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Edited by

J. H. PRICE

Department of Botany, British Museum (Natural History)

D. E. G. IRVINE

Department of Food and Biological Sciences, Polytechnic of North London

and

W. F. FARNHAM

Department of Biological Sciences, Portsmouth Polytechnic

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14 | Studies on Aliens in the Marine Flora of Southern England

W. F. FARNHAM

Department of Biological Sciences, Portsmouth Polytechnic Marine Laboratory, Hayling Island, England

Abstract: Many introduced species are known in the British marine flora. Some of the earlier introductions are by now so widespread and well-established that their exotic origins are overlooked, e.g. *Colpomenia peregrina* and *Codium fragile*. Other adventitious species have apparently arrived within recent years. The south coast of England, and in particular the Solent region, seems to provide suitable sites and habitats for the establishment and further spread of many immigrant species. Marine algae of alien origin which have been recorded within recent years include *Grateloupia filicina* var. *luxurians*, *G. doryphora*, *Solieria chordalis*, *S. tenera*, *Neoagardhiella gaudichaudii* and *Sargassum muticum*. The initial problem has usually been in recognizing an "unusual" seaweed as a species introduced from some other part of the world. Ecological observations have been made upon the above species to monitor any further changes in their distribution. Various vectors have been suggested as responsible for long-distance changes in distribution of marine organisms, as natural mechanisms for such dispersal are unlikely. Such transportation agents include shipping, with species carried as fouling organisms or in ballast tanks, and shellfish. It is concluded that early detection of alien species is important, so that any resultant changes in natural ecosystems can be discerned.

INTRODUCTION

1. A Survey of Previous Marine Algal Introductions into the British Isles

This chapter is concerned with the recent introduction of certain alien marine algae into British waters. Before these events are discussed, previous marine introductions will be reviewed. Taylor (1979) has recently described some of the characteristics shown by exotic species. In this chapter, an alien is broadly defined as any non-indigenous species, which has been fortuitously or deliberately introduced, not necessarily as a result of human activity, and which seems to have become an established member of the British flora or fauna.

The marine benthic algal flora of the British Isles has been well studied for the past two centuries. The culmination of the work of early British phycologists was "Phycologia Britannica" (W. H. Harvey, 1846–1851). A comparison of this compilation with more recent compendia of the British flora, such as "A Handbook of the British Seaweeds" (Newton, 1931) and the later "Check-list of British Marine Algae – third revision" (Parke and Dixon, 1976), shows that additional species of seaweeds have been recorded over the past century or so. This may be explained in various ways. First, some of these more recently recorded species reflect current taxonomic concepts, e.g. the recognition of *Ulva rigida** as a species separate from *U. lactuca.* Secondly, other additions are simply sightings of species which had hitherto been overlooked by collectors. This applies not only to smaller algae or to taxonomically difficult groups but also to larger algae from formerly inaccessible sites or habitats, especially in the sublittoral region. Thirdly, there have been some marine algae detected around the British Isles that actually do represent new-comers. Other aspects of change in the British marine flora were discussed by W. E. Jones (1974). Price *et al.* (1979) have recently described long-term distributional changes – both in time and space – of *Padina pavonica* (L.) Lamour. (= *P. pavonia*), which provides a rare example of a native alga for which the necessary data exist.

*Nomenclature of British algae cited follows that given by Parke and Dixon (1976).

Table I lists those marine algae which are considered to have been introduced but which by now are so well-established and extensively distributed that their alien origin is obscured. One of the surprising features of these introductions is that most of them appear to have originated from the Pacific Ocean, and have thus notably extended their geographical range. Fewer examples are known where the introduced species originated from a much nearer source. An example of the latter case is *Laminaria ochroleuca*, which was first reported for the British mainland by Parke (1948).

Many newly arrived species remain unnoticed for some time, this perhaps reflecting the paucity of collections (especially from the sublittoral), but resulting also from misidentifications. This can easily be so where differences from related, indigenous species are but minor. *L. ochroleuca* is illustrative on both accounts. It occurs in the shallow sublittoral which until recently was a poorly-collected area. Furthermore, plants could conceivably have been mistaken for *Laminaria digitata*. Nevertheless, it does seem to represent a relatively recent cross-Channel migrant, perhaps the result of a slight but significant increase in the temperature of the Channel over the past 50 years (Southward, 1960). However, most other algae introduced into this country, even if by way of the European mainland, represent overall incursions to the Atlantic from the Pacific. Often, recognition of these events has been hindered by taxonomic problems, as will be indicated below.

The brown alga, *Colpomenia peregrina*, attracted attention at the beginning of this century by causing considerable losses within the northern French oyster-beds. The problem was that the globose thalli became air-filled and accordingly buoyant, thus floating away with attached oysters. It was not initially appreciated that this alga differed from the previously known European species, *C. sinuosa* (Roth.) Derb. et Sol., until the studies of Sauvageau (1927). Blackler (1963) showed that *Colpomenia* in the Pacific, previously referred to as *C. sinuosa* Saunders, agreed anatomically with *C. peregrina*. It is thus likely that the *Colpomenia* associated with the Breton oyster-beds, viz. *C. peregrina*, came from the Pacific. *C. peregrina* has since spread further in European waters. It was soon noticed along the south-west coast of Britain (Cotton, 1908, although accidentally omitted from Newton, 1931) and later spread further round the British Isles.

Table I. Established introductions of marine algae into the British Isles

Species	Estimated place and date of introduction	Suggested origin	Reference
Codium fragile			
subsp. *atlanticum*	South-west Ireland; 1808	Pacific	Silva (1955)
subsp. *tomentosoides*	R. Yealm, Devon; 1939	Pacific	Silva (1955)
Bonnemaisonia hamifera	Falmouth, Cornwall; 1893	Japan	Holmes (1897)
Trailliella-phase	Dorset; 1890	Pacific	Westbrook (1930)
Colpomenia peregrina	Cornwall, Dorset; 1907	Pacific	Cotton (1908)
Antithamnion spirographidis (including *A. sarniensis*)	Plymouth, Devon; 1920s	S. Hemisphere?	Westbrook (1930)
Asparagopsis armata	Co. Galway, Ireland; 1941	Australia	De Valéra (1942)
Falkenbergia-phase	Co. Galway, Ireland; 1939	Australia	C. Harvey and Drew (1949)
Laminaria ochroleuca	Plymouth, Devon; 1940s	Channel Islands; N. France	Parke (1948)

The recognition of an earlier introduction into British (and European) waters was also obscured by taxonomic difficulties. *Codium fragile* was long confused with native, dichotomous species of *Codium*, namely *C. tomentosum* and *C. vermilara*, until Silva (1955) defined this assemblage. The two subspecies of *C. fragile* described by Silva (1955), subspp. *tomentosoides* and *atlanticum*, were probably introduced separately from the Pacific. The latter subspecies was considered by Silva (1955) to have been "introduced from the Pacific within historic times". The former subspecies is of more recent occurrence within the Atlantic. According to Silva (1955), it was first collected in Holland in 1900 and the first British record was from the River Yealm (south Devon) in 1939. Both of these subspecies have spread independently. In some areas, especially along the south coasts of England and Ireland (Parkes, 1975), the indigenous *C. tomentosum* has been outcompeted by *C. fragile*, which has also spread further by colonizing coastline free from *C. tomentosum*. *C. fragile* subsp. *tomentosoides* appeared on the Atlantic seaboard of North America in 1957 (Wood, 1962) and is still undergoing vigorous expansion of its distribution down that coastline (Malinowski and Ramus, 1973). It has now been recorded for the first time in New Zealand waters (Dromgoole, 1975).

