harbour compare well with those of Nicholls *et al.* (1981) who found similar species composition in areas with and without algae, but greater total density of fauna with algae. The findings for the infaunal survey in Strangford Lough contrast with those of Soulsby *et al.* (1982) and Nicholls *et al.* (1981), and have more similarity to Everett's (1994) observations of a pronounced impact of ephemeral algae, e.g. subtidal *Ulva* spp. and *Enteromorpha* spp., on infauna.

In Strangford Lough, the less diverse infaunal assemblage under the canopy suggested that some aspect of the introduced vegetation, either directly or indirectly, perturbed this community. By contrast, the Langstone Harbour infaunal community showed no signs of perturbation; rather, the presence of a canopy of *S. muticum* appeared to have enhanced the faunal abundance of the resident assemblage. It is clear that the presence of *S. muticum* does influence infaunal communities. However, perhaps due to site-specific differences, the influence of this introduced vegetation can vary, resulting in differing infaunal composition, but it is the differences within a site between vegetated and unvegetated areas that are interesting in highlighting localised responses of the infaunal assemblages to *S. muticum*. The duration of occupation by *S. muticum* may be another factor. In Langstone Harbour, *S. muticum* has been present since 1974, providing more time for the native assemblages to potentially adapt to and ultimately exploit the presence of, and processes associated with, this species. Neira *et al.* (2005), examined the impact of hybrid invasive *Spartina* spp. at three intertidal areas in San Francisco Bay. As with the Strong (2003) study, changes in the infaunal community between vegetated and unvegetated areas differed between sites. The reason for the lack of consistency was related to either the duration of *Spartina* spp. occupation at the sites, ranging from 10 to 30 years, or specific differences in the topography and sediment that mediated the presence of *Spartina* spp. in varied ways. Only continuing temporal surveillance in Strangford Lough could test whether the impact of this invasive species would decline with time.

Sediment composition (median size, sorting or silt/clay fraction) was not affected by the presence of a canopy of *S. muticum* in either Strangford Lough or Langstone Harbour. The finding that sediment particle size characteristics did not differ between canopy and non-canopy habitats at either Strangford Lough or Langstone Harbour was surprising considering that there was strong flow suppression. Suppression of current flow by *S. muticum* was not significantly different from that by *L. saccharina*. However, unlike *S. furcatum* and seagrass communities, which show similar levels of water flow, *S. muticum* sheds its canopy annually, leaving only the perennial holdfasts. This cycle leaves the sediment exposed for approximately four to five months each year, during which time wave action and currents could re-suspend and remove sediment accumulated during the vegetated phase. The effects on infauna associated with the presence of invasive algal canopies in Strangford Lough were therefore not due to changes in sediment characteristics.

Strong (2003) suggested that it could be concluded that the presence of *S. muticum* does influence infaunal communities. The enhancement of the community under *S. muticum* in Langstone Harbour could be related to two factors. Firstly, that the prevailing biotic and abiotic factors at this site 'modified' the presence of *S. muticum* and lessened its impact. Secondly, the 26-year residence of *S. muticum* may have allowed the infauna to adapt to and ultimately exploit the conditions under a canopy. Nonetheless, he pointed out the possibility that the long-term residence of *S. muticum* could diminish its impact and may actually enhance the infaunal community. Therefore, he hypothesized, the long-term presence of this alga might actually enhance the infaunal community in Strangford Lough.

The canopy of *S. muticum* had major effects on other aspects of the local environment. It had a strong shading effect, as previously observed, that was significantly greater than the native *L. saccharina* (Critchley *et al.,* 1990, Curiel *et al.,* 1998). In an unvegetated habitat, 89% of sub-surface irradiance penetrated to the substratum at low tide (depth 0.35 m), whereas under algal canopies this value was less than 5%. Canopies of *S. muticum* absorbed 97.2% of the sub-surface irradiance, compared to 95.6% for *Laminaria saccharina* canopies. In a native algal canopy, less than 5% of the light reaches the sub-canopy, so the extra 2% absorption by *S. muticum* potentially represents an approximate 40% loss of the available light for the sub-canopy macroalgae.

A 2°C warming was apparent in the canopy of *L. saccharina* when compared to the ambient seawater in unvegetated areas. Warming within the canopy of *S. muticum* was much greater, with the water temperature elevated by 11°C above ambient. Unlike *L. saccharina* canopies, evidence of a significant cooling to 2°C below ambient was observed under the canopy of *S. muticum*. Stands of *S. muticum* in Strangford Lough caused strong temperature stratification, including significant cooling of the water just above the sediment, as recorded in Lake Grevelingen, The Netherlands (Critchley *et al.,* 1990). The extreme heating of the water associated with the surface canopy is typically restricted to a thin layer at the very surface of the water. Within the sheltered environment of Strangford Lough, the high density of *S. muticum* tends to prevent the water within the stands of vegetation from being exchanged with non-canopy areas. In addition, the dark colour of the canopy absorbs much of the light, and on a sunny day the stagnant water can become extremely warm. Such stratification did not occur in *L. saccharina* beds, perhaps due to the lower standing biomass and because the vegetation does not ‘interlock’ as it does for *S. muticum*.

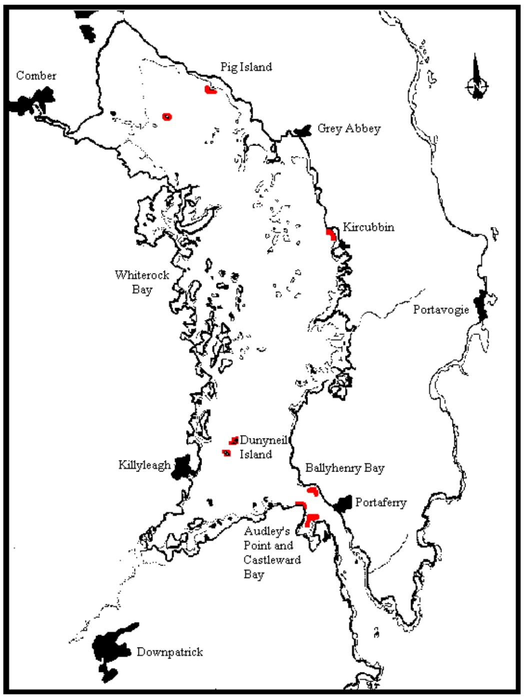
The temperature stratification documented in canopies of *S. muticum* raises some interesting questions about the interaction of the warming and the physiology of this species. Norton (1977) found that the optimum temperature for growth of *S. muticum* was 25°C, and that this species was also tolerant of temperatures up to 30°C. Strong *et al*. (2006) hypothesised that this localised warming within the canopy might actually benefit *S. muticum* and increase its growth rate. Bouts of increased warming within the canopy may also have an impact on the extent of epiphytic colonisation by less tolerant species, for example by reducing the fouling burden on *S. muticum*. To what extent the temperature stratification and flow suppression/water exchange persist over a tidal cycle and the implications of these factors for the infaunal community requires future investigation.

Strong *et al.* (2006) concluded that at both study sites (Strangford Lough and Langstone Harbour, English Channel), community analyses highlighted significant differences between the assemblages under the canopies and those in adjacent unvegetated areas. In Strangford Lough, the invertebrate community under the canopy contained a higher abundance of smaller, opportunistic, *r*-selected species than outside the canopy. By contrast, the communities under and outside the canopy at Langstone Harbour were similar in species composition, diversity and dominance, but overall the faunal abundance was greater under the canopy. *S. muticum* canopies did not affect sediment characteristics, but the infaunal changes may have been related to environmental modification; shading, flow suppression and temperature stratification. The differences between these two sites indicated that localised conditions as well as the period of colonisation by *S. muticum* are important in determining the nature of habitat modification.

9.4.2 Impacts of S. muticum on eel grass, Zostera marina

Strong (2003) investigated beds of *Zostera* spp. within Strangford Lough to assess whether any were being colonised by *S. muticum* and undertook transplanting experiments. The locations of *Zostera* spp. in Strangford Lough are shown in Figure 30.

Figure 30
Map illustrating the known distribution of subtidal Zostera spp. in Strangford Lough: 2002
(Strong, 2003)



9.4.2.1 Pig Island

The bed of *Zostera* spp. was extensive and lush in 2001 and 2002. A very low density of transient peripatetic thalli of *S. muticum*, with less than two plants per 10 metre^2 of *Zostera* spp., were present in 2001. The individuals of *S. muticum* observed in 2001 were typically less than one metre in length and in poor condition. No thalli of *S. muticum* were found in 2002.

9.4.2.2 Kircubbin Bay

Shallow sections of the *Zostera* spp. were exposed on low spring tides. There were consistently high biomasses of ectocarpoid species fouling the *Zostera* spp. and substratum surface. During 2001 and 2002, the density of *S. muticum* increased from approximately six plants per 10 metre^2 of *Zostera* spp. to 10 plants per 10 metre^2 of *Zostera* spp. Individuals of *S. muticum* were small, peripatetic and attached to pebbles. None of the plants in the bed were established, suggesting that this was a sink population of *S. muticum,* supplied by the other stands within Kircubbin Bay.

9.4.2.3 Ballyhenry Bay

The bed of *Zostera* spp. was located in a sheltered anchorage at approximately 5 m below mean low water. The bed in 2001 and 2002 was lush and had a high seagrass density. The substratum was very soft, despite moderate water motion. No *S. muticum* was found at this site in 2001 or 2002.

9.4.2.4 Castleward Bay

The bed of *Zostera* spp. was located in deeper water and no *S. muticum* was present in either 2001 or 2002. This was despite the fact that shallower sections of the bed are within the depth range of *S. muticum*. The nearest population of *S. muticum* to this bed was the small stand on Chapel Island (south) but the local currents and wind patterns would not disperse *S. muticum* from Chapel Island to this site. The eelgrass bed in Castleward Bay would be similar to that in Ballyhenry Bay in terms of depth and substratum type, hence only Ballyhenry Bay was selected for transplantation of *S. muticum*.

9.4.2.5 Audley's Point

The high-density and widespread bed of *Zostera* spp. was approximately 3-5 m below mean low water. The substratum was more sandy in the deeper areas and muddier in the shallows. No *S. muticum* was found in either 2000 or 2001.

Transplantation of *S. muticum* was undertaken into the deep water *Zostera* bed at Ballyhenry Bay and into the shallow water *Zostera* bed at Audley's Point. Transplantation of *S. muticum* into and outside the deep water bed of *Zostera* spp. in Ballyhenry Bay resulted in continuous primary lateral erosion and ultimately in plant death after three weeks. A similar decline was observed with transplants of *S. muticum* into and outside the shallow water *Zostera* bed at Audley's Point but this decline was much slower than that observed at Ballyhenry Bay.

