J. Mar. Biol. Ass. U.K. (2001), **81**, 931–937
Printed in the United Kingdom

Coexistence of introduced and native congeneric algae: *Codium fragile* and *C. tomentosum* on Irish rocky intertidal shores

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The coexistence of three taxa of *Codium* (Chlorophyta: Codiaceae) was examined on wave-swept shores of western Ireland: the introduced macroalgae *Codium fragile* ssp. *atlanticum* and ssp. *tomentosoides* and the native *Codium tomentosum*. In spring 1999 and 2000, four sites were monitored to evaluate whether past predictions regarding temporal changes and species replacement occurred. Introduced and native species of dichotomously branching *Codium* occurred at four tidal levels: in tidepools in (i) the upper barnacle zone; (ii) the mid barnacle/fucoid zone; (iii) the mussel zone, and (iv) on emergent substrata in the red algal turf/kelp zone. *Codium fragile* ssp. *atlanticum* and ssp. *tomentosoides* grew together in 11.9% of surveyed pools containing *Codium*. Compared to 1971 censuses, *C. fragile* ssp. *atlanticum* had increased in relative abundance at all tidal levels, and the dominance of *C. fragile* ssp. *tomentosoides* had declined. The native *C. tomentosum* constituted the same percentage of the population as it did in 1971. Pool availability and primary rock surfaces were not limiting at most sites, indicating that inter-subspecific and inter-specific competition could not account for temporal changes in *Codium* distribution on Irish shores. Ecological constraints other than intra-generic competition may have contributed to the purported long-term changes in *Codium* abundance.

INTRODUCTION

Introduced species of seaweeds are increasingly more frequent on many marine and estuarine shores. In some areas, exotics coexist with native congeners whereas in other areas they become established in communities lacking taxonomically or ecologically similar natives (i.e. 'naïve communities', *sensu* Trowbridge, 1995). The role of native species belonging to the same genus or at least the same family in modifying invasion success has not been well explored (but see Trowbridge, 1995; Trowbridge & Todd, 2001). This issue is directly pertinent to many introduced macrophytes including: (i) the invasive kelp *Undaria pinnatifida* on European and Australasian shores vs native kelps; (ii) the green algal pest *Caulerpa taxifolia* on Mediterranean and Australian shores vs native *Caulerpa* spp.; (iii) the introduced sea grass *Zostera japonica* on north-east Pacific shores vs the native eelgrass *Zostera marina*; and (iv) *Codium fragile* (Suringar) Hariot ssp. *tomentosoides* (van Goor) Silva on north-east Atlantic, north-east Pacific, and Australasian shores vs native *Codium* species. Despite the presumed ecological importance of such areas of sympatry, the frequency of herbivore host–plant changes (e.g. host–expansions vs shifts, *sensu* Trowbridge & Todd, 2001) or of macrophyte competition between introduced and natives has rarely been investigated. Although some introduced species such as *Caulerpa taxifolia* are clearly competitive dominants in their invaded range, the generality of competitively dominant invaders has generally been presumed rather than demonstrated.

One of the most widely distributed introduced macroalgal species is *Codium fragile* ssp. *tomentosoides*. This alga which apparently originated in or near Japan (Silva, 1955) has spread to north-east and north-west Atlantic, Mediterranean, north-east Pacific, and Australasian shores (reviewed by Carlton & Scanlon, 1985; Trowbridge, 1995, 1996, 1998a, 1999). Three introduced subspecies of *C. fragile* are recognized (ssp. *tomentosoides*, ssp. *atlanticum* (Cotton) Silva, and ssp. *scandinavicum*); two of these occur in the British Isles (Silva, 1955; Gibby, 1971; Parkes, 1975; Burrows, 1991; Trowbridge & Todd, 1999a,b). On the north-west Atlantic shores, *C. fragile* ssp. *tomentosoides* became extremely abundant in the absence of native congeners (reviewed by Carlton & Scanlon, 1985; Trowbridge, 1998a). In the north-east Atlantic, ssp. *tomentosoides* invaded an area with native congeners but no indigenous subspecies of *C. fragile* (Silva, 1955, 1957). On north-east Pacific and Australasian shores, ssp. *tomentosoides* invaded regions with both native congeners and conspecifics (Silva & Womersley, 1956; Goff et al., 1992; Trowbridge, 1995, 1996, 1999; references therein).

