



Unexpected abundance and long-term relative stability of the brown alga *Cystoseira amentacea*, hitherto regarded as a threatened species, in the north-western Mediterranean Sea



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ABSTRACT

Cystoseira amentacea is a Mediterranean endemic alga thriving on very shallow rocky substrates. It has been considered as a threatened species, having experienced a steady decline and is therefore protected by international conventions. The historical distribution of the species has been assessed along the French Mediterranean coast, on the basis of 467 articles and herbarium vouchers. We have produced an accurate map of its current distribution and abundance along 1832 km of coastline, through *in situ* surveys. *C. amentacea* was observed along 1125 km of shoreline, including 33% of almost continuous or continuous belt. In most of its range, there is no evidence of loss, except in 4 areas of Provence, French Riviera and Corsica. A significant relation was found between the absence or low abundance of *C. amentacea* and the vicinity of ports and large sewage outfalls. The status of conservation of the species should therefore be reassessed.

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1. Introduction

The coastal ecosystems are highly impacted all over the world, due to the cumulative impact of increasing human pressure (e.g. destruction of habitats, pollution, species introduction, overfishing, coastal aquaculture and global warming). None of the forms of impact affecting the coastal ecosystems exists in isolation. Different pressures act over time and in unison, with a possible synergy effect, to affect the species, the 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 biodiversity that is under siege due to high demographic pressure, a high percentage of worldwide shipping and tourism and the highest rate of biological invasions (Bianchi and Morri, 2000; Galil, 2000; Boudouresque and Verlaque, 2002; Lotze et al., 2006; Coll et al., 2010; Lejeune et al., 2010; Zenetos et al., 2010; UNEP/MAP, 2012; Bianchi et al., 2014).

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

(Fucales, Phaeophyceae, Ochrophyta) represent the dominant species in pristine environment (Dayton, 1985; Steneck et al., 2002; Schiel and Foster, 2006). They provide shelter, food, habitat and nurseries to a multitude of species; they provide high primary production involved in the maintaining of diversified trophic levels; the largest species attenuate wave action (Steneck et al., 2002). These seaweeds can be controlled by a top-down mechanism mainly in the case of the sublittoral species, while the subsurface species are controlled by a bottom-up mechanism (Hereu et al., 2008; Cardona et al., 2013). The decline of kelps and fucoids is a worldwide phenomenon due, directly or indirectly, to human activities (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). Some taxa, have been driven to regional extinction (Thibaut et al., 2005). These changes are leading to shifts in habitat structure from a state with canopy forming species to alternative states, in the worst cases to barren grounds composed of filamentous and encrusting species (Micheli et al., 2005; Perkol-Finkel and Airoldi, 2010; Sala et al., 2011, 2012; Parravicini et al., 2013; Filbee-Dexter and Scheibling, 2014).

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In the Mediterranean Sea, species of the genus *Cystoseira* C. Agardh are habitat-forming species dominating several benthic 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 is dependent on different environmental conditions (light, temperature, hydrodynamism and grazing) (Sauvageau, 1912; Ollivier, 1929; Vergés et al., 2009). Losses of fucoids have been reported all around the Mediterranean Sea caused by habitat destruction, eutrophication and overgrazing by herbivores leading to a shift to less structural complexity, such as turf-forming, filamentous or other ephemeral seaweeds or barrens grounds where urchin density is a driver of habitat homogenisation (Munda, 1974, 1982, 1993; Thibaut et al., 2005; Devescovi and Ivesa, 2007; Airoidi et al., 2008; Falace et al., 2010; Frascchetti et al., 2011; Giakoumi et al., 2012; Sala et al., 2012; Bianchi et al., 2014; Templado, 2014).

Seaweeds living in the rocky intertidal zone or in the sublittoral fringe can endure hard ecological conditions (desiccation, high variation of temperature, salinity and insolation, strong wave actions, etc.).