Eelgrass (*Zostera marina*) beds in Strangford Lough are in habitats generally inhospitable for *S. muticum*, suggesting that the substitution of eelgrass by *S. muticum* is highly unlikely. Some shallow eelgrass beds were found to contain a very low density of *S. muticum*, although these individuals are probably part of sink populations and without peripatetic movement would probably cease to exist. Three factors appear to prevent *S. muticum* colonisation in eelgrass beds, as follows:

- **Depth.** Three out of the seven eelgrass beds were located in water deeper than the maximum depth penetration of *S. muticum* in Strangford Lough. At Ballyhenry Bay, where transplants of *S. muticum* were undertaken into and outside a deep water bed of *Zostera*, the methodology lacked control transplants into shallower areas, hence preventing exact identification of the factor responsible for the decline. Field observations of *S. muticum* undertaken throughout Strangford Lough have never documented the permanent occupation of substratum under 3 m below mean low water. However, should this experiment be repeated, ideally controls for depth would be included to distinguish between the factors of depth and shading.
- **Substrata.** Although *S. muticum* occurs in soft sediment habitats, mixed substrata of loose rock and shell or bedrock is required for successful settlement of this species. Without some hard substrate, colonisation will only occur at the rate of peripatetic transport into the site.
- **Sedimentation** in soft sediment habitats has also been found to cause significant mortalities in the population of *S. muticum*, hence providing a mechanism for its exclusion in shallow eelgrass beds. Observations in the Dorn where *S. muticum* was transplanted into soft sediment areas without eelgrass also found that these plants

declined within weeks. This decline was attributed to greater sedimentation onto *S. muticum* and may explain why transplants into beds of eelgrass were unsuccessful.

Strong (2003) concluded that the probability of *S. muticum* replacing eelgrass in Strangford Lough is very slight. However, events that lead to the loss of eelgrass, such as storm damage or disease, might also result in the subsequent erosion of soft substrata. In shallow areas, any substratum exposed after this process is likely to be rapidly colonised by *S. muticum,* which could then prevent recolonisation by eelgrass.

10.0 THE CURRENT KNOWN DISTRIBUTION OF *SARGASSUM MUTICUM* AROUND SCOTLAND

10.1 The discovery and subsequent recording of current known populations in Scotland

The *S. muticum* colony in Loch Ryan, on the south west coast, was the first population discovered in Scotland. It was discovered in February 2004 by a survey team from the environmental consultancy, Royal Haskoning, whilst surveying the shore of Cairnryan Bay as part of an environmental assessment for a proposed ferry-terminal development (A. Davison, pers. comm.).

The initial discovery was subsequently confirmed by the Scottish Natural Heritage (SNH) Maritime Group, who found "*S. muticum* has become established at several other sites around the loch" (Reynolds, 2004). A more comprehensive survey of Loch Ryan was carried out on 25th March 2004, by Scottish Natural Heritage. Four locations were investigated, two on each side of the Loch. *S. muticum* was found at three survey sites, confirming the presence on both sides of the loch. *S. muticum* was present on the lower shore and the sublittoral fringe. All sites were mixed substrate with sediment, with cobbles and stones providing the attachment substrate for the algae. At the Cairnryan site there were about 100 individuals, along a 50 m stretch of shore. At the other sites, plants were distributed in a scattered manner along most of the shore visited by the surveyors, indicating a relatively well established population. Plants of a variety of sizes were collected at the Cairnryan site (Reynolds 2004; Pizzola 2005).

Other established populations were recorded subsequently on the west coast of Scotland. During 2004-5, two populations were found, one on the east coast of the Isle of Cumbrae and the other on the adjacent mainland shore at Hunterston Power Station, in the warm water plume (Ashton *et al.,* 2006a; Harries *et al.,* 2007a). During 2006, the Isle of Cumbrae population was found to have expanded and unattached drift *S. muticum* fragments were found at two sites; Clyde Marina, Ardrossan, Ayrshire and Loch Fyne, Argyll (Harries *et al.,* 2007a). During 2007, two populations were found, one in Whiting Bay, Isle of Arran and the other in Croy Bay, Culzean, Ayrshire (Harries *et al.,* 2007a). During 2007, unattached drift *S. muticum* fragments were found at four sites; one on the Isle of Arran at Corrie and three in Argyll at Kintyre, Firth of Lorn and Oban (Harries *et al.,* 2007a; F. Manson, pers. comm.).

It had been thought that the Kintyre Peninsula would provide a temporary physical barrier to the continued spread of this invasive species up the west coast of Scotland. However, unattached drift *S. muticum* fragments were found in the Firth of Lorn at the Garvellachs in May 2007 and at Ganavan, near Oban. These sites are over 100 km north of the southern end of the Mull of Kintyre (Harries *et al.,* 2007b).

There appears to be a colonising movement northwards along the west coast of Scotland and the occurrence of drift *S. muticum* as far north as Oban, indicates that other populations, not yet identified, may exist between Loch Ryan and Oban. Harries *et al.* (2007b) concluded that the rapid northwards spread of this species since the early 1990s, suggests that the colonisation of western Scotland by *S. muticum* is likely to occur in the next few years. The current records of *S. muticum* on the west coast of Scotland are shown in Figure 31 and are listed in Table 14.

Figure 31
Map illustrating the distribution of the records of Sargassum muticum on the west coast of Scotland: 2004 - 2007
(Harries *et al.,* 2007b)

Information on the sites is provided in Table 14

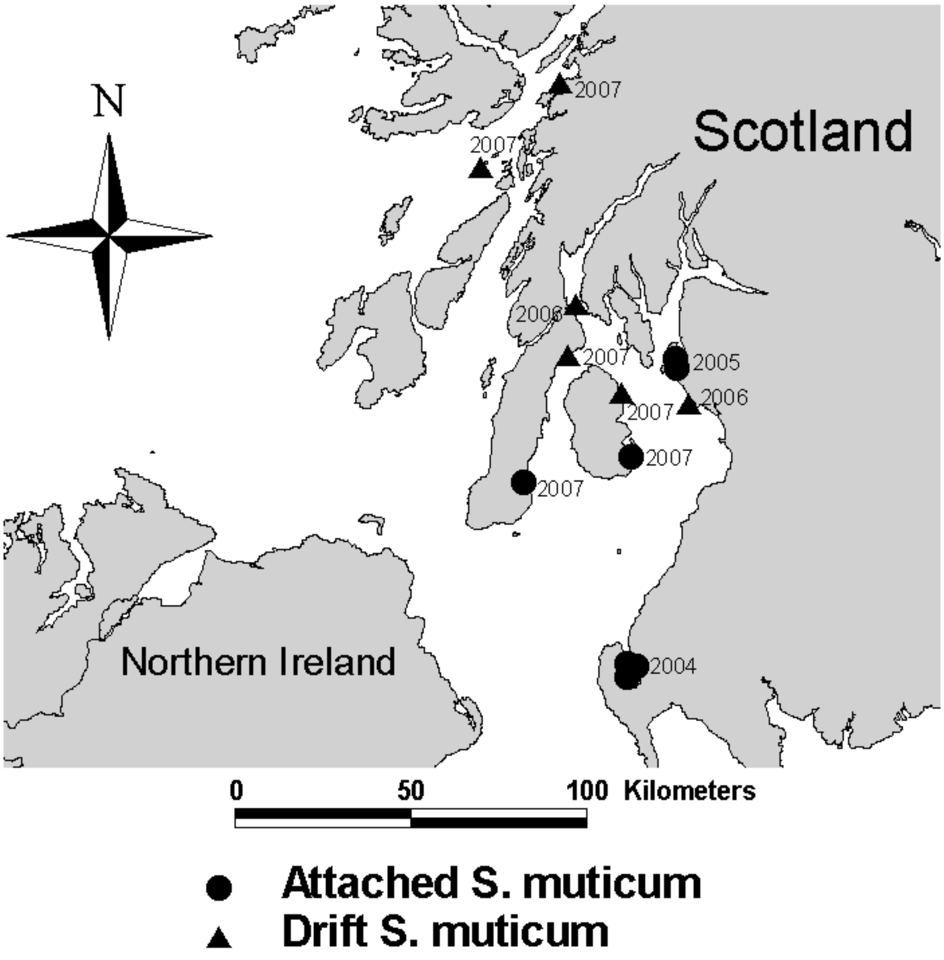


Table 14
Records of Sargassum muticum found around Scotland to date
(SNH)

Year **2004**	**Locations illustrated in Figure 31**	***S. muticum* notes**	**Position OSGB**	**Source**
1 February	Loch Ryan, Wigtownshire	Attached to scattered pebbles on sand, sparsely distributed on lower shore and sublittoral fringe	NX046681 NX069677 NX036648	Scottish Natural Heritage
2 August	Isle of Cumbrae, Ayrshire	Attached to cobbles and pebbles, forming dense canopy on lower shore and sublittoral fringe, on the sheltered east coast of island	NS175544 to NS182555	University Marine Biological Station, Millport
2005				
3	Hunterston Power Station, Ayrshire	Attached, within the warm water plume (Ashton *et al.,* 2006a)		University Marine Biological Station, Millport
2006				
4	Loch Fyne, Argyll	Unattached drift fragments	NR900700 (approx.)	Public Sighting Record
5	Isle of Cumbrae, Ayrshire	Attached, further expansion of bed noted in 2005	NS175543 to NS181593	Scottish Natural Heritage
6	Clyde Marina, Ardrossan, Ayrshire	Unattached drift fragments		Scottish Association for Marine Science
2007				
7	Corrie, Isle of Arran	Unattached drift fragments	NS026420	Scottish Natural Heritage
8	Whiting Bay, east coast of the Isle of Arran	Attached and well established	NS046259	Public Sighting Record
9	Clonaig, Kintyre, Argyll	Unattached drift fragments	NR875560	Scottish Natural Heritage
10	Davaar Bay near Campbeltown Loch, south east Mull of Kintyre, Argyll	Attached.		Scottish Association for Marine Science
11	Garvellachs, Firth of Lorn, Argyll	Unattached drift fragments	NM645096	Scottish Natural Heritage
12	Ganavan, near Oban, Argyll	Unattached drift fragments		Scottish Association for Marine Science
Not on map	Croy Bay, Culzean, Ayrshire	Attached, extensive cover	NS244126	Public Sighting Record

10.1.1 Loch Ryan

Loch Ryan is at the southern end of the Clyde Sea area and whilst open to the north, Loch Ryan is a moderately sheltered sea loch. Its large inner bay is rarely more than 5 m deep, with a mix of rocky and sediment substrates. Its open nature means that it is exposed to irregular but intense northerly storms.

Millar (1963) described surface water temperatures as being especially high for a northern locality, with a maximum of 21°C and a summer average between 15°C to 17°C, due to the enclosed and shallow nature of the Loch. Howson (1989) described the area as being fully marine, sheltered and containing many cobble shores. Therefore, it is no surprise that *S. muticum* was able to colonise this area.

The main established stands of *S. muticum* are found in the more protected areas of the western shore of the Loch. *S. muticum* was first observed in the upper sublittoral, with *S. muticum* present on cobbles and boulders on a matrix of muddy sand. There was limited algal cover, other than sparse red algae (A. Davison, pers. comm.).

Harrow (2005) described his survey site in Loch Ryan where *S. muticum* was observed as a sheltered, gradually sloping shore. The *S. muticum* was only observed subtidally, at a depth of approximately 0.3 m. This zone consisted of muddy sand (LMS: “Littoral muddy sands”) with occasional boulders dominated by *Semibalanus. balanoides* (B.Pat.Sem) and cobbles. The biota consisted mainly of small brown and red algae (*Chondrus. crispus*, *Chorda filum* and *Asperococcus* sp.) with ascidian species and *Hymeniacidon perleve* frequently observed.

10.1.2 The Isle of Cumbrae

The Isle of Cumbrae site, discovered in early August 2004, is approximately 85 km north of the Loch Ryan sites. As the Isle of Cumbrae and Hunterston are areas regular monitored by staff at the Millport Marine Station, it can be assumed that the appearance of *S. muticum* in these areas would be quickly noted. Consequently, until further evidence is forthcoming, the cautious assumption may be made that *S. muticum* established in Loch Ryan before spreading within the Firth of Clyde.