In contrast to numerous examples of regional and mesoscale coexistence, relatively few sites of local coexistence between native and introduced *Codium* taxa or between two subspecies of *C. fragile* have been described: west Ireland (Burrows & Dixon, 1959; Gibby, 1971; Parkes, 1975; Burrows, 1991), south-east Scotland (Hardy, 1990), north-east England (Hardy, 1981), south-east England (Culley et al., 1983; Baker, 1993; Hazelton, 1993) and south-east Australia (C.D.T., unpublished data) are the only reported locales. Past studies have reported morphological, physiological, and genetic variation between pairs of subspecies but such comparisons were based on collections from different locales (e.g. east vs west coasts of the US, New Zealand, and Scotland) and

even different habitats because areas of local coexistence had not yet occurred in the study regions (Malinowski, 1974; Dromgoole, 1979; Trowbridge, 1996; Trowbridge & Todd, 1999a,b). Local sites of coexistence are at the scale at which direct or indirect effects may be ecologically significant: interspecific competition, inter-subspecific competition, or *Codium*–herbivore interactions. This study focuses on one such area of local coexistence or sympatry.

Interspecific competition between introduced and native *Codium* species and the competitive exclusion of the native alga has been repeatedly assumed (e.g. Parkes, 1975; Farnham, 1980; Norton, 1985; Eno et al., 1997). While *C. fragile* may be competitively excluding the native congener, the ecological process has not actually been demonstrated. In fact, published records of the coexistence of *C. tomentosum* and *C. fragile* are extremely meagre. Furthermore, the possibility of hybridization has been raised for different combinations of subspecies of *C. fragile* (e.g. Silva, 1955, 1957; Silva & Womersley, 1956; Gibby, 1971; Burrows, 1991; Trowbridge, 1998a). However, the paucity of records of the frequency and magnitude that subspecies coexist makes it difficult to evaluate the possibility of gene flow.

On the west-coast shores of the Republic of Ireland and Northern Ireland, *C. fragile* subspecies *atlanticum* and ssp. *tomentosoides* have both encroached on the range of the native congener *C. tomentosum* (Cotton, 1912; Silva, 1955; Gibby, 1971; Norton, 1985; Burrows, 1991; Morton, 1994). Subspecies *atlanticum* apparently appeared in the region ~1808 whereas ssp. *tomentosoides* was first noted in Ireland in 1941 (Cotton, 1912; Silva, 1955; Parkes, 1975). Three workers have noted the coexistence of these taxa on the Irish shores of Counties Donegal, Mayo, Galway, Clare, and Kerry: (i) Parkes (1975) summarized all the known records of *C. fragile* and *C. tomentosum* from herbarium records and the literature; areas of coexistence are clearly visible from her maps and tables; (ii) Burrows (1991) investigated the distribution of *Codium* at several sites; although the data were never published, she does refer to the vertical zonation patterns in her book (Burrows, 1991); and (iii) Burrow's student Michael Gibby (1971) described the 1957–1958 distribution of *Codium* (data from E.M. Burrows and M. de Valéra) and 1971 situation (data collected by Gibby). He reported a reduction in the native *C. tomentosum* and introduced *C. fragile* ssp. *atlanticum* since 1957–1958 and an increase in *C. fragile* ssp. *tomentosoides*. Both Gibby (1971) and Parkes (1975) reported an 'apparent displacement' or 'exclusion' of the first two taxa by ssp. *tomentosoides* at Black Head (County Clare), although the basis of the reported change was neither explained nor the alternative hypothesis of replacement explicitly considered.

Because of the significance of this area of local coexistence, the limited distribution of Gibby's thesis and the fact that Gibby's thesis remains unpublished, the western Irish sites were reinvestigated to document the current situation of introduced vs native *Codium* and to compare them to past unpublished findings of Burrows and Gibby (in Gibby, 1971) for 1957–1958 and 1971. In addition, invaded and non-invaded communities are described to evaluate whether patterns on the shore are consistent with competition as the causal mechanism responsible for the observed long-term temporal changes.