Among the 51 taxonomically accepted taxa of the genus *Cystoseira* (Guiry and Guiry, 2014), 36 are present in the Mediterranean Sea, 30 are endemic to the Mediterranean, and only 3 live exclusively in the Mediterranean littoral fringe (i.e. the upper level of the sublittoral, from the mean sea level down to less than 1 m depth): *Cystoseira mediterranea* Sauvageau in the western basin, *Cystoseira tamarascifolia* (Hudson) Papenfuss in the Alboran Sea and *Cystoseira amentacea* (C. Agardh) Bory de Saint-Vincent in all the Mediterranean; two poorly characterised varieties var. *amentacea* and var. *stricta* Montagne, are sometimes considered (Ribera et al., 1992; Cormaci et al., 2012; Guiry and Guiry, 2014) but they will not be distinguished here. Because of their shallow habitat, these species escape overgrazing by most of the large herbivores, e.g. the sea urchins *Paracentrotus lividus* (Lamarck 1816) and *Arbacia lixula* (Linnaeus 1758) and the teleost *Sarpa salpa* (Linnaeus 1758) unlike the others subtidal fucoids (Cormaci and Furnari, 1999; Thibaut et al., 2005; Serio et al., 2006; Vergés et al., 2009). All these sub-surface species are considered as vulnerable to sea surface pollution, habitat destruction, trampling and a number of regression events have been reported all around the Mediterranean Sea (Bellan-Santini, 1968b; Desrosiers et al., 1982, 1986; Cecere et al., 1996; Rodriguez-Prieto and Polo, 1996; Cormaci et al., 2001; Soltan et al., 2001; Milazzo et al., 2002; Thibaut et al., 2005; Díez et al., 2009; Arévalo et al., 2007; Falace et al., 2010; Sales et al., 2011; Tsiamis et al., 2013). These taxa are also facing the low frequency natural disturbances called in Spanish 'minva' (very low tide for a long period of time, due to meteorological events), leading to mass mortality of the shallowest *Cystoseira* species (Huvé, 1970; Rodriguez-Prieto, 1992). In disturbed areas, *Cystoseira* species can be replaced by dense stands of fast growing *Corallina* spp. (Corallinales, Rhodophytes) and/or the mussel *Mytilus galloprovincialis* Lamarck, 1819 (Mytiloidea, molluscs), which become dominant, forming extensive and 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; Fernandez and Niell, 1982; Desrosiers et al., 1982, 1986; Thomas, 1983; Janssens et al., 1993; Soltan et al., 2001; Arévalo et al., 2007; Maggi et al., 2009; Falace et al., 2010). The interactions between *Cystoseira* species, turf-forming algae, herbivores and associated species have been extensively studied at different spatial and temporal scales and levels of protection (Benedetti-Cecchi and Cinelli, 1992a,b, 1995; Menconi et al., 1999; Ruitton et al., 2000; Benedetti-Cecchi, 2001; Benedetti-Cecchi et al., 2001; Bulleri et al., 2002; Maggi et al., 2009, 2012; Frascchetti et al., 2012; Tamburello et al.,

2013). *C. amentacea* can also be replaced by the tolerant *Cystoseira compressa* (Esper) Gerloff and Nizamuddin (Mangialajo et al., 2012).

Along the whole of the French Mediterranean coasts, two species are restricted to the upper sublittoral zone, *C. mediterranea* in the western part along the French Catalan coast (Sauvageau, 1912; Feldmann, 1937), and *C. amentacea* in Provence, French Riviera and Corsica. The latter taxon is widely distributed in the Mediterranean (Ribera et al., 1992). A non-Mediterranean record, from Sudan (East Africa) is regarded as a misidentification (Papenfuss, 1968). *C. amentacea* possesses a 40 cm high caespitose thallus and a basal holdfast a few centimetres wide. The species forms extensive stands on shallow rocky wave-exposed zones (Agardh, 1842; Molinier, 1960; Boudouresque, 1971a,b). As thalli are negatively buoyant and the maximum distance for egg dissemination is low (~few dozen cm, Mangialajo et al., 2012), the species is suspected of having low dispersal ability. *C. amentacea* is one of the most productive Mediterranean seaweeds (Bellan-Santini, 1963; Bellan and Bellan-Santini, 1972; Susini, 2006), because of steady exposure to turbulence (frequent emersion/immersion), which maintains a high nutrient uptake (Epiard-Lahaye et al., 1987).