The Isle of Cumbrae population, shown in Figure 32, was observed to have expanded greatly within one year (Harrow, 2005). Observations in 2004 described very sparse coverage, whereas a dense band of *S. muticum* was present in 2005, extending over 1.6 km of the east coast of the island, generally located between the Fucoid and Laminarian zones. Harrow’s (2005) study on the Isle of Cumbrae aimed to establish whether the biota associated with a site invaded by *S. muticum* was significantly different to a similar control site on the Isle of Cumbrae. The population structure of *S. muticum* found at two sites on the Isle of Cumbrae and Loch Ryan was also investigated.

Figure 32
Map illustrating the area colonised by Sargassum muticum (red line) on the Isle of Cumbrae: 2005
(Harrow, 2005)

Harrow's (2005) Isle of Cumbrae *S. muticum* survey site was east facing and moderately exposed. There were no anthropogenic influences, such as man-made structures or any indication of pollution. The biotope was classified as being IR.LIR.K.Sar: "*S. muticum* on shallow slightly tide-swept infralittoral mixed substrata", consisting of a band of *S. muticum* on a cobble substrate. Below this zone, in the sublittoral, a dense band of *S. muticum* was observed for the 1.6 km length of the coast.

Harrow (2005) found that the *S. muticum* plant density was higher at the Isle of Cumbrae site than at the Loch Ryan site, with a dense band of *S. muticum* being present and up to 100% *S. muticum* cover observed. This is likely to be due to the east coast of the Isle of Cumbrae having more available substrata suitable for colonisation by *S. muticum*, mainly cobbles and pebbles (70%) on the subtidal fringe. The Loch Ryan site consisted of mainly muddy sand (50%) with a low abundance of suitable substrata such as cobbles (5%). At both sites, *S. muticum* had colonised areas with relatively high algal cover; 50-80% at the Isle of Cumbrae.

The biota at both sites displayed similar species richness and diversity and the *S. muticum* site had a slightly larger standing stock of biota than the control site. In terms of population structure, it was found that *S. muticum* inhabited mixed substrata and sandy shores, although it favoured the mixed substrata. Plant lengths were indicative of populations that were growing in favourable conditions. The approximate age of plants suggested that the Loch Ryan population was older or that individual plants there were able to live longer (Harrow, 2005).

Wilson (2006) found that the *S. muticum* band on the Isle of Cumbrae was more dense in 2006 than in 2005. The band had also increased in length in that year, expanding its range further north and further south as shown in Figure 33. The increase to the south was thought to be limited by exposure to wave action, which increases towards the bay of Millport. The northern increase was not as great as that to the south, but further cast specimens were observed further north than shown by the band shown on Figure 33. These were not included as they were attached to small pebbles or molluscs and are likely to have stone-walked, carried by the current to Ballochmartin Bay, where the substratum is largely comprised of sand with cobbles and a few boulders. The amount of available space for further *S. muticum* colonisation is high but the band of *S. muticum* observed on the Isle of Cumbrae tends to be at the same level as that of the *L. digitata* and the *L. digitata* forms a dense band at the sublittoral zone in Ballochmartin Bay. *S. muticum* was found in tidal pools for the first time, at Farland Point and near the Butter Lump. Both pools were relatively deep (approximately 50 cm) and would only be covered at high tide for a short period of time (Wilson, 2006).

Figure 33
Map illustrating the area colonised by Sargassum muticum (blue line) on the Isle of Cumbrae: 2006
(Wilson, 2006)

The primary aim of Wilson's (2006) study was to investigate the impact of *S. muticum* on associated species and the corresponding community structure. It was found that *S. muticum* did have an impact on the associated species and the community structure of the receiving habitat. A *S. muticum* dominated community had lower variability in community composition (reduced richness of taxa) than that of a community made up of predominantly small brown and green ephemeral species. This was currently limited to the epibiota found on rocks but Wilson (2006) expressed concern that, as the density and area of the band of *S. muticum* on the Isle of Cumbrae had increased significantly in one year, then these impacts could increase in future years, if current increases in density and spread continued.

Wilson's (2006) secondary aim was to establish if the patterns of local spreading of *S. muticum* could be detected by examining the population's age structure and frond size. The conclusions concurred with the result of the study undertaken by Critchley (1981), that although the maximum lifespan of a *S. muticum* plant is likely to be three to four years, heavy losses caused by physical damage and detachment means that the average age of populations is more usually one or two years. The plants with the greatest age were found at a site where the substrate consisted of large boulders and bedrock in deeper water, providing a more stable and, critically, a more sheltered habitat. It is worth noting that one basal stump with 21 branches was recorded, which as the *S. muticum* population was discovered on the Isle of Cumbrae in 2004, may point to it being present at this location earlier. However, Wilson concluded that this method of counting basal branches to map the spread of *S. muticum* in terms of population age structure is flawed due to wave exposure affecting the plant mortality rate.

The longest plant length recorded in Wilson's (2006) study was 4.2 m which is greater than the maximum length of 4 m stated by Critchley (1983c) but plants 6 m long were found in the most sheltered sites within Strangford Lough, Northern Ireland by Davison (1999). However, the overall mean plant length had decreased since the study by Harrow (2005), which may be due to the increasing density causing overcrowding and a corresponding decrease in size due to competition for light and resources or due to increased exposure causing physical damage.

The most abundant epibiont was the banded chink shell, *Lacuna vincta*, which was found in almost equal numbers on both ephemeral algae and *S. muticum* fronds (Wilson, 2006).

Hoyle (2007) found that the distribution of *S. muticum* had extended by 2007 and was covering approximately 3 km of shoreline, as illustrated in Figure 34. Populations were found along much of the east side of Great Cumbrae and a population was found at one site on the Inner Eilean. For the first time a plant of *S. muticum* was also found at one site in the south west of the island. Around Great Cumbrae, *S. muticum* is found on a variety of substrates including rocks, rope, slipways, piers, and attached to shells and small rocks that may be buried in a sandy substrate.

Figure 34
Map illustrating the area colonised by Sargassum muticum
on the Isle of Cumbrae: 2007

Location of isolated plants or small populations (●), extended spread (———).
(Hoyle, 2007)

10.1.3 Hunterston nuclear power station

The third sighting of an attached *S. muticum* population was by the warm-water outfall of Hunterston nuclear power station (Harrow, 2005). There was a limited subtidal distribution, illustrated in Figure 35, extending a short way to the north and south of the cooling water outfall (Hoyle, 2007). The source of this population was likely to be fronds drifting from the Isle of Cumbrae. The warmer water temperature may provide more favourable conditions for *S. muticum*, allowing increased growth and reproduction to occur, as observed by Karlsson and Loo (1999) in Sweden where *S. muticum* was found close to Ringhals nuclear power station.

By 2007, the population had expanded considerably to both the north and the south of the initial population at the water outfall, covering approximately 2 km of shoreline (Figure 36). *S. muticum* was present both subtidally and intertidally in rockpools with a mixed sandy substrate, where the plants were mostly found attached to shells and stones, buried in the sandy substrate. The northern limit of the *S. muticum* population was where the mixed stony/sandy substrate of Stoney Port changed, becoming sandier at Hunterston Sands. The southern limit of the *S. muticum* population occurred where the shore became rocky and more exposed.

Figure 35
Map illustrating the area colonised by Sargassum muticum (black line) at Hunterston: 2005
(Hoyle, 2007)

Figure 36
Map illustrating the area colonised by Sargassum muticum (black line) at Hunterston: 2007
(Hoyle, 2007)
The stripes represent the presence of plants in intertidal rock pools.

10.2 The potential introduction vectors

The original point (or points) and time of introduction to the west coast of Scotland are uncertain. However, until further evidence is forthcoming, the cautious assumption will be made that the first record of *S. muticum* in Loch Ryan was the location of the first population in Scotland. An extensive survey of Loch Ryan was undertaken in 1989 (Howson, 1989) and since then no further surveys had been undertaken until February 2004, when *S. muticum* was first discovered (A. Davison, pers. comm.). Three possible modes of introduction can be considered for the introduction of *S. muticum* to Loch Ryan and Scotland in general.

Firstly, there is the possibility that *S. muticum* may have arrived by natural means, with fertile floating fronds drifting from the nearest known source populations in Northern Ireland and North Wales. Although *S. muticum* began spreading within Strangford Lough around 1998, having been introduced in 1987-88, it was not recorded outside Strangford Lough until 2005 when it was found in Carlingford Lough, where it is thought to have been introduced due to oyster movements (T. Mackie, pers. comm.). If natural movement from North Wales was the source of drift *S. muticum* material, it would be expected that other populations would have been recorded along the north west coast of England prior to discoveries in Scotland.

Consequently, the comparatively isolated populations within Loch Ryan are more likely to be attributable to an anthropogenic vector. The two vectors that have been linked to the introduction of non-native species are the transplantation of oysters and the movement of commercial and recreational vessels.

There is an oyster fishery in Loch Ryan and during the 1989 survey of Loch Ryan, it was noted that during the late 1980s, shipments of *Crassostrea gigas* oysters were being transported from Strangford Lough to Loch Ryan by Cuan Sea Fisheries due to Tributyltin (TBT) contamination of Strangford Lough (Howson, 1989). This coincides with the possible introduction of *S. muticum* to Strangford Lough in 1987-88 from the Channel Islands (Davison, 1999). Another invasive species that is present in Loch Ryan is *Styela clava*, the leathery sea squirt (Eno *et al.,* 1997). Like *S. muticum*, *S. clava* can also be transferred via oyster shells. It may be that both *S. muticum* and *S. clava* entered Loch Ryan via the transport of oysters, at some point after 1989.

It is possible that *S. muticum* could have remained undetected in Loch Ryan between 1989 and 2004. No extensive biological surveys were conducted in the area until 2004. The existing *S. muticum* population is sparsely distributed, due to the limited availability of hard substrate of scattered pebbles on sediment, so may have gone unnoticed during this time.

The other possible anthropogenic vector for the introduction of non-native species is the movement of commercial and recreational vessels. The ferry route between Loch Ryan and Belfast Lough and Larne Lough, Northern Ireland is one of the main routes from the UK mainland, with more than 2,500 crossings each year. The transfer of *S. muticum* from Northern Ireland to Loch Ryan by this means needs to be considered. However, *S. muticum* does not possess the characteristics to allow successful dispersal via a shipping vector, such as hull fouling or ballast water. While fertile *S. muticum* plant fragments may become entangled in the anchor chains and steering gear of recreational boats, given the speed of the ferry crossings and the distances covered, any entangled *S. muticum* fronds or fragments would be so physically damaged that they would be unlikely to be able to release viable germlings. Also, *S. muticum* does not yet occur at the sites of the ferry terminals in Belfast Lough and Larne Lough.

Fertile *S. muticum* plant fragments may become entangled in the anchor chains and steering gear of recreational boats and subsequently be carried to new locations short distances away and be capable of releasing viable germlings (Boalch and Potts, 1977; Critchley and Morrell, 1982; Critchley and Thorp, 1985; Farnham, pers. comm.). This has been observed in yachts arriving in the Channel Isles (Critchley and Morrell 1982; Critchley *et al.,* 1983) and in the Mediterranean where the spread of *S. muticum* has been partly attributed to transfer by pleasure boats and fishing boats (Knoepffler-Peguy *et al.,* 1985). Similarly, in Ireland there has been a high incidence of *S. muticum* establishment near moorings and pontoons, which implies a dispersal role for small boats (Kraan, 2004). The dispersal of *S. muticum* along the west coast of Scotland attached or entangled with small boats cannot be discounted.

