Journal of the Marine Biological Association of the United Kingdom, 2009, 89(2), 255–263.
doi:10.1017/S0025315408002609 Printed in the United Kingdom

Regional comparisons of *Codium* (Chlorophyta) assemblages in the northern versus southern English Channel

CYNTHIA D. TROWBRIDGE[1] AND WILLIAM F. FARNHAM[2]

[1]Department of Zoology, Oregon State University, PO Box 1995, Newport, OR 97365, USA, [2]Institute of Marine Sciences, University of Portsmouth, Eastney, Portsmouth PO4 9LY, UK

The cryptic invasion of the Asian macroalga Codium fragile *(Suringar) Hariot ssp.* fragile *on north-eastern Atlantic shores has been long considered a classical example of a successful invader that has competitively displaced native congeners. Yet, the lack of quantitative information about morphologically similar native congeners, namely* Codium tomentosum *Stackhouse and* C. vermilara *(Olivi) Delle Chiaje, has hindered interspecific comparisons and ecological predictions. From September 2002 to 2005, we made extensive intertidal surveys on 12 northern and 26 southern rocky shores of the English Channel, specifically documenting the abundance, distribution and identity of* Codium *assemblages. On the north side of the English Channel, the native* C. tomentosum *and alien* C. fragile *were both sparsely distributed in intertidal pools in Devon. In contrast, the natives were absent from and the alien was locally abundant in shallow lagoons and rocky reefs around Bembridge and Whitecliff on the Isle of Wight. Finally, in the Channel Islands off the Atlantic coast of France,* Codium *spp. were abundant in pools and on low-shore emergent substrata with native species predominating. Patterns of distribution varied substantially among Guernsey, Jersey and Alderney, despite their close proximity. The regional variation in the algal distributions merits further investigation to determine whether the pattern is produced by: (1) anthropogenic activities and effects; (2) ecological interactions; (3) oceanographic factors; or (4) some combination of these.*

Keywords: *Codium*, non-indigenous species, native species, north-eastern Atlantic, English Channel

Submitted 24 April 2008; accepted 18 June 2008

INTRODUCTION

Alien species of marine invertebrates, algae and fish are increasingly becoming important components and interactors in marine communities worldwide. In many cases, the non-indigenous species (NIS) have been noted due to increases in habitat-formers and ecosystem engineers such as invasive mussels, seagrass (Posey, 1988), or large seaweeds (Trowbridge, 2006). In other cases, NIS are detected by functional changes in species interactions. Quite often, the establishment and spread of NIS is visually obvious such as with the brown alga *Sargassum muticum* (Yendo) Fensholt. However, if the NIS are morphologically similar to resident species, the incursion can be cryptic, requiring detailed morphological and/or molecular analyses to elucidate the invasion dynamics. An important example of such cryptic invaders is the Asian green macroalga *Codium fragile*, originating from Japan, which has appeared on temperate shores throughout the world (Trowbridge, 1998; Provan *et al.*, 2005, 2007). In most invaded regions (except north-western Atlantic shores), this seaweed entered communities with native congeners and even non-weedy conspecifics. Untangling the invasion dynamics and documenting contemporary patterns of species occurrence is crucial to making realistic risk assessments of invasives and establishing a quantitative baseline from which future changes can be assessed.

Codium fragile ssp. *tomentosoides* was first collected on mainland European shores (Holland) ~1900 and described in 1955 (Silva, 1955). Until recently, the first recognized record for the British Isles was 1939 in Devon, south-west England (River Yealm estuary) (Silva, 1955). Exciting new molecular work, however, has demonstrated that the alga was in Ireland by 1845, Scotland by 1891 and England by 1894 (Provan *et al.*, 2007). Furthermore, based on the botanical code, the correct name of this invasive alga is *Codium fragile* ssp. *fragile* (Maggs & Kelley, 2007; Provan *et al.*, 2007). For simplicity, we refer herein to this introduced alga as *C. fragile*. The conspecific *C. fragile* ssp. *atlanticum* (A.D. Cotton) P.C. Silva does not occur in the English Channel (see Trowbridge *et al.*, 2004 and Provan *et al.*, 2007, regarding incorrect records) so our use of the binomial *C. fragile* herein is restricted to the invasive *C. fragile* ssp. *fragile*.

During the 20th Century, *Codium fragile* proliferated on north-western and north-eastern Atlantic shores (and elsewhere). In the former region, the invasive alga now dominates many shallow areas, competing with kelp in the Gulf of Maine (Levin *et al.*, 2002; Scheibling & Gagnon, 2006; Schmidt & Scheibling, 2006, 2007) and seagrass in shallow lagoons (Garbary *et al.*, 1997, 2004). It has also invaded rocky intertidal pools (Bégin & Scheibling, 2003;

Corresponding author:
C.D. Trowbridge
Email: trowbric@yahoo.com

Schmidt & Scheibling, 2005). The interspecific interactions have been well demonstrated (e.g. Levin *et al.*, 2002; Scheibling & Gagnon, 2006; Schmidt & Scheibling, 2005, 2007).

In contrast, work on north-eastern Atlantic shores has been more observational as field experiments with *Codium fragile* are illegal in the UK (Countryside Act of 1981). In the 1970s and 1980s, *C. fragile* formed extensive beds at Bembridge on the Isle of Wight (Benson *et al.*, 1983; Farnham, personal observation) and in Lough Hyne Marine Reserve, County Cork, Ireland (Norton, 1991). Some phycologists expressed concern that the introduced *C. fragile* would outcompete and displace native congeners (e.g. Farnham, 1980) (e.g. Figure 1A). Because there was no direct evidence of interspecific competition or a limiting resource, Trowbridge (1998, 2001) suggested the dynamics may involve temporal species' replacement (a decline of the native and unrelated increase of the introduced species; Figure 1B). A third hypothesis is that the cryptic invasion of *C. fragile* led to historical over-estimation of the native population abundance and geographical range with a subsequent readjusted perception after the description of *C. fragile* ssp. *tomentosoides* by Silva (1955) (Figure 1C). These three models are based on scientific observation and hypothesis formulation.

The species identification problem has been further exacerbated with *Codium tomentosum* and *C. vermilara* being considered warm-water species whose northward range expansion would be expected during climate warming (e.g. Hiscock *et al.*, 2004; Mieszkowska *et al.*, 2005) and *C. fragile* being considered constrained in the UK by cool summer temperatures (Elliott, 2006) when the alga already occurs north of Trondheim, Norway, and in the Canadian Maritimes. Climatic change predictions could lead to a fourth hypothetical pattern: southward range contraction of the native *Codium* species in cold winters (e.g. 1962/1963) and northward proliferation in warm periods (Figure 1D).

Without a detailed understanding of contemporary distributions of the native and introduced congeners, predictions about future ecological and environmental changes cannot be realistically evaluated. Our primary objective was to test the displacement hypothesis by comparing the frequency of the high-profile native and introduced *Codium* species at three locations within the English Channel where historical records and some historical specimens exist.