Other well-documented instances of introductions of Pacific algae relate to certain red algae. *Asparagopsis armata* was first described by W. H. Harvey (1855) from Australia and has since apparently spread from there into European waters. It was first recorded for the British Isles by De Valéra (1942) for County Galway and the first report of its occurrence in England was by Drew (1950). However, as Dixon (1965) indicated, reports relating to the subsequent spread of *Asparagopsis* in Europe have obscured more fundamental issues. *A. armata* is only known in the gametangial condition. Feldmann and Feldmann (1942) contended that its tetrasporangial generation was represented by a phase so morphologically dissimilar that it had been treated as the separate species *Falkenbergia rufolanosa* (Harvey) Schmitz. This had also been initially described from Australia by W. H. Harvey (1855) and was later reported to be spreading in the Atlantic and Mediterranean (Feldmann and Feldmann, 1942). It was first recorded for Britain by C. Harvey and Drew (1949) on Lundy, where it was later refound by D. Irvine *et al.* (1972). The *Falkenbergia*-phase is more widespread in the British Isles than

the *Asparagopsis*-phase. *Falkenbergia* has now been found as far east along the Channel as Lymington, Hampshire (Farnham, unpublished) and as far north as the Orkney and Shetland Isles (Irvine *et al.*, 1975), while the *Asparagopsis*-phase appears to be restricted to the south-west coasts of the British Isles. It would appear that both phases in this life history are spreading independently by vegetative means in the British Isles. *A. armata*, as its specific epithet indicates, produces spinous lateral branches which readily attach to other algae, while *Falkenbergia* grows as a mass of tangled filaments forming "balls" which float and can readily reattach themselves to suitable substrata. Dixon (1964) even questioned whether *A. armata/F. rufolanosa* is an Australian introduction. Another species of *Asparagopsis*, *A. taxiformis* (Delile) Trev., is also widely distributed in tropical waters and has been recorded for the Canary Islands (Boergesen, 1929) and the Mediterranean (Feldmann and Feldmann, 1942). It is distinguished from *A. armata* by the absence of spiny laterals but Dixon (1964) commented that British material of *Asparagopsis* is occasionally indistinguishable from *A. taxiformis* on this basis. This reinforces Schiffner's opinion (1931) that *A. armata* and *A. taxiformis* are conspecific. Furthermore, *Falkenbergia hillebrandii* (Born.) Falkenb., said to be the tetrasporangial phase of *A. taxiformis* (Chihara, 1960), is not apparently morphologically distinguishable from *F. rufolanosa* (Dixon, 1964). If these taxonomic opinions are confirmed, then the origins of the European *Asparagopsis* and *Falkenbergia* populations require further reconsideration.

The related alga *Bonnemaisonia hamifera* has also been regarded as an adventive from the Pacific, having first been described from Japanese material in 1891. The first British specimen was collected from Falmouth (south Cornwall) by Buffham in 1893, followed by a collection from Shanklin (Isle of Wight) by Holmes (1897). Westbrook (1930) commented that she had been unable to find *B. hamifera* at Shanklin or elsewhere on the Isle of Wight and this is also the current situation, although it is still to be found at Falmouth (Farnham, unpublished). Cotton (1912) had questioned whether *B. hamifera* was really alien as by then it was known to be more widely distributed in Europe, from Clare Island (west Ireland) to Cherbourg (north France). However, as he admitted (Cotton, 1912), it had been unknown in Europe before Buffham's discovery and accordingly seemed to be a recent arrival.

As with *Asparagopsis*, there is the complication of a pleomorphic life history to consider. Harder and Koch (1949) showed that *Trailliella intricata* Batt. was not an autonomous species but represented the tetrasporangial phase of *B. hamifera*. "*Trailliella*" was recorded in this country slightly earlier than its gametangial phase and has generally spread faster and also further northwards. It was first collected by Holmes at Studland (Dorset) in 1890 (as *Spermothamnion turneri* Aresch. f. *intricata* Holmes et Batt.). Westbrook (1930) discussed its further spread around Britain and Europe. McLachlan *et al.* (1969) reported on the current distribution of the phases, both of which are now present on the north-eastern and south-western coastlines of North America. A further complication is that *Bonnemaisonia nootkana* (Esper) Silva in the Pacific has a tetrasporangial phase morphologically indistuiguishable from *T. intricata*.

Although both phases of *B. hamifera* have greatly extended their geographical distributions during this century, there is no conclusive evidence pinpointing Japan as the country of origin. This general assumption (Westbrook, 1930; W. E. Jones, 1974) had been questioned by Cotton (1912), as mentioned previously, and more recently challenged by McLachlan *et al.* (1969). It does not necessarily follow that the country from which a species happened to be described first represents its place of origin. This is probably true for the tubeworm *Mercierella enigmatica* Fauvel (= *Ficoponatus enigmaticus* (Fauvel)), which was first described in France but is native to Australasia (Carlton, 1975). In view of the spread of *B. hamifera* and its *Trailliella*-phase on both sides of the Atlantic, it is surprising that it is not more widespread in the Pacific. The main indication that *B. hamifera* is indigenous to Japan comes from the occurrence of the full range of reproductive phases, i.e. spermatangial, carpogonial, carposporangial and tetrasporangial thalli, which is suggestive of the likely completion of its theoretical life history there.

Antithamnion spirographidis is "of somewhat problematic origin" (W. E. Jones, 1974). Jones cites its origin as from the southern hemisphere, although it was first described from the Adriatic in 1916. Westbrook (1930) discussed its occurrence and spread along both sides of the Channel (as *Antithamnionella sarniensis* Lyle). Sundene (1964) indicated that *Antithamnion sarniensis* (Lyle) G. Feldm. is conspecific with *A. spirographidis*, the former having been described by Lyle in 1922 from the Channel Islands. Westbrook (1930)

commented that *A. sarniensis* had not been found around Cherbourg last century by Thuret, but was found there for the first time in 1910 and later was quite abundant. Similarly, it had not been recorded in the Plymouth region by such assiduous collectors as Brebner and Holmes (last century) but Westbrook found it there in the 1920s. It has now been recorded for Lundy (D. Irvine *et al.*, 1972) and west Scotland (McAllister *et al.*, 1967; Price and Tittley, 1978), and so must be considered a well-established member of the British marine flora.

The introductions discussed above are not characterized by the same focal site of introduction into the British Isles, although in so far as can be determined they have usually made their first appearance somewhere along the southern or western coasts of the British Isles. As has been indicated, they have often been well established prior to being discovered and so the early events in their naturalization have been missed.

2. A Survey of Previous Marine Introductions into the Solent

One feature common to many marine species recently introduced into British waters is that they have first been discovered within the Solent region. (In this chapter, the "Solent region" refers to the shores around the Isle of Wight and the adjacent coastline of Hampshire.) Animal introductions are discussed here because similar general considerations apply to them as well as to algae in terms of their arrival, establishment and further spread. Marine introductions originating in the Solent are listed in Table II. Some of these are discussed further.

The Australasian barnacle, *Eliminius modestus* Darwin, has been a strikingly successful colonizer along considerable stretches of the British and European coastlines. *E. modestus* was first found by Bishop (1947) on test panels within Chichester Harbour. Later, Stubbings (1950) examined material collected earlier and concluded that it had been present before 1945. Since that time, *Elminius* has greatly increased its European distribution, as outlined by Crisp (1958). It has now spread round most of the English coastline and has more recently appeared in Ireland, Scotland and Shetland (Hiscock *et al.*, 1978). During the late 1940s, *Elminius* appeared on the European mainland and is now widespread from Germany to Spain. Lewis (1964, Fig. 70) depicts the rate of dispersal by *Elminius* in Europe.

Table II. Previous introductions reported for the Solent region

Species	Group	Date of earliest discovery	Suggested origin	Reference
Spartina alterniflora	Angiospermae	1829	east N. America	Marchant (1968)
Mercenaria mercenaria	Mollusca	1925	east N. America	Mitchell (1974)
Elminius modestus	Crustacea	1940s	Australasia	Crisp (1958)
Styela clava	Tunicata	1950s	Pacific	Houghton and Millar (1960)
Limnoria tripunctata	Crustacea	1957	temperate-tropical seas	Eltringham and Hockley (1958)

A later animal arrival, however, was not immediately identified as such. This was an ascidian reported by Carlisle (1954) as a previously undescribed species, *Styela mammiculata*. He recorded it from Plymouth, although it probably occurred more or less simultaneously in the area of Portsmouth Harbour (Houghton and Millar, 1960). Millar (1960) demonstrated that *S. mammiculata* Carlisle was synonymous with a species described earlier from the Pacific, *S. clava* Herdman, and concluded that *S. clava* constituted a new introduction into British waters from the Pacific. *S. clava* has since spread further along the south coast of England (Millar, 1970), across to Brittany (Dr L. Cabioch, personal communication) and more recently has been found in Cork Harbour, southern Ireland (Guiry and Guiry, 1973).

