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Decline and local extinction of Fucales in the French Riviera: the harbinger of future extinctions?

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Abstract

The French Riviera is among the Mediterranean areas that have been subject to the most long-lasting anthropogenic influences with severe impact on the marine environment. Fucales are long-lived, habitat forming brown algae that constitute a good model for studying human impact on species diversity. We gathered all historical data (literature and herbarium vouchers), since the early 19th century, to reconstruct their past distribution. The present distribution was established on the basis of an extensive 7-year (2007-2013) survey of the 212-km shoreline (measured on a 1/2 500 map), by means of boating, snorkelling and scuba diving. A total of 15 taxa of *Cystoseira* and 3 taxa of *Sargassum* were reported. Upon comparison with historical data, 5 taxa were no longer observed (*C. elegans*, *C. foeniculacea* f. *latiramosa*, *C. squarrosa*, *C. spinosa* var. *spinosa* and *S. hornschurchii*) while *C. jabukae*, previously unrecorded, was observed. In addition to the 5, possibly extinct taxa locally, *C. amentacea*, *C. barbata* f. *barbata*, *C. brachycarpa*, *C. crinita*, *C. sauvageauana* and *S. vulgare* suffered a decline, while *C. foeniculacea* f. *tenuiramosa*, *C. spinosa* var. *compressa* and *S. acinarium* became nearly extinct. *Cystoseira barbata* f. *barbata*, *C. brachycarpa*, *C. crinita* and *C. spinosa* var. *compressa* that played significant functional roles in coastal communities in the past, can be considered as functionally extinct. A similar situation has already been reported, although on a smaller scale, in other Mediterranean localities. The following question, therefore, arises regarding the ecology of Fucales in the Mediterranean: are some species on the brink of extinction? Is their decline or possible extinction, as documented on the French Riviera, the harbinger of their extinction Mediterranean-wide?

Keywords: *Cystoseira*, *Sargassum*, threatened species, Mediterranean.

Introduction

All over the world, coastal ecosystems are highly impacted due to the cumulative impacts of increasing human pressure (e.g. destruction of habitats, pollution, non-indigenous species, overfishing, coastal aquaculture and global warming). Different forms of stress act over time and in unison, with a possible synergistic effect, on species, ecosystems and their ability to deliver ecosystem services (e.g. Worm *et al.*, 2006; Halpern *et al.*, 2008; Waycott *et al.*, 2009). The Mediterranean Sea is a hotspot of marine species biodiversity that is under siege due to rapid demographic development, pollution, a high percentage of worldwide shipping and tourism and the highest rate of biological invasions (e.g. Bianchi & Morri, 2000; Galil, 2000; Boudouresque & Verlaque, 2002; Panayotidis *et al.*, 2004; Lotze *et al.*, 2006; Coll *et al.*, 2010; Lejeune *et al.*, 2010; Zenetos *et al.*, 2010; UNEP/ MAP, 2012; Bianchi *et al.*, 2014).

Along temperate rocky coasts worldwide, large canopy-forming kelps (Laminariales, Phaeophyceae, Ochrophyta) and fucoids (Fucales, Phaeophyceae, Ochrophyta)

represent the dominant species in pristine environments (Dayton, 1985; Steneck *et al.*, 2002; Schiel & Foster, 2006); they provide shelter, food, habitat and nursery areas to a multitude of species, and important primary production involved in the maintenance of diversified trophic levels, and they also attenuate wave action in the case of the largest species (Steneck *et al.*, 2002). These seaweeds can be controlled by top-down mechanisms, mainly in the case of the sublittoral species, while the subsurface species are controlled by a bottom-up mechanism (Hereu *et al.*, 2008a; Cardona *et al.*, 2013). The loss of kelps and fucoids is a worldwide phenomenon due, directly or indirectly, to human activities (Steneck *et al.*, 2002; Diez *et al.*, 2003; Helmuth *et al.*, 2006; Worm & Lotze, 2006; Airolidi & Beck, 2007; Hawkins *et al.*, 2008; Wernberg *et al.*, 2010; Schiel, 2011; Lamela-Silvarey *et al.*, 2012; Raybaud *et al.*, 2013; Filbee-Dexter & Scheibling, 2014). Some taxa have been driven to regional extinction (Thibaut *et al.*, 2005; Coleman *et al.*, 2008; Phillips & Blackshaw, 2011) or are threatened by climate warming that might drive them toward areas where retreat is impossible (Wernberg *et al.*, 2011). These impacts

are leading to shifts in habitat structure from a state with canopy forming species to alternative states, in the worst case to barren grounds composed of filamentous and encrusting species (Micheli *et al.*, 2005; Connell *et al.*, 2008; Perkol-Finkel & Airoidi, 2010; Sala *et al.*, 2012; Filbee-Dexter & Scheibling, 2014), with flow-on effects on adjacent communities (Bishop *et al.*, 2010).

In the Mediterranean Sea, species of the genus *Cystoseira* C. Agardh and *Sargassum* C. Agardh are habitat-forming species dominating several assemblages, from the littoral fringe down to the lower sublittoral zone (Feldmann, 1937; Molinier, 1960; Pignatti, 1962; Verlaque, 1987; Ballesteros, 1988, 1990a,b; Giaccone *et al.*, 1994). Their zonation depends on different environmental conditions (light, temperature, hydrodynamics and grazing) (Sauvageau, 1912; Ollivier, 1929; Vergés *et al.*, 2009). Loss of Mediterranean furoid algae has been reported all around the Mediterranean; caused by habitat destruction, eutrophication and overgrazing by herbivores and leading to a shift to lesser structural complexity, such as turf-forming, filamentous or other ephemeral seaweeds or urchin barren grounds where urchin density is a driver of habitat homogenization (Munda, 1974, 1982, 1993; Thibaut *et al.*, 2005; Devescovi and Ivesa, 2007; Airoidi *et al.*, 2008; Falace *et al.*, 2010; Frascchetti *et al.*, 2011; Orfanidis *et al.*, 2011; Giakoumi *et al.*, 2012; Sala *et al.*, 2012; Tsiamis *et al.*, 2013; Bianchi *et al.*, 2014; Templado, 2014).

In order to analyse the long-term patterns of distribution of *Cystoseira* and *Sargassum* species along the French Riviera coast (north-western Mediterranean), we collected all available data (herbarium vouchers, published and grey

literature) and we reconstructed their historical distribution. The aims of this study were i) to provide an up-to-date and exhaustive semi-quantitative map of the distribution of each taxon, ii) to compare this distribution with historical data, iii) to assess the status of the taxa: stable, in decline, functionally extinct or possibly locally extinct and iv) to analyse and identify the possible causes of the observed situation and its consequences at Mediterranean scale.

Materials and Methods

Study site

The French Riviera is located in the north-western Mediterranean and extends from Théoule-sur-Mer to the Italian border (Menton). The coast is rocky, interspersed with large sedimentary bays (Fig. 1). Densely urbanized and populated (more than one million permanent inhabitants), this coast is one of the most attractive coasts for tourism in the world, welcoming ~11 million tourists every year, with frequency peaking in August (600 000 visitors simultaneously present on August, 15th 2013) (Comité Régional du Tourisme Côte d'Azur, 2014).

Data collection

Historical data

There is a considerable amount of available historical data (published literature and herbarium collections) dealing with the occurrence of the genera *Cystoseira* and *Sargassum* along the French Riviera coastline. From the 19th to the early 21st century, numerous naturalists and

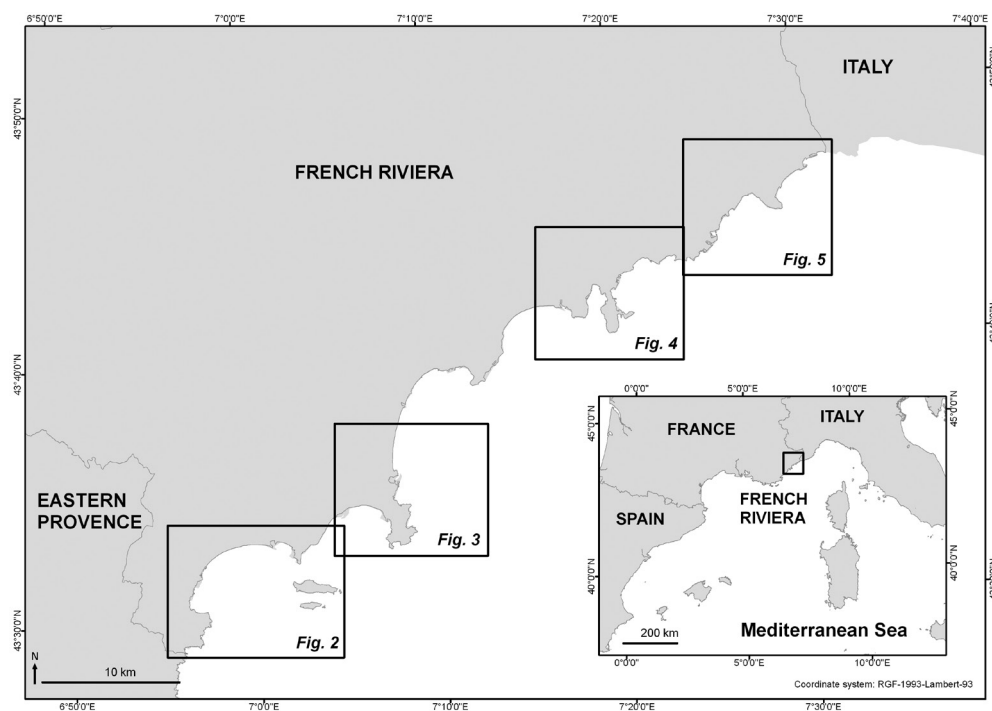


Fig. 1: The studied area; the French Riviera. We did not represent the shoreline between Antibes (Box Fig. 3) and Nice (Box Fig. 4) because it is only made of a large beach with the International Airport in the middle, any *Fucales* have never been observed in this area.

phycologists surveyed the French Mediterranean coasts. They received support from local natural history museums and they built up an efficient web of collectors providing large quantities of samples.