MATERIALS AND METHODS

Study regions

We surveyed three major regions of north-eastern Atlantic shores: the mainland of southern England, the Isle of Wight (IoW) and the Channel Islands. Of the six counties bordering the north side of the English Channel, we concentrated most of our surveys in Devon (Figure 2A, B; Table 1) due to the predominance of historical *Codium* records there; however, we did visit a site in Sussex (Pagham Harbour) and another in Dorset (Chesil Fleet) where the second author had previously collected *Codium* (Farnham, 1975). The IoW, directly south of Portsmouth, is separated from the Hampshire mainland by the Solent, a deep strait. We surveyed four sites on the east coast of the IoW: Bembridge/Lifeboat Station North, Whitecliff Ledge, Horse Ledge and Yellow Ledge (Figure 2C). These sites were selected based primarily on the

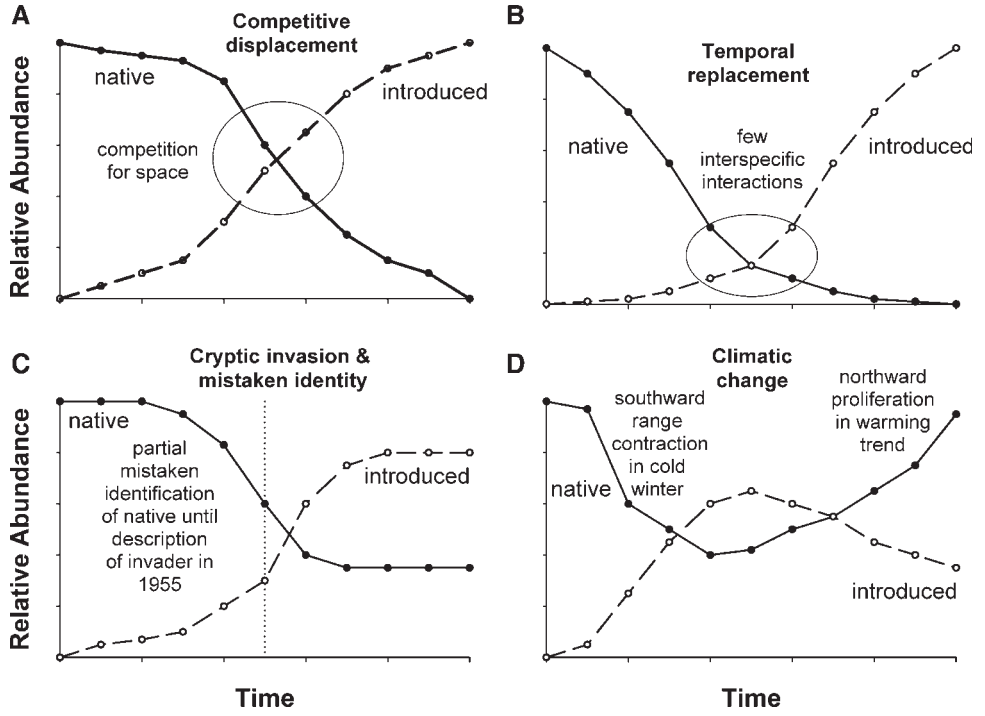

Fig. 1. Four schematic models of temporal change of native and introduced *Codium* spp. in the British Isles. Distinguishing between (A) competitive displacement and (B) temporal replacement depends on quantifying limiting resources (e.g. space) and interspecific interactions (or lack thereof). Phycological re-examination of historical specimens supports (C) but accurate population surveys are lacking. (D) Temporal changes of introduced and native species with known cold winters, warm summers and general climate changes have not been extensively evaluated.

https://doi.org/10.1017/S0025315408002609 Published online by Cambridge University Press

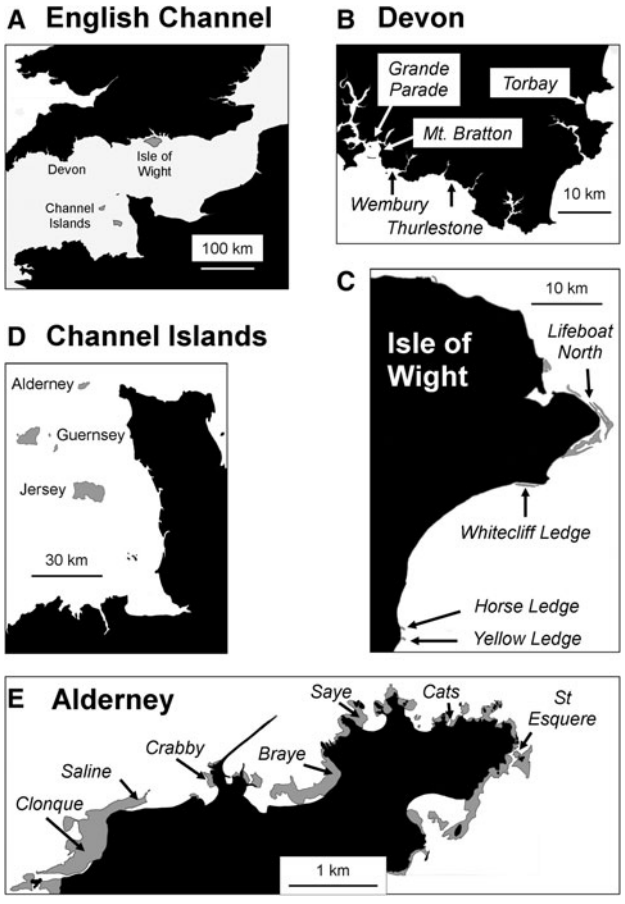

Fig. 2. Map of the survey regions and sites in the English Channel (north-eastern Atlantic shores). Scale bars are shown in each figure panel.

phycological literature (Foslie, 1893; Morey, 1909; Delf & Grubb, 1923; Norkett, 1947; Jones, 2000).

The Channel Islands in the Bay of St Malo off the Atlantic coast of France have received considerable phycological scrutiny (e.g. Lyle, 1920, 1923, 1937; Marquand, 1901, 1902, 1908; Van Heurck, 1908; Dixon, 1961; Feldmann, 1961; Culley *et al.*, 1983). We surveyed the three larger islands (Jersey, Guernsey and Alderney; Figure 2D) for logistical reasons of accessibility. Some results from Jersey and Guernsey have already been published (Trowbridge & Farnham, 2004; Trowbridge *et al.*, 2004). We concentrate herein on Alderney results, previously unpublished Guernsey and Jersey data and regional comparisons. We sampled ~1600 pools from seven Alderney sites from Clonque on the north-west shore to St Esquere on the north-east tip of the island (Figure 2E). Sites were selected based on accessibility and availability of rocky substrata.

