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Thriving populations of the native macroalga *Codium tomentosum* on Guernsey rocky shores

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Since the incursions of the introduced green macroalgae *Codium fragile* ssp. *tomentosoides* and ssp. *atlanticum* on European shores, the abundance and distribution of the native congeners *C. tomentosum* and *C. vermilara* have come under closer scrutiny. Hypotheses regarding the reported declines in the native(s) are largely speculative due to the paucity of quantitative information on the natives, the cryptic nature of the invaders and the unknown processes regulating *Codium* assemblages. As part of a field-based *Codium* study on north-eastern Atlantic shores, our surveys on Guernsey shores, Channel Islands, in September 2002 have revealed two unexpected and noteworthy results: (1) thriving populations of *C. tomentosum* are quite abundant on mid to low littoral shores; and (2) in marked contrast, sparse populations of *C. fragile* ssp. *tomentosoides* are restricted primarily to upper mid-littoral rock pools. Native *Codium* has not been displaced or eliminated from the southern end of the British Isles.

INTRODUCTION

Introduced species can negatively affect native species or resident exotics. Classic cases of marine pests include the ctenophore *Mnemiopsis leidyi* Agassiz, the brown alga *Sargassum muticum* (Yendo) Fensholt and the green alga *Caulerpa taxifolia* (Vahl) C. Ag. However, such effects may be spatially or temporally variable. Regional and geographic variation could be caused by variation in resistance of the recipient community or in efficacy of the exotic species; temporal variation could be caused by climatic changes, environmental degradation or synergistic interactions amongst exotics (Trowbridge, 1998; Chapman, 1999; Levin et al., 2002).

In this study, populations of the native European macroalga *Codium tomentosum* Stackhouse were investigated because of past suggestions that the alga's apparent decline throughout the British Isles was caused by interspecific competition with the invasive congener *C. fragile* (Suringar) Hariot ssp. *tomentosoides* (van Goor) Silva. Although many phycologists have come to the conclusion that the apparent decline may be an artefact of historical misidentifications of dichotomous species of *Codium* rather than a simple case of exotics outcompeting natives, invasion biologists have frequently overlooked this changed perception. Our objectives were to establish the species composition and community context of the *Codium* assemblages on Guernsey shores, Channel Islands. This study quantitatively demonstrates that thriving populations of the native *C. tomentosum* do occur in the British Isles.

Historical records

Basic phenological and distributional data on native *C. tomentosum* and *C. vermilara* in the British Isles, Atlantic France and Channel Islands are meagre (but see Silva, 1955; Parkes, 1975; Burrows, 1991; Morton, 1994; Trowbridge, 2001; Hardy & Guiry, 2003; references therein). Historical records for the Channel Islands (Lyle, 1920, 1923, 1937) indicate that there were three *Codium* spp. on Guernsey a century ago: *Codium tomentosum*, *C. adhaerens*, C. Agardh and *C. bursa* (Olivi) C. Agardh. *Codium tomentosum* was very common (Lyle, 1920), especially in rock pools on the lower part of the shore, and was reported from Guernsey, Jersey, Alderney and Sark (Lyle, 1923, 1937). Although Lyle (1923) also reported the alga from England, Scotland, Ireland, France and Spain (but not Wales), it is unclear whether Lyle's records refer to: (1) *C. tomentosum*; (2) *C. fragile* ssp. *atlanticum* (Cotton) Silva which appeared on Irish shores circa 1808 and spread around the British Isles; or (3) *C. fragile* ssp. *tomentosoides* which appeared on mainland European shores in the early 1900s and to the British Isles in the 1930s.