Vouchers held in herbaria are an exceptional source of data providing a basis for checking the identification of the specimens. We surveyed several thousand vouchers held in the following herbaria (names after *Index Herbariorum*). **AV**: The Muséum d'Histoire Naturelle d'Avignon; Herbarium Requier. **HCOM**: The herbaria held at Aix-Marseille University; Herbarium P. and H. Huvé, Herbarium Saint-Charles, Herbarium Thibaut, Herbarium M. Verlaque. **MPU**: The herbaria held at the University of Montpellier 2; Herbarium Flahault, Herbarium Général, Herbarium Raphaélis. **Musée Océanographique** of Monaco (not indexed); Herbarium Aguesse, Herbarium Mouret, Herbarium Prince Albert I. **NICE**: The Muséum d'Histoire Naturelle de Nice; Herbarium Camous, Herbarium Algues Marines tome III, Herbarium Algues vertes 1890-1910. **Nice-Sophia Antipolis** University (not indexed); Herbarium Meinesz. **PC**: The Muséum National d'Histoire Naturelle (MNHN) in Paris; Carnet de récolte de Feldmann, Herbarium Bory de Saint-Vincent, Herbarium B. de Revières, Herbarium J. Feldmann, Herbarium Général, Herbarium Lamouroux, Herbarium Leprieur in Herbarium Cosson, Herbarium Magne, Herbarium Montagne, Herbarium Sauvageau, Herbarium Thuret. **VTA**: The Botanical Garden of Villa Thuret in Antibes: a recently rediscovered collection of vouchers collected by Gustave Thuret and Edouard Bornet in the 19th century.

The '2007-2013' distribution

The field work was carried out during the period of maximum development of species (spring to autumn according to the taxon) from 2007 to 2013. When barely identifiable specimens were found, we returned to the site during the growth period in order to identify the species. We surveyed the whole shoreline with special attention to the sites sampled by previous phycologists. We used maps of the habitats, from the sea surface down to 50 m depth (Holon & Descamp, 2007, 2008), to locate the shallow and the deep reef habitats likely to harbour Fucales species; all these sites were investigated. Between the shallow reef habitats (usually less than 5 m depth and close to the shoreline) and the deep ones, most of the area is occupied by seagrass meadows and soft substrates unsuitable for Fucales species. Special attention was paid to *Cystoseira amentacea*, which thrives close to sea level, at less than 1 m depth, and can therefore be extensively mapped. Populations were drawn on black and white A3 format aerial photographs obtained from the IGN (French National Institute of Geographical and Forest Information: BD Ortho). The scale was 1:2 500. Three people were on board a small boat (length 5 m) moving at low speed (3 to 6 km h⁻¹) a few meters from the shore. *Cystoseira amentacea* populations were recorded within 50-m stretches of

shoreline, according to 6 classes, as defined by Ballesteros *et al.* (2007): C 0 = absence, C 1 = rare scattered individuals, C 2 = abundant scattered individuals, C 3 = abundant patches of dense stands, C 4 = almost continuous belt and C 5 = continuous belt of *C. amentacea*. For shallow water species, snorkelling was used to survey the reef habitats along the whole coast extensively, so that no surface area escaped observation. Finally, scuba diving was used in the deep areas down to 40 m depth; dives were focused on sites where Fucales were recorded in the past and on the hard bottom habitats suited to harbouring Fucales, together with the surrounding areas. It is worth noting that suitable deep habitats are only found in limited areas.

For species other than *C. amentacea*, sites hosting *Cystoseira* or *Sargassum* were geo-localised as points and their abundance was visually estimated: absent, isolated individuals, scattered population and dense population. Species were identified in the field if possible. Doubtful specimens were collected and identified at the laboratory, using appropriate bibliography (Sauvageau, 1912; Hamel, 1931-1939; Ercegović, 1952; Gómez-Garreta *et al.*, 2000; Cormaci *et al.*, 2012). Vouchers are deposited in the Thibaut Herbarium (HCOM) kept at the Mediterranean Institute of Oceanography of Aix-Marseille University.

The changes over time (past and present distribution) were analysed using a GIS (Geographical Information System) database (ArcGis10®) with Spatial Analyst tools. Each past or present location was geo-localised. All historical maps were digitalized to fit the same coastal line used for the present distribution (scale 1:2 500).

Results

The historical and '2007-2013' distributions of 15 and 3 taxa of *Cystoseira* spp. and *Sargassum* spp., respectively, are summarized in Tables S1-S17 and Figs. 2-5. Overall, 385 historical records have been listed since the beginning of the 19th century. Most of the historical records date back to the 19th and the beginning of the 20th century with extensive collections by several naturalists living or spending time on the Riviera, such as Stanislas Bonfils, Edouard Bornet, Auguste Camous, Charles Flahaut, Albert I of Monaco, Gaston-Maurice Ollivier, Alphonse Raphaélis, Antoine Risso, Camille Sauvageau and Gustave Thuret. The later 20th century collections are scarcer but several studies were undertaken (Raphaélis, 1907, 1924a,b,c; Ollivier, 1929, Gugliemi, 1969, Jaffrenou, *et al.*, 1996; Verlaque & Bernard 1998; Meinesz *et al.*, 2000) and specimens of *Cystoseira* and *Sargassum* were collected by phycologists such as Jean Feldmann, Francis Magne, Alexandre Meinesz and one of the authors (Marc Verlaque).

Cystoseira amentacea (C. Agardh) Bory de Saint-Vincent

Cystoseira amentacea occurs throughout the Mediterranean Sea. Two varieties are sometimes considered, var. *amentacea* and var. *stricta* Montagne, but they are poorly

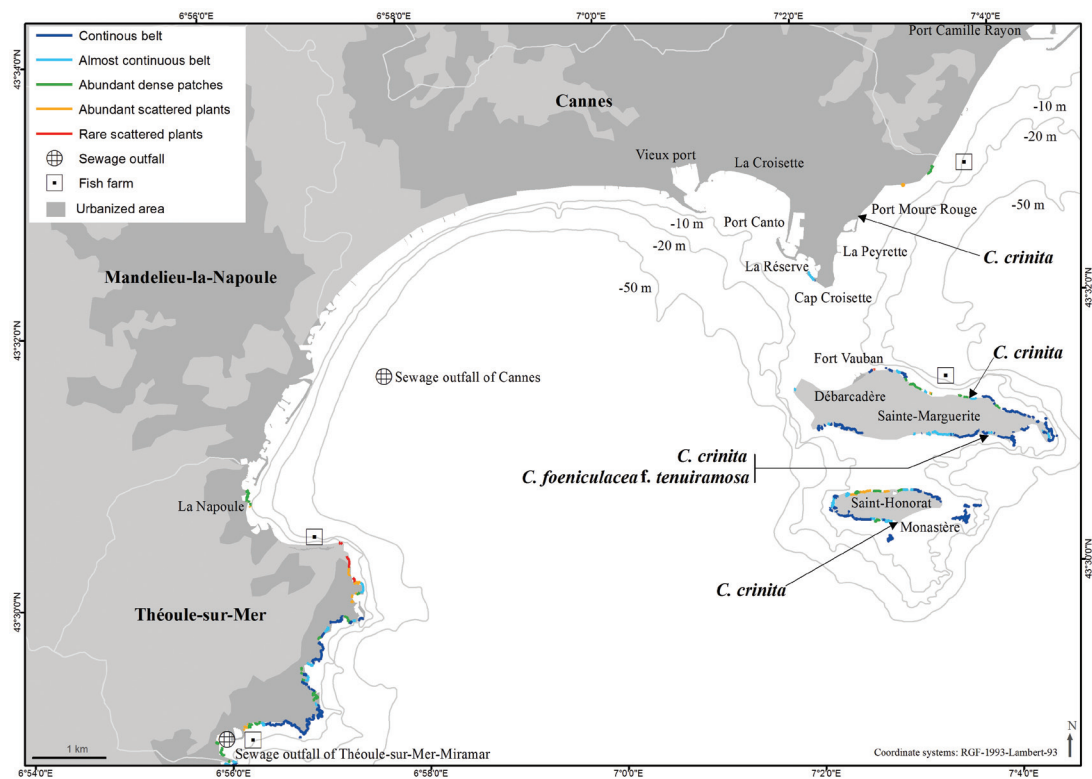


Fig. 2: Current distribution of *Cystoseira* and *Sargassum* species from the western limit of the French Riviera to Cannes. The colour indicates the presence and abundance of *C. amentacea*. No colour point or line means its absence. Other species, always present in very small patches, are located at the tip of the arrows. *C. compressa* subsp. *compressa*, which is present everywhere on hard substrates, is not cited. Lines correspond to depth contours.