Surveys

From September 2002–2005, we surveyed intertidal rock pools plus emergent substrata for the invasive *Codium fragile* and native congeners at 38 sites in the target regions (Table 1). Pools ranged in size from ~15 cm to 2–5 m in diameter with most being <1 m (notable exceptions were the vast intertidal lagoons at Bembridge, IoW). We quantified the percentage of rock pools occupied by *Codium* spp. at each site and, where possible, within each of four tidal levels, defined by the following zone-forming fucoids: the rockweeds *Pelvetia canaliculata* (Linnaeus) Decaisne & Thuret, *Fucus spiralis* Linnaeus, *F. vesiculosus* Linnaeus and *F. serratus* Linnaeus. At the upper end of the shore, *Codium* spp. were never on emergent substrata; on the lower half of the shore, *Codium* thalli were occasionally on emergent surfaces; we present results of pool-dwelling thalli (% occurrence) and densities of emergent thalli (based on 0.25 m^2 quadrats). Our sampling methodology was, for the most part, non-destructive. Branch tips of *Codium* thalli (2 cm from each thallus) were harvested to identify species, based on the morphology of the utricles, using an Olympus Mic-D digital compound microscope. Digital voucher specimens were captured for large numbers of thalli. Thallus length was measured to the nearest millimetre; size–frequency distributions of thallus length were compared for different regions, using pairwise Kolmogorov–Smirnov tests.

RESULTS

Sites in southern England (mainland)

At six sites in Devon (964 pools surveyed in April–May 2004), 1.2% of pools overall contained *Codium* spp. (Figure 3A), and <4% contained *Codium* spp. at any site. *Codium* spp. were sparsely distributed but did occur in pools at all tidal levels. We found 16 thalli of *C. fragile* and 23 of C. *tomentosum* in six days of low-tide surveys. The algal species averaged 3.2 and 3.3 thalli per occupied pool, respectively (Student's *t*-test, $t = 0.068$, $P = 0.947$). We found no *Codium* at Pagham Harbour in Sussex, despite the available habitats being characteristic of *C. fragile* (small rocks, large shells and other hard substrate) and the species having been collected there previously. Within the Chesil Fleet lagoon in Dorset, we found abundant native *C. vermilara* and introduced *C. fragile* on low-shore rocks below the *Ascophyllum* zone. Of the 31 thalli collected on 14 September 2002, 45% were *C. fragile* and 55% were *C. vermilara*.

On Devon intertidal shores, a wide range of sizes was present for *Codium tomentosum* and *C. fragile*. However, what was striking was the paucity of juvenile thalli of the latter (Figure 4A): there were no thalli or fronds <8 cm long. The size-structure of *C. fragile* (N = 16) on Devon shores was significantly different than that on Jersey shores (Giffard, Gréve de Lecq, Castle and Sauchet) sampled during the same 2-week period (Kolmogorov–Smirnov, $d_{max} = 0.458$, $P = 0.002$) but not that on Lihou and La Jaonneuse on Guernsey shores ($d_{max} = 0.283$, $P = 0.241$) (Figure 4; Table 2). Jersey pools had large numbers of incipient fronds (0–2 cm) as well as large ones (to 35 cm). When we repeated the analysis across all collections from 2002 to 2005, we found significant differences in populations of *C. fragile* in the different regions (Table 2). The paucity of juveniles in Devon relative to other areas was the main distinguishing factor.

Sites on the Isle of Wight

Only one species of *Codium* was recorded: *C. fragile* was widely distributed on the east side of the IoW. Thalli were large, abundant and heavily covered with epiphytes at Bembridge in the shallow lagoons and at Whitecliff on low

https://doi.org/10.1017/S0025315408002609 Published online by Cambridge University Press

Table 1. Spatial and temporal details of *Codium* surveys in the English Channel, north-eastern Atlantic Ocean.

Region	County or island	Sampling dates	Site locations	Latitude and longitude	Pools surveyed
Northern Channel					
	Devon	April 2004	Grande Parade, Plymouth	50°24.1′ N 4°09.0′ W	50
		April 2004	Mt Batten, Jennycliff Bay	50°21.5′ N 4°07.8′ W	125
		April 2004	Wembury	50°19.0′ N 4°05.6′ W	284
		April 2004	Thurlestone, Bigbury Bay	50°15.8′ N 3°51.7′ W	330
		April 2004	Torquay, Torbay	50°27.6′ N 3°32.4′ W	25
		April 2004	Brixham, Bigbury Bay	50°24.1′ N 3°30.0′ W	150
	Dorset	May 2003	Chesil Fleet	50°35.6′ N 2°29.6′ W	na
	Isle of Wight	May 2003, May and September 2005	Bembridge/Lifeboat Station North	50°41.6′ N 1°03.9′ W	na
		May 2005	Whitecliff Ledge	50°39.9′ N 1°06.5′ W	na
		May and September 2005	Horse Ledge	50°37.8′ N 1°10.4′ W	200
		May 2005	Yellow Ledge	50°36.7′ N 1°10.3′ W	100
	Sussex	September 2002	Pagham Harbour	50°35.6′ N 2°29.6′ W	na
Southern Channel					
	Guernsey	May 2004	La Jaonneuse	49°30.4′ N 2°32.0′ W	100
		June 2005	Site 3 near Albecq	49°29.8′ N 2°34.2′ W	240
		September 2002	Bordeaux	49°29.4′ N 2°30.0′ W	nd
		September 2002	Port Soif	49°29.3′ N 2°34.9′ W	nd
		September 2002	Grande Rocques	49°29.2′ N 2°35.4′ W	nd
		June 2005	Albecq Bay	49°28.5′ N 2°36.4′ W	231
		June 2005	Le Catioroc, Perelle Bay	49°27.6′ N 2°38.6′ W	123
		September 2002 and May 2004	Lihou Causeway	49°27.5′ N 2°39.6′ W	85
		September 2002	Moulin Huet	49°25.5′ N 2°32.9′ W	nd
	Jersey	May 2003	La Rocque	49°10.0′ N 2°01.5′ W	nd
		May 2003	Portelet Harbour	49°10.3′ N 2°10.6′ W	nd
		May 2004	Giffard Bay	49°15.0′ N 2°06.6′ W	130
		May 2004	Gréve de Lecq	49°14.9′ N 2°12.0′ W	59
		May 2004	Sauchet Bay	49°14.5′ N 2°03.0′ W	67
		May 2004	Queen Elizabeth Castle	49°10.5′ N 2°07.4′ W	226
		May 2004	Rozel Harbour	49°14.2′ N 2°02.6′ W	147
		May 2004	Fliquet Bay	49°13.6′ N 2°01.1′ W	59
		May 2003	L'Archirondel	49°12.9′ N 2°01.1′ W	nd
		May 2004	Corbière	49°10.9′ N 2°14.6′ W	133
	Alderney	June 2005	Saye Bay South	49°43.8′ N 2°11.0′ W	101
		June 2005	Cat's Bay	49°43.7′ N 2°09.7′ W	324
		June 2005	St Esquere Bay	49°43.6′ N 2°09.6′ W	290
		June 2005	Crabby Bay	49°43.4′ N 2°12.3′ W	119
		June 2005	Braye Bay	49°43.4′ N 2°11.3′ W	311
		June 2005	Saline Bay	49°43.3′ N 2°13.0′ W	149
		June 2005	Clonque Bay	49°43.0′ N 2°13.3′ W	325

na, pool habitat not available; nd, no data because pool occupancy was not measured (algal thalli were surveyed rather than pools *per se*).