The identity of the Channel Island *Codium* spp. was verified by Dixon (1961) and Feldmann (1961). The native *C. tomentosum* inhabited lower mid-littoral shores around Guernsey as well as on Herm and Sark (Dixon, 1961); the alga was also very abundant on Lihou Island, Guernsey (Feldmann, 1961). The congener *C. vermilara* occurred on mid-littoral shores of Guernsey, Herm and Sark (Dixon, 1961; Feldmann, 1961). The invasive *C. fragile* ssp. *tomentosoides* was found only on Guernsey (Port Soif and Portelet Harbour, Pleinmont) and Sark (Grande Greve). Specimens intermediate between *C. fragile* ssp. *atlanticum* and ssp. *tomentosoides* were reported; although many thalli were identified as the former during the phycological excursion, none examined later was actually ssp. *atlanticum* (Dixon, 1961). This issue is important, as there have been no verified and published reports of *C. fragile* ssp. *atlanticum* in the Channel Islands or the English Channel. The southern records of ssp. *atlanticum* shown in Hardy & Guiry (2003) are actually typographical and recording errors (Burrows, 1991; Biological Records Centre staff,

Table 1. *Study areas sampled around the island of Guernsey in September 2002.*

Study sites	Latitude and longitude	Wave exposure	Habitats sampled
Lihou Causeway	N 49°27.4′ W 2°39.5′	sheltered	high and mid littoral pools
Bordeaux	N 49°29.4′ W 2°30.1′	moderately sheltered	mid littoral pools low littoral walls low littoral cobbles
Port Soif	N 49°29.3′ W 2°34.9′	moderately exposed	high and mid littoral pools low littoral bench
Grande Rocques	N 49°29.2′ W 2°35.4′	moderately exposed	mid littoral pools low littoral bench
Moulin Huet	N 49°25.6′ W 2°32.9′	moderately sheltered	low littoral bench: *Fucus serratus* zone and *Mastocarpus stellatus* zone

personal communication). Finally, although *C. adhaerens* is still present on Guernsey (this study), the congener *C. bursa* was not recorded since Lyle (Dixon, 1961; Feldmann, 1961; Hardy & Guiry, 2003; this study).

MATERIALS AND METHODS

The *Codium* guild on Guernsey rocky shores was investigated in September 2002. A variety of sites around the island and at different tidal levels and microhabitats (Table 1) was surveyed. At each site, the population size-structure of *Codium* and the composition of the local community was documented. Thallus length was measured as the maximum length of the longest frond. For community structure, the per cent species coverage was estimated for canopy, turf and encrusting categories within 0.25-m^2 quadrats centred around *Codium* thalli. The number of molluscan herbivores per quadrat was also counted. Finally, species richness (S), i.e. total number of macrofaunal and macroalgal species, was calculated for each quadrat. This type of localized community analysis characterized the neighbouring taxa which would be potential interacting species (e.g. competitors or consumers).

To identify *Codium* species, branch tips of 27 to 106 thalli were harvested for each of the five sites. Specimens were brought back to the laboratory at the University of Portsmouth, Institute of Marine Sciences to examine. Disassociated utricles from each branch tip were examined under a compound microscope. Utricle length, width, mucron length (for *C. fragile*) and apical wall thickness were quantified for each thallus using an ocular micrometer; digital images of utricles were captured as jpg files for archival purposes. For reproductive thalli, the sex was determined based on gamete size and colour within gametangia.

RESULTS

Codium *assemblages*

Four *Codium* species were found on Guernsey shores. *Codium tomentosum* was found at all five study sites, *C. fragile* at three sites (Lihou, Port Soif and Grande Rocques), *C. vermilara* at one site (Bordeaux) and *C. adhaerens* at one site (Moulin Huet). Species identity of the dichotomously branching *Codium* was unambiguous (Figure 1). *Codium fragile* ssp. *tomentosoides* had long, wide utricles with a