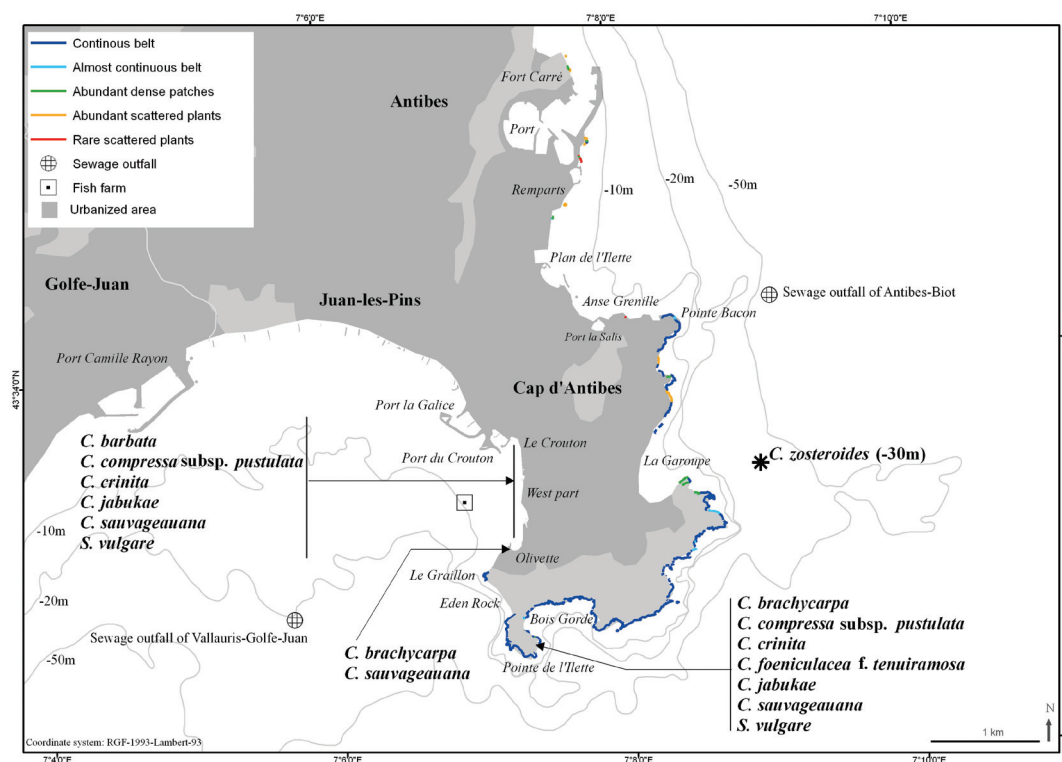


Fig. 3: Current distribution of *Cystoseira* and *Sargassum* species between Golfe-Juan and Antibes. The colour indicates the presence and abundance of *C. amentacea*. No colour point or line means its absence. Other species, always present in very small patches, are located at the tip of the arrows or beneath an asterisk. *C. compressa* subsp. *compressa*, which is present everywhere on hard substrates, is not cited. Lines correspond to depth contours.

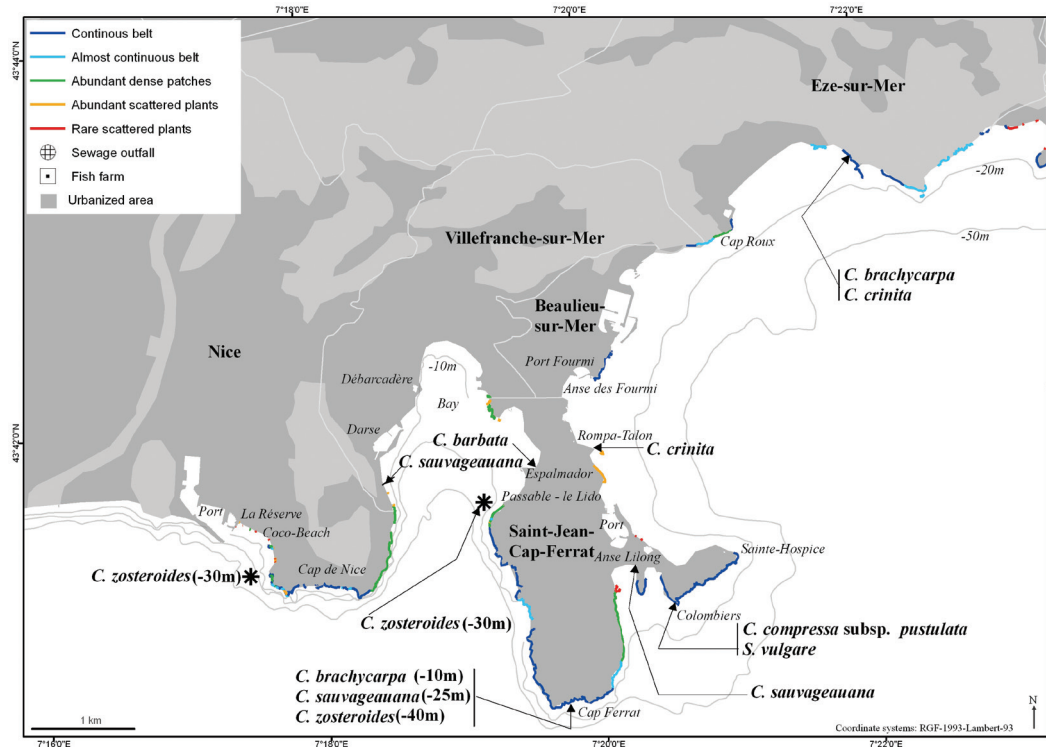


Fig. 4: Current distribution of *Cystoseira* and *Sargassum* species between Nice and Eze-sur-Mer. Colour indicates the presence and abundance of *C. amentacea*. No colour point or line means its absence. Other species, always present in very small patches, are located at the tip of the arrows or beneath an asterisk. *C. compressa* subs. *compressa*, which is present everywhere on hard substrates, is not cited. Lines correspond to depth contours.

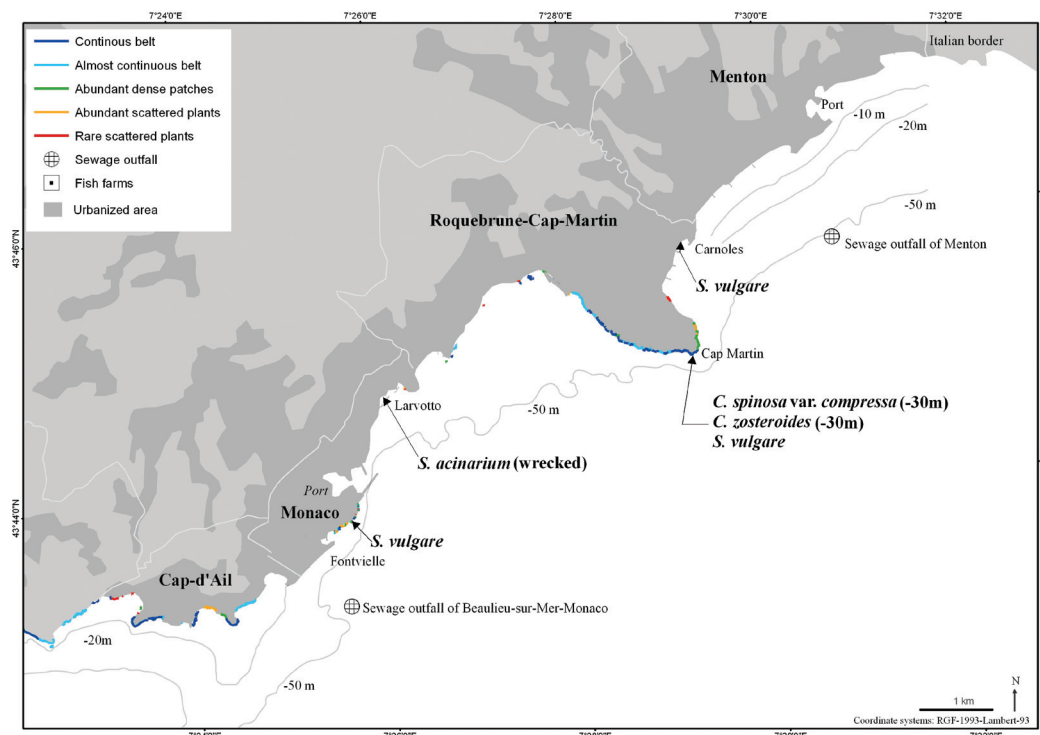


Fig. 5: Current distribution of *Cystoseira* and *Sargassum* species between Cap d'Ail and the Italian border. Colour indicates the presence and abundance of *C. amentacea*. No colour point or line means its absence. Other species, always present in very small patches, are located at the tip of the arrows or beneath an asterisk. *C. compressa* subs. *compressa*, which is present everywhere on hard substrates, is not cited. Lines correspond to depth contours.

characterized and will not be distinguished here (Ribera *et al.*, 1992; Cormaci *et al.*, 2012; Guiry & Guiry, 2014). *Cystoseira amentacea* was mentioned in the literature and herbaria under several other names, such as *Cystoseira stricta* Sauvageau, *Cystoseira ericoides* (Linnaeus) C. Agardh and *Cystoseira ericoides* var. *amentacea* C. Agardh.

The species was collected for the first time along the French Riviera coastline in 1826 at Nice by Antoine Risso (*in* Bory de Saint-Vincent Herbarium). During the 19th century, the species was frequently collected at Cannes, Antibes, Nice, and Roquebrune-Cap-Martin (Raphélis, 1907, 1924a,b,c). Agardh (1842) reported the species precisely ‘*ad Nizzam ipse*’ (in Nice). Montagne (1846) studied specimens collected by De Notaris ‘*ad Nicaeam*’ (in Nice). In the 20th century, Ollivier (1929) drew the first map of the species, from Cap Martin to Cap Roux (Eze-sur-Mer), described its distribution along the French Riviera coastline and highlighted that it was very abundant on exposed rocks and even in some bays. More recent authors noted that the species was still common (Guglielmi, 1969; Meinesz *et al.*, 2000; Susini, 2006) (Table S1).

In 2011, we mapped the entire populations of *C. amentacea* extensively (Figs. 2-5). *Cystoseira amentacea* was present along 44 km of shoreline. It was abundant on most of the suitable substrates and the populations are mainly constituted of continuous belts (Table 1). Populations were isolated from each other by large beaches and mostly located around the capes and islands. Regressions were localized around the entrance of ports and offshore from the cities (Antibes, Nice, Villefranche-sur-Mer, Saint-Jean-Cap-Ferrat), where *Mytilus galloprovincialis* and benthic assemblages of *Corallina* spp. dominated. In the vicinity of the Golfe-Juan fish farm, *C. compressa* subs. *compressa* was dominant over *C. amentacea*. In Monaco, a few *C. amentacea* patches subsisted at the foot of the old town (Le Rocher), the only natural coast remaining. On the man-made structures, *Corallina* spp. dominated.

Cystoseira barbata* (Stackhouse) C. Agardh f. *barbata

In the Mediterranean Sea, *Cystoseira barbata* f. *barbata* grows in the upper sub-littoral zone in sheltered places and shallow bays as well as in coastal lagoons. In the study area, some historical records were cited under the names: *Cystoseira hoppei* C. Agardh, *Cystoseira barbata* var. *hoppei* (C. Agardh) J. Agardh and *Cystoseira barbata* f. *hoppei* (C. Agardh) Woronichin.