intertidal, emergent substratum; high densities of juveniles were found under the adult canopies (Figure 5A, B). For example, at Whitecliff Bay, we recorded a mean of 3.0 large thalli and 19.0 small ones per 0.25-m^2 quadrat. In contrast, thalli were small and sparsely distributed in high pools at Horse and Yellow Ledges, Shanklin (Figure 5C, D). Of 300 pools surveyed, only nine contained *C. fragile* (3%); this value was significantly greater than the pool occupancy in Devon (Figure 3A). The derbesioid or vaucherioid stage of *Codium* carpeted the bottom of the pools; utricle examination of the small fronds (Figure 5C, D), arising from the mats, confirmed that the species was *C. fragile*. This size-structure and the vaucherioid stage were seen again when we re-visited the sites in June and August 2007. The size–frequency distributions differed significantly between each pairwise combination of sites (Kolmogorov–Smirnov, $P < 0.001$ for all except one (Horse Ledge versus Whitecliff), which was $P = 0.009$).

Sites on the Channel Islands

The situation on shores in the southern English Channel differed fundamentally. Three species of upright, branching *Codium* were recorded, and all were relatively abundant. By far the most abundant taxon was *C. tomentosum* that formed patchily distributed, high-density beds at many low-shore sites around Alderney. In addition, pool occupancy by *Codium* was greater in the Channel Islands than on Devon shores and IoW shores (except for the intertidal lagoons at Bembridge) (Figure 3A; Likelihood ratio Chi-square, $G = 210.2$, $N = 4483$, 2 df, $P < 0.001$). Furthermore, there was clear tidal-level variation in pool occupancy in the Channel Islands. In June 2005, *Codium* was present in 7% of pools surveyed on Guernsey in the high-shore, *Pelvetia* zone and 27% of the pools in the mid-shore, *Fucus spiralis* zone. This pattern was highly significant (Likelihood ratio Chi-square test, $N = 594$ pools, $P < 0.001$).

https://doi.org/10.1017/S0025315408002609 Published online by Cambridge University Press

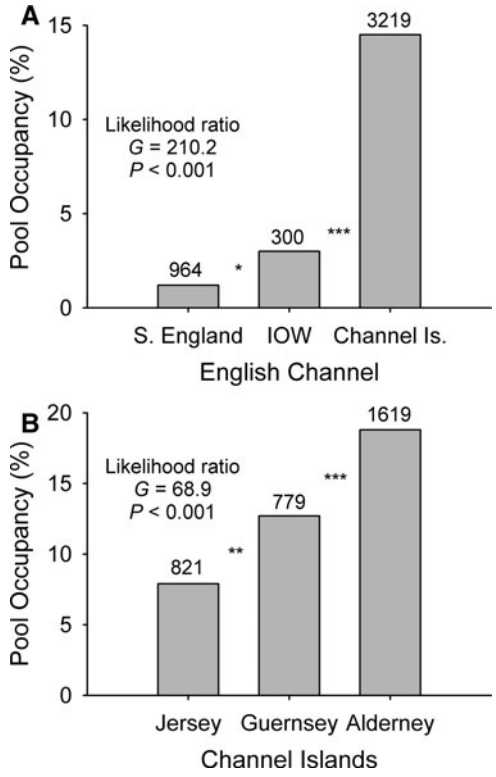

Fig. 3. Pool occupancy of *Codium* spp. in different areas of the English Channel: southern England, Isle of Wight (IoW) and the Channel Islands (CI). Survey sites and dates are listed in Table 1. Sample sizes over each bar indicate the number of pools surveyed that were used in the analyses.

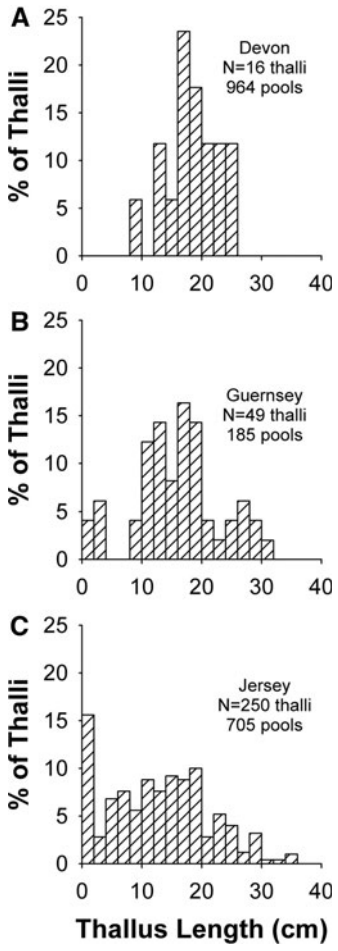

Fig. 4. Comparison of populations of *Codium fragile* in three different regions of the English Channel. All data were collected between 25 April and 9 May 2004. Devon data were from Wembury and Thurlestone; Guernsey data were from Lihou Causeway and La Jaonneuse; and Jersey data were from Sauchet Bay.

At sites on Alderney with extensive freshwater seepage from land and, thus, many ulvoid-dominated pools, *Codium* spp. were significantly less frequent in ulvoid than non-ulvoid pools (Likelihood ratio Chi-square test, $G = 10.5$, 1 df, $N = 426$ pools, $P = 0.002$). On Alderney, *Codium* spp. occurred in pools at all levels and on emergent substrata on lower parts of the shore. Of the ~1600 pools surveyed in June 2005, 19% contained *Codium* spp. (Figure 3B). There was considerable variation among sites and tidal levels. In the *Pelvetia* zone, the frequency of pool occupancy was high at Clonque but low elsewhere (overall: 8.2% of pools, $N = 574$). In the *Fucus spiralis* zone, *Codium* spp. occurred in 10–40% of the pools at all sites (overall: 24.3%, $N = 609$). In the *F. vesiculosus* zone, *Codium* spp. occurred in 20–60% of the pools at the four sites with pools at this tidal level (overall: 31.2%, $N = 311$). In the *F. serratus* zone, there were few pools at most sites but *Codium* occurred in 17.5% of the 80 surveyed. *Codium tomentosum* predominated in pools. On low-shore emergent substrata, we recorded a mean of 1.2 thalli per 0.25-m^2 quadrat ($N = 48$ quadrats at Clonque Bay).

Both *Codium vermilara* and *C. tomentosum* thrived throughout the Channel Islands surveyed (Guernsey, Jersey and Alderney). On Alderney shores, *C. tomentosum* predominated within the *Codium* assemblages at most sites and tidal levels (Figure 6). *Codium fragile* was present at the wave-protected Braye Bay (protected by the elongate breakwater; Figure 1E) but not at many other, more exposed sites (Figure 6). *Codium vermilara* was frequent at two sites on the north side of the island, Cats Bay and St Esquere Bay, high on the shore.