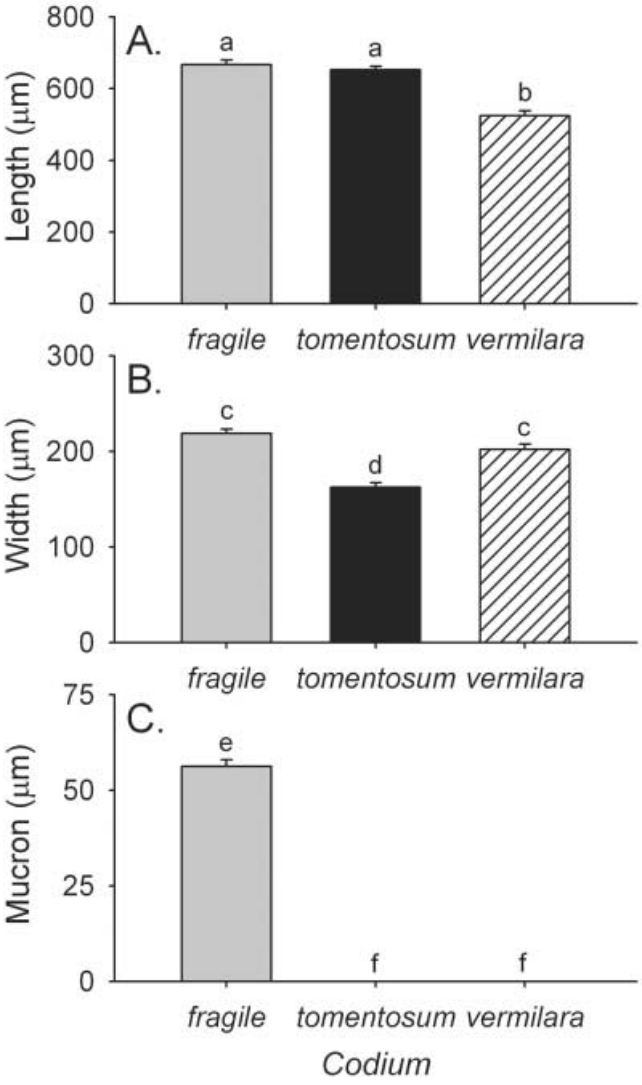

Figure 1. Mean size of utricles of *Codium* spp. from Guernsey. Similar letters indicate no significant differences (post-hoc tests, $P > 0.05$); different letters indicate highly significant statistical differences ($P < 0.001$). Error bars indicate +1 SE.

distinctly pointed apex $> 50\,\mu$m long (i.e. mucronate tips). The native *C. tomentosum* also had long utricles but they were significantly narrower than those of congeners (analysis of variance, post-hoc test, $P < 0.001$) and lacked mucronate tips. Finally, utricles of *C. vermilara* were significantly shorter (post-hoc test, $P < 0.001$) but wider

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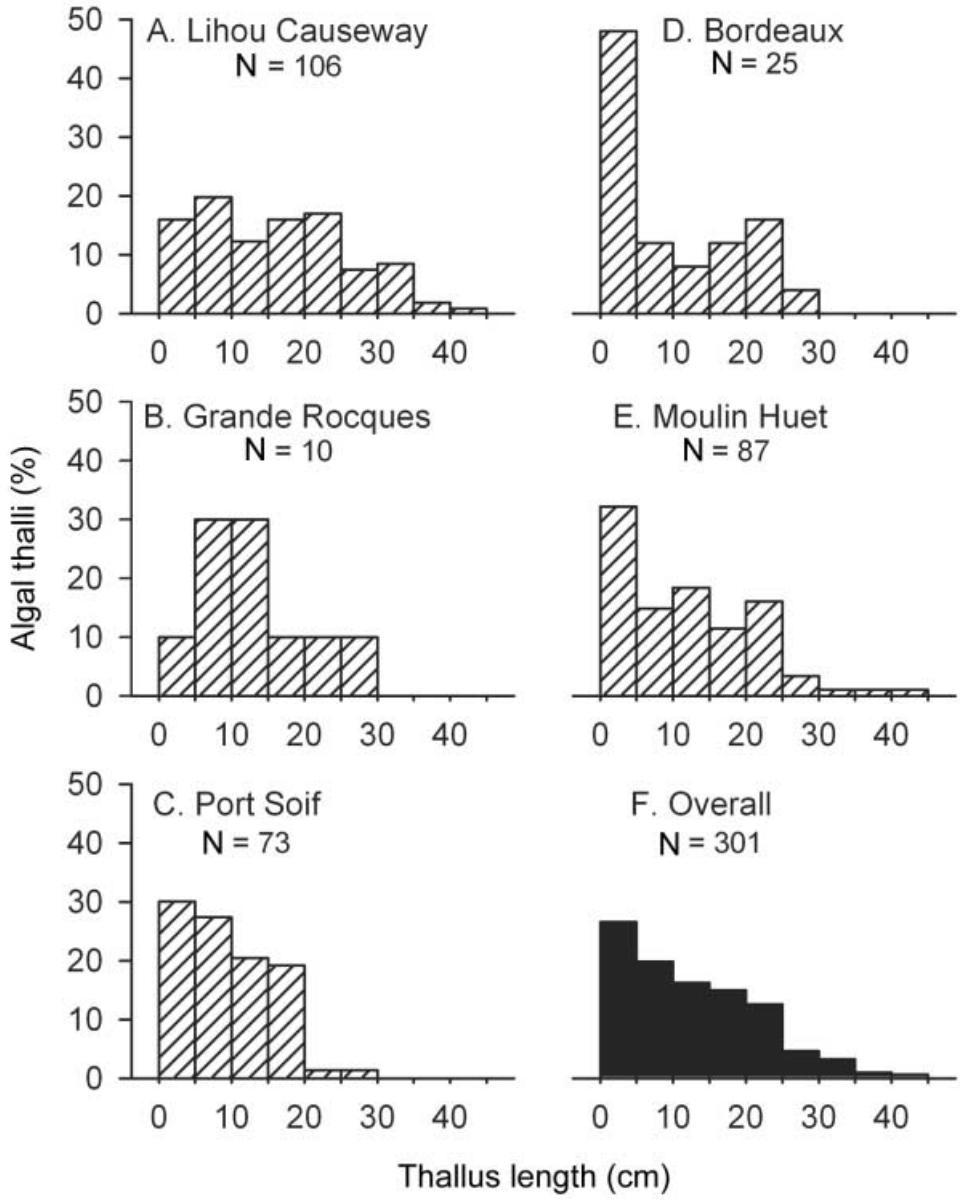