The bivalve *Mercenaria mercenaria* L. is widely distributed along the Atlantic coast of North America. This hard-shelled clam has often been deliberately introduced into European waters for commercial exploitation but usually without success. On the other hand, colonies have appeared in localities where there had been no attempted transplantations. This may be the explanation for the self-reproducing population in the Solent reported by Heppel (1961), although Mitchell (1974) suggested that this was a deliberate introduction. Naylor (1965) reviewed the biological effects of heated effluents on immigrant warm-water species. This is probably the explanation for the continued existence of *Mercenaria* in Southampton Water, and similarly for that of the wood-boring isopod, *Limnoria tripunctata* Menzies, recorded by Eltringham and Hockley (1958).

The cord-grass *Spartina* has perhaps had a greater overall ecological effect than any of the previous introductions discussed so far. Within the past century it has greatly altered the appearance of long stretches of British and European coastline, by virtue of its rapid spread and exceptional mud-binding properties.

The original species of *Spartina* to be found in Europe was *S. maritima* (Curtis) Fernald, which was widely distributed as small colonies. Those colonies at their northern limit of geographical distribution in Britain and Europe seemed to lack vigour and Marchant (1967) suggested that the species was sensitive to climatic fluctuations. Early in the eighteenth century, another species of *Spartina* appeared around Southampton Water and also in France. This was *S. alterniflora* Loisel, originating from the eastern North American seaboard. An unusual, if not unique, event then occurred around Southampton

Water. Rather than the newly arrived species itself becoming firmly established and spreading further, both species of *Spartina*, previously separated by the Atlantic Ocean, co-existed as outbreeding populations to create a natural hybrid. *S.* x *townsendii* H. and J. Groves. Records of this "species" date from 1870 and since then it has become widespread. This F_1 hybrid is sterile and accordingly can only spread vegetatively. Within the period 1870 to 1890, the initial expansion of *Spartina* took place. This has been explained by the production of a fertile amphidiploid, *S. anglica* Hubbard, derived from the sterile primary hybrid (*S.* x *townsendii*) by chromosomal doubling. As it is not always possible to separate these two hybrid forms in previous records and field collections, both types of hybrid can be collectively referred to as *S.* x *townsendii* agg. (Marchant, 1968). Since the turn of the century, *S.* x *townsendii* agg. has become widely distributed as a major colonizer of unstabilized tidal mudflats, around most of the British coastline and elsewhere in Europe.

Other alien species have been found around the Solent, additional to the list in Table II, but these appeared elsewhere in the British Isles before reaching the Solent. Examples include some of the algae given in Table I, i.e. *C. fragile*, subsp. *tomentosoides*, *B. hamifera* – both phases, *C. peregrina*, *A. spirographidis* and the *Falkenbergia*-phase of *A. armata*, and such animals as the slipper-limpet, *Crepidula fornicata* (L.), and the boring mollusc, *Petricola pholadiformis* Lamarck.

The algae recently introduced into the Solent will be discussed later in more detail, together with other apparently recent aliens occurring elsewhere in the British Isles, but especially along the coast of southern England.

3. A Discussion of Factors Responsible for the Introduction and Further Spread of Introduced Species

The geographical distributional patterns of organisms, whether plant or animal, marine or terrestrial, are not static and changes may occur from time to time. The advent of any species into a new region raises the initial query as to how the species was transported to its new locality. Subsequent investigation into the biology of an introduced species will usually concentrate on its "success", as exemplified by its rate of further spread from the initial site of

invasion and its effects upon indigenous members of the flora and fauna living in the same habitat.

The existing boundaries in the distribution of any species may respond to various environmental changes, such as climate, hydrography, and so on. Thus, the southward spread of such typically northern marine algae as *Ptilota plumosa* has been correlated with a general climatic improvement in the British Isles over the past century (Dixon, 1965). As previously mentioned, *Laminaria ochroleuca* is a recent cross-Channel migrant, perhaps in response to slightly elevated sea temperatures. These relatively minor expansions of the boundaries of existing populations are brought about by the natural methods of dissemination, which constitute what Crisp (1958) termed "marginal dispersal". Existing marine communities represent the climax of centuries during which processes of "marginal dispersal" have been operative and which are unlikely to result in any tremendous changes in the near future.

The majority of newly introduced species have been transported considerable distances by a variety of agencies or vectors, and this constitutes the process of "remote dispersal" (Crisp, 1958). Effectively, the difference between these two methods of dispersal is whether the species is transported a short distance or a greater distance away from its previous population. The term "vector" has been used in this context, e.g. Crisp (1958), W. E. Jones (1974), as an extension of its previous biological usage which related to the transmission of parasites only. However, the concept of a "vector" is a convenient one to employ in the wider connotation of the agency responsible for the introduction and spread of species. Doubtless many transportations of species occur but it must be exceptional for any such species to survive the journey and to have a large enough "inoculum" of breeding stock for the establishment of a population in a new area where conditions happen to be favourable. Once such a successful invasion has taken place, then further dispersal may be brought about by either, or a combination of, remote and marginal spread.

Various vectors for the long-distance transportation (remote dispersal) of marine organisms can be suggested. For most introductions, the nature of the vector is conjectural and frequently is suggested by circumstantial evidence related to their time of discovery and initial localities concerned.

An obvious marine vector is shipping, which may carry out this role in two ways. First, species may be transported as fouling organisms attached to the hull. This is the likeliest explanation for the introduction of *Elminius* and *Styela*, both of which are known to occur as components of the fouling community. As shown by Crisp (1958), *Elminius* probably arrived in British waters by the early 1940s. It is possible that wartime conditions may have helped in this introduction. A later war in the 1950s (Korean War) is thought to have resulted in the introduction of *Styela*, which may have been transported from the Pacific to England on naval vessels, such as landing craft. Further circumstantial evidence supporting the role of shipping as an important vector is that most introductions are first found in the vicinity of harbours, e.g. Portsmouth, Southampton, Plymouth, Falmouth and Cork. Involvement of shipping in the further spread of *Styela* is indicated by the recent report of its occurrence around Cork Harbour (Guiry and Guiry, 1973). Transportation of algae attached to ships has been suggested, particularly in those cases where the distribution of an introduced species is disjunct. De Valéra (1942) implicated shipping in the early spread of *Asparagopsis*.

Secondly, shipping can act as a vector by the discharge of ballast in foreign harbours. Marchant (1967) suggested this to be the method by which the North American *Spartina alterniflora* was introduced into Southampton. Discharge of ballast water has been implicated in the dispersal of planktonic species such as *Biddulphia sinensis* Grev. (Hardy, 1956). This diatom is of Indo-Pacific origin and first appeared in European waters at the beginning of the century but by now is an abundant member of the phytoplankton. Boalch and Harbour (1977) have recently reported the introduction of two more planktonic diatoms into the Channel.

Although it is an attractive proposition to cite international shipping as a main vector for introduced species, caution needs to be employed unless additional evidence is forthcoming. The application of antifouling paints to ships' hulls results in a reduced and cosmopolitan flora which is resistant to the toxins and also the varying hydrographic conditions (mainly salinity and temperature) encountered during passage. Additional factors militating against shipping as frequent vectors are the environments offered by harbours, often highly polluted and estuarine, and the quick turnabout times of modern commercial vessels. It may well be that the older forms

of shipping with less effective antifouling treatment were a much richer source of possible introductions. It used also to be the practice for at least the smaller trading boats, in the days of sail, to be run directly ashore to unload cargo without entering harbours. On the other hand, the faster speed of modern shipping does subject attached organisms to shorter periods at sea during which unfavourable conditions may be encountered, such as passage through tropical waters for temperate species.

In addition to fouled ships, floating objects such as timbers, buoys and fishing-pots also afford the possibility of transporting attached organisms considerable distances according to the prevailing currents. Lucas (1950) recorded a number of algae cast up on the Dutch coast, some attached to such objects as French fishing-floats. This is probably not an effective method leading to the establishment of successful introductions, because the biomass of attached organisms transported must be low. As Crisp (1958) discussed with respect to the spread of *Elminius*, one of the limiting factors for the establishment and further spread of an invading species must be the number of reproductive units produced to constitute a large enough inoculum. In those instances where only small amounts of a species are transported, a series of repetitious introductions is needed, in order to build up the biomass of the introduced species for its eventual successful establishment.

Another important way by which long-distance introductions are brought about involves the deliberate introduction by Man of commercially important species. This is less true for the marine environment, in which the practice of "mariculture" is still in its infancy as compared with the terrestrial flora and fauna, which has been affected all over the world by international exchanges (see Salisbury, 1964). Marine organisms deliberately introduced into European waters are listed in the report prepared for the International Council for the Exploration of the Sea, I.C.E.S. (Anon., 1972), and are included in the world-wide inventory prepared by Walford and Wicklund (1973).