In August 2006, the ten largest marinas in Scotland were surveyed for the presence of seven non-native species, known to occur at other locations within the UK, including *S. muticum* (Ashton *et al.,* 2006a). A variety of structures, including pontoon floats, chains and harbour walls were inspected to a depth of 0.5 m for the presence of these non-native species. Seven of the marinas had one or more of the target species and *S. muticum was* found unattached and free-floating near pontoons at a single marina, the Clyde Marina, Ardrossan, where it was observed free-floating again in 2007 and 2008 (Ashton *et al.,* 2006a; Wilson, 2006, E. Cook, pers. comm.).

Assuming that the Isle of Cumbrae population developed after the Loch Ryan population, there are two possible introduction scenarios to consider. There are no oyster farms on the Isle of Cumbrae but recreational boating could be an introduction vector. However, in this case, there is a very high likelihood that drift dispersal of *S. muticum* is the source of introduction, due to the prevailing south-westerly wind direction and the northerly net flow of water in this area (McKay and Baxter, 1985). If this was the case, Wilson (2006) predicted that other populations would be found at suitable habitats along the Ayrshire coast and in 2007, a population was found at Croy Bay, near Culzean, Ayrshire.

11.0 THE PROJECTED EXPANSION OF THE SCOTTISH DISTRIBUTION OF *SARGASSUM MUTICUM*

It is the local, secondary spread within a country that will ultimately determine the extent of the economic and environmental impact of a non-native species (Lodge *et al.,* 1998).

The evidence from the colonisation of other areas indicates that the sighting of drifting *S. muticum* fronds is typically followed by the discovery of the first attached plants, two to three years later. There are two phases of colonisation displayed by *S. muticum*. Initially, there is a relatively slow establishment phase, where the population develops, with an increase in the number of individuals, coupled with an increase in the number of mature plants. This is followed by a rapid expansion due to the large reproductive output from the number of individual plants and an increased number of fronds on the mature plants, each able to reproduce (Critchley, 1983a; Critchley, 1983b).

Often, the inoculation site may not provide ideal habitat or environmental conditions for *S. muticum* to flourish initially, as was the case in Strangford Lough. There may be a delay of between two and ten years, while the 'inoculant' populations consolidate and slowly develop sufficient breeding stock to provide a large resource of drift *S. muticum* material for dispersion. As other sites are colonised, the chances of one of these new sites providing more favourable habitats and environmental conditions for *S. muticum* increases and typically, these sites provide the dense, rapidly growing and vigorous breeding stock that facilitates a period of rapid expansion.

After the initial discovery of established plants on the Isle of Wight in 1973, *S. muticum* was confined to the Solent region for approximately three years before travelling westwards. The population then entered a very rapid phase of growth and dispersal, in areas with suitable substrata (Critchley, 1983a). In Sweden, the sighting of drifting fronds was followed two years later by the first attached plants. A further two year delay was then followed by rapid expansion (Karlsson and Loo, 1999). Karlsson and Loo (1999) predicted that around Sweden, shores that are very sheltered, with a lack of algal cover and which receive large amount of drifting marine debris would be particularly vulnerable to colonisation by *S. muticum*, as would shallow areas subject to large water temperature increases during summer months.

11.1 Dispersal mechanisms and vectors for *Sargassum muticum* along the Scottish coastline

Predictions of the future expansion of *S. muticum* along the Scottish coast need to be based on dispersal mechanisms and vectors, environmental tolerances and habitat preferences to determine which regions within Scottish waters are at greatest risk to the negative impacts of *S. muticum*.

S. muticum appears to be dispersing rapidly northwards along the west coast of Scotland. Northerly dispersal via natural drift is likely to be facilitated by the prevailing wind and current directions, although anthropogenic vectors, such as the movement of shellfish stock and recreational boating are likely to play important roles in its dispersal. It is worth reiterating the significant role of movements of oyster stock for cultivation as the main anthropogenic vector in the global dispersal of *S. muticum*.

In Scotland the predominant wind direction, although highly variable, is from the south west and Scotland experiences a greater frequency of strong winds than the rest of the UK (Met Office, 2007). Near-surface water currents are highly influenced by local geography, generally moving northwards up the west coast and southwards down the east coast (BODC, 1998). It is, therefore, highly likely that the apparent northwards dispersal of *S. muticum* along the west coast of Scotland is the result of drift fragments being driven north and east by the prevailing south westerly winds and the northward water flow in this region (McKay and Baxter, 1985). The source of the drift *S. muticum* fragments might include the known *S. muticum* populations in the Clyde Sea area, populations in the Irish Sea, such as Strangford Lough (Davison, 1999) or the north west coast of Ireland.

The coastline of western Scotland is highly complex and many drifting *S. muticum* fragments could become trapped within the semi-enclosed sea lochs, with prevailing winds likely to drive fragments towards the heads of lochs, rather than towards the open coast to the west.

There are several locations, especially in Scotland and Ireland, where poor water exchange within sheltered water bodies may result in localised warming in shallow or surface waters. These shallow waters may become more amenable to species that thrive in warm water during the summer, including the non-native alga *S. muticum* (Hiscock *et al.,* 2001).

Dispersal rates for *S. muticum* on the west coast of the UK have averaged approximately 44 km per year since the population was recorded on the north coast of Cornwall in the early 1990s. Harrow (2005) predicted that the rate of spread is likely to be between five and 30 km per year and that colonisation would be restricted to sheltered or moderately exposed shores, in areas that do not have a high abundance of large macroalgae. It is potentially possible that *S. muticum* could reach the Outer Hebrides and the north coast of Scotland within the next few years (Harries *et al.,* 2007b).

Dispersal beyond Cape Wrath to the north coast of Scotland and onward down the east coast is likely to be slower and establishment less pronounced. Prevailing winds are likely to drive drifting *S. muticum* fragments away from the coast and many shores in the north of Scotland are unsuitable for the establishment of *S. muticum* because of high levels of wave exposure. Although surface currents may carry drifting *S. muticum* fragments round the north of Scotland and down into the North Sea most fragments which reach the shore are likely to end up at exposed locations where *S. muticum* would probably be unable to establish (Harries *et al.,* 2007b).

There is a risk that the Scottish aquaculture industry could contribute to the subsequent spread of *S. muticum* within Scotland, and may already have done so. As 95% of Pacific oyster production is concentrated in Argyll and the Clyde sea area (FRS, 2006) there is therefore the potential for significant movements of oyster stock in and out of this area (Harries *et al.,* 2007b). There are 69 sites in Scotland that grow Pacific oysters, *Crassostrea gigas,* and 42 of these are in the Strathclyde area. These are grown for direct human consumption or for “on-growing”, where sites grow oysters but then transfer them to other producers, both within the UK and to mainland Europe (FRS, 2005). It is important that current and defunct of Pacific oyster production and processing sites are surveyed for the presence of *S. muticum*.

The results of the August 2006 survey for the presence of seven non-native species in the ten largest marinas in Scotland suggests that recreational boating is an important vector for the dispersal of marine non-native species, and that marinas may act as a refuge for such species. In August 2006, up to 100 yachts in each of the ten largest marinas in Scotland were ranked using a fouling index (Ashton *et al.,* 2006b). 59% of the yachts surveyed were found to have macrofouling attached to their hulls, suggesting that recreational boating has a high potential for distributing marine species throughout Scotland. Recreational yachts frequently travel short distances and there is a high probability, therefore, that the source and recipient areas will be within the same climatic region, and that the fouling species will survive in the receiving habitat if similar environmental conditions exist. There is strong variation, however, in the potential of domestic craft to spread non-native species (Minchin *et al.,* 2006). The increasing age of the antifouling paint, the long periods that yachts remain stationary and the reduced sailing activity found in the survey, increases the risk of macrofouling species attaching to hulls and consequently, recreational boating must be considered as a high risk vector for non-native species in Scotland (Ashton *et al.,* 2006b).

It is worth noting that one of the six other non-native species, *Caprella mutica*, recorded in the 2006 Scottish marina survey was found at seven of the ten surveyed marinas. This caprellid attaches to *S. muticum* within its native range (Kawashima *et al.,* 1999) and *C. mutica* was the most widely distributed non-native species recorded, occurring on east and west coasts of Scotland and was also the most abundant species recorded, appearing in medium or high densities. Further and regular marina surveys throughout the UK are recommended to provide an effective early warning system for invasive non-native species (Ashton *et al.,* 2006a).

11.2 Habitat preferences and environmental tolerances of *Sargassum muticum* in Scotland

Please refer to Section 3.0 for further information on habitat preferences and environmental tolerances. *S. muticum* occurs in many shallow habitats in Norway suggesting that the current restricted distribution around Britain and Ireland is, in part, due to lack of dispersal, by natural mechanisms or anthropogenic vectors, rather than physiological limitations. Hiscock *et al.* (2001) predicted that *S. muticum* will extend its northerly distribution and the two current *S. muticum* biotopes will become established further north but the role of seawater warming in encouraging spread is unclear.

To date, two UK biotopes have been identified that contain *S. muticum*:
IR.LIR.K.Sar: *S. muticum* on shallow, slightly tide-swept infralittoral mixed substrata with a depth band of 0-5 m
LR.FLR.Rkp.FK.Sar: *S. muticum* in eulittoral rockpools.

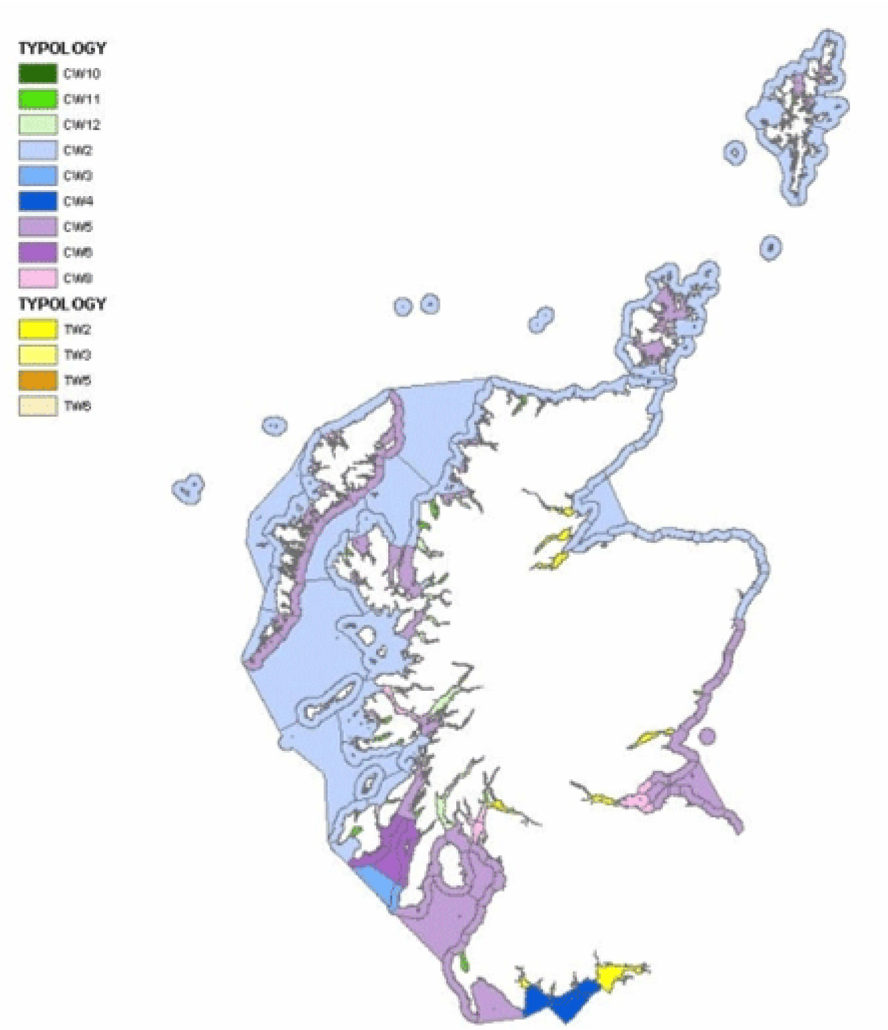
11.2.1 Zonation and exposure tolerances

The west coast of Scotland offers numerous sites that are likely to be favourable for *S. muticum* establishment in terms of their physical environment. This coastline is highly complex, with a high proportion of the shoreline falling within the exposure range suitable for *S. muticum*. This is illustrated on the map provided in Figure 37.