Figure 2. Population size-structure of *Codium tomentosum* at five sites. Sample sizes indicate the number of thalli measured.

than those of *C. tomentosum* (post-hoc test, $P<0.001$). Furthermore, the placement of hair scars also contributed to definitive species identification.

Thriving native

The majority (>66%) of *Codium* thalli examined in September 2002 were the native *C. tomentosum*. The alga's populations were abundant, particularly in mid and low-littoral rock pools and on low-zone benches and boulder fields. Thalli grew to 45 cm long on west- and south-coast shores (Figure 2). At all sites, there were large adults >20 cm long, many of which were fertile, as well as many small thalli <5 cm long, indicative of recent reproduction and growth (Figure 2). Thus, Guernsey populations had size–frequency distributions consistent with continued persistence and contained both sexes (Figure 3A) so sexual reproduction was presumably occurring.

Codium tomentosum occurred in a variety of different communities on Guernsey. At Lihou Causeway, the alga coexisted with abundant ulvoids and polysiphonous red algae. At other sites, the alga also coexisted with fucoids, *Mastocarpus stellatus* (Stackhouse) Guiry and *Chondrus crispus* Stackhouse. Understory taxa included corallines, various red algal turfs and algal crusts. The native alga occurred in the presence of either high or low amount of bare space as well as either moderate or low amount of sand on the rocky shore. Herbivore densities (Figure 4A) varied considerably among sites and habitats but averaged 4.4 limpets (*Patella* spp.), 16.9 topshells (*Gibbula*, *Monodonta* and *Calliostoma*) and 3.0 sacoglossans (*Elysia viridis* (Montagu)) per 0.25 m^2. Peak densities were 10 limpets, 64 topshells and 16 sacoglossans per 0.25 m^2. In many cases, *C. tomentosum* was attached to the shells of live limpets. The native alga coexisted with about eight other macroalgal species and three molluscan herbivores per quadrat (Figure 4B). Thus, the native alga inhabited diverse types of communities.