Because of its habitat preferences, *C. amentacea* has been considered as one of the species most severely impacted by coastal development and sewage outfalls (Bellan-Santini, 1964, 1965, 1966, 1968b; Bellan and Pérès, 1970; Arnoux and Bellan-Santini, 1972; Bellan and Bellan-Santini, 1972; Astier, 1975; Belsher, 1977; Desrosiers et al., 1982, 1986; Thomas, 1983; Janssens et al., 1993; Sinnassamy et al., 1993; Soltan et al., 2001; Bulleri et al., 2002; Falace et al., 2010). *C. amentacea* is also harvested for the cosmetics industry (Max Pellegrini, pers. comm.). Furthermore, the species is thought to be vulnerable to oil spills and chemical releases at the sea surface (Bellan-Santini, 1968b). The species is considered to have a high ecological status within the framework of the EU Water-Framework Directive (2000/60/EC) (Orfanidis et al., 2001; Panayotidis et al., 2004; Ballesteros et al., 2007; Mangialajo et al., 2008; Cecchi et al., 2009; Sfriso and Facca, 2011; Nikolic et al., 2013).

C. amentacea is currently listed as a species strictly protected under the Berne Convention (Annex I 1979), together with 4 other taxa (*C. mediterranea*, *C. sedoides*, *C. spinosa*, *C. zosteroides*); all the Mediterranean species of the genus *Cystoseira*, except *C. compressa* have been listed under Annex II of the Barcelona convention (2010). All the Mediterranean *Cystoseira* species are under surveillance by international organizations such as the IUCN, the RAC/ASP and MedPan. Like all the species of the genus *Cystoseira*, *C. amentacea's* stands are an habitat and listed as Habitat of Community Interest by the UE (Micheli et al., 2013).

The use of historical data in marine ecology is growing, as they provide a baseline of animal and plant populations in very lightly disturbed areas so changes can be analysed over a long time period (Jackson et al., 2001; Thibaut et al., 2005; Sáenz-Arroyo et al., 2005; Barsanti et al., 2007; Babalis, 2011; Lotze et al., 2010; Montefalcone et al., 2013; Husa et al., 2014). Most studies of habitat loss or coastal urbanisation, however, focus only on local scales and short periods over contemporary times. Whilst this focus is also necessary, the preoccupation with these local and present-day drivers means that we are often not aware of the past extension of the species and of the regional context of local studies.

In order to analyse the long-term changes in *C. amentacea* populations along the French Mediterranean coasts, we collected all available data (herbarium vouchers, published and grey literature) and we have compared them to our field surveys. Because most of the data collected over the last centuries are qualitative, the aim of this study was: (i) to give a present exhaustive quantitative map of the distribution of *C. amentacea* along the French Mediterranean

coasts, including Corsica; (ii) to compare the present distribution with historical data; (iii) and to highlight the eventual sites of regression and identify the possible causes.

2. Materials and methods

2.1. Study area

In France, *Cystoseira amentacea* was reported from four regions: the western and eastern Provence, the French Riviera (including the Principality of Monaco) and Corsica (Fig. 1). The species is absent from French Catalonia and Languedoc where it can be replaced on suitable hard substrates by *C. mediterranea*.

2.2. Data collection

2.2.1. Literature and herbaria

Historical data available concerning *C. amentacea* along the French Mediterranean coasts are numerous (Supplementary material Tables S1–S4). The species is easy to identify and to collect and, from the 18–19th to the early 21st century, many naturalists and phycologists surveyed the French Mediterranean coasts. They received the support of local natural history museums and they built an efficient web of collectors providing a large quantities of samples.