DISCUSSION

At most sites surveyed in the UK and the Channel Islands, native *Codium* spp. were equally or more abundant and widely distributed than the invasive *C. fragile*; displacement or elimination of native congeners has not occurred. *Codium tomentosum* dominated the *Codium* assemblage on Alderney (Figure 6) and Guernsey (White, 2003; Trowbridge *et al.*, 2004), and was the most frequent species in Devon. This alga is also frequent on rocky intertidal shores of western Ireland (Trowbridge, 2001 and unpublished data). *Codium vermilara* was abundant intertidally on Alderney and Jersey, and present in small amounts elsewhere in the Channel Islands; this species is abundant subtidally on the western shore of Lough Hyne, County Cork, southwestern Ireland (Trowbridge *et al.*, unpublished data). In summary: (1) the displacement and replacement scenarios (Figures 1A, B & 7) have not occurred; and (2) pool occupancy in southern England does not support interspecific competition among native and introduced congeners as a causal mechanism.

Sites on the Isle of Wight

The only area we surveyed that had dense populations of *Codium fragile* was the IoW, particularly the Bembridge to

https://doi.org/10.1017/S0025315408002609 Published online by Cambridge University Press

Table 2. Results of pairwise comparisons between regions of size distribution of *Codium fragile*, using Kolmogorov–Smirnov two-sample tests. Left part of table includes all data collected (N = 1159 thalli from 2002 to 2005); right part of table includes data collected from 25 April to 9 May 2004 (N = 315 thalli).

Regions	d_{max} 2002–2005				d_{max} 2004		
	Devon	IoW	Guernsey	Jersey	Devon	Guernsey	Jersey
Devon	0.000	–	–	–	0.000	–	–
IoW	0.670^{***}	0.000	–	–	–	–	–
Guernsey	0.550^{***}	0.486^{***}	0.000	–	0.283^{ns}	0.000	–
Jersey	0.433^{**}	0.445^{***}	0.142^{ns}	0.000	0.458^{**}	0.278^{**}	0.000

***, $P < 0.001$; **, $P < 0.010$; ^{ns}, $P > 0.050$.

Whitecliff Bay series of intertidal lagoons. Here the invasion history of the species is unclear. Based on molecular analyses of herbarium specimens (Provan *et al.*, 2007), the first verified record of *C. fragile* in England was in 1894 in Swanage, Dorset. Three sets of early records on the IoW may also indicate the unrecognized incursion of the introduced alga: (1) Delf & Grubb (1923) reported *Vaucheria velutina* C. Agardh as common on upper rocks on Shanklin Ledge (where we recorded *C. fragile*); (2) *Vaucheria litorea* C. Agardh was 'very common on the sand-covered rocks at Horse Ledge and growing as a mat at the bottom of some rockpools' (Norkett, 1947: 59); and (3) Foslie (1893) collected *C. tomentosum* at Steephill, IoW; Morey (1909) referred to *C. tomentosum* at Steephill and West Cowes (based on the Batters 'Catalogue' (Batters, 1902)); Delf & Grubb (1923) reported *C. tomentosum* from Puckaster Cove and Shanklin Ledge in tidepools; and Kain (1958) reported *C. tomentosum* from Bembridge. The first two records may refer to the derbesioid or vaucherioid stage of *Codium fragile* (see Blunden *et al.*, 1989; Fletcher *et al.*, 1989; Yang *et al.*, 1997; Trowbridge, 1998). This conjecture is based on the absence of genuine

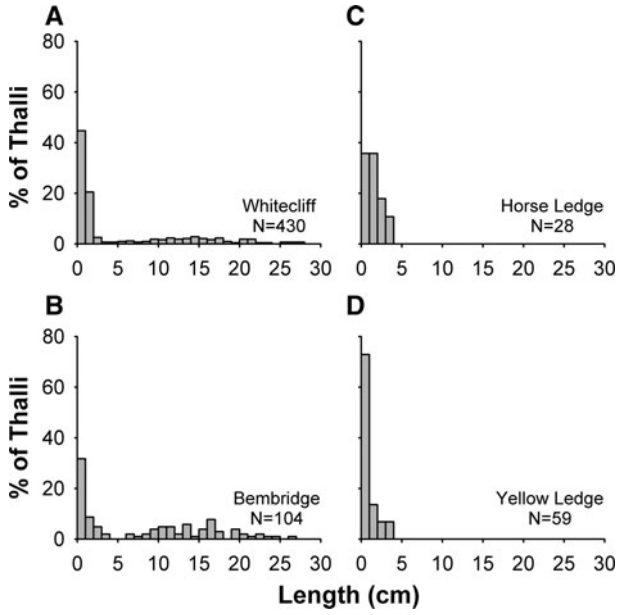

Fig. 5. Population size–frequency distributions of *Codium fragile* at four sites on the Isle of Wight. Data were collected in May 2005 with subsequent verification in September 2005 and June and August 2007. The number of thalli of *Codium fragile* sampled from each site is indicated. Identifications were confirmed by utricle examinations.

Vaucheria during our surveys, the presence of *C. fragile* and the known historical confusion between the two taxa. This juvenile vegetative stage can persist for years on docks or the shore. While it is possible that the vaucherioid stage could have belonged to *C. tomentosum*, there are no verified records of the alga at the IoW. Either *Codium tomentosum* (*sensu stricto*) occurred on the IoW historically but not now and/or *C. fragile* was present on the IoW by the 1890s (Foslie, 1893). This conclusion is based on the current absence of *C. tomentosum* during our surveys, the absence of verified historical specimens of the native from the IoW, the known historical confusion about *C. tomentosum* (*sensu lato*) and the contemporary occurrence of *C. fragile* at most of these locations. The first author has searched historical herbaria in the British Isles; the requisite specimens were not available to distinguish between the two hypotheses. Given that the invasive *C. fragile* was present in the British Isles by the mid to late 1800s (Provan *et al.*, 2007), there is circumstantial support for the second hypothesis.

What factors would explain the contemporary, dense populations of *Codium fragile* at Bembridge and Whitecliff Bay (IoW) and the comparative scarcity of the alga elsewhere? At least four possible explanations have been suggested.

(1) The habitat *per se* may contribute to alga's abundance at the IoW: the shallow, expansive, intertidal lagoons are ideal environments for the *Codium fragile*. Although the Wildlife and Countryside Act (1981) of the UK forbids experiments 'planting' listed species (such as *C. fragile*), experimental work in Korea demonstrated that growth of *Codium fragile* was greatest at shallow sublittoral depths (Hwang *et al.*, 2007).

(2) The tidal patterns around the IoW are unusual (Kain, 1958; Collins *et al.*, 1990) with double or prolonged high and low waters; spring high tides occur around midday. Thus, desiccation and light stress during early morning and early evening low tides would be comparatively less than in other areas that experience daytime low tides. Recent papers on desiccation tolerance (Schaffelke & Deane, 2005; Kim & Garbary, 2007) indicate that *C. fragile* is susceptible to desiccation but exhibits impressive recovery. On European shores, there is no direct experimental evidence that desiccation is a major problem. However, sunny weather does contribute to periodic thallus destruction and disintegration of *Codium fragile* (and congeners) in the British Isles and Japan (Trowbridge, personal observation). Similarly, cold damage to apical tips exposed to cold air in winter may influence littoral *Codium* distribution.