It has been common practice for many centuries to transplant or relay the indigenous European oyster, *Ostrea edulis* L., into new beds or to augment existing populations. In recent years, many oyster-beds in this country and elsewhere in Europe have been greatly depleted by pollution and disease. Re-stocking of these beds

has been attempted with other, hardier or faster-growing species. The Portuguese oyster, *Crassostrea angulata* L., has been successfully transplanted around Europe and later consignments of the Pacific oyster, *Crassostrea gigas* (Thunberg), were exported from Japan and British Columbia. Such deliberate introductions will not be dealt with in detail here. However, as a consequence of deliberate transplantations, many accidental introductions have been effected, e.g. imported oysters themselves acting as vectors. As Elton (1958) commented, "the greatest agency of all that spreads marine animals to new quarters of the world must be the business of oyster culture". This is a regrettable consequence of the initial lack of stringent precautions and quarantining, since many of these accidentally introduced species have proved detrimental to the oyster industry, e.g. the slipper-limpet, *Crepidula fornicata* L., and the oyster-drill, *Urosalpinx cinerea* (Say), (Cole, 1942).

The geographical spread of *Codium fragile* has already been discussed. Ramus (1971) suggested that the *Codium* may have been introduced into eastern North America attached to oysters. Perhaps the same explanation holds good for the initial appearance of *Colpomenia peregrina* in Brittany, also associated with oyster beds there. However, the further colonization of the European coastline by *Colpomenia* probably occurred by marginal dispersal. The thalli of *Colpomenia* are hollow, becoming air-filled and buoyant, and spread by floating away. This is exceptional in that the majority of seaweeds are not likely to float for any significant time or distance when detached. However, a few remarkable instances exist where drift specimens have been found considerable distances away from the nearest site of attached plants. Holmes (1900) found *Gelidium versicolor* (S. Gmel.) Lamour. (as *G. cartilagineum* J. Ag.) unattached on the Isle of Wight. According to Dixon and L. Irvine (1977), the Canary Islands are the nearest site for attached plants of this species. It is probably easier for many marine animals to extend their range because of their production of planktonic larval stages which can be dispersed by water movements. This has probably been an important factor in the subsequent colonization of the European coastline by *Elminius*.

Little is known about the methods of marginal dispersal in the benthic marine algae. The buoyant thallus of *Colpomenia* has been mentioned but this is the exception rather than the rule.

Fragmentation of various algae can occur with the possibility of rhizoidal reattachment, as was shown by Chemin (1928) for a range of red algae. Some algae have become specialized towards this method by the development of tendrils or hooked branches, as in *Asparagopsis armata* and *Bonnemaisonia hamifera*, which facilitate the further spread of such algae by attachment onto floating objects. In other algae, there is the possibility of spores or microscopic germling stages being transported either in the plankton or attached to such vectors as shipping. Virtually nothing is known about the viability and longevity of such stages in the life histories of algae. It is generally assumed that the thin-walled spores produced by marine algae sink and germinate quickly, and are thus unlikely to spread far in the plankton. However, the ability of swarmers of *Enteromorpha intestinalis* to be motile for up to 8 days (W. E. Jones and Babb, 1968) suggests that considerable dispersal of this alga, and any other with comparable swarmers, could take place in the plankton. Many summer annuals are thought to overwinter as multicellular sporelings (Dixon, 1960) and it is these phases which may survive transportation by vectors from one country to another. Usually, major changes in the distribution of macroalgae have been attributed to transportation by vectors rather than to passive dispersal of spores, or other reproductive elements, by water currents but little direct evidence is available to confirm either hypothesis.

As can be appreciated from the varied nature of vectors involved, many potential introductions may be made. That is to say, a wide variety of species is probably transported into new regions without any further development because of unsuitable conditions. Factors required for a successful introduction include the following: suitable vector(s); survival during the transit period; arrival in a new region offering the same or similar habitats to those in the country of origin (e.g. suitable water temperatures; salinity; substratum); the establishment of a large enough breeding-stock from either a single massive inoculum or from a repetitious series of invasions; suitable conditions and vectors for the further spread of the introduced species.

4. A Discussion of Effects Caused by Introduced Species

Little is known of the effects produced by the successful invasion and subsequent spread of most introduced species. This is particularly

true for the algae already discussed; the consequences of faunal introductions are perhaps better known because of the commercial interests involved, as in the case of introduced oyster-pests which were discussed by Quayle (1964).

Some introductions appear to have had little discernible effect upon the indigenous biota and simply provide additional components to the ecosystem. *Colpomenia* would seem to be in this category. Despite its present wide European distribution and abundance, especially in summer in rock-pools, no obvious effect has been apparent upon the established flora. In other cases, effects of competition are apparent, and particularly so where related species were established in the host flora. *Codium tomentosum* used to be widely distributed on the south and west coast of the British Isles. Since the introduction of *Codium fragile*, which grows in the same habitats, the former has diminished in abundance whereas the introduced *Codium* has spread further round the British Isles, even into areas where *C. tomentosum* did not grow. This greater competitive ability and "aggressiveness" seems to be a general feature of many introduced species and is not easy to explain. Salisbury (1964), in discussing terrestrial invasions, cites instances where species are easily manageable in their native or original environments but then become rampant in alien environments. This may be explained, easily if not precisely, on the grounds that controlling factors in the country of origin, such as predators or competitors for space, will not have been introduced along with the invading species. In the absence of such constraint, more vigorous biological activities, e.g. growth rate, reproductive strategy and output, may be manifest by the successful alien species.

Certainly the advent of *Elminius* has affected the British native barnacles (Crisp, 1958) and in particular *Balanus balanoides* L., with which it is in direct competition for space and food. There may be further, less obvious, effects resulting from indirect competition. *Elminius* produces a much larger number of larval stages in the summer than does *B. balanoides* and these may then reduce or displace other components of the zooplankton, leading to a smaller adult settlement of other species. In this manner, *Elminius* may affect a wide range of other marine animals through loss of their planktonic larvae.

It is appropriate to mention here the introduced freshwater aquatic plant *Elodea canadensis* Michx. Canadian Pondweed was

first noted in England around the middle of the last century and may have been brought in by Canadian timber. *Elodea* quickly became widely dispersed along many rivers and canals throughout the British Isles in such abundance that it hindered the passage of canal barges and choked many land-drainage systems. The spread of *Elodea* was by purely vegetative means, since it is a dioecious species with only female plants having been introduced. However, in recent years there has been a marked decline in *Elodea* populations. The causes of this decline are unknown; grazing is not likely to be a significant factor. Reduced genetic vigour as a result of the vegetative methods of propagation, or limitation by trace elements have been suggested (Salisbury, 1964). This population decrease may well be a general phenomenon for many introduced species. The initial colonizing phase consists of vigorous expansion, either in conditions where resources are available or at the expense of some established members of the native flora and fauna. This pioneer phase may be followed by a decline leading perhaps to a more stable system and better balance within the ecosystem. The relative amounts of ecological disturbance and the time-scale leading to the stabilized phase will vary for each particular case. It is factors such as these which must be taken into consideration when attempting to evaluate the biological effects of introduced species, as and when they are first reported, in case any early remedial action is warranted.

RECENT ALGAL INTRODUCTIONS INTO THE SOLENT

Marine algae which are considered to have been introduced into the Solent are given in Table III. These will be discussed in turn, mainly to provide some account of their initial discovery and present distribution.

1. *Grateloupia filicina* var. *luxurians*

(a) Occurrence and identification. Since 1947 specimens of a large, distinctive red alga have been found around the Solent which had been variously ascribed to such diverse genera as *Helminthocladia*, *Calliblepharis*, etc. Investigations into their anatomy and reproduction showed that none of these identifications was correct and that these specimens must be referred to the polymorphic genus *Grateloupia*

Table III. Recent introductions of algae into the Solent

Species	Date of earliest discovery	Suggested origin	Reference
Grateloupia filicina var. *luxurians*	1947	Pacific	Farnham and L. Irvine (1968)
Grateloupia doryphora	1969	Pacific	Farnham and L. Irvine (1973)
Sargassum muticum	1971	Pacific	Farnham *et al.* (1973)
Neoagardhiella gaudichaudii	1973	Pacific	Farnham and L. Irvine (1979)

(Florideophyceae, Cryptonemiales). Nearly 40 species of this genus have been described and are widely distributed in tropical and temperate seas (Kylin, 1956). Examination of foreign specimens in the British Museum (Natural History) showed closest resemblance between this Solent *Grateloupia* and specimens of *G. filicina* from such countries as Australia and Japan, in particular. The difficulty in identifying the Solent specimens as *G. filicina* was because this same species had already been included in the British flora in such early accounts as W. H. Harvey (1846–1851). Specimens in the British Isles previously ascribed to this species were regarded as rare, being restricted to the south-west, and were very much smaller than the Solent plants.