In addition to its present taxonomical status (Guiry and Guiry, 2014) *C. amentacea* has been mentioned in the literature and herbariums under several nomenclatural synonyms, with correct or

incorrect authorities: *C. amentacea* (C. Agardh) Bory de St-Vincent, *C. amentacea* var. *stricta* Montagne, *Cystoseira stricta* Sauvageau, *Cystoseira ericoides* (Linnaeus) C. Agardh var. *amentacea* C. Agardh. Its name was also misspelled as *C. amantacea*, *C. amentacea* Agardh and *C. amentacea* Bory. Finally, it was sometimes misidentified as *C. mediterranea* or as *Fucus ericoides* Linnaeus, *Fucus selaginoides* Linnaeus and *Fucus tamarascifolius* Hudson.

Vouchers held in herbaria are a valuable source of data providing a basis for checking the identification of the specimens. We surveyed several thousand of vouchers held in the following herbaria named after *Index Herbariorum*. **AIX**: The Muséum d'Histoire Naturelle d'Aix-en-Provence: Herbarium Berner. **ARAGO**: The herbaria held at Pierre and Marie Curie University – Laboratoire Arago: Herbarium Feldmann. **AV**: The Muséum d'Histoire Naturelle d'Avignon: Herbarium Requien. **HCOM**: The herbaria held at Aix-Marseille University: Herbarium C.F. Boudouresque, Herbarium Berner, Herbarium P. and H. Huvé, Herbarium Saint-Charles, Herbarium T. Thibaut, Herbarium M. Verlaque, **LAU**: The online herbarium of the Musée Botanique de Lausanne: Herbarium Ducommun. **MPU**: The herbaria held at the University of Montpellier: Herbarium Flahaut, Herbarium Général, Herbarium Lenormand, Herbarium Raphélis, Herbarium Salzmann, Herbarium Schousboe. **Musée Océanographique of Monaco** (not indexed): Herbarium Mouret, Herbarium Prince Albert I. **NICE**: The Muséum d'Histoire Naturelle de Nice: Herbarium Algues Vertes 1890–1910, Herbarium Camous. **Nice-Sophia Antipolis University** (not indexed): Herbarium Meinesz. **PC**: The Muséum National d'Histoire naturelle (MNHN) in Paris: Carnet de Récolte de Feldmann,