In contrast, the north and east coasts of Scotland are characterised by more open linear shorelines, where exposure levels are likely to be too high for the establishment of *S. muticum* (Harries *et al.,* 2007b).

Figure 37
Map illustrating exposure levels around Scotland's coastline
(SEPA, 2005)

(CW2, CW3: exposed; CW5, CW6: moderately exposed; CW12 (sea lochs): sheltered)



11.2.2 Substrate preferences

The west coast of Scotland has a high proportion of mixed substrate, as well as artificial floating substrates, including aquaculture infrastructure and marinas. Long stretches of shoreline in many lochs are composed of loose cobbles and pebbles overlying sediments. This substrate tends to extend subtidally to several metres depth, with cobbles and pebbles becoming increasingly sparse with increasing depth and beyond this habitat, the substrate tends to be predominantly sedimentary, generally composed of poorly sorted muddy sand (e.g. Black *et al.,* 2000; Bates *et al.,* 2004; ERT (Scotland) Ltd., 2006).

Mixed substrates on the lower shore and sublittoral fringe, in sheltered conditions, will provide a suitable environment for the establishment of *S. muticum*. As the shores and shallow sublittoral margins of sea lochs are often relatively steep, the zone available for *S. muticum* colonisation will tend to be narrow. Where cobbles are larger and more numerous, their increased stability is likely to allow a persistent canopy of native algae to develop which can present a physical barrier to the settlement of *S. muticum* germlings and can totally inhibit colonisation (Deysher and Norton, 1982; De Wreede, 1983; De Wreede and Vandermeulen, 1988; Andrew and Viejo, 1998a; Britton-Simmons, 2006).

One Scottish coast type unlikely to be colonised is steep bedrock, with narrow or no sublittoral shelves, as *S. muticum* appears to be unable to colonise such areas in Sweden (Karlsson and Loo, 1999).

11.2.3 Growth conditions: temperature and salinity

11.2.3.1 Temperature

On the basis of distribution patterns, Van den Hoek (1982) distinguished 10 phytogeographic distribution groups of wide applicability. *S. muticum* belongs to "Group 8"; north east American temperate / Japanese temperate, for which the critical temperatures, determined experimentally, were found to be:

Northern lethal limit = -1˚C winter isotherm
Northern growth boundary = 12˚C summer isotherm
Southern growth boundary = 25˚C winter isotherm
Southern lethal limit = 27˚C winter isotherm

Previous studies indicate that *S. muticum* may colonise areas with wide temperature ranges, between 5°C and 30°C, with optimum conditions between 15°C and 25°C. The fact that *S. muticum* has been able to establish itself in Alaska (Hales and Fletcher, 1989) and Sweden (Karlsson and Loo, 1999), where ice cover may occur over winter, is proof that *S. muticum* will be able to tolerate Scottish temperatures. It is, therefore, unlikely that sea temperature will limit the establishment of *S. muticum* in Scotland (Hales and Fletcher, 1989). The surface temperatures in the Irish Sea and around south west Scotland are illustrated in Figure 38.

While optimum temperature conditions are less likely in cooler Scottish waters, Hales and Fletcher (1990) state that the cumulative effect of temperature, irradiance and day length is a critical factor which determines whether a permanent *S. muticum* population will become established in any area. It could be predicted that the longer summer days in Scotland would enhance the onset of fertility, whereas the colder, shorter winter days will retard growth and delay maturation, possibly leading to a shorter fertile season in Scotland.

It is probable that climate change and warming sea temperatures will facilitate the northerly dispersal of *S. muticum*. The importance or impact of this effect is unknown.

11.2.3.2 Salinity

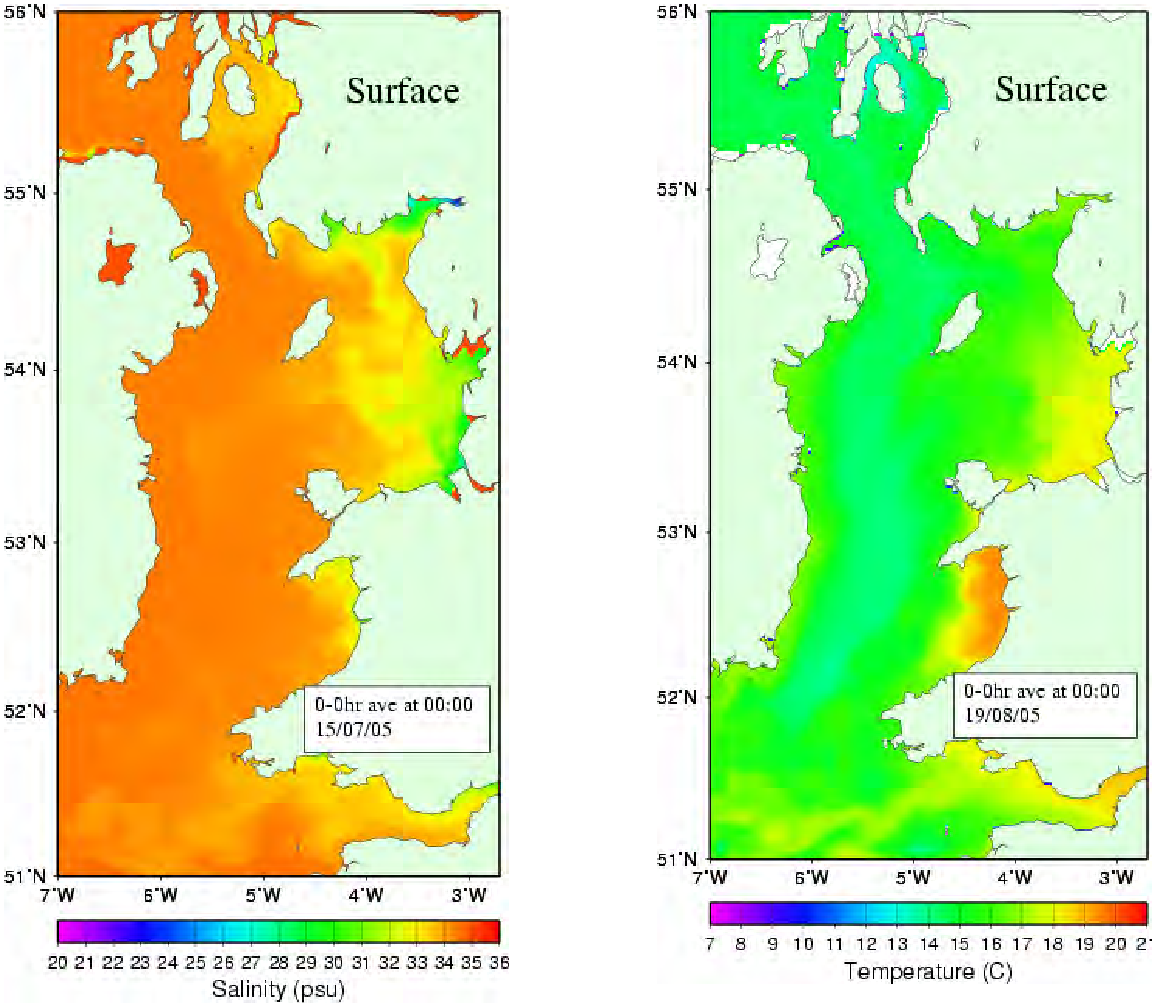
In Scotland, particularly on the west coast, many of the more enclosed sea lochs are subject to conditions of reduced or variable salinity and at locations where this is pronounced, the establishment of *S. muticum* may be constrained. The surface salinities in the Irish Sea and around south west Scotland are illustrated in Figure 38.

Such conditions are likely to occur at the inland head of sea lochs, where seawater exchange is reduced and freshwater input is greatest. However, salinity levels are likely to remain relatively higher during the summer reproductive growth period, when freshwater input is lowest and the dormant holdfasts are likely to survive the reduced salinity associated with increased freshwater input in the winter. Consequently, the pseudo-perennial lifecycle of *S. muticum* may allow it to survive despite the potential constraints of reduced salinity in sea lochs (Harries *et al.,* 2007b).

S. muticum will therefore be able to advance into the sea lochs, until salinities reach 15 ppt, although values of 25 ppt may inhibit ability to compete with native algae (Steen, 2004).

Harrow (2005) concluded that in terms of continued spread, *S. muticum* is likely to colonise available substrata in the Clyde area and possibly beyond, as environmental conditions in Scotland of exposure, salinity and temperature are suitable for colonisation.

Figure 38
Maps illustrating the summer surface salinities and temperatures in the Irish Sea and south west Scotland
(Coastal Observatory, 2005)



11.2.4 Competitive ability with native algae

It appears that *S. muticum* is likely to become an established member of the Scottish marine flora. Current evidence suggests that ecological effects are inevitable, but not necessarily deleterious.

Harrow (2005) investigated the biota associated with *S. muticum* on the Isle of Cumbrae and suggested that there were minimal differences in community structure between a site inhabited by *S. muticum* and one that was not. However, he did find that the site inhabited by *S. muticum* displayed a community with a slightly larger standing stock. He concluded that *S. muticum* had not, in this area and at that point in time, caused any major changes in the community structure and has had no significant effect on species richness or diversity.

Wilson (2006) found that *S. muticum* and *Laminaria digitata* formed very distinct bands on the Isle of Cumbrae and that in only two years, *S. muticum* had established itself, forming an almost complete band, normally at the level of *L. digitata*. This may indicate that *S. muticum* was displacing or out-competing *L. digitata* in only a short time frame at this site (Wilson, 2006).