As suggested by Farnham and L. Irvine (1968), the occurrence of the large plants of *G. filicina* around the Solent could be given various explanations. Their luxuriant growth could be a genetic or ecological response to certain local conditions, such as thermal or organic pollution, promoting enhanced growth. Berthold (1884), Boergesen (1916) and Gayral (1958) all commented that *Grateloupia* spp., including *G. filicina*, show increased growth in waters near towns or rich in organic matter, but none of these authors indicated that the increase in size is of such proportions as would account for the degree of difference between the specimens from the Solent and elsewhere in Britain. Alternatively, the Solent population could belong to a taxon distinct from the usual British *G. filicina*. This could either have passed unnoticed until recent times (which is improbable in view of the careful records kept in this country along the south coast around the turn of the century by such assiduous
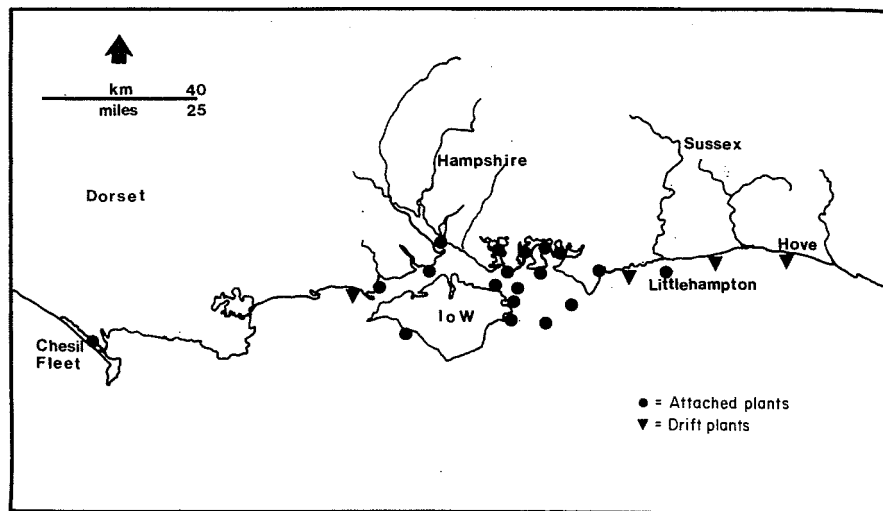
Fig. 1. Distribution of *Grateloupia filicina* var. *luxurians* on the south coast of England. The Solent region is shown in more detail in Fig. 2.

collectors as E. M. Holmes, E. A. L. Batters and their contemporaries), or is a comparatively recent introduction.

Gepp and Gepp (1906) reported on a collection of marine algae from New South Wales, Australia, which included "the finest specimen of *Grateloupia filicina* that we have ever seen". These large plants were described as a new variety *luxurians*. The Solent *Grateloupia* is similar to their type material.

(b) Distribution. *G. filicina* var. *luxurians* is widely distributed in the Pacific, Indian and warmer parts of the Atlantic Oceans. Figure 1 shows its present English distribution, which is centred around the Solent region. Abundant populations occur on the Isle of Wight at Bembridge and St Helens. On the mainland of Hampshire, var. *luxurians* is to be found within the local harbour complexes. It used to be particularly abundant within Portsmouth Harbour around Horsea Island, until the construction of the M275 motorway and land-reclamation schemes in 1971. Var. *luxurians* is found along Southsea beach and at a similar site between Lepe and Calshot. Within Southampton Water, it has only been found once, growing

on a buoy in the Hamble. Var. *luxurians* extends further west along the Hampshire coast to Lymington (Normandy salterns); drift plants have been found at Milford-on-Sea. The variety has a rather sporadic sublittoral distribution around the Solent.

The only site west of the Solent where var. *luxurians* has been found is in Chesil Fleet, Dorset (Burrows and Farnham, cited by Whittaker, in press). Since this interesting locality had been neglected phycologically for much of this century, it is possible that var. *luxurians* may have appeared in the Fleet before the Solent. Var. *luxurians* has been found further east along the south coast, with drift plants common at Bognor Regis (Sussex) since at least 1966. It was dredged off Littlehampton in 1953 by Drs W. E. Jones and A. Austin. More drift plants have been found between Hove and Brighton.

(c) Ecological observations. The most abundant population occurs at Bembridge. This site consists of an intertidal system of undulating limestone ledges, in between which at low tide are formed extensive shallow lagoons. The flora of these lagoons is rich, with such species as *Cordylecladia erecta*, *Cylindrocarpus microscopicus*, *Derbesia marina* and *Gracilaria bursa-pastoris*. This was one of the reasons for the recent designation of this locality as a Site of Special Scientific Interest (SSSI). Plants are also distributed around the more sheltered local harbours (Portsmouth, Langstone, Chichester and Pagham), where they occur in shallow pools or drainage channels, attached to stones or shells buried in the mud or sand. Associated algae here include *Chondria coerulescens*, *Chondrus crispus*, *Laminaria saccharina* and *Nitophyllum punctatum*.

Seawater temperature and salinity measurements have been made throughout the year at various sites. The lowest temperatures occur in February–March (3–4°C) with summer temperatures in the lagoons and channels exceptionally up to 25°C. Around the Solent, LWST occurs in early morning and late afternoon so that, in summer, the *Grateloupia* plants are not exposed to the full rigours of the midday sun. Lewis (1964) suggested that the time of LWST could be a factor modifying the distribution of certain intertidal organisms. Salinity does not usually vary much but, in parts of Chichester Harbour near freshwater inputs, *Grateloupia* plants may be subjected to salinities of 10–15 ‰ at low water, although for only 1–3 h.

Fertile plants bearing tetrasporangia or carposporangia can be found throughout the year, with greatest fertility in June–July. Tetrasporangial plants generally tend to be more abundant. The seasonal reproductive cycle is not so well-defined as in such other red algae as *Gracilaria verrucosa* (W. E. Jones, 1959).

Numbers of plants within permanent quadrats were counted monthly for one year at Bembridge and Horsea. At both sites, the overall trends were similar, with numbers decreasing from November to midsummer and then a sudden increase of mainly young plants. At this time of year, day length and water temperature are at their maxima.

"Tagged" plants and sporelings grew much faster in summer than in winter; sporelings 50 mm long in May were up to 200 mm in the following month, whereas a sporeling of 58 mm length in November had grown to only 75 mm by the following March. Some "tagged" plants were observed to develop cystocarps, which existed for up to 3 months before discharging spores.

G. filicina var. *filicina* has been only infrequently collected around the Solent, although it has been found at the same sites as var. *luxurians*. Thalli of both varieties have even been found on the same stones, but as quite separate plants. Specimens of var. *filicina* were transplanted from West Looe (Cornwall) into Portsmouth Harbour. They were there found to grow more slowly than var. *luxurians* plants and remained morphologically different. In laboratory culture from spores, sporelings of both varieties, resembling field-material, have been produced. Only in var. *filicina* has the complete *Polysiphonia*-type life history been obtained. These observations indicate that both varieties of *G. filicina* are genetically different and are not ecological variants. We can therefore conclude that var. *luxurians* is a recent introduction into the Solent.

2. Grateloupia doryphora

(a) Occurrence and Identification. A blade-like red alga was collected from Southsea beach in May 1969; it had not been found at that site or elsewhere in the Solent previously. Although it was morphologically quite different from *G. filicina* var. *luxurians*, details of its structure and reproduction established it as another *Grateloupia* species. A foliose *Grateloupia* had not hitherto been recorded for the

British Isles, so that this discovery provided yet another example of introduction into the Solent (Farnham and L. Irvine, 1973).