Unsuccessful invader

High and upper mid-littoral pools at Lihou Causeway, Port Soif and Grand Rocques contained sparse populations

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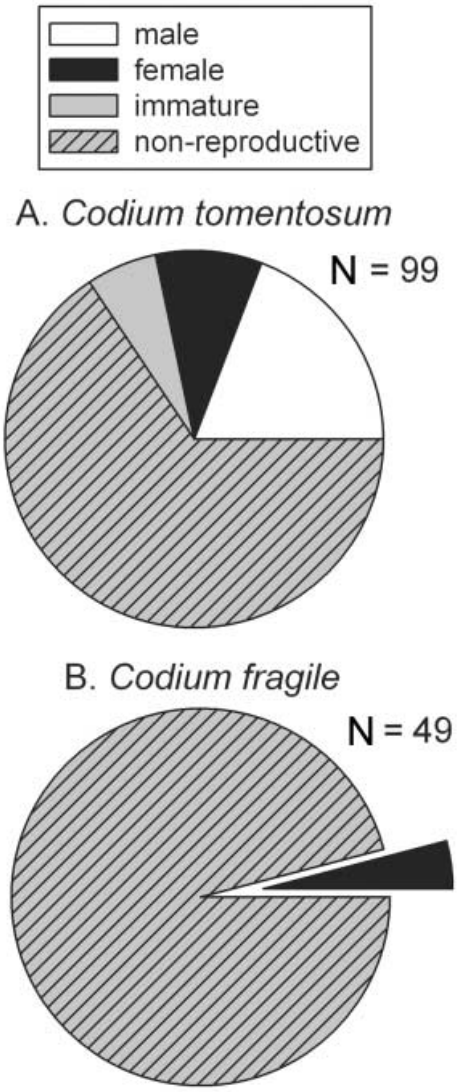

Figure 3. Relative abundance of male, female, immature and non-fertile thalli of *Codium tomentosum* and *C. fragile* ssp. *tomentosoides* on Guernsey rocky shores. Sample sizes indicate the number of thalli examined.

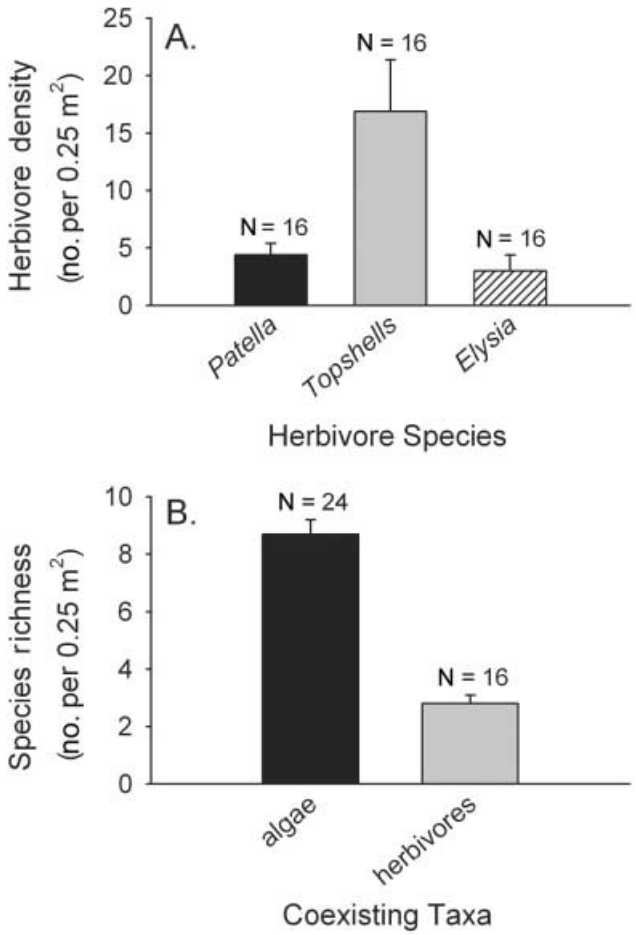

Figure 4. Density of herbivores and number of species in 0.25-m^2 quadrats centred around *Codium tomentosum* on Guernsey shores. Sample sizes indicate the number of quadrats examined.