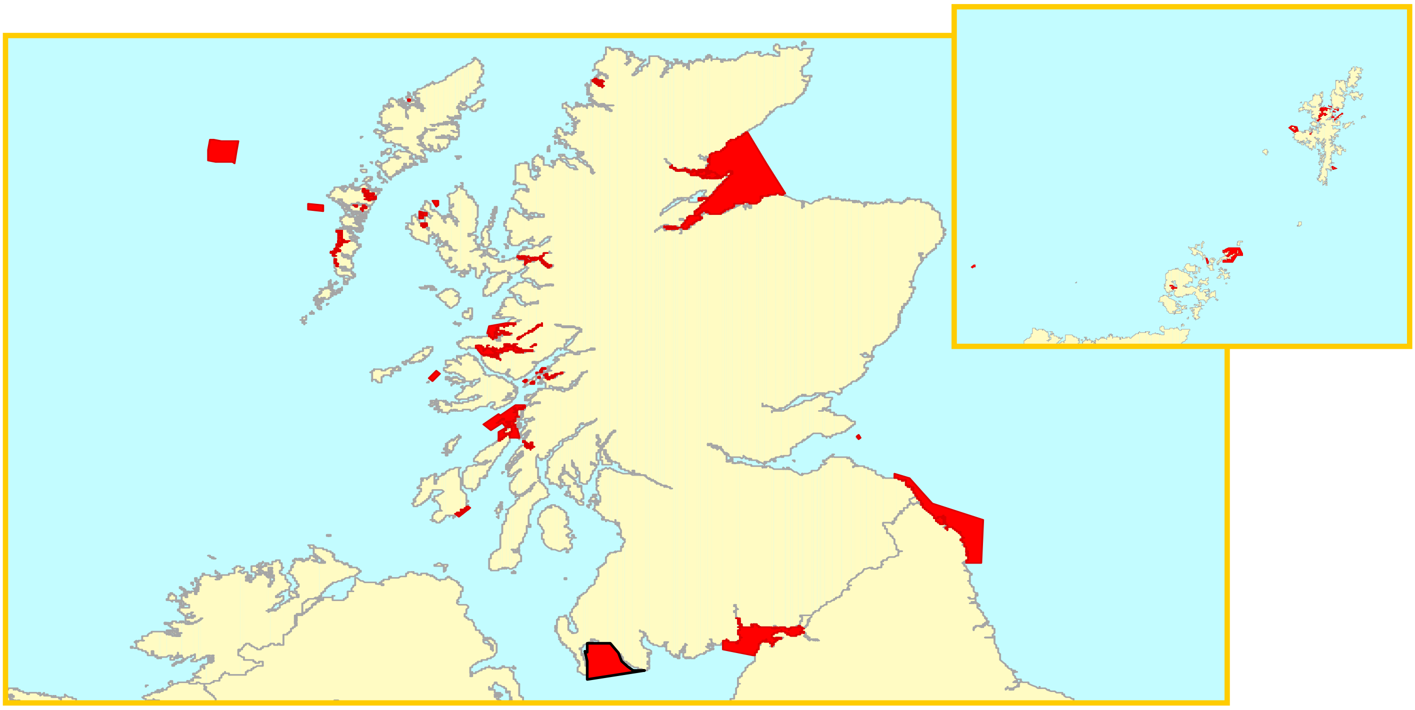
11.2.5 Susceptibility to herbivorous grazing

The sea urchin, *Psammechinus miliaris,* is a common macroalgivore in many of the sea lochs on the west coast of Scotland (Kelly, 2000). However, it is unlikely that this species would be able to control the spread of *S. muticum*, unless populations were artificially enhanced with commercially reared sea urchins.

11.3 Predicting the future dispersal of *Sargassum muticum* around Scotland's coastline

A significant proportion of the Scottish coastline is designated as Special Areas of Conservation (SAC) and Special Protected Areas (SPA), as well as Sites of Special Scientific Interest (SSSI). The marine Special Areas of Conservation are shown on the map in Figure 39.

Figure 39
Map illustrating the Scottish marine Special Areas of Conservation (SAC)
(SNH)



11.3.1 The Clyde Sea area and inner Clyde

The purpose of this short section is to provide context for discussion of the likely spread of *S. muticum* in Scotland and inform any response or action plan when further sites are discovered. *S. muticum* is spreading up the west coast of Scotland, which offers one of the most diverse coastlines in Europe. This diversity reflects both the physiography of the coastline, with its many indentations, bays, islands and sea lochs, as well as the particularly high biodiversity and conservation value of much of Scotland's western seaboard.

Loch Ryan's open nature facing up the Firth of Clyde makes it likely to be a significant source of drift *S. muticum* material being released into the wider Clyde Sea Area. Once released, prevailing winds would drive drift material northwards along the Ayrshire and North Ayrshire coast. Whilst much of this area of coast is likely to be too wave exposed and sand dominated to allow extensive colonisation by *S. muticum*, pockets of shelter may be found on most stretches of coast as the recently discovered extensive *S. muticum* bed at Croy Bay, Culzean demonstrates.

Assuming the Great Cumbrae population of *S. muticum* and its satellite stock in Hunterston was the result of drift *S. muticum* material released from Loch Ryan or Strangford Lough, this illustrates the effectiveness of *S. muticum*'s long distance dispersion strategy. It is also noteworthy that Great Cumbrae is in one of the first areas of comparative shelter up the

Ayrshire coast, as it is protected from the north by the Cowal Peninsula, from the west by the Isle of Bute and to a lesser extent, to the south by Arran and Little Cumbrae. The habitat colonised by *S. muticum* is a mixture of cobble, boulder and bedrock interspersed with sediment. This habitat is relatively common and widespread throughout the Firth of Clyde, until more mud and silt dominated shores take over in the Inner Firth at Dumbarton and upstream.

The outer Firth of Clyde encompasses Arran and a number of smaller islands, along with the Mull of Kintyre, which encloses and protects the Firth of Clyde to the west. The known distribution of established *S. muticum* in this first affected area in Scotland shows a number of interesting points. The outer Firth is subject to significant wave action yet *S. muticum* has established itself in small areas of shelter in Campbeltown Loch and Whiting Bay on the eastern, lee side of Arran. It is possible that some initial colonisation of areas may be sub-optimal and will not establish the very extensive stands of *S. muticum* noted elsewhere. However, these areas could act as sources of further drift *S. muticum* material that would be able to colonise more suitable sheltered habitats of the inner Firth of Clyde and its sea lochs.

The Clyde sea lochs are extensive areas of enclosed, sheltered to very sheltered marine habitat. The shoreline and upper sublittoral areas are known to encompass a typical range of sea loch habitats: bedrock, boulders and mixed habitats of cobbles and pebbles set in a matrix of gravel sand and silt. These habitats are typical of the upper reaches of the sea lochs. Wave exposure generally decreases the further away from the mouth of the sea lochs, as does tidal current exposures, except where constrictions or tidal straits are noted.

It is reasonable to suggest that areas of all the Clyde sea lochs, from the Kyles of Bute, Loch Striven, Holy Loch, Gare Loch, Loch Gilp, Loch Long, Loch Goil to Loch Fyne, would have significant areas of open stony habitat in wave sheltered conditions suitable for *S. muticum* colonisation.

On the basis of current UK dispersal rates, previously outlined in Section 6.1, Harrow (2006) predicted that, in a worst case scenario, *S. muticum* may be able to reach the Isle of Bute, Loch Striven and Holy Loch within one year and Gare Loch and Loch Long within two years. However, he pointed out that the rate of spread would depend on many factors, such as availability of substrate, movement of water and environmental conditions, so until *S. muticum* had been observed moving within the Clyde, dispersal rate estimates would be very hard to make.

11.3.2 The west coast sea lochs

It is possible that a small number of the more open, south west facing 'bay like' sea lochs such as Loch Caolisport, Loch Na Keal, Loch Gairloch and Loch Indaal may generally be too wave exposed to support large stands of *S. muticum*. However the majority of the other sea lochs are likely to be suitable, and sensitive, to some degree of colonisation by *S. muticum* and may be vulnerable if *S. muticum* continues to spread. Sea lochs are particularly vulnerable for a number of reasons. In general, once inside the sea loch, the shorelines are moderately to extremely wave sheltered. The conditions grade up the sea loch, becoming very or extremely wave sheltered towards the head of the loch. The habitats and marine communities found in the lower littoral and shallow sublittoral reflect this gradation, shifting from wave exposed bedrock and boulder communities typically found at the mouth of the lochs to more sheltered boulder and cobble shores in the outer areas, grading through typical cobbles and pebbles on mixed sediment until finally more sediment-dominated mud or silt habitats are found at the head of the loch. The gradation means that if drifting *S. muticum* material which is actively dropping germlings drifts up the coast of a sea loch, it is likely that at least some of the germlings will find highly suitable habitat.

11.3.3 Islands

Islands, by their nature, have a predominantly sheltered side. The settlement pattern of *S. muticum* on Whiting Bay in Arran demonstrates that even in comparatively offshore islands, it is possible to have pockets of suitable shelter that can allow the settlement of *S. muticum*.

Most of the islands on Scotland's west coast will have areas of shelter, which could offer suitable settlement habitat for *S. muticum*. Areas where there are complexes of islands, offering a greater range of wave exposure conditions are likely to be particularly vulnerable. The Firth of Lorn SAC, where *S. muticum* drift has been recorded, is an example of a complex of islands separated by tidal straits, which would offer a range of habitat and wave shelter conditions suitable for *S. muticum* settlement.

11.3.4 Lagoons

Scotland has one of the largest resources of lagoons in Europe. They are considered as priority habitat under the Habitats Directive. Scotland's lagoons are rich and varied, ranging from the extensive and diverse linked pools and lochans of the Western Isles to the largest lagoons in Scotland in Orkney and the Houbs and Vadills of Shetland. Reflecting their conservation importance and comparative rarity, the lagoons of Scotland have been comparatively well studied, notably by SNH and the JNCC.

The Scottish lagoons are, by their nature, wave sheltered. Most have little current movement but many are linked to the sea by a channel, through which strong tidal currents are often noted. The Western Isles lagoons vary from low salinity peat pools, which are unlikely to be suitable habitat for *S. muticum* to more commonly extensive areas of mixed and diverse shallow sublittoral habitats, which are subject to lowered salinity but within the tolerance range of *S. muticum.* Much of the area of the Western Isles lagoons should be considered to be suitable for *S. muticum* colonisation. Should colonisation occur, large areas of the lagoons would be vulnerable. This would include most of the designated European Marine Site lagoons.

In Orkney, the Loch of Stenness (SAC) and Loch of Harray (SSSI) are large lagoons, subject to low or very low salinity. As a result, they may not offer suitable habitat for *S. muticum* throughout their area. However, the mixed cobble and boulder habitat at the mouth of Loch of Stenness may offer suitable sheltered, open rocky habitat for *S. muticum* colonisation.

The lagoons at the head of many Shetland Voes are small, enclosed bodies of water, often separated from the main Voe by a shingle or cobble bank. They enclose sheltered rocky and peat habitats, which are likely to offer some areas that would be suitable for *S. muticum* colonisation.

It is likely that *S. muticum* will extend throughout the west coast of Scotland within the next few years, becoming established on mixed substrate in sheltered or moderately exposed areas. Where conditions are optimal, dense canopies of *S. muticum* will develop, although these are likely to be restricted to narrow fringing bands around the margins of sea lochs due to seabed topography. Where there are extensive shallow areas of mixed substrates more extensive beds of *S. muticum* may develop.

Many locations on the west coast are likely to provide favourable conditions for *S. muticum* establishment in terms of exposure and substrate, including several designated European marine sites. The north and east coasts of Scotland offer less favourable conditions on a predominantly open and linear coastline and the prevailing wind direction is also less favourable for dispersing drift *S. muticum* fragments along these coasts.