The first record dates back to 1825, with specimens collected along the coast at Nice (‘*côtes de Nice*’) (specimens held in the Sauvageau Herbarium). During the 19th and 20th century, the species was collected 49 times along the French Riviera. In the 19th century, *C. barbata* f. *barbata* was collected at Cannes (Raphélis Herbarium, Raphélis, 1924a), at Antibes (Saint-Charles Herbarium, Huvé Herbarium, Sauvageau Herbarium, Flahaut Herbarium, Le Prieur Herbarium, Villa Thuret Herbarium,

Table 1. Structure of the *Cystoseira amentacea* populations along the French Riviera coasts (% of hard substrate coastline). C 0: absence; C 1: Rare scattered plants; C 2: Abundant scattered plants; C 3: Abundant patches of dense stands; C 4: Almost continuous belts; C 5: Continuous belts.

| C 0 | C 1 | C 2 | C 3 | C 4 | C 5 |
|-------|------|------|------|------|-------|
| 57.51 | 0.91 | 2.12 | 5.67 | 6.54 | 27.24 |

Bornet & Flahault, 1883), at Nice (Sauvageau Herbarium, Montagne Herbarium, Algue Vertes Herbarium), and at Menton (Bonfils *in* Raphélis 1924b).

At the beginning of the 20th century, vouchers and records remained numerous and the species was collected at Saint-Jean-Cap-Ferrat (J. Feldmann Herbarium, Carnet de récolte Feldmann, Ollivier 1929), Beaulieu-sur-Mer (Ollivier 1929), Roquebrune Cap-Martin (Bonfils *in* Raphélis 1924), and Menton (Raphélis Herbarium). The species was reported as common at Théoule (Raphélis Herbarium), Cannes (Raphélis Herbarium; Raphélis, 1924a), Golfe-Juan (Raphélis, 1924a), Antibes (Ollivier, 1929), Nice (Camous Herbarium) and between Saint-Jean-Cap-Ferrat and Eze-sur-Mer in 1912 (Camous, 1912). Ollivier (1929) described the species as very abundant in the shallow bays in the eastern and the western parts of Antibes but he noted that on the steep coast from Nice to Menton, the species was rare and located in Passable, Beaulieu-sur-Mer and Pointe Sainte-Hospice (Saint-Jean-Cap-Ferrat). Finally, Guglielmi (1969) reported the species as common at Villefranche-sur-Mer (rock pools on Pointe Colombier), Saint-Cap-Ferrat (Espalmador), and Beaulieu-sur-Mer (Baie de Fourmi). The species has become rare since the 1970s: only one citation (Debrat, 1974) and two specimens collected at Saint-Jean-Cap-Ferrat in the 1970s and Antibes in the 1980s (Meinesz Herbarium) (Table S2).

The ‘2007-2013’ situation of *C. barbata* f. *barbata* is critical. The species was not found at most of its previously recorded localities. We observed it at only 3 sites: a sheltered shallow site of the western part of Cap d’Antibes and adjacent to Le Crouton, where individuals are scattered over several dozen square meters, mixed with *C. compressa* subsp. *compressa*, *C. crinita*, *C. jabukae* and *C. sauvageauana*. A few individuals have been observed behind a *Posidonia oceanica* (Linnaeus) Delile barrier reef, in the Anse de l’Espalmador at Saint-Jean-Cap-Ferrat, on very shallow rocks surrounded by hundreds of individuals of the sea urchins *Paracentrotus lividus* (Lamarck 1816) and *Arbacia lixula* (Linnaeus 1758). *Cystoseira barbata* f. *barbata* was observed during the entire study period at all sites.

***Cystoseira brachycarpa* J. Agardh**

Cystoseira brachycarpa grows in littoral pools and sublittoral habitats, in moderately exposed and high light intensity sites. Some historical records were cited under the names: *Cystoseira balearica* Sauvageau, *Cystoseira*

brachycarpa var. *balearica* (Sauvageau) Giaccone and *Cystoseira caespitosa* Sauvageau.

Historical data concerning *C. brachycarpa* are scarce. The species has been recorded only 5 times: in 1899, as drift on a beach in Golfe-Juan (Raphélis Herbarium); frequent in Nice (Camous, 1912); collected in Antibes in 1928 (Raphélis in Général Herbarium); reported at Villefranche-sur-Mer by Hamel (1931-1939) by P. Dangeard; and two specimens collected at Antibes (Port Rousse Chaffa, now called Port La Salis) in 1979 (Verlaque Herbarium) (Table S3).

During the field study, the species was observed at 4 sites. At Cap d'Antibes, the species constituted a narrow belt below *C. amentacea* at l'Olivette and a dense monospecific assemblage in a rock pool of the Pointe de L'Ilette; at Cap Ferrat (Saint-Jean-Cap-Ferrat), a few sparse individuals, highly grazed, were growing at 10 m depth; some individuals were found slightly deeper than the *C. amentacea* belt at Eze-sur-Mer. *Cystoseira brachycarpa* was observed during the whole study period at all sites.

Cystoseira compressa* (Esper) Gerloff & Nizamuddin subsp. *compressa

Cystoseira compressa subsp. *compressa* (hereafter *C. compressa*) grows in the upper sublittoral zone from the sea surface down to 15 m, at both sheltered and exposed sites, in pristine and moderately polluted areas. Some individuals have occasionally been observed at depths down to 40 m. Some historical records were cited under the names: *Cystoseira abrotanifolia* (Linnaeus) C. Agardh, *C. abrotanifolia* f. *fimbriata* Sauvageau, and *C. fimbriata* Bory de Saint-Vincent.

Cystoseira compressa was first collected in 1839 at Nice (C. Agardh in Requier Herbarium, Algues Vertes Herbarium). In the 19th century, the species was collected and reported at Cannes (Raphélis Herbarium; Raphélis, 1924a), Antibes (Saint-Charles, Général and Flahault Herbaria), Nice (Requier, Montagne and Lamouroux Herbaria; Raphélis, 1924c), Menton (Bonfils in Raphélis, 1924b).

In the 20th century, *C. compressa* was observed 'everywhere' between Eze-sur-Mer and Nice (Camous, 1912). Ollivier (1929) described the species as ubiquitous and abundant everywhere from the surface down to several meters depth. Gugliemi (1969) reported the species as very common, everywhere in sheltered and exposed locations. The species was also observed by Gilet (1954) and Huvé & Huvé (1963).

Voucher specimens were collected at Mandelieu-la-Napoule (Raphélis Herbarium), Cannes, where the species was noted as abundant in 1900 (Général Herbarium, Raphélis Herbarium), Golfe-Juan (Raphélis Herbarium), Juan-les-Pins (J. Feldmann Herbarium), Antibes (Villa Thuret Herbarium, Raphélis Herbarium, Verlaque Herbarium), Nice (Raphélis Herbarium, Camous Herbarium, Algues Marines tome III Herbarium), Villefranche-

sur-Mer (J. Feldmann Herbarium, Aguesse Herbarium, Magne Herbarium), Saint-Jean-Cap-Ferrat (J. Feldmann Herbarium, Meinesz Herbarium), Beaulieu-sur-Mer (Meinesz Herbarium), Monaco (Mouret Herbarium) and Menton (Général Herbarium) (Table S4).

During the field study, the species was not only very common still, but was by far the most common Fucales along the French Riviera coastline.

***Cystoseira compressa* subsp. *pustulata* (Ercegović) Verlaque comb. nov.¹**

In the studied area, *C. compressa* subsp. *pustulata* grew in the shallow sublittoral zone. It was only sampled at Cannes in 1899 and 1912 (Général Herbarium) (Table S5) where it is still present.

We also found the species in the western part of Antibes and in shallow waters and two rock pools at Pointe Colombier at Saint-Jean-Cap-Ferrat. *Cystoseira compressa* subsp. *pustulata* was observed during the entire study period at all sites.

***Cystoseira crinita* Duby**

Cystoseira crinita grows in the upper sublittoral zone, near the sea surface, in sheltered locations with high light intensity and warm temperatures in summer.

The first record of the species along the French Riviera dates back to 1826, with a specimen collected at Nice (Thuret Herbarium). In the 19th century, voucher specimens and records come from Golfe-Juan (Saint-Charles Herbarium), Antibes (Thuret Herbarium, Sauvageau Herbarium, Bornet & Flahault, 1883). Hamel (1931-1939) reported the species referring to a record of de Notaris in the 20th century, in Nice (Thuret Herbarium, Lamouroux Herbarium; Duby, 1830; Agardh, 1842) and in Villefranche-sur-Mer (Thuret Herbarium).

At the beginning of the 20th century, *C. crinita* was present at Antibes (Villa Thuret Herbarium, J. Feldmann Herbarium; Ollivier, 1929), Saint-Jean-Cap-Ferrat (Camous, 1912), Beaulieu-sur-Mer (Ollivier, 1929) and Cap-d'Ail (Ollivier, 1929). Ollivier (1929) mentioned the species as abundant between Juan-les-Pins and Le Crouton in the western part of Antibes and in the Bay of Beaulieu. In the 1960s, the species was collected at Saint-Jean-Cap-Ferrat (Meinesz Herbarium) (Table S6).

During the field study, *C. crinita* was observed at 7 sites. A few individuals were found near the Mouret Rouge port, at Cannes, a few square meters below the monastery of Saint-Honorat Island and a number of individuals were found at Sainte-Marguerite Island. In the western part of Antibes, over a few dozen square meters, *C. crinita* was mixed with *C. barbata* f. *barbata*, *C. compressa* subsp. *compressa* and subsp. *pustulata*, *C. jabukae* and *C. sau-*

1. See Nomenclatural note

vageauana. At Pointe de l'Ilette, the species occurred in a single rock pool. We also observed a few heavily grazed individuals in shallow waters at Rumpa Talon (Saint-Jean-Cap-Ferrat) and at Eze-sur-Mer. *Cystoseira crinita* was observed during the entire study period at all sites, but, it is no longer present at most of the historical localities. Where still present, populations have become fragmented and have dramatically declined to a few individuals.