MATERIALS AND METHODS

In May 1999 and June 2000, the following four sites were visited: Spiddal (County Galway) and Black Head, Spanish Point and Duggerna Rocks, Kilkee (County Clare) on the west coast of Ireland. Burrows & Dixon (1959) reported *Codium* spp. from these locales. Also, Gibby (1971) reported that, at Quilty, Spanish Point and Kilkee, *Codium fragile* ssp. *atlanticum* and ssp. *tomentosoides* "grow in the same rock pool and are frequently found within inches of each other."

In 1999 at each site, the pools and emergent substrata were surveyed for *Codium* spp. For each thallus found, the following attributes were measured: thallus length, width of the terminal internode, number of fronds arising from the basal holdfast, and number of dichotomies or orders of branching. Measurements were taken for 70 thalli of *Codium fragile* ssp. *tomentosoides*, 28 thalli of ssp. *atlanticum*, and 34 of *Codium tomentosum*. Discriminant analysis was used to determine the accuracy of classification of specimens based on the four morphological attributes recorded. In the first analysis, species differences were compared (*C. fragile* vs *C. tomentosum*); in the second analysis, morphological differences amongst the three taxa were evaluated. Branch tips were harvested for subsequent microscopic examination; the area 2 cm from the tips was used for identification as advocated by Silva (1957). During utricle examination, the presence or absence of the central constriction in utricles was noted (indicative of *C. fragile* ssp. *tomentosoides*) and the length of the mucronate utricle tip was measured (when present). *Codium tomentosum* has non-mucronate utricle tips, *C. fragile* ssp. *atlanticum* has short mucronate tips, and *C. fragile* ssp. *tomentosoides* typically has long ones ($<68\,\mu$m) (Silva, 1957).

In June 2000, the four sites were revisited to collect supplementary data regarding potential competition (between species and subspecies of *Codium*). The availability of primary and secondary space was documented because the competition hypothesis implicitly assumes that space is a limiting resource. At Kilkee, the following were quantified: (i) the per cent coverage of species within 0.25 m^2 quadrats centred upon *C. fragile* thalli, using the 100 random dot technique; (ii) the distance between each *C. fragile* thallus and its nearest neighbour; and (iii) the substrata to which *Codium* thalli were attached. The community structure was also documented for sympatric non-invaded tide pools at the same tidal level to evaluate whether there were certain community attributes associated with invaded pools. Because of the paucity of published data about the native *C. tomentosum* (but see Baker, 1993; Hazelton, 1993), comparable data were collected at Spanish Point South (County Clare) where the native species was abundant.

RESULTS

Distribution

On the shores of County Galway and County Clare, Ireland, *Codium* spp. occurred at four tidal levels: in tidepools in the barnacle, fucoid, and mussel zones and on emergent substrata in the red algal turf/kelp zone (Figure 1). At no site were these pools at all tidal levels

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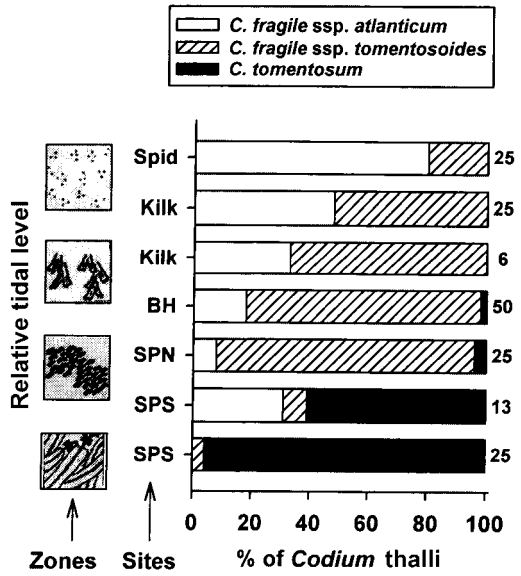

Figure 1. Relative abundance of introduced and native *Codium* species on rocky shores of County Galway and County Clare, Ireland. Numbers indicate the number of algal thalli examined at each site. Floral and faunal assemblages designating zones are based on Lewis (1964).

but at two sites, Kilkee and Spanish Point, tidepools with *Codium* occurred at two or three tidal levels.