Many foliose species of the genus have been described, often based upon limited material. Ardré and Gayral (1961) made a preliminary taxonomic revision of certain foliose species occurring within the Atlantic and Pacific. They concluded that most species could be reduced to synonymy with *G. lanceola* J. Ag. Later, Dawson *et al.* (1964) agreed with Howe (1914) that *G. doryphora* (Mont.) Howe was representative of the foliose complex in *Grateloupia* and had taxonomic priority. Material of Solent *G. doryphora* agrees well with foreign specimens and in particular with material, illustrated by Abbott and Hollenberg (1976), from the Pacific coast of North America.

(b) Distribution. As indicated in the previous section, *G. doryphora* is widely distributed in the Pacific and Atlantic Oceans. Since the original discovery at Southsea further sites have been noted; these are mainly local harbours although it has not been detected in Portsmouth Harbour (Fig. 2). Its present eastern limit along the English coast is Pagham Harbour (Sussex), where it occurs along with var. *luxurians* (Farnham, 1975), and its western limit in Lepe. *G. doryphora* has not yet been found on the Isle of Wight.
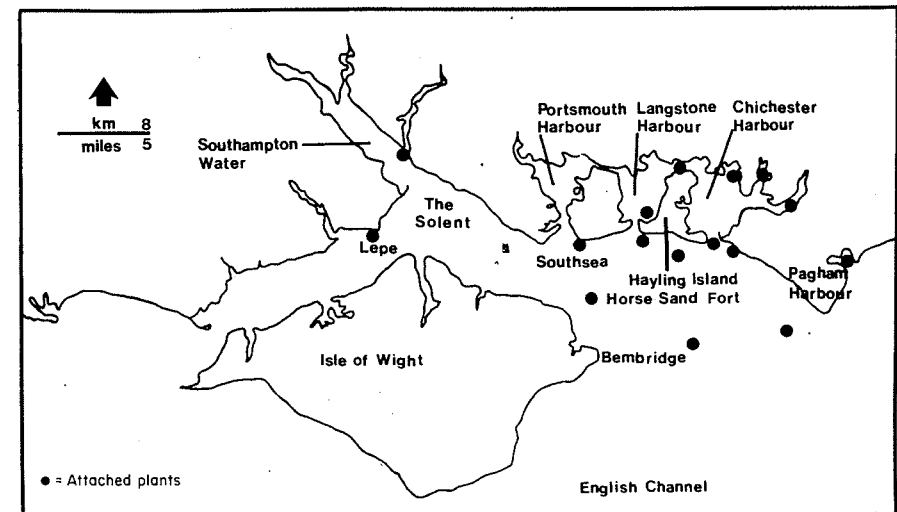

Fig. 2. Distribution of *Grateloupia doryphora* around the Solent region.

(c) Ecological observations. G. doryphora occurs in relatively sheltered sites, as in the Solent harbours, but can also withstand a certain amount of wave action, as indicated by its presence at Southsea. Here, both introduced Grateloupia spp. occur in the lower eulittoral-sublittoral fringe. Since 1969, G. doryphora has increased in cover at Southsea, while var. luxurians has become less abundant.

G. doryphora grows well in the creeks of Langstone and Chichester Harbours. Plants measuring up to 1.0 x 0.2 m have been found, which must make this one of the largest British red algae. Reasons for this enhanced growth probably include the eutrophic conditions in the harbours (Dunn, 1972), little wave action but fast tidal movements, and elevated seawater temperatures (up to 25°C) in summer. G. doryphora is more tolerant than var. luxurians of reduced salinity; plants have been found in runnels experiencing 5–10 $^o/_{oo}$ for 2–4 h before the incoming tide restores the salinity to its full value of 33–34 $^o/_{oo}$.

Only a few, small plants (up to 100 mm) have been found in the sublittoral, down to a depth of 5–6 m below C.D. Clearly, G. dorphora has not yet colonized the sublittoral zone as effectively as it has the lower eulittoral. This may be due to competition from the indigenous sublittoral algae. In addition, the rather turbid conditions of Solent waters and consequent reduced light penetration in the Solent may inhibit the growth of G. doryphora in the sublittoral.

3. Sargassum muticum

(a) Occurrence and identification. Sargassum muticum (Phaeophyceae, Fucales) was first reported for the British Isles, and for the Atlantic, when Farnham et al. (1973) reported some 30 plants growing in the Bembridge lagoons. However, S. muticum must have been present at Bembridge since at least 1971, since a visit shortly after its discovery revealed larger numbers of plants which were subsequently estimated as at least 2 years old. In June 1971, a mature drift Sargassum plant had been found at Southsea; this was initially misidentified as one of the pelagic species originating from the Sargasso Sea. It was later correctly identified as S. muticum.

Sargassum is a problematical genus, credited with over 200 species. Yendo (1907) described S. kjellmanianum f. muticus (sic) from Japan, which Fensholt (1955) elevated to specific status. Yoshida

(1978) has recently placed S. kjellmanianum Yendo in synonymy with S. miyabei Yendo. Tseng and Chang (1954) described a new forma, longifolia, of S. kjellmanianum from China, which Yoshida (1978) transferred to S. muticum. Because Tseng and Chang's paper has not yet been translated from Chinese, it is not known whether f. longifolia is present in the Atlantic population of S. muticum.

(b) Distribution. S. muticum occurs in the Pacific in Japan (Yendo, 1907), in China (Tseng and Chang, 1954), and along the North American coast, where it was introduced in the early 1940s around southern British Columbia (Scagel, 1956). As Norton (in press) has pointed out, the rate of spread by S. muticum down the Pacific American coast has been disjunct and uneven. It had reached Baja California by the early 1970s (Abbott and North, 1972). This represents a spread of over 2000 km in some 30 years. Nicholson et al. (in press) consider that this species has not yet reached its southern limit in distribution.

The means of introduction and dispersal of S. muticum along the American coastline probably involve both "remote" and "marginal" methods. Circumstantial evidence indicates that the arrival of S. muticum into Canada was caused by the importation of Japanese oysters, which were used to restock oyster-beds there (Scagel, 1956). The further spread of S. muticum may have been caused not only by the relaying of oysters from British Columbia into new beds, but also by the flotation of unattached Sargassum plants, rendered buoyant by their vesicles and subsequently dispersed by currents.

The European distribution has been monitored since 1973, and its rate of spread can be obtained from E. B. G. Jones et al. (1974), Lewey (1976), Gray and Jones (1977), Farnham (1978) and Critchley (in press). This alga now occurs along the south coast of England from as far west as Plymouth, south Devon (Boalch and Potts, 1977) to Eastbourne (Sussex) in the east – a distance of over 300 km (see Fig. 3).

The discovery of Sargassum on the English coast prompted marine biologists to look for this species on the other side of the Channel. An attached population was found by Gruet (1976) and Cosson et al. (1977) at Saint-Vaast-la-Hougue in Normandy. The oyster-parks there have been refurbished with spat of Crassostrea gigas imported from Japan, Korea and British Columbia. Gruet et al. (1976) pointed
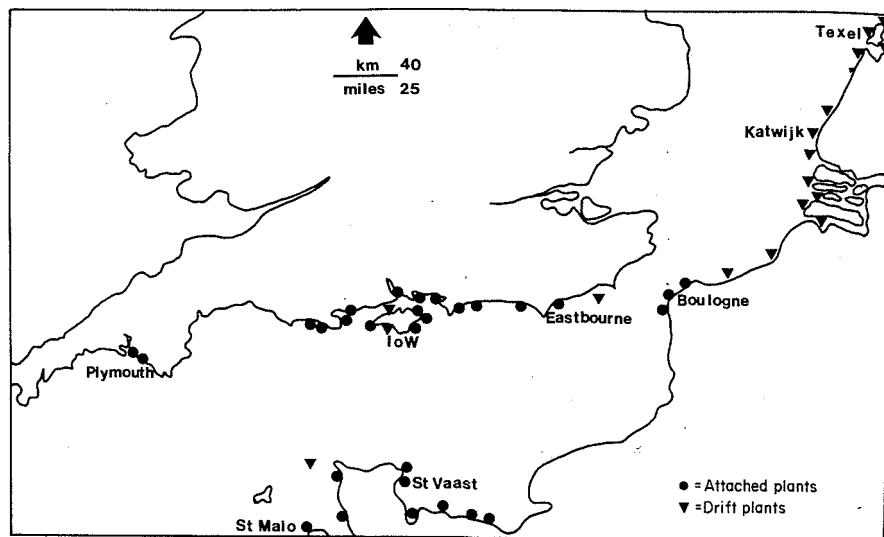
Fig. 3. European distribution of *Sargassum muticum*.

out that various sedentary Pacific animals were also being introduced with the oyster-shells. Since this importation of *C. gigas* into France has been in progress for some years (since at least 1966), it is possible that this population at St Vaast may have been established before the one in the Solent, although the latter happened to have been discovered first. Druehl (1973) expressed the view that international marine transplantations should be controlled more strictly because of the risk of accidental transportation of undesirable species. He predicted "the establishment of *Sargassum muticum* in the eastern Atlantic as a result of this transplant", i.e. importation ·of Pacific oysters into France. His prophecy has been substantiated! Other sightings of *S. muticum* have been recorded on the Continent. Kopp (1976) found a plant growing in the sublittoral off Barfleur, Compère (1977) collected drift material near Boulogne, and Prud'homme van Reine (1977) recently reported drift plants in the Netherlands.