***Cystoseira elegans* Sauvageau**

Cystoseira elegans grows in the upper sublittoral zone, from the sea surface to a few meters depth, usually in moderately sheltered conditions. The species was only collected at Cannes in 1912 and 1926 (Raphélis in Général Herbarium) and at Antibes in 1961 (Huvé & Huvé, 1963) (Table S7).

We never found the species during our surveys. Considering its preference for a shallow habitat and that it is relatively easy to survey, its local extinction constitutes a likely hypothesis.

***Cystoseira foeniculacea* (Linnaeus) Greville f. *tenuiramosa* (Ercegović) A. Gómez Garreta, M.C. Barceló, M.A. Ribera & J.R. Lluch**

Cystoseira foeniculacea f. *tenuiramosa* grows in sheltered places in the littoral zone to 1 m depth (sometimes in rock pools). It is primarily an Atlantic species and the specimens that we observed in the herbaria all belong to the Mediterranean form *tenuiramosa*. Some historical records were cited under the names *Cystoseira discors* (Linnaeus) C. Agardh, *Cystoseira concatenata* C. Agardh and *Cystoseira schiffneri* Hamel.

Cystoseira foeniculacea f. *tenuiramosa* was first collected in 1825 by Thuret at Nice (Thuret Herbarium). In the 19th century, the species was collected at Cannes (Requien Herbarium, Raphélis, 1907), Antibes (Sauvageau Herbarium; Bornet & Flahault, 1883), Nice (Thuret Herbarium, Montagne Herbarium, Lamouroux Herbarium; Agardh, 1842), Villefranche-sur-Mer (Montagne Herbarium), Saint-Jean-Cap-Ferrat (Algues Vertes Herbarium) and Menton (Bonfils in Raphélis, 1924b).

In the first half of the 20th century, the taxon was collected at Cannes (Raphélis in Général Herbarium; Raphélis, 1907). The collector mentioned that the species was very abundant at Cannes (La réserve), between the two Islands of Lérins where it formed real forests (Raphélis, 1907). The taxon was also collected at Théoule-sur-Mer (Raphélis, 1907), Golfe-Juan (Raphélis, 1907), Antibes (J. Feldmann Herbarium; Ollivier, 1929), Villefranche-sur-Mer (J. Feldmann Herbarium, J. Feldmann: carnet de récolte; Ollivier, 1929), Saint-Jean-Cap-Ferrat (J. Feldmann Herbarium; Ollivier, 1929), Roquebrune-Cap-Martin (Mouret Herbarium) and Menton (Raphélis in Général Herbarium). Ollivier (1929) observed that *C. foeniculacea* f. *tenuiramosa* was abundant in the rock

pools of Pointe de l'Ilette (Antibes) and within the port of La Darse (Villefranche-sur-Mer). In the 1950s, the species was only collected once at Villefranche-sur-Mer (Magne Herbarium). In the 1970-1980s, *C. foeniculacea* f. *tenuiramosa* was collected at Golfe-Juan (Meinesz Herbarium), Antibes (Verlaque Herbarium) and Beaulieu-sur-Mer (Meinesz Herbarium) (Table S8).

During the field study, *C. foeniculacea* f. *tenuiramosa* was only observed at 2 sites: a single individual in shallow water at Sainte-Marguerite Island, in June 2007, and a dense population in a rock pool of a few square metres at Pointe de l'Ilette, Cap d'Antibes. This population was observed during the entire study period. The extensive exploration of the historical sites was unsuccessful in locating the taxon, with the exception of Pointe de l'Ilette; we can therefore consider that it is nearly extinct locally.

***Cystoseira foeniculacea* f. *latiramosa* (Ercegović) A. Gómez Garreta, M.C. Barceló, M.A. Ribera & J.R. Lluch**

A specimen dredged off Cap-Ferrat at 10-20 m depth and referred to as *C. discors* by Ollivier (1929) (Table S9), probably belonged to *C. foeniculacea* f. *latiramosa*, the deep form of the species.

We did not find this taxon during our surveys.

***Cystoseira jabukae* Ercegović**

Cystoseira jabukae has not been previously recorded along the French Riviera, and our two records are therefore the first. It has been regularly observed since 2007, growing in shallow waters (less than 1 m depth) in two moderately exposed areas: in the western part of Antibes, where a few individuals occurred together with *C. barbata* f. *barbata*, *C. compressa* (including subsp. *pustulata*), *C. crinita* and *C. sauvageauana*, and in rock pools at Pointe de l'Ilette with *C. crinita*.

***Cystoseira sauvageauana* Hamel**

Cystoseira sauvageauana usually grows in sheltered places in the littoral and sublittoral zones, down to several metres depth. Some early records were cited as *Cystoseira selaginoides* Sauvageau.

The species was first collected in 1840 at Antibes (Saint-Charles Herbarium) and another specimen collected in the 19th century (not dated) was found at Antibes (Général Herbarium).

All the other records date back to the beginning of the 20th century when the species was collected at Cannes (Raphélis in Général Herbarium), Antibes (Ollivier, 1929), Villefranche-sur-Mer (Ollivier, 1929; J. Feldmann: carnet de récolte), Saint-Jean-Cap-Ferrat (Ollivier, 1929; J. Feldmann: carnet de récolte) and Beaulieu-sur-Mer (Ollivier, 1929). According to Ollivier (1929) the species could be found in rock pools and in all the rocky bays along the entire French Riviera; the species was also abundant on the *jetée septentrionale du Fort Carré* (Antibes), at the

entrance of the Port of La Darse (Villefranche-sur-Mer), at l'Espalmador (Saint-Jean-Cap-Ferrat), between the rocks at Anse Lilong (Saint-Jean-Cap-Ferrat), in the north of Rumpa-Talon (Beaulieu-sur-Mer), while a few stunted individuals were growing in large rock pools dominated by *C. barbata* f. *barbata* at Pointe Sainte-Hospice (Saint-Jean-Cap-Ferrat). In 1999, the species was collected at Antibes (Verlaque Herbarium) (Table S10).

During the field study, *C. sauvageauana* was observed at 5 sites. Some specimens were found in the western part of Cap d'Antibes (regularly observed since 2007) in a mixed population with *C. barbata* f. *barbata*, *C. compressa* (including subsp. *pustulata*), *C. crinita* and *C. jabukae*, a few individuals of the species were also observed at Pointe de L'Îlette in rock pools (regularly observed since 2007), and some individuals in shallow waters (1 m depth), off the Marine Station of Villefranche-sur-Mer (2007 and 2010) and at Anse de Lilong (Saint-Jean-Cap-Ferrat) (2013), and off Cap-Ferrat at 25 m depth (2010). The latter record constitutes the deepest observation ever made for this species.

***Cystoseira squarrosa* De Notaris**

The species was originally described by De Notaris from material collected at Nice (Agardh, 1842) and has also been found growing near the sea surface at the entrance of the port of Nice in 1871 (Montagne Herbarium). Raphaélis (1907) mentioned drift specimens on the beach of Cannes. Ollivier (1929) reported, with doubts, from De Notaris' observations in the 19th century, some individuals at the same Nice site (Table S11).

We did not find this species during our surveys, which nowadays lies within the port of Nice. The species can therefore be considered as locally extinct.

Cystoseira spinosa* Sauvageau var. *spinosa

Ollivier (1929) reported the two varieties of *C. spinosa*: var. *spinosa* and var. *compressa*. He described a *C. spinosa* 'facies' from the sea surface rock pools down to 30-50 m depth, at Pointe de Lilong (Saint-Jean-Cap-Ferrat), with var. *spinosa* in shallow habitats and var. *compressa* in the deep habitats (Table S12).

We did not find *Cystoseira spinosa* var. *spinosa* during our survey, including at the above-mentioned site.

***Cystoseira spinosa* var. *compressa* Cormaci, Furnari, Giaccone, Scamaca & Serio**

According to Cormaci, Furnari, Giaccone, Scamaca & Serio, *Cystoseira spinosa* var. *compressa* grows in the sublittoral zone down to 70 m depth. Some early records were quoted as *Cystoseira spinosa* Sauvageau (without mentioning the variety).

The first specimen of *Cystoseira spinosa* var. *compressa* collected at Antibes (Saint-Charles Herbarium) dates back to 1840. The taxon was collected in the 19th century

at Nice (Risso in Lamouroux Herbarium, De Notaris in Montagne Herbarium). In the first half of the 20th century, the taxon was collected off Saint-Honorat Island (Raphélis, 1930), round the Islands of Lérins at 70 m depth (Peyrisol in Général Herbarium), at Pointe de Lilong, Cap-Ferrat (Ollivier, 1929), on the western side of Cap Ferrat (J. Feldmann: carnet de récolte). Sauvageau collected the species at Cap-Ferrat at 40 m depth between 1930 and 1935 (Sauvageau, 1931, 1936). Finally, the taxon was collected in 1997 at Larvotto (Monaco), at 32 m depth (Verlaque Herbarium; Verlaque & Bernard, 1998) (Table S13).

During our field study, we observed a few isolated individuals at Cap Martin (30 m depth) in 2010.

***Cystoseira zosteroides* C. Agardh**

Cystoseira zosteroides grows in the sublittoral zone down to 80 m depth. Some historical records were cited as *C. opuntioides* Bory de Saint-Vincent ex Montagne.

The species was first reported off the Port of Nice and in the Bay of Beaulieu-sur-Mer (Ollivier, 1929); this author noted that the species was less common than *C. spinosa*. Then, the species was only recorded in 1967 and 1968 at Cap Martin (Meinesz Herbarium) at 30 m depth (Gugliemi, 1969) (Table S14).

During the field study, we found a few specimens in Antibes, off La Garoupe (2008), at the entrance of the port of Nice (2007-2010), in the eastern part of the Bay of Villefranche-sur-Mer, off Le Lido-Passable, off Cap Ferrat (regularly observed since 2007), and off Cap Martin (2010), always between 30 and 40 m depth.