At Spiddal, *Codium fragile* inhabited tidepools in the barnacle zone above the tidal level of *Fucus* (Figure 1). The pools were surrounded by the barnacle *Balanus balanoides* and lichens; *B. balanoides* and the fucoid *Pelvetia canaliculata*; or just *B. balanoides*. Littorine snails (*Littorina littorea*) and limpets (*Patella* spp.) were common in the pools. Only 3% of pools surveyed in June 2000 were occupied by *Codium* spp., and there were few thalli per pool (range 1–7) (Figure 2A). In most cases, there was low secondary cover; at least half of each pool was either bare space or covered by encrusting coralline algae. Thus, pool availability and space for macroalgal attachment were not limiting. The predominant *Codium* at this site in May 1999 (Figure 1) was *C. fragile* ssp. *atlanticum* (N=25 thalli).

At Kilkee, *Codium* inhabited pools in the barnacle zone (Figure 1); neighbouring pool dwellers included the brown alga *Bifurcaria bifurcata*, the coralline red alga *Corallina officinalis*, and the purple urchin *Paracentrotus lividus*. *Codium* was most common in shallow pools with considerable bare space and/or extensive coralline algal crust with a relatively open canopy; only the two introduced subspecies were found. In deeper pools and those lower on the shore (e.g. Duggerna Rocks), other algal species monopolized the space and *Codium* was not found, not even in the understorey.

At Black Head, all three *Codium* taxa occurred in tidepools in the barnacle/*Fucus* zone. Pools had high densities of purple urchins (*Paracentrotus lividus*) in cracks, crevices, and depressions carved into the limestone rock; herbivorous sacoglossan sea slugs were also abundant at this site. *Codium* occupied 54% of the upper pools (N=50 pools) and 20% of the lower ones (N=70 pools). Thus, *Codium* was more frequent at Kilkee and Black Head than at Spiddal, and there were up to six thalli of *Codium* per invaded pool (Figure 2A,B).

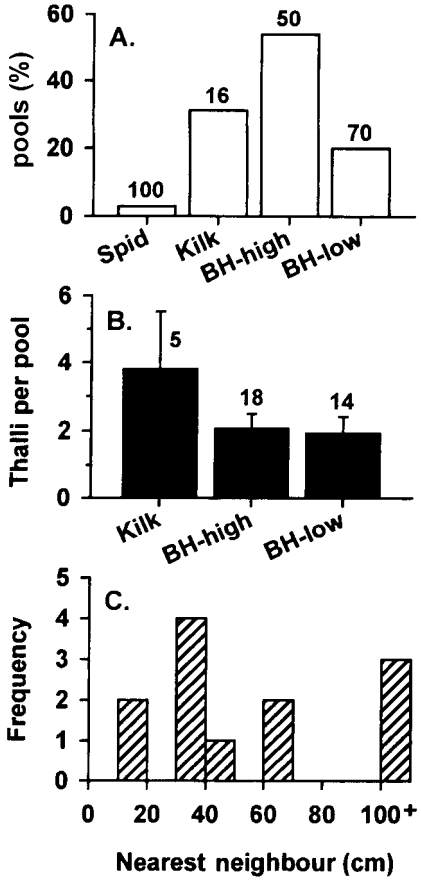

Figure 2. Different abundance indices of *Codium* spp.: (A) percentage of pools occupied per site; (B) number of *Codium* thalli per pool; and (C) frequency pattern of nearest *Codium* neighbour. Data collected from Spiddal, Black Head, and Kilkee in June 2000; site names are abbreviated Spid, BH, and Kilk, respectively. Error bars indicate 1SE; numbers above bars indicate number of pools or thalli (A and B, respectively).

At Spanish Point, *Codium* inhabited several different types of habitats, including pools and emergent substrata in the mussel and kelp zones (Figure 1). *Codium tomentosum* occurred on low intertidal, generally emergent, substrata. Neighbouring species included various kelp species, red algal turf species, the fucoid *Himanthalia elongata*, and the green alga *Cladophora ?rupestris*. Sacoglossan slugs (*Elysia viridis* and *Placida dendritica*) were frequent on *Codium* at this site as well. In tidepools filled with urchins (*Paracentrotus lividus*) within the mussel zone (*Mytilus edulis*), *C. fragile* ssp. *tomentosoides* was the most common *Codium* at the north end of the site; in contrast, *C. fragile* ssp. *atlanticum* and *C. tomentosum* were also common in pools and on emergent substrata at the south end of Spanish Point.