11.4 Potential ecological, economic and natural heritage consequences

11.4.1 Potential ecological consequences

Predicting the ecological consequences of the establishment of a new marine biotope is highly speculative. Dense canopies of *S. muticum* will alter the community structure in the immediate surrounding area, but are unlikely to cause radical reductions in the abundance of native biota on a wide scale. It is most probable that some existing macroalgal species will be displaced and that their abundance will decrease locally but, due to habitat patchiness, it is highly unlikely that any will become rare or endangered as a result of encroachment by *S. muticum*. The evidence indicates that the existing epibiont species are unlikely to be adversely affected. In fact, it is probable that the development of a *S. muticum* zone may increase standing stock (Wernberg *et al.,* 2004) of many species, by providing increased habitat area and greater habitat diversity. Epifaunal communities existing below the *S. muticum* canopy are likely to undergo structural changes but as yet there is no evidence to suggest that a net loss in diversity or abundance is probable. In certain circumstances, the development of patches of *S. muticum* could be viewed as providing increased habitat diversity (Buschbaum *et al.,* 2006). The effects on the infauna of mixed sediments are uncertain and currently there is insufficient evidence to accurately predict the nature of any changes. However, the presence of dense *S. muticum* is likely to increase primary productivity (Pedersen *et al.,* 2005; Sánchez *et al.,* 2005) and the increased input of detrital material to the sediment is likely to modify the trophic structure of the infaunal community (Harries *et al.,* 2007a). By colonising areas of mixed substrate where algal cover was formerly sparse (Jephson and Gray, 1977) *S. muticum* may increase local productivity (Viejo, 1999; Pedersen *et al.,* 2005; Sanchez *et al.,* 2005), increase habitat heterogeneity (Buschbaum *et al.,* 2006) and provide cover for mobile macrofauna and fish (Critchley, 1983b). Harries *et al.,* (2007a) concluded that such changes are unlikely to constitute serious ecological degradation or result in significant loss of biodiversity.

Wilson (2006) found that *S. muticum* and *Laminaria digitata* formed very distinct bands on the Isle of Cumbrae and that in only two years, *S. muticum* had established itself, forming an almost complete band, normally at the level of *L. digitata*. This may indicate that *S. muticum* was displacing or out-competing *L. digitata* in only a short time frame at this site (Wilson, 2006).

11.4.2 Potential economic consequences

The economic impact of *S. muticum* in the UK appears to be minimal and Harries *et al.* (2007a) reported that they were not aware of documented evidence of this species having had a significant negative impact on economic activities in UK waters. When *S. muticum* first became established on the south coast of England in the early 1970s there was considerable concern, based on reports from British Columbia, Canada where it was considered a serious pest in terms of causing ecological damage and economic damage through fouling (Fletcher and Fletcher, 1975). For the most part, these concerns have not been realised on the south coast of England. However, it is worth noting that British Columbia has a complex, highly indented coast that is hydrographically more similar to the west coast of Scotland than to the south coast of England. It is possible that Scotland's experience of *S. muticum* will prove to be more similar to that of British Columbia than to the outcome experienced on the south coast of England.

Scottish coastal waters are monitored under the Water Framework Directive, which requires that the presence of alien species in water bodies is recorded. The presence of *S. muticum* within a water body will automatically lead to its water quality status being downgraded.

The west coast of Scotland accounts for a large proportion of the UK's aquaculture production, concentrating on the farming of Atlantic salmon (*Salmo salar*) with 278 active sites (FRS, 2006), the blue mussel (*Mytilus edulis*) and the Pacific Oyster (*Crassostrea gigas*) with 90 active sites (FRS 2007). *S. muticum* is known to densely grow on floating structures (Fletcher and Fletcher, 1975a) and has the potential to cause economic damage due to the fouling of salmon cages and mussel ropes. It has also caused similar problems to commercially farmed oysters (Critchley *et al.,* 1986). On the west coast of Scotland, the large number of aquaculture operations, located in the sheltered sea lochs, are likely to be affected by fouling by *S. muticum*, both due to their sheltered locations, which are suitable for *S. muticum* growth, and also due to the fact that *S. muticum* commonly attaches itself to artificial substrata. There are a large number of commercial shellfish farms, which may be negatively impacted by *S. muticum* and other species of invasive algae, fouling equipment and shellfish shells, thereby increasing maintenance and product preparation costs. It would be prudent, therefore, to develop effective control methods for *S. muticum* both in areas of aquaculture activity to prevent the transfer of this alga when commercial species are moved to new areas for on-growing.

The fishing industry may be affected, with sports fishermen (Critchley *et al.,* 1983) complaining about the large floating mats, and oyster farmers in the Netherlands and British Columbia complaining of stock losses and difficulties locating their stock (Critchley and Dijkema, 1984).

Dense growth may also create a nuisance in some small harbours (Fletcher and Fletcher 1975a; Critchley, 1983b; Critchley *et al.,* 1983), but extensive free-floating rafts like those which created problems off the south coast of England (Critchley *et al.,* 1983) are unlikely to occur unless *S. muticum* beds are particularly extensive, such as in shallow lagoons.

There may be implications for the tourism industry, in terms of blocking waterways, which may entangle boat engines, and damaging the aesthetic value of an area.

11.4.3 Potential natural heritage consequences

A number of the sea lochs are designated as European Marine Sites. There is a duty on all regulators to assist in managing these sites to maintain their conservation status and quality, as defined by a series of conservation objectives. It is unclear if the accidental introduction of *S. muticum* to one of the many European Marine Sites would be considered as a significant impact on the sites' integrity.

When it comes to policy for the conservation of the natural heritage there are additional grounds for concern. Non-native species in general are unwelcome in designated sites, whether under UK or European legislation, which have been selected due to the presence of special or characteristic biotopes. *S. muticum* has been identified for inclusion in Scottish Natural Heritage's Species Action Framework as an active invasive with high potential for adverse impact on important biodiversity features. *S. muticum* is likely to form a visually distinct band on the lower shore and in the shallow subtidal, with dense summer surface canopies, appearing quite different in character to the native shoreline. However, while the eradication of *S. muticum* from Scottish coasts may already be logistically and economically impractical to achieve, there may be merit in exploring the feasibility of controlling *S. muticum* within marine protected sites (Harries *et al.,* 2007a; Harries *et al.,* 2007b).

Many of the designated European marine sites (SAC and SPA) in Scotland may be vulnerable to colonisation by *S. muticum*. The impact of *S. muticum* on these sites' integrity is unclear but is likely to be considered a negative impact.

A significant concern is the degradation of the landscape value of Scottish shorelines as a consequence of the establishment of highly visible dense canopies of *S. muticum*. The concern applies particularly to the suite of nationally and internationally important marine protected areas that have been established around the Scottish coast.

11.5 Management strategies for *Sargassum muticum* in Scottish coastal waters

An understanding of the patterns and processes involved in non-native introductions are necessary to implement appropriate management strategies. Ashton *et al. (*2006a) stated that without surveys, the range and abundance of species cannot be assessed (Ruiz *et al.,* 2000, Herborg *et al.,* 2003), and their potential impact (Parker *et al.,* 1999) and predicted expansion is uncertain (Arbaciauskas, 2002; Telesh and Ojaveer, 2002). Frequent monitoring also enables some ability to deduce source regions, vectors and rates of introduction (Cohen, 2004).

It has been suggested that small-scale removal of *S. muticum* may be possible, if focused on an ecologically important area, such as a marine reserve (Wootton, 2005) although the long-term success has not been proven. For containment of *S. muticum* and other invasive macroalgae to have any chances of success, several factors need to be considered.

Early identification of non-native species is critical for successful eradication (Simberloff, 2003; Anderson, 2005; Hewitt *et al.,* 2005). Early discovery of an introduction greatly increases the probability of a successful eradication. The probability of finding new marine introductions will be increased with improved monitoring of high-risk vectors and sites such as mariculture facilities, marinas and ports. Public awareness programs will also limit the number of introductions and speed the detection of new species. Ideally, the public should be informed about introduced species, including those not yet found in the local area. The E.H.S. produced a leaflet about *S. muticum* after its introduction but if it had been produced and widely circulated earlier, the probability that populations in Strangford Lough would remain undetected for approximately eight years may have been decreased. Enlightened policy regarding invasive species deals more with prevention and early detection, than with eradication after the introduction.

The efficacy of *S. muticum* clearance would be greatly increased if the introduced population can be identified early in the season. Clearance *before* the reproductive period will prevent the build up of a ‘seed bank’. Many invasive algal species are able to disperse by drifting and eradication programs that minimise the fragmentation of the collected material are more likely to prevent dispersal. Then, if non-reproductive drift plants are liberated during the containment, the drifting *S. muticum* will have to remain afloat until it becomes fertile and the longer the planktonic existence, the greater the probability of this material being cast on the shore or being transported to inhospitable habitats (e.g. deep water). Finally, the hand picking of material must be repeated several times within a year to prevent any individuals becoming reproductive. The fecundity of most invasive species means that very few individuals are required to repopulate an area.

Previous attempts at controlling or eradicating *S. muticum* have proved fruitless and have sometimes been counter-productive (Critchley *et al.,* 1986; Davison, 1999). Manual or mechanical removal of plants failed to remove all the holdfasts and small plants allowing re-growth to occur (Fletcher and Fletcher, 1975b). Re-growth was often more dense and vigorous than the previous population because the removal of the algal canopy and the creation of patches of bare substrate were favourable to *S. muticum*’s ‘gap-grabbing’ strategy. It has also been suggested that such attempts could facilitate dispersal by creating large quantities of drift *S. muticum* fragments (Fletcher and Fletcher, 1975a). The potential for control by biocides has been investigated and discounted due to environmental concerns (Davison, 1999). There is no species-specific effective biocide available and dilution effects would require very high dosages, creating unacceptable levels of non-target mortality. The potential for biological control also appears to be limited (Critchley *et al.,* 1986), although observations on the coast of British Columbia, Canada suggest that in certain circumstances grazers (e.g. *Strongylocentrotus droebachiensis*) can control *S. muticum* abundance (De Wreede, 1983). However, it has also been suggested that grazing pressure may accelerate dispersal by increasing fragmentation of *S. muticum* fronds (Critchley *et al.,* 1986).

Eradication of other introduced macroalgae has rarely been successful (Strong, 2003). Attempts to remove *Codium fragile* ssp. *tomentosoides* with manual and mechanical removal techniques were unsuccessful as the species can reproduce asexually from fragments and regrow from holdfast attachments if not removed completely (McEnnulty *et al.,* 2001). It also has microscopic lifestages that are cryptic and difficult to target. Thalli with mature propagules, which may became detached by control techniques further contributed to the enhanced translocation of the species (Wassmann and Ramus, 1973).

In the Mediterranean Sea, the attempts to eradicate *Caulerpa taxifolia* were unsuccessful (Strong, 2003). Once again, the ability of fragmented material to reproduce asexually hampered the eradication (Ceccherelli and Cinelli, 1999). However, this species was successfully exterminated from San Diego when a small patch was discovered (Jousson *et al.,* 2000). Herbicides, algicides and light exclusion were all ineffective at killing *C. taxifolia*. The only reliable poison found was concentrated chlorine bleach pumped under a chamber constructed from plastic sheets and pvc pipes along the edge of the sheets. This method lacked specificity and had a significant impact on the native community.

Eradication of *Undaria pinnatifida* was unsuccessful on European coastlines yet was successful in New Zealand (Strong, 2003). In New Zealand, the population was discovered soon after its introduction. The population was small and attached to a sunken boat hull. Repeated clearance was successful in preventing this species from establishing. Care was also taken to remove microscopic stages of *U. pinnatifida* and not to fragment the sporophytes, which aid the dispersal of this species (McEnnulty *et al.,* 2001).