***Sargassum acinarium* (Linnaeus) Setchell**

Sargassum acinarium usually grows in the sublittoral zone at several dozen meters depth. Some historical records were cited under the names: *S. linifolium* C. Agardh, and *S. vulgare* var. *linifolium* (C. Agardh) Zanardini.

The first record of the species dates back to 1821 at Cannes (Raphélis, 1907). In the 19th century, the species was collected at Cannes (Raphélis, 1907; Sarato in Raphaélis, 1924c), Golfe-Juan (Raphélis, 1907), Antibes (Thuret Herbarium; Bornet & Flahault 1883), Nice (Algues Vertes Herbarium, Risso in Requier Herbarium; Algues Vertes Herbarium; Sarato in Raphaélis, 1924c) and Menton (Bonfils in Raphaélis 1924b). In the 20th century the species was collected as drift at Saint-Jean-Cap-Ferrat in 1910 and at Cannes in 1926 (Raphélis in Général Herbarium) (Table S15).

We found a single drift fertile specimen cast ashore on a beach of Larvotto (Monaco) in 2007.

***Sargassum hornschurchii* C. Agardh**

Sargassum hornschurchii usually grows in the sublittoral zone at several dozen metres depth. The first specimen was collected in 1821 at Cannes (Raphélis, 1907). A few specimens were collected in the 19th century at Cannes

(Raphélis in Général Herbarium; Raphélis, 1907), Antibes (Sauvageau Herbarium), and Villefranche-sur-Mer (Algues Vertes Herbarium). In the 20th century, *S. hornschruchii* was collected at Théoule-sur-Mer (Raphélis in Général Herbarium), Cannes (Raphélis in Général Herbarium), Antibes (J. Feldmann Herbarium), Villefranche-sur-mer (J. Feldmann in Hamel, 1931-1939) and Cap-Ferrat (J. Feldmann herbarium; J. Feldmann: carnet de récolte) (Table S16).

We did not find this species during our surveys.

***Sargassum trichocarpum* J. Agardh**

Sargassum trichocarpum has been quoted by Raphélis (1907) as *Sargassum boryanum* Montagne. It was found in a fishing net, off Cannes. In the synonymy, Raphélis (1907) included *S. salicifolium* Bory, which is considered to be the very common *S. vulgare*. Raphélis' specimen was not located in his herbarium. Therefore, we consider this record as a probable misidentification, as doubt arises both from the proposed synonymy as well as the fact that this species has never previously been collected in France in natural habitats.

***Sargassum vulgare* C. Agardh**

Sargassum vulgare grows in rock pools, on moderately wave-exposed rocks, and in the sublittoral zone down to ca. 40 m depth. Some historical records were cited under the names: *Sargassum salicifolium* auctorum (non Montagne) and *S. megalophyllum* Montagne.

The species was first mentioned as *S. salicifolium* Bory at Antibes (Agardh, 1842) and the first voucher specimen dates from 1849 as *S. vulgare* (Saint-Charles Herbarium). In the 19th century, the species was collected and observed at Cannes (Raphélis in Général Herbarium, Lenormand in Général Herbarium), Antibes (Saint-Charles Herbarium, Flahault Herbarium, Villa Thuret Herbarium; Agardh, 1842) and Nice (Hamel, 1931-1939, from De Notaris).

In the first half of the 20th century, observations of the species were made at Cannes (Raphélis & Séraillier in Général Herbarium; Raphélis, 1907, 1924a), Nice (Camous, 1912) and Saint-Jean-Cap-Ferrat (Raphélis in Général Herbarium). In the second half of the 20th century, the species was collected at Juan-les-Pins (Meinesz Herbarium), Nice (Meinesz Herbarium), Villefranche-sur-Mer (Magne Herbarium; Meinesz Herbarium; Hamel, 1931-1939 from J. Feldmann), Beaulieu-sur-Mer (De Reviere Herbarium; Meinesz Herbarium) and Monaco (Meinesz Herbarium). In 2000, one of us (T. Thibaut) observed a large population at Carnoles (Roquebrune-Cap-Martin) in a shallow bay, off a beach, growing on pebbles. Individuals were tall (around 50 cm height) and numerous, covering several dozen square metres. A year later, these populations had disappeared. Thereafter, a few small scarce individuals were sampled in a rock pool at Pointe Sainte-Hospice (Saint-Jean-Cap-Ferrat) (Herbarium T.

Thibaut), Pointe Bacon, Antibes, at 20 m depth (Herbarium Meinesz), Larvotto, Monaco at 31 m depth, and Cap Martin, at 30 m depth (Herbarium T. Thibaut) (Table S17).

During the field study, we regularly observed a few specimens of *S. vulgare* at Pointe Sainte Hospice (Saint-Jean-Cap-Ferrat), at Pointe de L'Ilette (Antibes), and on the dykes in Monaco.

Taxa excludenda

Cystoseira dubia Valiante was recorded in 1992 in Monaco at 43 m depth (Fredj *et al.*, 1993). This determination, made by a non-specialist, is doubtful as this rare Mediterranean species is hitherto unknown in France and the record was only based on a video observation. Raphélis (1907) mentioned several species of the genera *Cystoseira* and *Sargassum* that constitute obvious misidentifications: *Cystoseira corniculata* (Turner) Zanardini, *C. baccata* (S.G. Gmelin) P.C. Silva (as *C. fibrosa* (Hudson) C. Agardh), an Atlantic species, *C. squamosa* Kützinger, a possible misspelling for *C. squarrosa* and *Sargassum natans* (Linnaeus) Gaillon (as *S. bacciferum* (Turner) C. Agardh), an Atlantic species (Guiry & Guiry 2014). Camille Sauvageau, who examined the Raphélis herbarium, left a manuscript letter kept with it, casting doubt on most of Raphélis' determinations.

Discussion

The loss of species

The Mediterranean treatment of the genera *Cystoseira* and *Sargassum* differs according to the authors (Ribera *et al.*, 1992; Gómez Garreta *et al.*, 2000; Coll *et al.*, 2010; Draisma *et al.*, 2010; Cormaci *et al.*, 2012; Rožić *et al.*, 2012; Guiry & Guiry, 2014). The taxonomy of these genera is complex and progress will depend on molecular studies unravelling the relationships between the species, varieties and forms.

On the French Riviera, 15 and 3 taxa of *Cystoseira* and *Sargassum* were reported, respectively (if the taxa *excludenda* are not taken into consideration). If we compare the historical data with the '2007-2013' distribution, the decline in the number of species is real although far from conspicuous: 5 species were no longer observed (*C. elegans*, *C. foeniculacea* f. *latiramosa*, *C. squarrosa*, *C. spinosavar. spinosa* and *S. hornschruchii*) while *C. jabuka*, previously unrecorded, was observed. In addition to these taxa, probably extinct at the scale of the French Riviera, 9 other taxa suffered a decline (*C. amentacea*, *C. barbata* f. *barbata*, *C. brachycarpa*, *C. crinita*, *C. Sauvageauana* and *S. vulgare*) or became nearly extinct (*C. foeniculacea* f. *tenuiramosa*, *C. spinosa* var. *compressa* and *S. acinarium*) (Table 2). In the past, four of them (*C. barbata* f. *barbata*, *C. brachycarpa*, *C. crinita*, *C. spinosa* var. *compressa*) played a significant functional role in the Mediterranean sublittoral reef ecosystem with large pho-

Table 2. Status of the *Cystoseira* and *Sargassum* taxa along the French Riviera coasts over time. Mis-id: probable misidentification.

| Taxon | Before 1950 | After 1950 | Current | Comment |
|--|-------------------|------------------|-----------------|----------------------|
| <i>Cystoseira amentacea</i> | Very common | Very common | Very common | Slight decline |
| <i>C. baccata</i> | Record (mis-id.) | ? | Absent | Excludendum |
| <i>C. barbata</i> f. <i>barbata</i> | Common | Less common | Very rare | Dramatic decline |
| <i>C. brachycarpa</i> | Common | ? | Rare | Decline |
| <i>C. compressa</i> subs. <i>compressa</i> | Very common | Very common | Very common | Stable |
| <i>C. compressa</i> subs. <i>pustulata</i> | Rare? | ? | Rare | Stable? |
| <i>C. corniculata</i> | Record (mis-id.) | ? | Absent | Excludendum |
| <i>C. crinita</i> | Common | Rare | Very rare | Dramatic decline |
| <i>C. dubia</i> | ? | Record (mis-id.) | Absent | Excludendum |
| <i>C. elegans</i> | Very rare | Very rare | Absent | Locally extinct |
| <i>C. fibrosa</i> | Record (mis-id.) | ? | Absent | Excludendum |
| <i>C. foeniculacea</i> f. <i>latiramosa</i> | Very rare | ? | Absent? | Stable? |
| <i>C. foeniculacea</i> f. <i>tenuiramosa</i> | Common | Rare | Very rare | Locally near Extinct |
| <i>C. jabukae</i> | ? | ? | Very rare | Stable? |
| <i>C. sauvageauana</i> | Common | Rare | Relatively rare | Decline |
| <i>C. squarrosa</i> | Very rare | ? | Absent | Locally extinct |
| <i>C. spinosa</i> var. <i>spinosa</i> | Common? | ? | Absent | Locally extinct |
| <i>C. spinosa</i> var. <i>compressa</i> | Common | Very rare | Very rare | Dramatic decline |
| <i>C. zosteroides</i> | Rare | Rare | Rare | Stable |
| <i>Sargassum acinarium</i> | Common | ? | Very rare | Dramatic decline |
| <i>S. hornschurchii</i> | Rare | ? | Absent | Locally extinct? |
| <i>S. natans</i> | Record (mis-id.) | ? | Absent | Excludendum |
| <i>S. trichocarpum</i> | Record (mis-id.)? | ? | Absent | Excludendum |
| <i>S. vulgare</i> | Common | Common? | Rare | Decline |
| Number of taxa (not excludenda) | 17 | 10 | 13 | |

tophilaous seaweeds (Molinier, 1960; Ballesteros I Sagarra, 1992; Sala *et al.*, 2012); on this basis, we can claim that they are functionally extinct, i.e. the reduced population no longer plays a significant role in ecosystem functioning (Sala & Knowlton, 2006). The Mediterranean Fucales belong to perennial species that structure the habitats. Their tolerance to disturbances (Ecological plasticity) varies according to the species (Orfanidis *et al.*, 2011). Certain species such as *C. barbata*, *C. compressa* or *S. vulgare* have higher ecological plasticity than others. However, along the French Riviera, only one taxon, namely *C. compressa* subsp. *compressa*, which was very common in the past, is still very common and can therefore undoubtedly be considered as stable over the last two centuries.