Morphological variation

When discriminant analysis was used to determine the accuracy of classification of species based on four macrostructural attributes (thallus length, branch width, number of axes, orders of branching), 95% of the thalli of *Codium fragile* and 88% of *C. tomentosum* were correctly assigned for an overall value of 93% of correct classification (Wilks' Lambda, $F=46.9$, 4 df, $P<0.001$). In a three-way comparison, 67% of the thalli were correctly

https://doi.org/10.1017/S0025315401004854 Published online by Cambridge University Press

classified, with the two subspecies of *C. fragile* being the least accurately assigned. The inaccurate classifications were primarily due to extensive overlap in gross morphology between subspecies (despite the statistically significant differences: Wilks' Lambda, $F=3.8$, 4 df, $P=0.007$).

The relative length of the mucron or point on the utricle tips of the three *Codium* taxa varied significantly (one-way ANOVA, $F=532.4$, $P<0.001$, N=169). *Codium fragile* ssp. *tomentosoides* had mucronate tips more than twice as long as those of *C. fragile* ssp. *atlanticum*, and *C. tomentosum* had no mucron at all (mean values were all statistically different, based on post-hoc Tukey tests). Thus, at the population level, there was no statistically significant overlap in utricle characters; the *Codium* taxa could be unambiguously distinguished on the basis of utricle morphology.

Temporal changes

Comparisons of frequency data from 1958 (Burrows in Gibby, 1971), 1971 (Gibby, 1971), and 1999 (this study) indicate highly significant temporal changes in relative *Codium* abundance (*G*-test, $G=180.4$, 4 df, $P<0.001$, N=302, Figure 3). In 1958, Burrows found a preponderance of *C. fragile* ssp. *atlanticum* at County Mayo, Galway, and Clare sites. In 1971, ssp. *tomentosoides* predominated. In 1999, although ssp. *tomentosoides* still predominated (Figure 3), the reported replacement process had not gone to completion. Furthermore, comparisons of the frequency of different *Codium* taxa with respect to tidal level (Figure 4) indicate that *C. fragile* ssp. *atlanticum* increased in abundance between 1971 and 1999, not only overall ($G=31.2$, 1 df, $P<0.001$) but also across tidal levels ($G=25.6$, 1 df, $P<0.001$). The frequency of occurrence of *C. tomentosum*, however, remained constant ($G=0.587$, 1 df, $P=0.444$; Figure 4).

Coexistence and competition

Patterns anticipated if inter-specific or inter-subspecific competition was occurring were: (i) limited space (for attachment); and/or (ii) partial coexistence. Documented patterns of community structure at Kilkee (Figure 5A,B) indicate that while bare space *per se* was perhaps limiting, attachment space on encrusting and erect coralline algae or sessile invertebrates (barnacles, mussels, serpulid polychaetes) was not limiting despite the fact that sampling was conducted in early summer when the abundance of ephemeral algae was at an annual peak. Invaded pools tended to have more algal canopy by the macroalgae *Bifurcaria*, *Laminaria*, and *Ectocarpus* than uninvaded pools (Figure 5B). The frequency of pool occupancy was 30% at Kilkee at tidal levels that *Codium* inhabited (Figure 2A).

Partial coexistence did occur between species and subspecies of *Codium*. The number of thalli per pool averaged about four at Kilkee and two at Black Head (Figure 2B). The thalli did not form high-density beds but were frequently widely spaced tens to hundreds of centimetres (Figure 2C). During the 1999 survey, 4.8% of the 42 pools with *Codium* contained two species (*Codium tomentosum* and *Codium fragile*); the remaining 95.2% contained a single species (usually *C. fragile*). Furthermore, 11.9% of the pools contained both ssp. *atlanticum* and ssp. *tomentosoides*; the remaining pools contained either one or the other.

The majority of thalli of *C. tomentosum* were observed on emergent substrata. The native alga was most abundant on a series of sloping benches or ledges at Spanish Point South that were scoured by sand. *Codium fragile* comprised only 4% of the 150 *Codium* found in this habitat. A wide size-range of thalli was found (Figure 5C) from small germlings to large, mature thalli. Other neighbouring species were red algal turf, *Corallina*, kelp, *Fucus*, and sessile invertebrates (Figure 5D).

