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The fate of *Cystoseira crinita*, a forest-forming Fucale (Phaeophyceae, Stramenopiles), in France (North Western Mediterranean Sea)

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ABSTRACT

In the Mediterranean Sea, Fucales, and in particular the species of the genus *Cystoseira* C. Agardh, are habitat-forming species dominating several benthic assemblages from the littoral fringe down to 70–80 m depth in the clearest waters. They generate high primary production involved in the maintenance of diversified trophic levels, they provide shelter, food, habitat and nursery areas to many species, and they are long-lived species that constitute a good model for studying human impact on species diversity. *Cystoseira crinita* Duby is a Mediterranean endemic cespitose species, living in shallow waters (0–5 m depth), in places with little wave action and high solar irradiance. To reconstruct the long-term patterns of change in its distribution along the French Mediterranean coast (French Catalonia, Languedoc, Provence, French Riviera and Corsica), all the historical data (published articles, unpublished reports and herbarium vouchers) collected since the 18th century were searched and analysed. To assess the current status of the species, several field surveys were conducted between 2010 and 2016 by snorkelling and SCUBA diving. *Cystoseira crinita* is currently extinct in French Catalonia, near-extinct in Languedoc and western Provence, and functionally extinct on the French Riviera coast, while the eastern Provence and Corsican populations have remained stable. The main probable causes of decline are habitat destruction and overgrazing by herbivores.

1. Introduction

Along the temperate rocky coasts, the large canopy-forming kelps (Laminariales) and fucoids (Fucales) (Phaeophyceae, Stramenopiles) represent the dominant species in pristine environments (Dayton, 1985; Steneck et al., 2002; Schiel and Foster, 2006). They generate high primary production contributing to sustaining diversified trophic levels, they provide shelter, food, habitat and nurseries to a multitude of species, and the larger species reduce the wave action (Steneck et al., 2002). The kelp beds and fucoid assemblages are highly impacted worldwide, due to the cumulative impact of increasing human pressures (e.g. destruction of habitats, pollution, species introduction, overfishing, coastal aquaculture and global warming) (e.g. Steneck et al., 2002; Díez et al., 2003; Helmuth et al., 2006; Worm and Lotze, 2006; Airoldi and Beck, 2007; Hawkins et al., 2008; Wernberg et al., 2010; Schiel, 2011; Lamela-Silvarrey et al., 2012; Raybaud et al., 2013; Filbee-Dexter and Scheibling, 2014; Vergés et al., 2014). Different pressures act over time and in unison, with possible synergistic effects, affecting species, ecosystems and their ability to deliver ecosystem services. After destruction, the habitat-forming algae usually take a long time to recover when water quality is improving (Coleman et al., 2008; Connell et al., 2008; Díez et al., 2009).

In the Mediterranean Sea, fucoid species of the genera *Cystoseira* C. Agardh and *Sargassum* C. Agardh are the main habitat-forming species of the photophilous rocky substrates from the littoral fringe to the lower sublittoral zone (down to 70–80 m depth in the clearest waters) (Feldmann, 1937; Molinier, 1960; Pignatti, 1962; Boudouresque, 1971, 1972; Verlaque, 1987a; Ballesteros, 1988, 1990a,b; Giaccone et al., 1994). Of the 289 taxa of *Cystoseira* described worldwide, 29 species and more than fifteen infraspecific taxons are currently accepted taxonomically in the Mediterranean Sea, most of them having specific ecological constraints that limit their development to specific habitats (Gómez-Garetta et al., 2001; Guiry and Guiry, 2015).