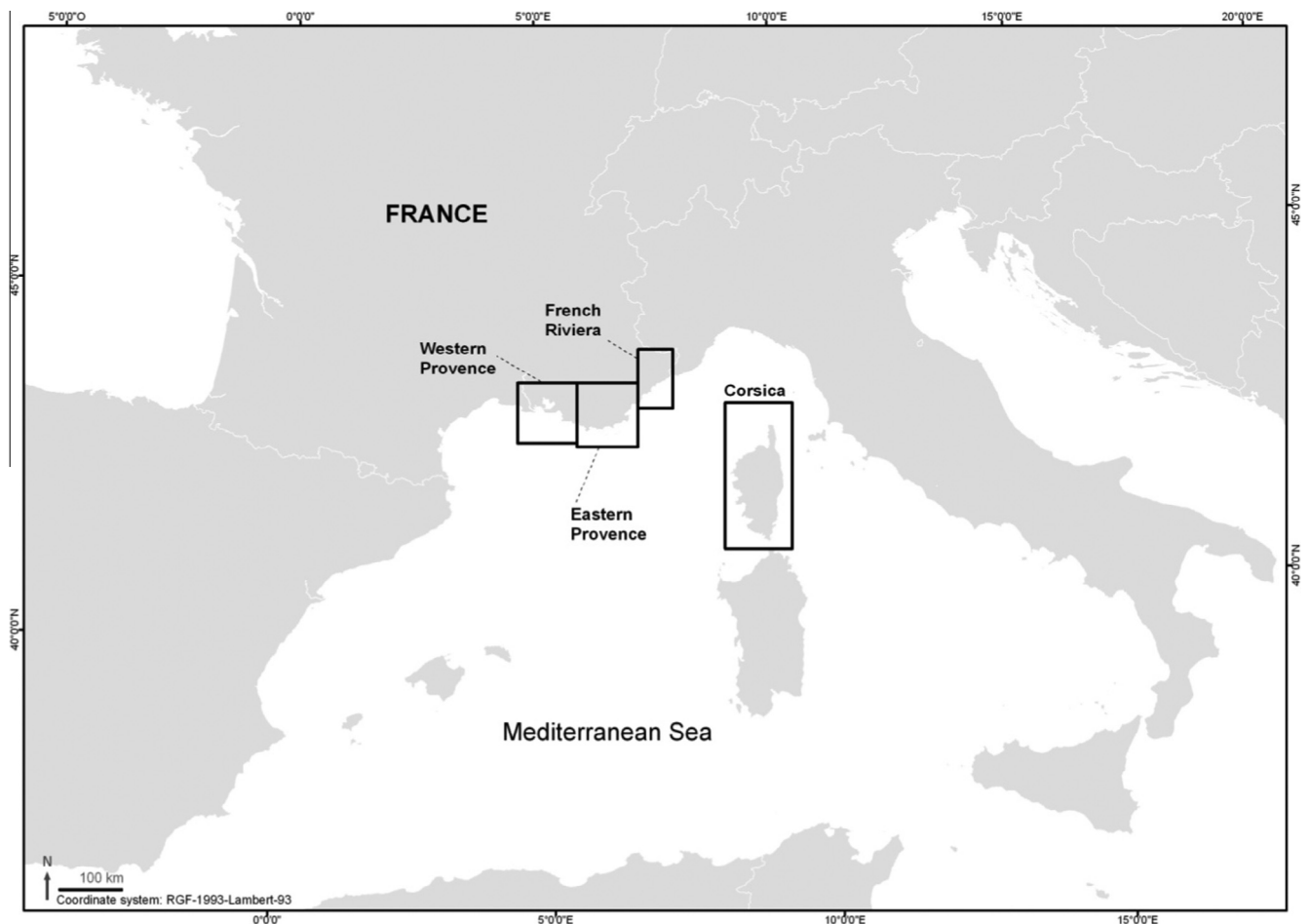


Fig. 1. Studied areas.

Herbarium Algues de France non trié, Herbarium J. Arènes, Herbarium Bornet, Herbarium Bory de Saint-Vincent, Herbarium A. Bunge, Herbarium O. Debeaux, Herbarium Fabre, Herbarium Feldmann, Herbarium Général, Herbarium R. Lami, Herbarium Lebel, Herbarium Le Sourd, Herbarium Lamouroux, Herbarium Lenormand, Herbarium Magne, Herbarium Roger Melin, Herbarium Montagne, Herbarium Moquin-Tandon, Herbarium Roussel, Herbarium Sauvageau, Herbarium Schousboe, Herbarium Soleirol, Herbarium Solier, Herbarium Thuret, Herbarium Sébastien Vaillant, Herbarium A. Vickers, Excicata O. Debeaux, Excicata G. Hamel. **TLON**: The Muséum d'Histoire Naturelle de Toulon; Herbarium Mouret, Algues de Provence. **VTA**: The Botanical Garden of Villa Thuret in Antibes: a recently rediscovered collection of vouchers gathered by Gustave Thuret and Edouard Bornet in the 19th century.

2.2.2. Fieldwork

The fieldwork was carried out during four campaigns from April to June in 2008 and 2009 for the continental Mediterranean French coasts and from April to June 2010 and 2011 for Corsica. Late spring is the best season for fieldwork as primary branches of *C. amentacea* are fully developed.