(3) Local diversity within a community might influence invasion success of some NIS (White & Shurin, 2007). Certainly, *C. fragile* has proliferated on north-western

https://doi.org/10.1017/S0025315408002609 Published online by Cambridge University Press

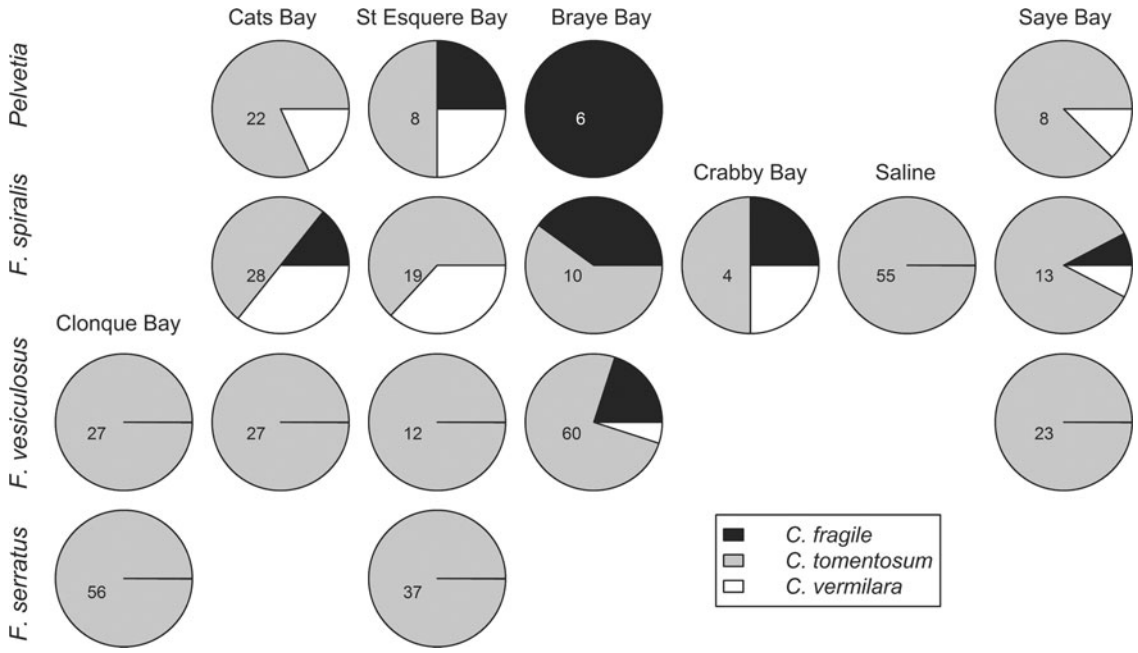

Fig. 6. Species composition of the *Codium* assemblages at seven Alderney sites and different tidal levels, based on utricle examination of thalli. Sample sizes indicate number of thalli examined microscopically. Data collected in June 2005.

Atlantic shores, a region with comparatively low species richness, compared to its response on the north-eastern Atlantic shores. The local-diversity hypothesis is not supported at Bembridge as the IoW is regarded as floristically rich (Farnham, 1982, 1994), particularly on the east coast (Figure 1C) in the intertidal lagoons. The entire coastline is listed as SMAs (Sensitive Marine Areas) by English Nature and large sections of the coastline are also SSSIs (Sites of Special Scientific Interest) due to high biodiversity.

(4) The Solent appears to be a UK hotspot of introduced macroalgae (Farnham, 1980; Collins *et al.*, 1990), in part due to extensive shipping and ferry traffic among Southampton and Portsmouth ports and continental ones. Bembridge could, thus, receive a comparatively high influx of NIS propagules relative to the Devon open-coast shoreline or to the complex, Channel Island shores.

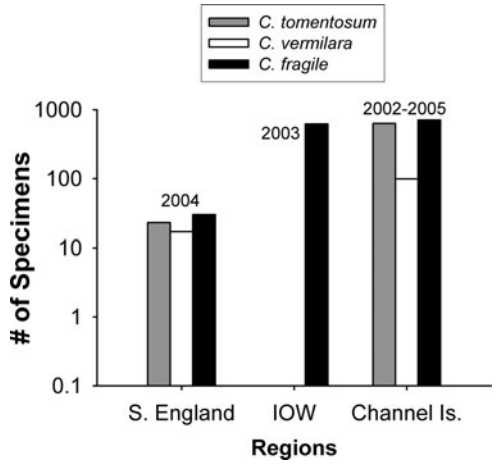

Fig. 7. Contemporary specimens of native and introduced *Codium* in southern England, Isle of Wight (IoW) and the Channel Islands. Data based on surveys made at sites and locations listed in Table 1.

Sites on the Channel Islands

Codium vermilara and *C. fragile* were first recorded on the Channel Islands by Dixon (1961) and Feldmann (1961). Lyle's voucher specimen of *C. tomentosum* (collected on 17 November 1921 and lodged in the Guernsey Museum and Galleries) is correctly identified (verified by Trowbridge). Although Kain (1961) made a subtidal algal collection at Braye Harbour at the breakwater, she did not record *Codium* spp., presumably due its intertidal location. Thus, the arrival date of *C. fragile* to the Channel Islands is not known.

Jersey and Guernsey both have a history of Pacific oyster cultivation, whereas Alderney does not. Given that the translocation of Pacific oysters is considered a primary vector in the spread of *C. fragile*, oyster mariculture activities may have contributed to the algal distributions. If this were the sole contributory factor, Alderney should have little or no *C. fragile*. Although Alderney does have appreciably less *C. fragile* than Jersey and Guernsey, it would be hard to accept that many decades of time (and generations of *C. fragile*) did not enable the invasive alga to disperse, establish and proliferate to most local areas.

Alternative explanations include current levels of disturbance. Jersey, as the most commercially developed of the three largest Channel Islands, presumably has the highest level of anthropogenic disturbance and it does have appreciable populations of *C. fragile*. Alderney, the least developed of the three islands, has substantial, thriving populations of *C. tomentosum*, *C. vermilara* and some *C. fragile*. However, direct experimental evidence of the stimulatory effects of anthropogenic effects (human trampling, nitrogen effluent, other pollution, mariculture and ship hull transport) has not been demonstrated anywhere in the alga's invaded range. Furthermore, the native congeners have not been experimentally manipulated to evaluate their presumed sensitivities. Anthropogenic effects do not provide a simple explanation

https://doi.org/10.1017/S0025315408002609 Published online by Cambridge University Press

that could account for the spatial variation in *Codium* populations between sides of the English Channel.

