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Spatio-temporal dynamics of *Codium* populations along the rocky shores of N and NW Spain

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ABSTRACT

The green alga *Codium fragile* ssp. *fragile* (hereafter *C. fragile*) has long been assumed to outcompete and displace its native congeners via cryptic invasion. We analysed the population dynamics of the exotic *C. fragile* and native congeners and their relative abundance on intertidal shores in N-NW Spain. Our results did not support the existence of current competitive displacement by the exotic species. The presence of *C. fragile* was clearly seasonal, while the native *C. tomentosum* was more persistent throughout the year, due to a higher frequency of frond sprouting from perennial basal fragments. However, our results also indicated an increase in the proportion of *C. fragile* relative to native species towards inner areas of the Bay of Biscay, which was correlated with environmental gradients. The greater tolerance of *C. fragile* to environmental stress and its opportunistic abilities may favour establishment and spread of the species under a warming scenario.

1. Introduction

The introduction and establishment of non-indigenous species (NIS) is considered one of the greatest threats to the integrity of most ecosystems on earth (Simberloff et al., 2014; Davidson et al., 2015) and continues to be one the most commonly studied processes (Davidson et al., 2015). Although only a small proportion of introduced NIS become invasive (Blackburn et al., 2011), these species may have measurable effects on the recipient habitats. The impacts include displacement of native species, biodiversity loss, changes in community structure and food webs, and alterations in ecosystem processes (Molnar et al., 2008; Simberloff et al., 2014).

Climate change is expected to alter spatial and temporal patterns of species distribution and resource availability, thus enhancing biological invasions (Occhipinti-Ambrogi, 2007). For instance, NIS that are capable of tolerating a wider range of thermal regimes may be more successful under a scenario of increasing temperature (Hellmann et al., 2008; Walther et al., 2009). Human activities such as maritime transport and aquaculture have also contributed to increased numbers and impacts of NIS on marine systems in recent decades (e.g. Cohen and Carlton, 1998; Occhipinti-Ambrogi, 2007).

Seaweeds are an important component of marine invasions worldwide, with around 300 species detected in coastal systems (Trowbridge, 1998, 2006; Johnson and Chapman, 2007; Williams and Smith, 2007). Recent meta-analyses indicate strong negative impacts of invasive seaweeds on resident assemblages, particularly at the same trophic level through competitive interactions, although the number of species analysed was small relative to the total number detected (Thomsen et al., 2009; Maggi et al., 2015). Moreover, the number of NIS may still be underestimated, mainly due to cryptic invasions, i.e. in cases where NIS are morphologically similar to native species (Carlton and Scanlon, 1985; Mackie et al., 2012). Detection of cryptic invasions is crucial for quantifying both the numbers of invaders and their impacts on ecosystems. Several incidences of cryptic invasions involving both algae and invertebrate groups have been reported in marine environments (Thomsen et al., 2006; Lee, 2016).

The siphonous green macroalga *Codium fragile* ssp. *fragile* (Suringar) Hariot (Provan et al., 2008) (hereafter *C. fragile*) is a typical example of a cryptic invasive species. Originating in Japan, *C. fragile* is now widely distributed across the world (Trowbridge, 1996; Campbell, 1999; Provan et al., 2008; Guiry and Guiry, 2017). Although considered a warm-temperate alga (Fralick and Mathieson, 1972; Carlton and Scanlon, 1985), its distribution spans from across temperate and cold regions of the NW and NE Atlantic (Trowbridge, 1998; Matheson et al., 2014). The potential impacts of the introduction of *C. fragile* have been widely studied, and both negative and positive effects have been identified (Bulleri et al., 2006; Scheibling and Gagnon, 2006; Drouin et al., 2016). *C. fragile* has long been assumed to outcompete and

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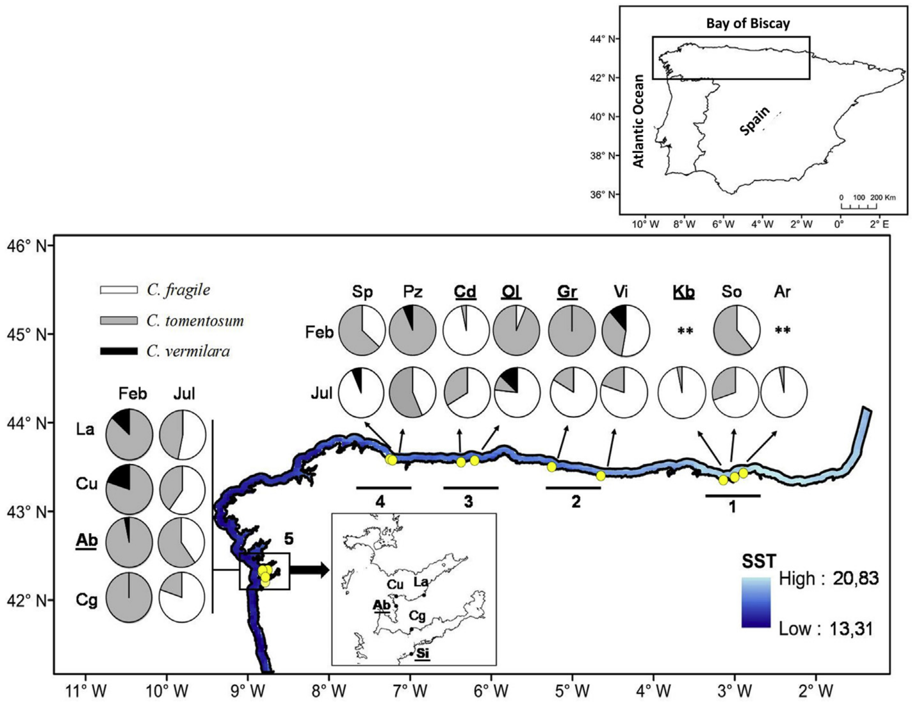