The question is, how reliable is the overview of the situation of *Cystoseira* and *Sargassum* species along the French Riviera coastline presented here? The baseline, consisting of a large number of collectors who published their data or left extensive herbariums, is probably biased, at least as regards deep water species, i.e. *C. foeniculacea* f. *tenuiramosa*, *C. spinosa* var. *compressa* and *Sargassum* spp. Most of these collectors did not dive (whether snorkelling or scuba diving). Indications of abundance, often based on a few access points to the sea, or on casual records in

fishing nets or grapnels, must be considered with caution (see Coleman & Brawley, 2005, for a thorough discussion on problems with herbarium specimens). With regard to the shallow water species, historical data are probably more reliable. As regards species that were so common and thus easy to collect, despite the poor means available, for which our thorough and comprehensive exploration, lasting six years and using the whole range of modern methods and tools, all year round, resulted in a very limited number of sightings, it is unrealistic to claim that the decline could be due to sampling bias. In addition, in other areas (such as eastern Provence and Corsica), using the very same protocol, we had no difficulty in reporting the conspicuous abundance of species, such as *C. brachycarpa*, *C. crinita* and *C. barbata* f. *barbata* (results not shown).

Possible causes of decline

Why such a near-total loss? The possible causes of the decline of Fucales along the French Riviera are multiple and cumulative, but some have yet to be clearly identified.

The most severe probable cause of decline is habitat destruction; in the French Riviera and Monaco, 19 % and 88 % of the shallow waters between 0 and 10 m depth ,

respectively, have been irremediably destroyed by road enlargement, ports, dykes, jetties, embankments, artificial beaches, urbanization and airport construction (Meinesz *et al.*, 2013). The most severely impacted species are shallow water species such as *C. barbata* f. *barbata* and *C. crinita*, the populations of which have been destroyed, especially because of port constructions or enlargements at Cannes, Golfe-Juan, Antibes, Nice, Saint-Jean-Cap-Ferrat, Beaulieu-sur-Mer and Roquebrune-Cap-Martin. The population of *C. squarrosa*, located at the entrance of the port of Nice, has been destroyed by port enlargement. *Cystoseira amentacea* is the least severely impacted by habitat destruction because of its dwelling under exposed conditions. However, in some areas, *C. amentacea* has experienced major losses in relation to habitat destruction: widening of the road in the 1950's on the Italian border; widening of the road to Eze-sur-Mer around 1975 and construction of the port in 1969 at Beaulieu-sur-Mer; port, embankments and artificial beaches in Monaco from 1963 to 2002; enlargement of the port and construction of an embankment in Le Lido in 1972, Saint-Jean-Cap-Ferrat (Meinesz *et al.*, 2013) (Table 3). These losses represent c.a. 6.5 km of shoreline compared to 44 km of living populations mapped during this study. Other populations of *C. amentacea* have probably been lost through coastal urban development and port enlargements at Mandelieu-la-Napoule, Cannes, Antibes and Nice.

In contrast with habitat destruction, pollution appears to be a less important cause of decline with regard to *C. amentacea*, in contrast to observations from other Mediterranean areas (e.g. Arnoux & Bellan-Santini, 1972). It is only in the immediate vicinity of port facilities and fish farms (sources of pollution) that *C. amentacea* has been replaced by *Corallina* spp. or *C. compressa* subsp. *compressa*. Ollivier (1929) noticed that the species was not impacted by sea surface outfall of untreated sewage located at Cap-Ferrat. Since the 1990s, the sewage of the French Riviera cannot impact *C. amentacea* because of the location of outlets between 20 and 100 m depth and the setting up of sewage treatment plants (Agence de l'Eau Rhône Méditerranée & Corse, 2014). Trace metal contamination could have also impacted the survival of *C. barbata* f. *barbata* and the growth of *C. crinita*, as reported by Sales *et al.* (2011).

It is now well known that overgrazing by the sea urchins *Paracentrotus lividus* and *Arbacia lixula* is a cause of decline of the sublittoral species of *Cystoseira* and *Sargassum* (e.g. Cormaci & Furnari 1999; Thibaut *et al.*, 2005; Serio *et al.*, 2006). *Paracentrotus lividus* is known to feed preferentially on these erect macrophytes, while *A. lixula* feeds on plantlets and prevents new settlement (Verlaque & Nédélec 1983; Verlaque 1984; Knoepffler-Péguy *et al.*, 1987; Frantzis *et al.*, 1988; Hereu *et al.*, 2008a). The major causes of the spread of sea urchins are the reduction of populations of sea urchin predators (mainly Labridae and Sparidae) due to overfishing (e.g. Sala *et al.*, 1998; Hereu

Table 3. Comparison of the coastline occupied by *Cystoseira amentacea* between historical maps and the current situation.

| Reference | Concerned area | Difference (%) |
|----------------------------|---|----------------|
| Ollivier, 1929 | Eze-sur-Mer to Cap Martin | -24.8 |
| Guglielmi, 1969 | Beaulieu-sur-Mer to Saint-Jean-Cap-Ferrat | -29.9 |
| Meinesz <i>et al.</i> 2000 | Coastline of Nice | -3.8 |

2006; Hereu *et al.*, 2005, 2008a) and regulation of sea urchin harvesting. On the French Riviera, the harvesting of *P. lividus* is regulated by period (banned for ~6 months) and quantity (up to 120 individuals/ person⁻¹ d⁻¹) (DIRM Méditerranée, 2014). *Arbacia lixula* is not collected because of a low organoleptic value. Depletion of *Cystoseira* and *Sargassum* by the teleost *Sarpa salpa* (Linnaeus 1758) has also been documented (Thibaut *et al.*, 2005; Vergés *et al.*, 2014). On the French Riviera, this species is rarely fished because of low interest by consumers. On the French Riviera, loss due to the alien herbivorous fishes *Siganus luridus* (Rüppel 1829) and *S. rivulatus* (Forsskal & Niebuhr 1775), as observed in the eastern Mediterranean Sea (Sala *et al.*, 2011; Bianchi *et al.*, 2014), is currently unlikely, even if a school of dozens of individuals of *Siganus* sp. has been observed once in the Bay of Villefranche-sur-Mer in 2012 (Heike Molenaar, pers. comm.).

Competition with two invasive macroalgae, *Caulerpa taxifolia* (Vahl) C. Agardh and *C. cylindracea* Sonder, which are extensively present along the French Riviera coastline, over a wide depth range and with high cover rate, can also contribute to outcompeting *Cystoseira* spp. (Verlaque & Fritayre, 1994a,b; Boudouresque *et al.*, 1995; Boudouresque, 1997; Ferrer *et al.*, 1997; Rollino *et al.*, 2001; Piazzzi & Ceccherelli, 2006).

Collection by scientists and students in rock pools at Pointe de Colombier at Saint-Jean-Cap-Ferrat may also be blamed. There, one of the main sites of the French Riviera for *C. barbata* f. *barbata* and *C. sauvageauana* was steadily pillaged to total depletion by various phycologists during a course in phycology at the University of Nice. The same occurred in the rocks pools at Collioure (French Catalonia) where several species of *Cystoseira* have been extirpated by 5 decades of extensive collecting (Thibaut *et al.*, 2005).

Concerning the deep water species, the maps of benthic assemblages (Meinesz *et al.*, 1994, 2000; Belsher & Houlgatte, 2000, Francour *et al.*, 2003, Holon & Descamp, 2007, 2008; Leblond, 2010) and our survey did not show any large populations such as those reported in the National Park of Port-Cros (Hereu *et al.*, 2008b) and the MPA (Marine Protected Area) of Scandola (Ballesteros *et al.*, 2009). This could be due to fishing activities, as specimens are easily ripped by fishing nets and the increase in turbidity can affect the deep population (Thibaut *et al.* 2005;

Hereu *et al.*, 2014). The extreme rarefaction of *C. spinosa* var. *compressa* versus *C. zosteroides* could be due to lower photosynthetic efficiency, which makes the former taxon sensitive to an increase in turbidity (Sant Funk, 2003).

Consequences

The loss of habitat structuring species is worrying. We are witnessing a typical regime shift with a replacement of macroalgal forests by less structured algal assemblages dominated by *Halopteris scoparia*, *Padina* spp., *Dasycladus vermicularis*, *Cladostephus spongiosus*, *Laurencia* spp. Dictyotales and Corallinales or by barren grounds dominated by encrusting species, filamentous algae and sea urchins. It is clear that vestigial isolated populations of Fucales have lost most of their functional role. Only few small and dispersed shallow water populations remain along the coasts of the French Riviera, i.e. 3 sites with *C. barbata* f. *barbata*, 4 with *C. brachycarpa*, 7 with *C. crinita*, 2 with *C. foeniculacea* f. *tenuiramosa*, 2 with *C. jabukae* and 4 with *C. sauvageauana*, along more than 212 km of coastline. We can consider that these habitat forming species (engineer species) are functionally extinct. In addition, the decline of *Cystoseira* species results in a decrease of benthic assemblage diversity (i.e. homogenization of seascapes).

For example, *Cystoseira brachycarpa*, which still grows in dense subtidal forests down to 15 m depth in undisturbed areas such as Corsica (Ballesteros *et al.*, 2002; Thibaut *et al.*, 2008; Sales & Ballesteros 2010; Cheminée, 2012), is known to be a nursery for some teleost species (Cheminée *et al.*, 2013); obviously, it no longer plays this role along the French Riviera.