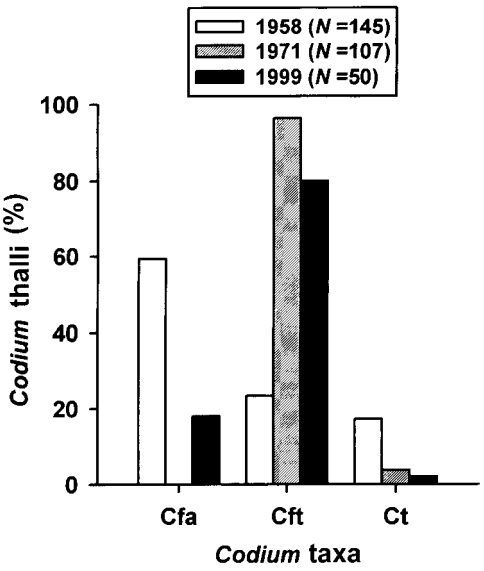

Figure 3. Relative abundance of introduced and native *Codium* spp. at Black Head, County Clare, Ireland. Algae are abbreviated as follows: Cfa, *C. fragile* ssp. *atlanticum*; Cft, *C. fragile* ssp. *tomentosoides*; and Ct, *C. tomentosum*. Numbers indicate number of algal thalli examined. The 1958 and 1971 data are from Gibby (1971).

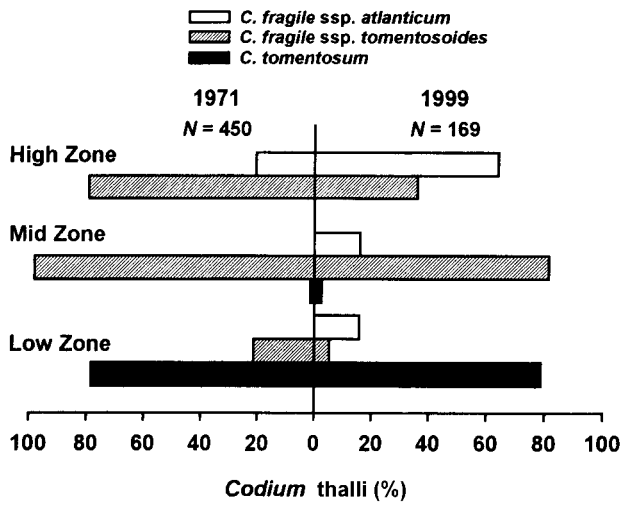

Figure 4. Temporal change of introduced and native *Codium* species on rocky shores of County Galway and County Clare, Ireland. The 1971 data are from Gibby (1971); 1999 data are pooled from four sites (Spiddal, Black Head, Spanish Point, and Kilkee).

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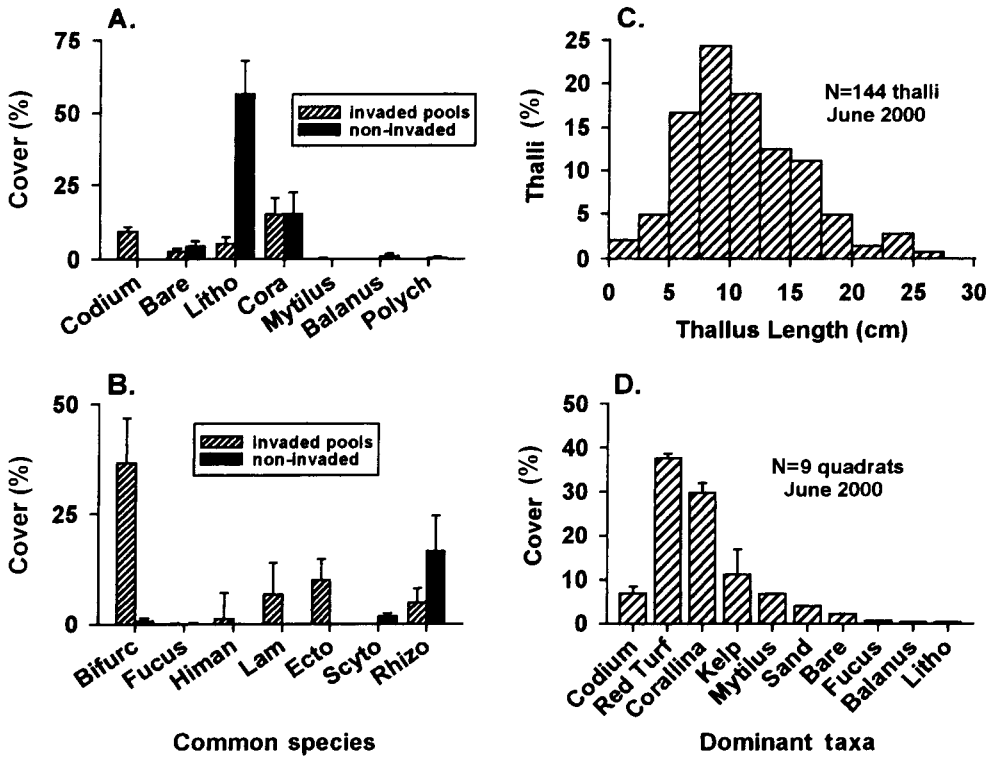