It is therefore apparent that *S. muticum* is increasing its present distribution in European waters and may even colonize a similar extent of coastline in Europe as that in North America. Hydrographic conditions in terms of salinity and water temperature are generally

similar along both these continential coastlines. In the Pacific, *S. muticum* is found in British Columbia with a winter minimum temperature of 1–3°C, whereas in shallow bays in southern California, sea temperatures up to 18°C may be encountered in summer. Kjeldsen and Phinney (1972) demonstrated that estuarine populations of *S. muticum* in Oregon were metabolically tolerant of sea water diluted down to $20^{\circ}/_{00}$. Norton (1977) has shown that *S. muticum* sporelings and detached laterals grow in culture over the temperature range 5–25°C. Thus, the potential distribution of *S. muticum* in Europe is considerable – the entire British Isles, and in continental Europe perhaps from Scandinavia down to Spain or Portugal, or even into North Africa. In a shorter space of time, *S. muticum* has spread further from the Solent than either *Grateloupia doryphora* or *G. filicina* var. *luxurians*.

(c) *Ecological Observations*. *Sargassum muticum* is found in fairly sheltered sites around the Solent; there, it grows in lower eulittoral lagoons, as at Bembridge and St Helens on the Isle of Wight, in low-water channels within Langstone Harbour, and along the waterline of floating pontoons and landing stages in Portsmouth Harbour. Few plants have been found in the sublittoral and it is considered that, in the rather turbid waters around the Solent, growth of such plants is likely to be poor. It is anticipated that in clearer waters, such as off Dorset and Devon, *Sargassum* may colonize the shallow sublittoral (Jephson and Farnham, 1974). Short accounts of the ecology of *S. muticum* in Britain have been given by E. B. G. Jones *et al.* (1974), Fletcher and Fletcher (1975), Withers *et al.* (1975), Jephson and Gray (1977), Lewey and Farnham (in press), and Critchley (in press).

The rationale for the decision to attempt control of the newly introduced *S. muticum* in English waters is summarized here. An account of this has already been given in E. B. G. Jones and Farnham (1973) and in Farnham and E. B. G. Jones (1974).

The possible effects of the spread of *S. muticum* down the Pacific American coast caused concern to at least some marine biologists there. Druehl (1973), for example, suggested that *S. muticum* might be replacing the eel-grass, *Zostera marina* L. Replacement of native marine plants in English waters by *S. muticum* could disrupt existing ecological relationships and food nets. Furthermore, *Sargassum* plants

can also become detached from their holdfasts and float away, forming large free-floating masses. These may become such a nuisance as to affect the recreational usage and amenities of sheltered waters, for example, fouling fishing-lines, tangling round propellers of outboard-powered boats, and rotting on resort beaches. Commercial organizations could be harmed by the blocking of intake pipes or cooling seawater conduits to larger ships and shore installations, such as electricity generating stations. These problems caused by other seaweeds, already occur in England, and the establishment and spread of S. muticum would only compound them.

Thus, once marine botanists became aware of the implications of finding Sargassum in the Solent, a meeting was held at Portsmouth Polytechnic, on 4–5 May 1973. Eighteen marine biologists from various institutions in the United Kingdom attended to debate what, if any, action might be taken concerning S. muticum. This meeting had no official status but was justified by the lack of any Governmental legislation to cover this type of situation in the United Kingdom, although there are controls regulating the importation of land plants. Arguments in favour of eradicating S. muticum were proposed principally by Dr D. E. G. Irvine (Polytechnic of North London), supported by Dr G. Boalch (MBA, Plymouth). With regard to the practicality of eradication, most biologists present were not convinced as to the chances of a successful outcome, as the Sargassum population in Britain would need to be completely destroyed. However, the decision of this meeting was that the Sargassum found in the Solent region represented an undesirable addition to the British marine flora and should therefore be eliminated. Of the methods discussed, the one most acceptable was picking plants by hand. It was estimated that such man-power – made up of volunteers from the general public – would be required over an indefinite period. Gray and E. B. G. Jones (1977) have given a further account of the attempted clearance of S. muticum from British shores. It is now clear that hand-picking, even by large parties of enthusiastic volunteers, can only be an interim or palliative measure, rather than a real control, for Sargassum populations, because the plants have such a fast growth rate, immense reproductive output, and high regenerative ability. Other approaches which are currently under investigation include the evaluation of suitable herbicides, which would ideally affect only S. muticum in the sea (Lewey and

E. B. G. Jones, 1977), and various designs for mechanical clearance, ranging from simple hardware such as tractors fitted with harrows to more sophisticated project-orientated devices.

Despite the above attempts, it is certain that S. muticum has established itself along the south coast of England and is likely to colonize further stretches of suitable shoreline around the British Isles.

4. Neoagardhiella gaudichaudii

(a) Occurrence and identification. During a recent investigation into the Solent population of Gracilaria bursa-pastoris, it became apparent that another red alga, morphologically similar to G. bursa-pastoris, had also been collected under the same name. This is generically different from Gracilaria, as indicated by its filamentous medulla, zonate tetrasporangia, and ostiolate cystocarps with a central mass of sterile cells. These features are indicative of the genus Neoagardhiella (Florideophyceae, Gigartinales), which was defined by Wynne and Taylor (1973). There are two similar species in this genus, N. baileyi (Kütz.) Wynne et Taylor, on the North American Atlantic coast, and N. gaudichaudii (Mont.) Abbott, on the Pacific coast. The latter was confused with N. baileyi, until Abbott's (1978) investigation. The Solent Neoagardhiella seemingly fits more closely in habit, anatomical detail, and reproductive detail the description given by Abbott (1978) for N. gaudichaudii than that given for N. baileyi (Wynne and Taylor, 1973). The earliest collection of N. gaudichaudii from the Solent was made in August, 1973. In view of the confusion with G. bursa-pastoris, it could well have been present earlier. N. baileyi has been re-named Agardhiella subulata (C. Ag.) Kraft and Wynne (1979), while N. gaudichaudii has been transferred to Agardhiella by Ganesan (in press) and to Sarcodiotheca by Gabrielson and Hommersand (1980).

(b) Distribution. N. gaudichaudii has a limited distribution in the Solent, having been found only within parts of Langstone and Chichester Harbours and around Hayling Island (see Fig. 4).

(c) Ecological Observations. Only sporadic collections of this alien species have been made in the past 6 years, so that information is
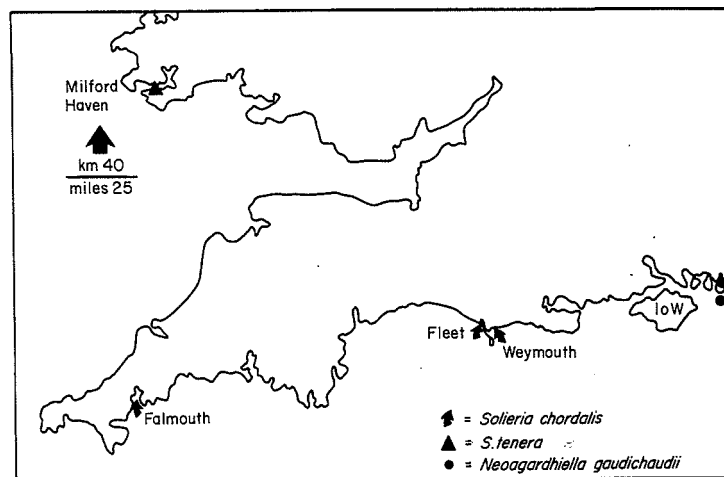
Fig. 4. Distribution of members of the Solieriaceae in Britain.

scanty. Plants have been found mainly in summer, occasionally in great abundance. They are found either unattached, or growing in clumps in the harbour creeks or in the shallow sublittoral (0–5 m). Associated algae include *Brongniartella byssoides*, *Cryptopleura ramosa*, *Desmarestia* spp., *Grateloupia* spp., *Laminaria saccharina* and *Ulva lactuca*. *Neogardhiella* is probably still in the early or pioneer phase of becoming established in the Solent and perhaps cannot even be regarded as a legitimate member of the British marine flora at this stage.