Fig. 1. Frequency of occurrence of *Codium* species in each stretch of coast and location studied, and SST satellite data (annual average values from the period 2013–2016). *Codium* occurrence, n = 30 for all locations, except Vidiago (Vi) in February (n = 11). Coastal stretches are represented by numbers and underlined with a dashed line (1 = Basque Country, 2 = E Asturias, 3 = W Asturias, 4 = N Galicia, 5 = western Atlantic shores). Ar: Armintza; So: Sopela; Kb: Kobaron; Vi: Vidiago; Gr: La Griega; Ol: Oleiros; Cd: Cadavedo; Pz: Peizás; Sp: San Pedro; La: Lapamán; Cu: Cabo Udra; Ab: Área de Bon; Cg: Cangas; Si: Sirenita. The name of those locations where the temporal dynamics of *Codium* spp. were determined are shown in bold type and underlined. ** indicates locations that were visited but no *Codium* fronds were found.

ultimately displace its native congeners (Trowbridge, 2001 and references therein). However, elucidating, rather than assuming, the dynamics of the relationships between congeners (i.e. displacement *vs* coexistence) demands quantitative information about population growth and the phenology of *Codium* species in the different regions where *C. fragile* has been introduced (e.g. Trowbridge, 2001; Trowbridge and Farnham, 2004; Trowbridge and Farnham, 2009; Geraldi et al., 2014).

The success of *C. fragile* has been linked to its various modes of reproduction (Trowbridge, 1998; Bégin and Scheibling, 2003) and to its greater tolerance to high seawater temperature, irradiance and desiccation stress than in the native congeners (Burrows, 1991; Yang et al., 1997; Trowbridge, 1998). As this species may be nitrogen-limited during most of the growing season, its growth and spread may also be favoured increased concentrations of nutrients in seawater (e.g. eutrophication, upwelling events) (Trowbridge, 1998). In this context, the presence of utricle hairs may be important for enhancing nitrogen assimilation in this species (Oates and Cole, 1994; Harrison and Hurd, 2001).

The establishment and regional spread of NIS depends on propagule pressure (Williamson, 1996), biotic resistance and life history traits of the invader (Sakai et al., 2001; Lockwood et al., 2005), as well as on the presence of suitable environmental conditions (Sakai et al., 2001). In N-NW Spain, there are regional differences in abiotic factors, such as seawater temperature and inorganic nutrient content (Ramos et al., 2012), mainly as a result of upwelling phenomena that occur during spring-summer, generally towards western areas (Botas et al., 1990; Álvarez et al., 2010). In this region, *C. fragile* coexists on intertidal rocky shores with three erect native *Codium* species: *C. tomentosum* Stackhouse, *C. vermilara* (Olivi) Chiaje, and *C. decorticatum* (Woodward) Howe (Fernández-Montero et al., 1998; Bárbara et al., 2005; Rodríguez and Moliner, 2010; Rojo et al., 2014). Invasive and native species are all dichotomously branched and morphologically very similar. The subspecies *C. fragile* ssp. *atlanticum* (Cotton) Silva is now considered a native of the British Isles (Provan et al., 2008) and has been also cited in N Spain. However, no specimens have been identified by molecular analysis in the area (Rojo et al., 2014).

The results of some preliminary studies in the region indicated that, relative to its native congeners, *C. fragile* occurs more frequently towards the inner part of the Bay of Biscay, either on emergent substrata or in tide pools (Cires Rodríguez and Rico Ordás, 2007; Rojo et al., 2014). This suggests that increases in SST, already observed in N-NW Spain (Gómez-Gesteira et al., 2008; Costoya et al., 2015), may lead to changes in abundance, survival and persistence of *C. fragile*, as also suggested Armitage and Sjøtun (2017) in a study conducted on Norwegian shores.

The present study constitutes an extended analysis of the relative abundance and population dynamics of native and exotic *Codium* species along N-NW coasts of Spain. We focused on the phenology and growth patterns of invasive and native congeners, which are very variable in invaded regions and essential for understanding the invasive process and for enabling realistic predictions to be made about ecological impacts (Trowbridge, 1998). We also discussed the potential impact of the exotic species in a region in which a sharp environmental gradient is predicted under future climate change scenarios. The present study is one of few to quantitatively evaluate population dynamics of *Codium* species on intertidal shores (Trowbridge, 1996; Campbell, 1999; Bégin and Scheibling, 2003; Schmidt and Scheibling, 2005).

2. Material and methods

2.1. Study sites

The study was conducted at low intertidal levels in 14 locations in 5 selected stretches of coasts in N − NW Spain. The distribution of the coastal stretches ranged from the inner part of the Bay of Biscay to western Atlantic shores (in the outer part of rias or coastal inlets). Specifically, four stretches were located on the northern coasts, in the Bay of Biscay (Basque Country, E Asturias, W Asturias and Lugo), and another was located in the western Atlantic coast (stretches numbered 1 to 5 in Fig. 1). Between 2 and 5 sampling locations, all gently sloping rocky platforms semi-exposed to wave action, were chosen within the coastal stretches. Well-developed *Bifurcaria bifurcata* R. Ross beds dominate at low intertidal levels in these locations, and this perennial seaweed is abundant all along the N and NW coasts of Spain, co-dominating with *Himanthalia elongata* on Atlantic shores (Niell, 1977; Fernández et al., 1983). *Codium* species appeared at low intertidal levels and in tide pools (when present) in these locations. The tidal