Comparison with other Mediterranean areas

It is not the first time that similar local extinction of Fucales populations has been reported in the Mediterranean; *C. foeniculacea* (as *C. ercegovicii*), *C. sauvageauana* and *C. spinosa* in Mar Piccolo, Southern Italy (Cecere *et al.*, 1991); *C. dubia* (as *C. fucoides* Ercegović), *C. foeniculacea* (as *C. ercegovicii*), and all the species of *Sargassum* in the Northern Adriatic (Munda, 1993); *C. crinita*, *C. foeniculacea*, *C. humilis*, *C. spinosa*, *S. acinarium* and *S. hornschochii* at Tremiti Islands, Sicily (Cormaci & Furnari, 1999); *C. brachycarpa*, *C. sauvageauana*, *C. spinosa*, *C. zosteroides*, *S. acinarium* and *S. trichocarpum* at Linosa Island, off Tunisia (Serio *et al.*, 2006); *C. corniculata*, *C. foeniculacea* f. *tenuiramosa*, *C. spinosa*, *S. acinarium* and *S. hornschochii* along the Adriatic Italian coastline (Cecere *et al.*, 2001; Falace *et al.*, 2006); half of the species historically present in the Gulf of Naples were no longer collected (Buia *et al.*, 2013); *C. crinitophylla* in the Gulf of Saronikos, Greece (Tsiamis *et al.*, 2013); *C. brachycarpa*, *C. corniculata*, *C. crinita*, *foeniculacea* and *S. vulgare* at Kos Island, Greece (Bianchi *et al.*, 2014). Finally, in French Catalonia, Thibaut

et al. (2005) reported the local extinction of 11 taxa out of 15 initially reported; only 2 species, *C. compressa* subsp. *compressa* and *C. mediterranea* (the vicariant species of *C. amentacea* in this region) were still abundant, the other species formed small and isolated populations without the functional role of habitat forming species.

It is surprising to note the total absence along the French Riviera of *C. funkii*, a deep-water species common in Provence and Corsica (Hereu *et al.*, 2008b). We did not dive deeper than 50 m, so we cannot exclude the possibility that some populations have been missed on isolated rocks and detritic bottoms. Information on the situation of deep water species is lacking and calls for further study.

Conservation questions

Despite the dramatic decline or local extinction of most *Cystoseira* and *Sargassum* species along most of the French Riviera coastline, we discovered a kind of small 'oasis' that harbours, along only 3 km of coast (from the port of Crouton to Pointe de L'Illette; on the western side of Cap d'Antibes), 10 taxa, i.e. most of the surviving taxa in the study area. Unfortunately, this site does not belong to the EU Natura 2000 site of Cap d'Antibes (n° FR9301573). We suggest the inclusion of this area within the Natura 2000 site.

Most of the species of the genus *Cystoseira* are under protection within the framework of international conventions (Berne Convention, Barcelona Convention). Obviously, these conventions are far from sufficient in effectively protecting these species, not only on the French Riviera, but also at Mediterranean scale.

The causes of decline of Mediterranean Sargassaceae are multiple and act not only in a cumulative but also in a synergic way. Dynamics, vulnerability to disturbances and regime shift are well known for certain *Cystoseira* species (e.g. *C. amentacea*, *C. brachycarpa*, *C. crinita* and *C. zosteroides*) (e.g. Hereu *et al.*, 2008a; Sales & Ballesteros, 2010; Sala *et al.*, 2011, 2012; Sales *et al.*, 2011; Maggi *et al.*, 2012; Mangialajo *et al.*, 2012; Cardona *et al.*, 2013). For the other species, more long-term field surveys and experimental and physiological studies are required. To stimulate the natural restoration of lost populations, the setting up of MPAs is necessary but is probably not sufficient. The conservation of habitats, the improvement of sewage treatment systems and the limitation of sea urchin populations are also required. As far as *Sargassum* species are concerned, the presence of aerocysts allows the drifting of fertile fragments and their remote dispersal; thus, the recovery of lost populations from distant areas is possible. The best example is that of the rapid invasion of European coasts by the introduced species *Sargassum muticum* (Yendo) Fensholt (Critchley *et al.*, 1990). In the case of *Cystoseira* species, similar recoveries can be expected for the taxa bearing aerocysts (i.e. *C. barbata*, *C. compressa* subsp.

compressa, *C. foeniculacea*). Some natural recoveries of *Cystoseira* species from nearby populations were reported in the Rovinj region (Croatia) (Hanel, 2002; Iveša *et al.*, 2014). Such a phenomenon has never been reported in France. Whatever the species of *Cystoseira*, a natural recovery seems unlikely on the French Riviera because of the loss of suitable habitats, the small number of vestigial populations and the low dispersal range of *Cystoseira* zygotes (Susini, 2006). Transplantation has been suggested as a tool to improve the restoration of extinct populations. Techniques are available (Falace *et al.*, 2006; Susini *et al.*, 2007; Perkol-Finkel & Airoidi, 2010; Sales *et al.*, 2011, Gianni *et al.*, 2014). Attempts have been made on the French Riviera to restore small populations of *C. barbata* f. *barbata*, *C. crinita*, *C. foeniculacea* and *S. vulgare* at sites (Saint-Jean-Cap-Ferrat) known to have hosted Fucales in the past. However, the transplants never survived, due to waves, human presence and grazing pressure, even when the sea urchin *P. lividus* was removed prior to the experiment (Robvieux, 2013). These attempts, therefore, clearly question the usefulness of the restoration strategy in small areas subjected to multiple pressures. Restoring populations and their ecological functions makes sense only over a large area and within the framework of an integrated management policy.

Conclusion

Such a comprehensive exploration of coastal habitats, over 7 years (2007-2013) along a significant stretch of coastline (~212 km, measured on a 1/2 500 map), has never before been undertaken in the Mediterranean Sea. In addition, the production of a check-list of all historical records, since the early 19th century, from both shallow and deep water habitats, made it possible to localize and thoroughly explore historical habitats. As a result, the non-observation of a species, or its scarcity, enables us to conclude with reasonable certainty, at least for shallow water species, on its extinction or near-extinction, respectively, along the French Riviera.

The worrying situation for the *Cystoseira* and *Sargassum* species on the French Riviera is far from being a local case, linked for example to exceptionally intensive human impact. Similar studies, although concerning less extensive areas, in other parts of the Mediterranean, ranging from west (Catalonia) to east (Greece) and from north (French Riviera) to south (Linosa, off Tunisia), all lead to the same conclusions. These species could, therefore, really be on the brink of extinction. Will their actual extinction be the next step? The local recoveries reported from the Adriatic Sea show that the decline can be stopped if we take immediate action to reduce disturbances (eutrophication, sea urchin populations).

Another question arises: is it the tip of an iceberg of local and functional species extinction? Fucales constitute good material for such a study: they are long-lived,

large-sized, easy to observe year-round and relatively stable at sites where they are established. In contrast, most other Mediterranean macroalgae are more or less seasonal, often present a complex life-cycle with several phases that may be microscopic or encrusting (and therefore difficult to observe) and experience multi-annual phases of abundance and rarity. Phycologists do not worry when they fail to observe them for years, even decades. Could these less visible species actually be threatened in the same way, as being in fact the hidden part of the iceberg?

Nomenclatural note

In 1952, Ercegović described *Cystoseira abrotanifolia* subsp. *pustulata* Ercegović from the Adriatic Sea. Giaccone and Bruni (1972-1973) reduced this taxon to a heterotypic synonym of *C. myriophylloides* Sauvageau (= *C. humilis* Schousboe ex Kützinger), a species described from Atlantic France (Sauvageau, 1912). Verlaque (1988) rejected this synonymy and reported the Ercegović entity as '*Cystoseira compressa* (Esper) Gerloff & Nizamuddin var. *pustulata* Ercegović' from Corsica. On the basis of a study of genuine Atlantic specimens of *C. humilis* from the Canary Islands, Spain and Morocco, we can confirm the distinction between the two taxa. In *Cystoseira humilis*, the axes are always cylindrical, the branches are never distichously inserted (thallus with pyramidal outline) and the cryptostomata are inconspicuous (branches smooth), whereas in *Cystoseira compressa* subsp. *pustulata*, the axes are frequently compressed at the basis, the branches are more or less distichously inserted in one plane and the cryptostomata are large and prominent (whence the name '*pustulata*'). As we frequently observed, the taxon '*pustulata*' in mixed populations with *C. compressa* subsp. *compressa*, cannot be considered as an ecotype. Given that the currently accepted name for *C. abrotanifolia* C. Agardh is *C. compressa* (Esper) Gerloff & Nizamuddin, we propose the ranking of subspecies and we validate, hereafter, the transfer of this entity from *C. abrotanifolia* to *C. compressa*.

Cystoseira compressa subsp. *pustulata* (Ercegović) Verlaque comb. nov.

Basionym: *Cystoseira abrotanifolia* subsp. *pustulata* Ercegović (1952). *Fauna i Flora Jadrana. Jadranske cistozire. Njihova morfologija, ekologija i razvitak / Fauna et Flora Adriatica. Sur les Cystoseira adriatiques. Leur morphologie, écologie et évolution*. Vol. 2: 113, plates XXX, XXIVe.g. Syntype localities: Split, Lovište and Pelješcu, Croatia.

Comment: *Cystoseira epiphytica* Schiffner ex Gerloff & Nizamuddin (1976: 165-167, pls 1-3) was hitherto treated as a later heterotypic synonym of *C. humilis* (Guiry and Guiry, 2014). However, when Gerloff and Nizamuddin (1976) validated '*Cystoseira epiphytica* Schiffner' (nomen in sched.) from the Adriatic Sea, they specified: "*C. epiphytica* resembles *C. compressa* (Esper)

Gerloff and Nizam. in possessing flat, primary axes (if and when present)...”, and “*C. epiphytica* appears to be nearer to *C. abrotanifolia* subsp. *pustulata* of Ercegović (1952) which has the similar arrangement of cryptostomata”. In our opinion, the only difference between *C. epiphytica* and *C. compressa* subsp. *pustulata* is its epiphytic development on other species of *Cystoseira*, and we consider the two taxa as putative synonyms..

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