RECENT ALGAL INTRODUCTIONS OUTSIDE THE SOLENT

The Solent is not the only area which has provided new records of marine algae for the British Isles. Table IV lists certain of these, which will be briefly discussed.

It is remarkable that two species of *Solieria* should have been discovered within such a short time of each other, and perhaps even more surprising because *Solieria* occurs in the same family (Solieriaceae) as *Neogardhiella*. *S. chordalis* was first found in April 1976, during a sublittoral survey of Falmouth Harbour (Farnham and Jephson, 1977) where the plants were growing on maerl and shell. Later that year, *S. chordalis* was also found in Chesil Fleet and in Weymouth Bay, Dorset (see Fig. 4). Such a disjunct distribution is suggestive of remote dispersal, involving a vector such as shipping. *S. chordalis* is found in northern France

Table IV. Recent additions of marine algae to the British flora

Species	British distribution	Date of discovery	Suggested origin	Reference
Solieria chordalis	Falmouth, S. Cornwall	1976	N. France	Farnham and Jephson (1977)
	Fleet, Dorset	1976		
Solieria tenera	Milford Haven, Pembrokeshire	1978	Atlantic	Farnham and L. Irvine (1979)
Cruoria cruoriaeformis	Falmouth, S. Cornwall	1976	N. France	Blunden et al. (in press)
	Galway, W. Ireland	1977		
"Foliose red alga"	Falmouth, S. Cornwall	1977	?	Farnham and Jephson (1977)

and thus seems to be a cross-Channel migrant similar to *L. ochroleuca*.
The record by Ardré (1970) for *S. chordalis* in England is erroneous
(Mlle F. Ardré, personal communication). The addition of *S. chordalis*
to the English flora was anticipated by Holmes and Batters (1891). As
with other aliens, it is possible that *Solieria* was always present and
has been unnoticed or misidentified. Its life history requires further
investigation, since only tetrasporangial plants have been found in
this country.

S. *tenera* (J. Ag.) Wynne et Taylor was first collected by S. Hiscock
in July 1978 (as ? *Gracilaria* sp.) at East Pennar Point, Milford Haven,
during the Southwest Britain Sublittoral Survey. This material
differed from *S. chordalis* in its more robust axes and less proliferous
appearance, thus agreeing with specimens of *S. tenera*. This is a
warm-water species occurring in the Atlantic (Caribbean, Gulf of
Mexico and West Africa). Both carposporangial and tetrasporangial
plants have now been collected. In all three of these solieriaceous
algae, it has been found that although spores have been discharged
in culture from fertile material, none has ever germinated. This
could indicate that these species may reproduce more by vegetative
propagation than by spore development It has been observed that
plants of *S. chordalis*, in particular, easily fragment and undergo
rhizoidal reattachment.

An encrusting red alga, *Cruoria cruoriaeformis* (Crouan frat.)
Denizot (Florideophyceae, Gigartinales), has been found growing on
maerl in Falmouth and Galway. It has not previously been recorded
for the British Isles, but Dixon and Irvine (1977) suggested that it
was likely to be present. *C. cruoriaeformis* is probably not an intro-
duction from northern France but is much more likely to have been
previously undetected. A further foliose red alga has also been found
at Falmouth; it is not only unlike any previously known British
species but cannot even be given provisional generic identification
due to the lack of appropriate reproductive structures. Whether this
represents an undescribed indigenous species or an exotic alien
therefore cannot yet be stated.

DISCUSSION

Some authors (e.g. Carlton, 1975) stipulate that alien species are
only properly so if introduced as the result of human activities,
which may be unintentional, as in the case of *Elminius*, or deliberate,

as for *C. gigas*. The arrival of other immigrant species may be
merely by the process of marginal dispersal, e.g. *L. ochroleuca*.
However, the mode of arrival for many adventitious species can
only be surmised. Thus, it seems advisable to regard any exotic
species which has established itself in a new country as constituting
an introduction.

Discoveries of introduced species in the British Isles, especially
along the south coast of England, seem to be continuous, particularly
within sublittoral harbour areas. This is suggestive of shipping as
a vector but may also be a reflection on the "distribution of
collectors", especially divers who have recently been surveying
these localities. Areas like the Solent may also be conductive to
the establishment of alien species, which are usually characterized
as pioneer or opportunist, through the occurrence of "open" com-
munities, combined with relative freedom from "closed" communities
dominated by fucoids and kelps.

Like many of the established introductions, e.g. *C. fragile*, some
of the recent arrivals may also have originated from the Pacific. The
main "donor" area for algae introduced into the British Isles could
be the Pacific coast of North America, since this is a region common
to the geographical distribution of many of our alien species. It is
appropriate to note here that the movement of immigrant species
is not a one-way process. Successful introductions have occurred
from the Atlantic into the Pacific, e.g. the barnacle *Balanus amphitrite*
Darwin (Carlton, 1975) and the red alga *Schottera nicaeensis* (Lewis
and Kraft, 1979).

As has been indicated, many introduced species are difficult
to identify when first found. They may either be confused with
native species, e.g. *N. gaudichaudii* and *G. bursa-pastoris*, or may be
treated as previously undescribed species. *Cryptonemia hibernica*
was described as a new species from Cork Harbour, Ireland, by
Guiry and L. Irvine (1974), who considered that this Irish material
was taxonomically distinct from a complex of species in the eastern
Pacific. Further investigation may indicate that only one polymorphic
species of *Cryptonemia* is involved, and that this Irish population
represents another Pacific introduction. Inconspicuous species
which have recently been recorded for the British Isles, e.g. *C.
cruoriaeformis* and *Fosliella limitata* (Chamberlain, 1977), are
almost certainly indigenous.

Introduced species may vary in their responses to a new environment. Some may remain locally restricted in their distribution; G. doryphora, for example, is still a "Solent species", while others such as S. muticum have spread faster and further. Some successful aliens may outcompete indigenous species, as has been suggested for C. fragile and S. muticum. One alien may even act as vector whereby further adventitious species are introduced; this may be the explanation for the two immigrant spirorbid polychaetes found on Sargassum in Portsmouth Harbour by Knight-Jones et al. (1975). Ecological consequences of marine transplantations, whether intended or inadvertent, cannot be predicted, as Druehl (1973) pointed out. This should be borne in mind when deliberate introductions are proposed, as in the suggestion to introduce the South Atlantic and Pacific kelp Macrocystis pyrifera (L.) C. Ag. into Brittany (Franklin, 1974).

Continuous surveillance of marine communities is required to detect any ecological changes, including the initial arrival of such alien species as discussed here.

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15 | Control of Algal Life-history by Daylength and Temperature

K. LÜNING

Biologische Anstalt Helgoland, Meeresstation, 2192 Helgoland, West Germany

Abstract: How are the characteristic patterns of seasonal growth and reproduction in benthic marine algae controlled by the environment? From what is known of higher plants, which are much better understood at present than algae, it can be expected that photoperiod and temperature are the main controlling factors. A culture system was developed in which various benthic algae were cultivated at 12 combinations of temperature and photoperiod. A night-break regime was included to test for genuine photoperiodic responses. New photoperiodic reactions were found in the *Trailliella*-phase of the red alga *Bonnemaisonia hamifera* Hariot, which formed tetrasporangia only in short days, at 15°C, as well as in the *Codiolum*-stage of the green alga *Monostroma grevillei* (Thur.) Wittr., which became reproductive again only under short-day conditions, at lower temperatures. In the brown alga *Scytosiphon lomentaria* (Lyngb.) Link, which forms erect thalli under short-day conditions, various photoperiodic ecotypes exist, all with different critical daylengths and obviously adapted to the latitudes at which they are growing. Two species of *Petalonia* also exhibited genuine photoperiodic responses. Various stages of other algae were found to react definitely to temperature, not to photoperiod. Among these are the gametophytes of several representatives of the Desmarestiales and Laminariales, which mature only in a certain range of lower temperatures. The ecological significance of these reactions, which enable the plants to occupy a niche in space and time, is discussed.