C. amentacea populations were drawn on black and white A3 format aerial photographs from the IGN (French National Institute of Geographical and Forest Information): BD Ortho; Google Earth was also used). The scale was 1:2500. Three people were on board a small boat (length 5 m) moving at low speed (3–6 km h⁻¹) at few metres offshore. Identification of the species is easy and it cannot be confused with any other species, with the exception of *C. mediterranea*. For this reason, every 1-km, the presence of a caespitose base, the easiest to observe distinctive character of *C. amentacea*, absent in *C. mediterranea*, was checked via snorkelling. *C. amentacea* populations were recorded within 6 classes as defined by Ballesteros et al. (2007): C0 = absence, C1 = rare scattered individuals, C2 = abundant scattered individuals, C3 = abundant patches of dense stands, C4 = almost continuous belt and C5 = continuous belt.

For each 50-m sector, corresponding to a class of *C. amentacea* (C0–C5), we also recorded the slope of the substrate in three classes (vertical, sub-vertical, sub-horizontal to horizontal), the height of coast (High coast: vertical cliff >15 m; Low coast: all the other cases, including decimetric blocks), the nature of the substrate (natural or artificial including stone blocks used for jetties, ports, etc.) and when present the dominant taxa and functional groups other than *C. amentacea* (e.g. *Corallina* spp., *C. compressa*, turf algae and the mussel *M. galloprovincialis*).

2.3. GIS analysis

The changes over time of *C. amentacea* (past and present distribution) were analysed on a GIS (Geographical Information System) database (ArcGis10[®]) with Spatial Analyst tools. Each past or present location has been geo-localised. All historical maps have been digitized to fit the same coastal line used for the present distribution (scale 1:2500). Because no ready-to-use coastal line was available, the entire shoreline of the French Mediterranean coasts was drawn at a scale 1:2500.

The current distribution of *C. amentacea* was analysed regarding possible perturbations (i.e. sewage outfalls, fish farms, vicinity of ports). Although the general pattern of currents in the study area is well known, with the northern Mediterranean current flowing westward along the continental French coast (Millot, 1987; Albérola and Millot, 2003; Taupier-Letage et al., 2013), the near shore local currents are more variable in direction and intensity,

depending upon wind, swell, shore topography, bathymetry and season. For this reason, we drew a 500 m radius circular buffer from the centre of each source of possible perturbation and the *C. amentacea* populations and accompanying species were analysed within this area. In the studied area, are located 275 ports, 43 sewage outfalls and 13 fish farms (Supplementary material Table S5). Ports localised on a rocky shore (193 ports out of 275) were taken into consideration (Supplementary material Table S6), and classified according to their size, i.e. the surface area of the enclosed water body. As regards fish farms, the parameter considered was their distance to the nearest shore, since reared fish volume, a proxy of the pollution generated, was not available. As regards the sewage outfalls, only those where the pipe end is located at less than 500 m from a rocky shore (20 outfalls out of 43) were considered, as their effluents are prone to reach the shore and to impact coastal shallow assemblages (Supplementary material Table S7). The study parameter is the effluent volume (Agence de l'Eau Rhône Méditerranée Corse, 2014). It is worth noting that all these outfalls come from sewage treatment plants.

2.4. Statistical analysis

We tested the influence of (i) the size of ports (surface area, ha), (ii) the mean effluent flow (m³ d⁻¹) of sewage outfalls and (iii) the distance from the coast of fish cages on the abundance of *C. amentacea* and associated species along the natural coast and suitable substrate. Effects on assemblages (*C. amentacea*, and dominant taxon or functional group) composition were first studied through a multivariate exploratory approach using a non-metric multi-dimensional scaling (nMDS) (Clarke and Gorley, 2006). Similarity measure matrixes were calculated from the initial data matrix containing for each sample the percentage of coast occupied by each taxon or functional group, after square root transformation. The chosen similarity measure was the S17 Bray Curtis similarity, (Clarke and Warwick, 1994; Clarke and Gorley, 2006); nMDS represents samples as points in low-dimensional space such as the relative distances apart of all points are in the same rank order as the relative similarities of the samples. Finally, for each taxon or functional group, correlations of taxa-specific abundance with the 2-D ordination plot of samples were plotted by displaying correlation vectors. Spearman correlation was used given its non-parametric properties.