Other regional issues

Differential oceanographic conditions might account for cross-channel differences in *Codium* assemblages. The IoW is at a biogeographical boundary between western oceanic and eastern continental communities (Collins *et al.*, 1990; Herbert *et al.*, 2007). The water masses carrying *Codium* propagules to Devon shores might be hydrodynamically distinct from those moving into and around the Bay of St Malo where the Channel Islands occur. Yet, it is hard to see how this mechanism could account for the flourishing population of *C. fragile* at Bembridge.

The three Channel Islands do have dramatically different environmental situations from southern England, including large tidal ranges (9–11 m) and rapid tidal currents (e.g. Alderney Race). Native and introduced *Codium* species occur intertidally in the southern English Channel where tidal ranges are huge; the species are often in lower intertidal pools and/or in subtidal areas at the northern channel sites (Devon and IoW) where tidal ranges are much smaller (3–4 m). However, western Ireland also has a small tidal range as well as a diverse and abundant assemblage of *Codium* on many rocky shores (e.g. Trowbridge, 2001). Thus, tidal range *per se* is not a sufficient regional explanation.

Regional differences in wave action may contribute to differential patterns of littoral *Codium* distributions. *Codium fragile* can propagate vegetatively via fragmentation and subsequent attachment of fragments. Perhaps the Channel Islands have comparatively higher wave exposure and *Codium* fragmentation than Devon or IoW shores. This testable hypothesis could account for the broad-scale patterns documented in this study.

In summary, simplistic explanations of algal distributional constraints are fraught with peril. Past accounts of temporal *Codium* changes have postulated anthropogenic effects and/or ecological interactions (Figure 1); while one or more of these mechanisms may be true, the hypotheses have not been well supported scientifically. Alternative oceanographic explanations such as tidal patterns, tidal range and tidal streams have never been seriously evaluated for spatial variation in the distribution of NIS on north-eastern Atlantic shores. The classical case of an introduced species displacing a native congener is still speculative after three decades of scientific study and alternative mechanisms have been generally ignored.

ACKNOWLEDGEMENTS

We greatly appreciate the assistance of numerous people, particularly Tricia Farnham and Hal Ross for field assistance and moral support. Richard and Dorothé Lord provided gracious hospitality and valuable logistical advice of Channel Island contacts, survey sites and biology. We thank Alan Howell (Guernsey Museum and Galleries) for access to the Lyle Collection of seaweeds and Moria Sleeman and Brian Bonnard for valuable discussions of Alderney shores. This paper was significantly improved by constructive comments from Colin Little, Bob Scheibling and David Garbary. This material is based upon work supported by the National Science Foundation under International Program Grant No. INT-0211186 to C.D.T., with W.F.F. as a UK collaborator.

REFERENCES

Batters E.A.L. (1902) A catalogue of the British marine algae. *Journal of Botany* 40 (Supplement), 1–107.

Bégin C. and Scheibling R.E. (2003) Growth and survival of the invasive green alga *Codium fragile* ssp. *tomentosoides* in tide pools on a rocky shore in Nova Scotia. *Botanica Marina* 46, 404–412.

Benson E.E., Rutter J.C. and Cobb A.H. (1983) Seasonal variation in frond morphology and chloroplast physiology of the intertidal alga *Codium fragile* (Suringar) Hariot. *New Phytologist* 95, 569–580.

Blunden G., Fletcher R.L., Smith B.E., Rogers D.J. and Fish B.C. (1989) An unusual growth form of *Codium fragile* (Sur.) Hariot subspecies *tomentosoides* (Goor) Silva found on floating structures in the Solent. *British Phycological Journal* 24, 299.

Collins K.J., Herbert R.J.H. and Mallinson J.J. (1990) The marine flora and fauna of Bembridge and St. Helens, Isle of Wight. *Proceedings of the Isle of Wight Natural History and Archaeological Society* 9, 41–85.

Culley M.B., Farnham W.F., Thomas W.S. and Thorp C.H. (1983) *Portelet Bay, Jersey: an ecological investigation and analysis*. Portsmouth: Portsmouth Polytechnic.

Delf E.M. and Grubb V.M. (1923) Marine algae. *Proceedings of the Isle of Wight Natural History and Archaeological Society* 1, 181–185.

Dixon P.S. (1961) List of marine algae collected in the Channel Islands during the joint meeting of the British Phycological Society and the Société Phycologique de France, September 1960. *British Phycological Bulletin* 2, 71–80.

Elliot P. (2006) Impacts of climate change on non-native species. In Marine Climate Change Impacts Partnership annual report card 2006. In Buckley P.J., Dye S.R. and Baxter J.M. (eds) *Online Summary Reports, MCCIP, Lowestoft*. Available at www.mccip.org.uk

Farnham W.F. (1975) Seaweeds and their allies (algae). In Rayner R.W. (ed.) *The natural history of Pagham Harbour, Part II Plants and animals other than birds and mammals*. Bognor Regis: The Bognor Regis Natural Science Society, pp. 37–46.

Farnham W.F. (1980) Studies on aliens in the marine flora of southern England. In Price J.H., Irvine D.E.G. and Farnham W.F. (eds) *The shore environment. Volume 2: ecosystems*. London: Academic Press, pp. 875–914.

Farnham W.F. (1982) *Species list of the benthic algae of the Isle of Wight. Report to the Department of the Environment*. Portsmouth: Portsmouth Polytechnic, pp. 14.

Farnham W.F. (1994) Species list from the British Phycological Society field meeting, Isle of Wight (1993). *The Phycologist* 39, 24–28.

Feldmann J. (1961) Field meeting at Guernsey, Channel Islands, September 1st–8th 1960. *British Phycological Bulletin* 2, 96–97.

Fletcher R.L., Blunden G., Smith B.E., Rogers D.J. and Fish B.C. (1989) Occurrence of a fouling, juvenile, stage of *Codium fragile* ssp. *tomentosoides* (Goor) Silva (Chlorophyceae, Codiales). *Journal of Applied Phycology* 1, 227–237.

Foslie M. (1893) List of the marine algae of the Isle of Wight. *Det Kongelige Norske videnskabers selskabs skrifter* 1891, 267–282.

Garbary D.J., Vandermeulen H. and Kim K.Y. (1997) *Codium fragile* ssp. *tomentosoides* (Chlorophyta) invades the Gulf of St Lawrence, Atlantic Canada. *Botanica Marina* 40, 537–540.

Garbary D.J., Fraser S.J., Hubbard C. and Kim K.Y. (2004) *Codium fragile*: rhizomatous growth in the *Zostera* thief of eastern Canada. *Helgoland Marine Research* 58, 141–146.

Herbert R.J.H., Southward A.J., Sheader M. and Hawkins S.J. (2007) Influence of recruitment and temperature on distribution of intertidal

barnacles in the English Channel. *Journal of the Marine Biological Association of the United Kingdom* 87, 487–499.

Hiscock K., Southward A., Tittley I. and Hawkins S. (2004) Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14, 333–362.