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Decline and losses of populations of *Cystoseira* species have been reported throughout the Mediterranean Sea caused by habitat destruction, eutrophication and overgrazing by herbivores, leading to a shift from highly structured ecosystems to poorly organised benthic assemblages such as filamentous algal turfs, ephemeral seaweed assemblages and barren grounds dominated by encrusting algae and sea urchins (Munda, 1974, 1982, 1993; Verlaque, 1987a,b; Benedetti-Cecchi and Cinelli, 1992a,b; 1995; Chryssovergis-Bacoyannis and Panayotidis, 1993; Menconi et al., 1999; Ruitton et al., 2000; Benedetti-Cecchi, 2001; Benedetti-Cecchi et al., 2001; Bulleri et al., 2002; Micheli et al., 2005; Thibaut et al., 2005; Devescovi and Iveša, 2007; Airoldi et al., 2008; Maggi et al., 2009, 2012; Falace et al., 2010; Perkol-Finkel and Airoldi, 2010; Fraschetti et al., 2011, 2012; Giakoumi et al., 2012; Sala et al., 2012; Tamburello et al., 2013; Boudouresque and Verlaque, 2013; Bianchi et al., 2014; Templado, 2014; Vergés et al., 2014). As regards the putative impact of warming, either positive or negative, upon *Cystoseira* species (including *C. crinita*), no evidence has as yet been published.

As a consequence, the Mediterranean species of *Cystoseira* are under surveillance by international organizations, such as the Council of Europe, the United Nations, the IUCN, the RAC/ASP and the WWF. Five species, *C. amentacea* (C. Agardh) Bory, *C. mediterranea* Sauvageau, *C. sedoides* (Desfontaines) C. Agardh, *C. spinosa* Sauvageau and *C. zosteroides* C. Agardh are on the list of strictly protected species (Annex I) of the Berne Convention (Council of Europe (1979), and all the species, except *C. compressa,* are on the Annex II List of endangered and threatened species of the Barcelona Convention (UNEP/MAP, 2009).

Among the shallow Mediterranean species, *Cystoseira crinita* Duby (Duby, 1830) is a perennial cespitose plant, living in shallow waters (0–5 m depth), up to 50 cm in height, fixed by an encrusting base from which rise up to 20 primary erect axes. The species is living in the upper sublittoral zone, near the surface, in places with little wave action, high light intensity and high temperature (Gómez-Garreta et al., 2001). *Cystoseira crinita* is a strictly Mediterranean endemic species mainly distributed in the Western Mediterranean and the Adriatic Sea (Ribera et al., 1992). Berov et al. (2015) consider all the Black Sea records of *C. crinita* as misidentifications of *C. bosphorica* Sauvageau, and the records from the Canary Islands (Santos Guerra et al., 1970; Santos Guerra, 1972) as erroneous (MV). Two infraspecific taxa described from the Adriatic Sea, *C. crinita* f. *semispinosa* Ercegovic (Ercegović, 1952) and *C. crinita* var. *flaccida* (Kützing) Schiffner (Schiffner, 1933), require further investigation (Cormaci et al., 2012; Guiry and Guiry, 2015).

Cystoseira crinita is probably a long-lived species, with low seasonal and year-to-year fluctuations. This assertion is not based upon the accurate ageing of individuals: in the absence of growth rings, no ageing method is currently available. Rather, it is based upon the expertise resulting from 40 years experience of the senior authors (CFB, MV), who checked the persistence and stability of precisely located *C. crinita* stands, with regard to both density and number of erect trunks, over seasons and years, at undisturbed sites. For these reasons, *C. crinita* is a relevant indicator of possible long-term changes.

Benthic assemblages dominated by *C. crinita* were originally described as an algal association (*Cystoseiretum crinitae*) from Cap Corse (Capicorsu, northern Corsica) (Molinier, 1960). The author considered them as the most complex photophilic Mediterranean seaweed assemblage that develops in shallow rocky habitats. According to Sales (2010), Sales and Ballesteros (2010) and Sales et al. (2012), *C. crinita* assemblages are restricted to shallow sheltered areas (usually < 1 m depth) and host 234 species of flora and fauna.