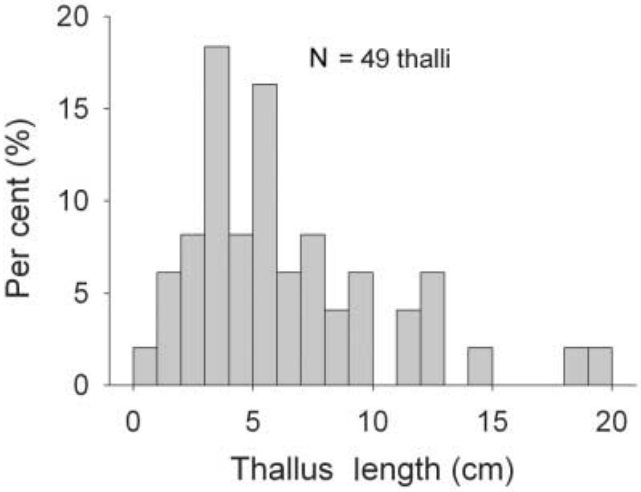

Figure 5. Population size-structure of *Codium fragile* ssp. *tomentosoides* on Guernsey shores. Sample size indicates the number of thalli measured.

of the invasive *C. fragile* ssp. *tomentosoides*. All three sites were on the north-western side of the island, suggesting similarity of conditions; Bordeaux on the east coast and Moulin Huet on the south coast had no detectable populations of the invasive alga. This species did not typically coexist with its congeners at these Guernsey sites (although it did at the nearby Sark and Jersey). The majority of the thalli were <10 cm long with a maximum observed length of 19.1 cm (Figure 5). Few thalli were large enough to be sexually mature. Microscopic examination of 49 thalli indicated that few (4%) had gametangia; all thalli with gametes present were female (Figure 3B).

DISCUSSION

Thriving native

The fact that the native *Codium tomentosum* dominated the local *Codium* assemblage is noteworthy as many marine scientists have considered the alga to be declining to low levels in the British Isles. Whether the Channel Islands represent a refuge due to reduced pollution, trampling and other anthropogenic effects is an intriguing question. Clearly the native alga is flourishing on Guernsey shores and has so for the last century.

On Guernsey shores, *C. tomentosum* grew to at least 45 cm; this value was much larger than the 20 cm reported

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by Burrows (1991). The alga thrived at mid and low-littoral levels in pools and on emergent benches. The maximum development (length) occurred in winter with peak fertility between August and March (Burrows, 1991). Thus, we were examining the alga at the presumed start of its reproductive period. More detailed aspects of its biology (distribution, growth, etc.) were recorded by White as part of her BSc (Honours) thesis. Not only was *C. tomentosum* abundant but also it occurred in a variety of littoral communities. At some sites, it coexisted with ulvoids and other ephemerals whereas at other sites, the alga coexisted with fucoids, *Chondrus crispus* or *Mastocarpus stellatus*.

Unsuccessful invader

The second striking result was that *C. fragile* ssp. *tomentosoides* was restricted to upper mid-shore pools. This alga has the capacity to inhabit a wide range of habitats from high and mid-littoral splash pools (Trowbridge, 1998, 2001; Bégin & Scheibling, 2003) to shallow sublittoral areas. Yet, on Guernsey, no invasive thalli were found low on the shore (in pools or on emergent surfaces) and few coexisting with the native congener. Ecological factors restricting the alga to this habitat on Guernsey merit investigation given the alga's well-documented physiological tolerance of environmental stresses (reviewed by Trowbridge, 1998). The paucity of a limiting but shared resource (e.g. space) and little coexistence of congeners (Trowbridge, 2001; this study) weakens hypotheses of intrageneric competition.

An associated result was that *C. fragile* ssp. *tomentosoides* was primarily non-reproductive. Elsewhere, thalli over about 10–15 cm are generally sexually mature (Trowbridge, 1998), and previous reports demonstrate a broad season of fertility. Invasive pests are often fecund although some macroalgal pests propagate either exclusively or primarily via fragmentation and regeneration. Thus, the observed paucity of gametangia on Guernsey was intriguing. Trowbridge has observed a comparable pattern of low fecundity in *C. fragile* ssp. *tomentosoides* in Lough Hyne, Ireland in 2002 and 2003. On Atlantic European shores, the alga is exhibiting a long-term decline (Trowbridge, 2001). The cause of this decline could be ecological and/or physiological; potential causal processes include (1) the accumulation of specialist herbivores, resident epibionts and pathogens or (2) long-term climatic changes. Spatio-temporal variation in invasion resistance could contribute to changes in incursions of exotics and in recovery of natives.

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