Figure 5. Structure of the (A,B) invaded community at Kilkee and (C,D) native community at Spanish Point South, County Clare in June 2000. (A) Primary and secondary cover of species; (B) tertiary or canopy cover of species in pools occupied and not occupied by the introduced alga *Codium fragile* (either subspecies); (C) size–frequency distribution of native *C. tomentosum*; and (D) community structure. (A) Bare, bare space; *Bifurc*, *Bifurcaria*; *Cora*, *Corallina*; *Codium*, *Codium tomentosum*; *Ecto*, *Ectocarpus*; *Himan*, *Himanthalia*; Kelp, *Alaria* and *Laminaria*; *Lam*, *Laminaria*; *Litho*, *Lithothamnion*; Polych, polychaete worms; *Rhizo*, *Rhizoclonium*; *Scyto*, *Scytosiphon*.

DISCUSSION

Morphological variation

Cotton (1912) remarked that the introduced *Codium fragile* ssp. *atlanticum* "attracted attention on the first day spent on Clare Island, and on one or two occasions only was there the slightest difficulty in distinguishing it at a glance from *Codium tomentosum*" (p. 16). The main distinctions between the species are the narrower branches, the smaller non-mucronate utricles, and typically darker colour in *C. tomentosum* than in the invaders (Cotton, 1912; Silva, 1955; Gibby, 1971; Trowbridge & Todd, 1999a,b). The microscopic analyses of utricle tips (Gibby, 1971; Trowbridge, this study) and the discriminate analyses strongly support the morphological bases for Cotton's astute observations and Silva's (1955) classic paper distinguishing dichotomously branching *Codium* spp. of the region.

Distribution, coexistence and competition

Cotton (1912) compared the spatial and temporal distributions of the native *Codium tomentosum* and the introduced *Codium fragile* ssp. *atlanticum* (as *C. mucronatum* var. *atlanticum*) during his Clare Island survey. For example, the native alga occurred near the "low-watermark usually semi-exposed, or in deep or shady rock-pools" (p. 114) and the introduced alga occurred high on the shore. There were also temporal differences with the native maturing in the winter and the invader in the summer. More recently, Gibby (1971) and Burrows (1991) quantified the spatio–temporal variation of *Codium* taxa on Irish shores; they reported that the native alga occurred slightly lower on the shore than the two invaders although the distributions overlapped extensively. This study supports the vertical zonation patterns with *C. fragile* ssp. *atlanticum* inhabiting slightly higher pools than ssp. *tomentosoides*, although local coexistence was certainly frequent (e.g. 11.9% of pools with *Codium* spp.). Thus, these results support earlier work in Jersey, south-east England (Culley et al., 1983; Baker, 1993; Hazelton, 1993).