Because of the shallow habitat, *C. crinita* and the other subsurface *Cystoseira* species are particularly vulnerable to sea surface pollution, habitat destruction, trampling and overgrazing by large herbivores, e.g. the sea urchins *Paracentrotus lividus* (Lamarck 1816) and *Arbacia lixula* (Linnaeus 1758) and the teleosts *Sarpa salpa* (Linnaeus 1758), *Diplodus* spp. and *Siganus* spp., as evidenced by the numerous regressive events reported throughout the Mediterranean Sea (Bellan-Santini, 1968b; Desrosiers et al., 1982, 1986; Cecere et al., 1996; Rodríguez-Prieto and Polo, 1996; Cormaci and Furnari, 1999; Cormaci et al., 2001; Soltan et al., 2001; Milazzo et al., 2002; Thibaut et al., 2005, 2015a; Burkepile and Hay, 2006; Serio et al., 2006; Arévalo et al., 2007; Díez et al., 2009; Vergés et al., 2009; Falace et al., 2010; Sala et al., 2011; Sales et al., 2011; Tsiamis et al., 2013; Bianchi et al., 2014).

In disturbed areas, the bathymetric range of *C. crinita* decreases and the ecosystem exhibits a shift to less structural complexity and the homogenization of the habitat. When *C. crinita* and the other shallow water species of *Cystoseira* disappear, the benthic assemblage is replaced by articulated Corallinales (*Corallina* spp.), mussel beds (*Mytilus galloprovincialis* Lamarck, 1819), which become dominant, forming extensive, wide belts along the shore (Berner, 1931; Bellan-Santini, 1964, 1965, 1968a,b; Huvé, 1970; Arnoux and Bellan-Santini, 1972; Bellan and Bellan-Santini, 1972; Astier, 1975; Augier, 1977; Desrosiers et al., 1982, 1986; Fernández and Niell, 1982; Thomas, 1983; Janssens et al., 1993; Soltan et al., 2001; Arévalo et al., 2007; Maggi et al., 2009; Falace et al., 2010). The ultimate regressive stage being barren ground dominated by encrusting Corallinales and grazer invertebrates (sea urchins and gastropods), *Cystoseira* spp. then finds refuge in rocks pools (free of herbivorous species) and in very shallow waters of sheltered coves (Munda, 1974, 1982, 1993; Chryssovergis-Bacoyannis and Panayotidis, 1993; Micheli et al., 2005; Thibaut et al., 2005; Devescovi and Iveša, 2007; Airoldi et al., 2008; Perkol-Finkel and Airoldi, 2010; Falace et al., 2010; Fraschetti et al., 2011; Giakoumi et al., 2012; Sala et al., 2012; Templado, 2014; Vergés et al., 2014). When the herbivory pressure decreases, recolonization by Fucales has been reported (Hanel, 2002; Zavodnik et al., 2002).

Most studies of habitat loss or coastal urban development only focus on local scales and short, recent periods of time. While this focus is also necessary, the preoccupation with these local and present-day drivers means that we are often not aware of the past range of species and of the regional context of local studies. In order to analyze the long-term patterns of change in the distribution of the *C. crinita* populations along the French Mediterranean coasts, we have used all possible available data (herbarium vouchers, published and grey literature) for comparison with the current distribution of the species investigated by field surveys. The use of historical data in marine ecology is becoming more frequent, as they provide a baseline for animal and plant populations in very slightly disturbed areas so that changes can be analysed over a long time period (Jackson et al., 2001; Sáenz-Arroyo et al., 2005; Thibaut et al., 2005, 2014, 2015a,b; Lotze et al., 2010; Babalis, 2011; Husa et al., 2014; Gatti et al., 2015). Because most of the data collected over the last centuries are qualitative, the aim of this study was (i) to provide an exhaustive map of the current distribution of *C. crinita* over the entire French Mediterranean coast including Corsica; (ii) to compare this distribution with historical data to assess losses; (iii) to identify and analyze the possible causes of decline.

2. Material and methods

2.1. Study area

We considered all the Mediterranean coasts of France from Cerbère (Spanish border) to Menton (Italian border), including Corsica (Fig. 1). We divided the studied area into 6 administrative regions: French Catalonia (Pyrénées-Orientales), Languedoc (Aude, Hérault, Gard), Western Provence (Bouches-du-Rhône), Eastern