In order to compare assemblage composition as a function of the various factors of our design, we performed a PERMutational multivariate ANalysis Of VAriance (PERMANOVA) (Anderson, 2001) based on the S17 Bray Curtis similarity matrixes, as for the nMDS. *P*-values were obtained by 999 permutations of residuals under a reduced model. Monte Carlo *P*-values were considered when there were not enough possible permutations (<200). In order to compare assemblage abundances between levels of factors we performed the PERMANOVA on the model including terms and all interactions (Underwood, 1981).

Three separate models were successively applied, in order to test the effect of each factor was fit to assemblage abundances in order to test its response to 'size of port', 'effluent flow' and 'cages distance'. Factor 'size of port' has 4 levels (surface area: <2 ha, between 2.1 and 6 ha, between 6.1 and 100 ha, >101 ha) and is fixed; Factor 'effluent flow' has 5 levels (<100 m³ d⁻¹, between 100 and 1000 m³ d⁻¹, between 1000 and 10000 m³ d⁻¹, between 10000 m³ d⁻¹ and 100000 m³ d⁻¹, >100000 m³ d⁻¹ and is fixed; Factor 'cages distances' has 3 levels (<100 m, between 100 and 200 m, between 200 and 500 m) and is fixed. Since ecological data are by nature highly variable, terms were considered significant for

P-values < 0.01. Post-hoc pair-wise analysis were performed when necessary.

3. Results

3.1. Historical data

The first putative mention of *C. amentacea* in the literature dates back to the Roman naturalist Pliny the Elder (23–70 CE; CE means Common Era) in his *Naturalis Historiae* (liber XIII, 48–168 and 170) where Fée (1833) interpreted the description of a Mediterranean marine plant as corresponding to *C. ericoides*. This name is currently regarded as a taxonomic synonym of *Cystoseira tamariscifolia* (Hudson) Papenfuss (Guiry and Guiry, 2014), but we can hypothesise that Fée (1833) was actually thinking of the current *C. amentacea*.

467 Historical records of *C. amentacea* have been found from the 18th to the 21st centuries (Table 1, Figs. 2A–6A).

3.1.1. 18th century

We found the oldest specimen of *C. amentacea* in the Sébastien Vaillant herbarium held in PC in Paris, identified as *F. selaginoides*, collected in Marseilles in 1700, this specimen was most probably collected in March of that year by Joseph Pitton de Tournefort while waiting for a boat in Marseilles for his expedition to the Levantine coasts (Tournefort, 1717). We also found three non-dated samples of *C. amentacea* collected in Toulon (as *Fucus ericoides*) and one in Marseilles (as *F. selaginoides*) in two bundles of vouchers from the 18th century (respectively herbarium Roussel and herbarium Lamouroux, both also held in PC).

3.1.2. 19th century

The 19th century was the golden age for the collection of *Cystoseira* along the French Mediterranean coasts, with famous botanists such as Jacob Georg Agardh (1813–1901), Edouard Bornet (1828–1911), Jean-Baptiste Bory de Saint-Vincent (1778–1846), Jean-Louis Martin Castagne (1785–1858); Jean Odon Debeaux (1826–1910), Camille Montagne (1784–1866), Jean Vincent Felix Lamouroux (1779–1825), Antoine Risso (1777–1845), Camille Sauvageau (1861–1936), Peter Schousboe (1766–1832), Gustave Thuret (1817–1875); they all collected specimens of *C. amentacea* in France. We found 106 specimens of *C. amentacea* collected in the 19th century. Some descriptions give information on its abundance. According to Agardh (1842), the species lives on the most sea-exposed rocks, very frequent on the French Mediterranean shore ('*Hab. ad rupes in ipso limite vehementiori mari expositas, ad littora Galloprovinciae frequentissima*'); he also reported the species precisely '*ad Nizzam ipse* (in Nice), *prope Frejus* (near Fréjus)'. Montagne (1846) studied specimens collected by De Notaris '*Ad Nicaeam*' (in Nice) and by J. Agardh '*Ad Massilliam*' (in Marseilles). Peter Schousboe, Danish consul in Tangier, while waiting for his boat in Marseilles, collected *C. amentacea* in 1818–1820 (Bornet, 1892): '*Sat frequens circa Massilliam per totum fere annum cum*