As eradication programmes are unlikely to halt the progress of *S. muticum* in Scotland, the vectors that are potentially responsible for initial introduction throughout the world, principally the transfer of oysters, should be more tightly controlled. Although oyster fisheries have been implicated in the initial introduction of *S. muticum* to mainland Europe, North America and the UK, the UK, EU and international laws regulating transfers focus on the elimination of diseases and parasites rather than non-native species (Fasham and Trumper, 2001; Brown *et al.*, 2006). The regulations that aim to ensure that oysters transferred between sites and countries are clear of invasive species before being transported should be better enforced and the issues of illegal movements of oysters should be addressed. There is a risk that the Scottish aquaculture industry could contribute to the subsequent spread of *S. muticum* within Scotland, and may already have done so. It is important that current and defunct of Pacific oyster production and processing sites are surveyed for the presence of *S. muticum*.

The possibility that pleasure boats may be enabling *S. muticum* to disperse around Ireland (Kraan, 2004) should also be actively investigated around Scotland. Focussing on all possible vectors may prevent additional introductions and thus slow the spread or prevent it reaching areas that would not be reached naturally by frond drifting. It may also slow down or prevent the introduction of any other non-native species. The 2006 Scottish marina survey showed that marinas provide suitable habitat for non-native species in Scottish waters. Recreational yachting activity may be an important vector for the spread of these species (Ashton *et al.,* 2006b). The new records of non-native species found in this survey of selected Scottish marinas demonstrates the need for more regular and expanded studies. Most usually, the number of non-native species identified in an area underestimates the real numbers present (Ruiz *et al.,* 1997). This survey demonstrates the need for more detailed port surveys throughout Britain, from which future introductions can be evaluated (Ross *et al.,* 2003) and to aid better informed decisions in managing the problems of invasive non-native species (Cohen, 2004).

Under the Water Framework Directive (WFD), the recorded presence of alien species is considered sufficient to place the water body at risk of failing to meet its environmental objectives of good ecological status. The UK Technical Advisory Group (UKTAG) on the Water Framework Directive has divided alien species into three categories of impact: high, low and unknown. To make the task of assessing risk to the water environment manageable, characterisation work has concentrated on ten key high impact species, including *S. muticum*. These species were selected because their impact is known to be severe and information on these alien species is usually available for the water bodies in which they occur. Addressing the problem of alien species preventing the achievement of good ecological status, will require action within the specific water bodies and the consideration of potential sources of re-infestation in the surrounding area. A three-level hierarchical approach adopted by the Convention on Biological Diversity (CBD) identifies prevention, detection/surveillance and control/eradication as the three main ways of dealing with invasive species. The objectives are to develop and instigate a programme of work to tackle existing aquatic alien species problems, prevent the further spread of invasive alien species already present and prevent new introductions of invasive alien species. This approach is being adopted by the developing GB Framework Strategy for Invasive Non-Native Species, the implementation of which in Scotland is being overseen and informed by the work of the Scottish Working Group on Invasive Non-Native Species lead by the Scottish Government. This approach is proposed for the Scotland river basin management plan (RBMP) in combination with other relevant activities. Through the Area Advisory Groups and the RBMP, the Scottish Environment Protection Agency (SEPA) will seek to engage with and involve partners.

In Ireland, the Invasive Species Ireland project was established as a cross-border joint venture between the Northern Ireland Environment Agency and the National Parks and Wildlife Service to implement the recommendations of the 2004 Invasive Species Ireland Report. Extensive consultation has been undertaken on developing a series of codes of practice for aquaculture, recreational water users and marina operators. The National Biodiversity Data Centre is currently developing the aquatic component of the National Invasive Species Database. Thirty established and potential high impact species including invertebrates, fish, and aquatic and riparian plants, have been identified as priorities for record collection. Once collated, the location of these species will be displayed on the Data Centre's web GIS mapping system. Aquatic records will be displayed in a way that is biologically meaningful, for example by lake-catchment unit and river systems. It can be viewed against other GIS map layers on the Centre's web mapping system, such as Water Framework Directive water bodies and environmental quality indicators. The public display of such data will help to inform research, assessment of spread, monitoring and control options. The availability of having one central, easily accessible portal of information on the spatial distribution of invasive species throughout the island of Ireland will greatly assist those interested in combating the threat of invasive species to Ireland's natural environment and economy.

Invasive alien species are a major and increasing threat to European biodiversity, habitats, and economy. In order to improve the ability of European states and institutions to respond to the threats posed to biological diversity in the major European ecosystems and marine areas by invasive alien species, the European Environment Agency (EEA) has initiated a survey aimed at:

- Assessing the existing information and mechanisms for risk assessment to respond to new arrivals of unwanted alien species which may threaten biodiversity and impact ecosystems, and

- Identifying the main limits and constraints to rapid and effective action.

The consultation information provided will be used as background material to help develop a proposal for a European co-ordinated early warning and information system for invasive alien species threatening biodiversity.

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13.0 GLOSSARY OF TERMS

Absciss	The ability of the algae to sever and release laterals. Typically reproductive growth is followed by the onset of senescence, with laterals being cast and the plant dying back to the main axis and holdfast. Laterals can also be severed as a result of physical damage or herbivorous grazing.
Acid mucopolysaccharide	The natural adhesive produced by germlings to aid their attachment to the substrate.
Antheridia	The male sex organ (gametes) of algae, located in conceptacles upon the receptacle.
Apex	The tip of an axis or lateral branches.
Apical meristem	The growing point at the tip of the axis. In *S. muticum*, this exerts apical dominance upon the secondary lateral extensions. The loss of or damage to the primary lateral may result in the loss of apical dominance. This can stimulate the increased elongation of secondary laterals, particularly nearest the point of injury. Occasionally, a single secondary lateral may take over the role of primary lateral apex and maintain an apical dominance effect.
Axil	The position where leafy laminae issue from the laterals. Air vesicles and reproductive receptacles arise in the axils of lanceolate lamina of tertiary laterals.
Axis	Main branch or stalk from which laterals arise. There may be one (main) axis or several. In *S. muticum*, it is a stumpy stalk, up to 5 cm high.
Conceptacle	Tiny cavities containing the reproductive gametes, arranged spirally upon the receptacle. As the receptacles mature, the conceptacles become visible as minute pale spots.
Culch	Crushed shell materi*al (*oysters or mussels) traditionally used to encourage natural settlement of bivalve mollusc spat, typically oyster spat.
Dormancy period	When the plants die back to the perennial holdfast and main axis, typically between mid-summer and late autumn. The occurrence and duration varies with latitude.
Epibiont	Plants and animal species that grow upon another species, using the other species as a substrate.
Epiflora / Epiphyte	Algal epibionts that grow upon other plants, not acting as a parasite, but utilising the other plant as a substrate.
Epifauna	Animal epibionts that grow upon other plants, not acting as a parasite, but utilising the other plant as a substrate.
Fouling	The growth of algae on structures and other species, where this growth may have a detrimental impact.
Gap-grabber	Ability to opportunistically colonise open patches within an area of dense algal cover, before re-colonisation by native algal species can occur.

Germling	Tiny multi-cellular plantlet, released from the surface of the reproductive receptacles after a short incubation period.
Holdfast	The basal structure that attaches the algae to the substrate. *S. muticum*'s small perennial conical discoid holdfast can reach 5 cm in diameter.
Inoculum	A significant introduction incident into a new area.
Introduced species	Those taxa transported by human activity to regions where they did not exist in historical time. It includes established non-native species and non-established or alien species. "Historical time" is taken as being since the beginning of the Neolithic Age: c. 3500 BC.
K-selected species	Species with a high thallus differentiation and a long lifespan
Lamina	Leaf-like parts of algae. Basal laminae arise from the main axis. Leaves from sterile secondary and tertiary laterals, known as "winter" leaves, are up to 30 mm long and 15 mm wide. "Summer" leaves are generally linear-lanceolate and up to 15 mm long and 3-5 mm wide.
Lanceolate	Long and pointed (lance-shaped). Often used to describe the shape of lamina found on tertiary laterals and reproductive receptacles.
Laterals	Side branches that arise from the main axis (primary laterals) and from other laterals (secondary and tertiary laterals), creating the plant's structure.
Main axis	See axis.
Monoecious	Possessing both male and female reproductive organs on the same individual plant, facilitating self-fertilisation.
Mono-specific	Comprising one species.
Non-native species	A species which has been introduced directly or indirectly by human agency (deliberate or otherwise), to an area where it has not occurred in historical times and which is separate from and lies outside the area where natural range extension could be expected. The species has become established in the wild and has self-maintaining populations; the term also includes hybrid taxa derived from such introductions.
Non-established introductions or aliens	Species which are introduced through the agency of man but which have not become established and are incapable of establishing self-sustaining or self-propagating populations without the interference of man.
Oogonia	Female sex organ (gametes) in algae, located in conceptacles upon the receptacle.
Ostiole	Single opening or pore in the conceptacles through which the reproductive gametes are discharged into the surrounding seawater.
Peripatetic	See Stone-walking
Pre-emption	The passive prior occupation of limited substratum

Primary laterals	These 'branches' arise annually from the main axis. The primary laterals of *S. muticum* are 4-6 mm wide and in warm southern waters, over one season they can grow up to a maximum recorded length of 12 m. They typically reach 1–4+m in the UK. They are tough and wiry, hence the common name of 'wire weed'.
Phyto-geographic	On the basis of distribution patterns, algal species can be grouped according to upper and lower critical temperatures.
r-selected species	Species with a high growth rate and large propagule production
Receptacle	The stalked rough-surfaced, jelly filled lanceolate-shaped structures that contain male and female gametes. In *S. muticum*, self-fertilisation can occur as male and female gametes occur in the same receptacle but in separate conceptacles. Up to 50-70 conceptacles can mature on a single receptacle, with up to 90% of these conceptacles being female. Receptacles develop in the axil of leafy lamina on the tertiary laterals.
Rhizoid	Germlings' root-like attachment structure, used to secure attachment to the substrate.
Rugosity	The rough texture of potential substrates. Settlement success and germling survival increases with greater rugosity of the substrate. Optimum rugosity is provided by substrates where the depths of the troughs or depressions are greater than the height of the germling.
Secondary laterals	These branch off the primary laterals and in *S. muticum* are typically 30 - 40 cm long and 2–3 mm wide.
Senescence	Seasonal dieback to the perennial holdfast and main axis.
Space-filler	See 'Gap-grabber'.
Stone-walking / wandering / rafting	As the algae grows and more laterals with air vesicles are produced, the buoyancy of the algae can exceed the weight of its substrate (usually a shell or small stone). Currents, the wind or waves can carry the buoyant plant and its attachment substrate to new sites, an effective dispersal mechanism.
Tertiary laterals	These branch off the secondary laterals and in *S. muticum* they create the feathery fronds.
Vector	Method of transmission or introduction i.e. an organism that transmits a disease-causing agent.
Vesicles	Air bladders. In *S. muticum*, these are small (2-6 mm), smooth-surfaced and stalked and provide the buoyancy that lifts the laterals to the surface. They arise in the axil of leafy lamina on laterals, predominantly tertiary laterals. Their shape varies, with lower vesicles being spheroidal, while upper vesicles are pyriform (having a pointed tip).
Zygotes	Fertilised eggs, incubated on the receptacle surface for 2-3 days, before undergoing cleavage and become multi-cellular germlings.

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