Hwang E.K., Baek J.M. and Park C.S. (2007) Cultivation of the green alga, *Codium fragile* (Suringar) Hariot, by artificial seed production in Korea. *Journal of Applied Phycology*, DOI 10.1007/s10811-007-9265-5.

Jones L.A. (2000) The history of phycology on the Isle of Wight. *Proceedings of the Isle of Wight Natural History and Archaeological Society* 16, 47–56.

Kain J.M. (1958) Observations on the littoral algae of the Isle of Wight. *Journal of the Marine Biological Association of the United Kingdom* 37, 769–780.

Kain J.M. (1961) Some sub-littoral records. (a) Alderney; (b) West of Scotland. *British Phycological Bulletin* 2, 80–86.

Kim K.Y. and Garbary D.J. (2007) Photosynthesis in *Codium fragile* (Chlorophyta) from a Nova Scotia estuary: responses to desiccation and hyposalinity. *Marine Biology* 151, 99–107.

Levin P.S., Coyer J.A., Petrik R. and Good T.P. (2002) Community-wide effects of non-indigenous species on temperate rocky reefs. *Ecology* 83, 3182–3193.

Lyle L. (1920) The marine algae of Guernsey. *Journal of Botany*, 58 (Supplement 2), 1–53.

Lyle L. (1923) Distribution of the marine flora of the Channel Islands compared with that of the coasts of Western Europe. *Journal of Ecology* 11, 77–92.

Lyle L. (1937) Additions to the marine flora of Sark. *Journal of Botany* 75, 18–22.

Maggs C.A. and Kelley J. (2007) *Codium*. In Brodie J., Maggs C.A. and John D.M. (eds) *Green seaweeds of Britain and Ireland*. UK: British Phycological Society, pp. 189–201.

Marquand E.D. (1901) *Flora of Guernsey and the Lesser Channel Islands: namely, Alderney, Sark, Herm, Jethou, and the adjacent islets*. London: Dulau & Co.

Marquand E.D. (1902) Additions to the flora of Alderney. *Transactions of the Guernsey Society of Natural Science for 1902*, 4 pp.

Marquand E.D. (1908) Botanical notes. *Transactions of the Guernsey Society of Natural Science for 1908*, 11 pp.

Mieszkowska N., Leaper R., Moore P., Kendall M.A., Burrows M.T., Lear D., Poloczanska E., Hiscock K., Moschella P.S., Thompson R.C., Herbert R.J., Laffoley D., Baxter J., Southward A.J. and Hawkins S.J. (2005) Marine biodiversity and climate change: assessing and predicting the influence of climatic change using intertidal rocky shore biota. *Occasional Publication, Marine Biological Association of the United Kingdom* 20, 1–53.

Morey F. (1909) *A guide to the natural history of the Isle of Wight*. Newport and London: County Press.

Norkett A.H. (1947) Marine algae of the Isle of Wight. *Proceedings of the Isle of Wight Natural History and Archaeological Society* 4, 59.

Norton T.A. (1991) The algal vegetation. In *The ecology of Lough Hyne. Proceedings of a conference 4–5 September, 1990*. Dublin: Royal Irish Academy, pp.117–126.

Posey M.H. (1988) Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. *Ecology* 69, 974–983.

Provan J., Murphy S. and Maggs C.A. (2005) Tracking the invasive history of the green alga *Codium fragile* ssp. *tomentosoides*. *Molecular Ecology* 14, 189–194.

Provan J., Booth D., Todd N.P., Beatty G.E. and Maggs C.A. (2007) Tracking biological invasions in space and time: elucidating the invasive history of the green alga *Codium fragile* using old DNA. *Diversity and Distributions* 14, 343–354. DOI: 10.1111/j.1472-4642.2007.00420.x

Schaffelke B. and Deane D. (2005) Desiccation tolerance of the introduced marine green alga *Codium fragile* ssp. *tomentosoides*—clues for likely transport vectors? *Biological Invasions* 7, 557–565.

Scheibling R.E. and Gagnon P. (2006) Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). *Marine Ecology Progress Series* 325, 1–14.

Schmidt A.L. and Scheibling R.E. (2005) Population dynamics of an invasive green alga, *Codium fragile* subsp. *tomentosoides*, in tidepools on a rocky shore in Nova Scotia, Canada. *Ecoscience* 12, 403–411.

Schmidt A.L. and Scheibling R.E. (2006) A comparison of epifauna and epiphytes on native kelps (*Laminaria* species) and an invasive alga (*Codium fragile* ssp. *tomentosoides*) in Nova Scotia, Canada. *Botanica Marina*, 49, 315–330.

Schmidt A.L. and Scheibling R.E. (2007) Effects of native and invasive macroalgal canopies on composition and abundance of mobile benthic macrofauna and turf-forming algae. *Journal of Experimental Marine Biology and Ecology* 344, 110–130.

Silva P.C. (1955) The dichotomous species of *Codium* in Britain. *Journal of the Marine Biological Association of the United Kingdom* 34, 565–577.

Trowbridge C.D. (1998) Ecology of the green macroalga *Codium fragile* (Suringar) Hariot 1889: invasive and non-invasive subspecies. *Oceanography and Marine Biology: an Annual Review* 36, 1–64.

Trowbridge C.D. (2001) Coexistence of introduced and native congeneric algae: *Codium fragile* and *C. tomentosum* on Irish rocky intertidal shores. *Journal of the Marine Biological Association of the United Kingdom* 81, 931–937.

Trowbridge C.D. (2006) A global proliferation of non-native marine and brackish macroalgae. In Critchley A.T., Ohno M. and Largo D.B. (eds) *World seaweed resources—an authoritative reference system*. DVD-ROM, version 1.0. Amsterdam: ETI Bioinformatics.

Trowbridge C.D. and Farnham W.F. (2004) Spatial variation in littoral *Codium* assemblages on Jersey, Channel Islands (southern English Channel). *Botanica Marina* 47, 501–503.

Trowbridge C.D., Farnham W.F. and White L.F. (2004) Thriving populations of the native macroalga *Codium tomentosum* on Guernsey rocky shores. *Journal of the Marine Biological Association of the United Kingdom* 84, 873–877.

Van Heurck H. (1908) *Prodrome de la flore des algues marines des Iles Anglo-Normandes et des Côtes Nord-Ouest de la France*. Jersey: Labey and Blampied.

White L.F. (2003) *An investigation into* Codium *species on Guernsey rocky shores*. BSc (Hons) thesis. University of Portsmouth, UK.

White L.F. and Shurin J.B. (2007) Diversity effects on invasion vary with life history stage in marine macroalgae. *Oikos* 116, 1193–1203.

and

Yang M.-H., Blunden G., Huang F.-L. and Fletcher R.L. (1997) Growth of a dissociated, filamentous stage of *Codium* species in laboratory culture. *Journal of Applied Phycology* 9, 1–3.

Correspondence should be addressed to:
C.D. Trowbridge
Department of Zoology, Oregon State University
PO Box 1995, Newport, OR 97365, USA
email: trowbric@yahoo.com