Long-term temporal changes of the *Codium* assemblage are more difficult to evaluate. The two introduced subspecies of *C. fragile* predominate high on the shore but the status of the native has really never been quantitatively demonstrated. Perhaps *C. tomentosum* was never in the high and mid intertidal pools at these sites or was extremely sparse. To infer that the invaders are displacing or replacing the native pre-supposes that the native was indeed in the pools before the appearance of *C. fragile*. Parkes (1975) stated that Professor Valéra recorded *C. fragile* ssp. *tomentosoides* at Spiddal and Mweenish "at the expense of *C. fragile* ssp. *atlanticum* which can no longer be found in these areas" (p. 130). Nowhere in the British Isles has *C. tomentosum* been studied sufficiently to warrant blaming the exotics for the native's decline. Even if competition did occur in southern England as suggested by Farnham (1980), the biotic and abiotic processes controlling *Codium* abundance may well differ in western Ireland, Scotland, and north-eastern England; ecological

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processes are not typically uniform in different regions. Thus, alternative hypotheses for the purported decline of *C. tomentosum* should be assessed, including intergeneric competition (proposed by Culley et al., 1983) and herbivory. Furthermore, several studies (Baker, 1993; Hazelton, 1993; Trowbridge, this study) demonstrate that *C. tomentosum* is not only still present but also may be increasing in local abundance relative to earlier surveys (Gibby, 1971; Culley et al., 1983).

Other alternatives

The role of herbivory by generalist or specialist herbivores in modifying the abundance or distribution of Irish *Codium* spp. has not been well investigated except in Lough Hyne (e.g. Kitching & Thain, 1983; Kitching, 1987). In contrast to the statement by Eno et al. (1997) that the lack of grazers probably contributed to establishment success, *C. fragile* ssp. *atlanticum* is palatable to the herbivorous snail *Littorina littorea* and is consumed at much greater rates than neighbouring pool-dwelling algae (Trowbridge & Todd, 1999a). The importance of urchin and limpet grazing merits investigation given the high densities of the grazers in pools with *Codium*.

Colgan (1911) reported the high abundance of the herbivorous sea slugs *Elysia viridis* and *Placida dendritica* on *Codium* during the Clare Island survey, County Mayo: "No less than 93 specimens [of *P. dendritica*] were found living on two medium-sized plants of *Codium* taken from rock-pools" (pp. 21–22). Although Colgan reported the sea slugs "always occurring on *Codium tomentosum*" (p. 21), it is not clear whether Colgan was aware of the presence of *C. fragile* ssp. *atlanticum* found by Cotton during the algal part of the Clare Island survey. What is clear, however, is that the west coast of Ireland has a high rate of slug attack of *Codium* relative to most other reported regions in the world. Colgan (1911) also noted that *P. dendritica* was abundant near the low-water mark; almost all the specimens of *P. dendritica* were found on *Codium tomentosum* on low intertidal emergent benches. Trowbridge (1998b) demonstrated that sacoglossan attack of *Codium* spp. was frequently concentrated on desiccation-stressed thalli on Oregon, New Zealand and Scottish shores. Thus, thalli in pools should be less vulnerable to attack than those on emergent surfaces. *Elysia viridis*, however, frequently occurs in low and mid intertidal pools throughout the British Isles; fluctuations in water temperature and/or salinity may exclude this slug species from high pools (see Hagerman, 1970) where *C. fragile* ssp. *atlanticum* generally occurs.

Finally, the autecology of *Codium tomentosum* or *C. fragile* ssp. *tomentosum* has not yet been investigated. Differential growth rates, fecundity, temperature and salinity tolerances, and many other factors may account for apparent changes in algal distributions. Yang et al. (1997) made a preliminary assessment of these factors. Unfortunately, they did not present quantitative results (e.g. graphs or tables) or conduct statistical tests, so unambiguous conclusions cannot be drawn from their study. Furthermore, the role of photobiology, nutrient dynamics, and pollutants to *Codium* dynamics are obvious alternative hypotheses. In conclusion, the questions of whether *C. tomentosum* is actually declining in abundance in the British Isles and what the causal mechanism may be is still an open issue.

I thank W. Farnham for generously sending me the MSc thesis of Michael Gibby and two unpublished student reports (Baker, 1993; Hazelton, 1993) and G. Hardy for sharing his information about his work on Northumbrian and Berwickshire shores. Constructive comments and suggestions by W. Farnham, G. Hardy, A. Pulsford, and one anonymous referee significantly improved this paper: to all, I am very grateful. I am also indebted to my husband H. Ross for his ever-cheerful field assistance. This research was supported by the kindness of colleagues and friends.

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Submitted 14 March 2001. Accepted 8 August 2001.