fructificatione reperitur' (stand near Marseilles throughout the year with fructifications observed). Castagne (1845) reported the species everywhere (in French '*partout*') around Marseilles. Debeaux (1873) recorded the species is Corsica. Marion (1883) reported the species as abundant throughout the Gulf of Marseilles including the islands and the Côte Bleue (west part of the gulf), but he first noticed that the species is replaced by the articulate Rhodophytes *Corallina officinalis* or the mussel *M. galloprovincialis* when the waters are polluted. He described massive developments of Ulvales all around Marseilles in small bays; at that time, domestic and industrial non-treated outflows to the sea were numerous to the north and the south of the city.

Despite these few records, very localised in space (the vicinity of large cities: Marseilles, Nice, Toulon), accurate maps are non-existent and large portions of the coast have not been surveyed. As a result, the absence of records of *C. amentacea* along most of the coastline only means that we did not find any historical observation. We can hypothesise that rest of the coast was pristine (witnessing all the paintings from this period held in art Museums) and poorly urbanised. Thus, when the favourable ecological conditions were met, it is highly probable that *C. amentacea* was abundant outside the large cities in the 19th century.

3.1.3. 20th century

During the first half of 20th century, the records and collections remained numerous along the whole of the French continental coasts (Anonymous, 1911; Mouret, 1911; Camous, 1912; Decrock, 1914; Raphéris, 1924a,b,c; Jahandiez, 1929; Ollivier, 1929; Berner, 1931; Hamel, 1931–1939). For Corsica the records are rarer (Leblond, 1924; Hamel, 1931–1939). The species was reported as abundant and no evidence of regression was noted along most of the coast except at Marseilles, where Berner (1931) reported heavy pollution of the coast and the development of large stands of *Corallina* spp., *M. galloprovincialis* and proliferations of Ulvales interfering with navigation in some small bays. At that time, Marseilles was still an active industrial city.

From 1950 to 1989, the number of works concerning *C. amentacea* considerably increased with algal inventories, phytosociological and chemical studies. The species was collected along the whole coast, in western Provence (Magne, 1956; Huvé, 1960, 1970; Bellan-Santini, 1961, 1962, 1964, 1965, 1966, 1968a,b; Bellan and Pérès, 1970; Pellegrini and Pellegrini, 1970, 1972; Boudouresque, 1971a,b, 1972; Arnoux and Bellan-Santini, 1972; Bellan and Bellan-Santini, 1972; Belsher, 1975, 1977; Picard and Bourcier, 1975; Belsher and Boudouresque, 1976; Bitar, 1980, 1982; Desrosiers et al., 1982, 1986; Epiard-Lahaye, 1988; Gravez et al., 1988), Eastern Provence (Molinier, 1956; Bellan-Santini, 1961, 1962; Augarde and Molinier, 1964; Vignes, 1965; Augier et al., 1966; Bensimon et al., 1966; Bensimon, 1967; Augier and Boudouresque, 1967, 1969, 1970a,b, 1976; Augier, 1974, 1978, 1981, 1985; Gadea, 1967; Maggi, 1967; Canamella, 1968; Carvou, 1967; Carvou et al., 1968; Gasquet, 1968; Boudouresque, 1969, 1971a,b; Pellegrini and Pellegrini, 1970; Coppejans, 1972, 1977; Astier, 1975; Belsher et al., 1976; Verlaque and Tiné, 1979; Artaud et al., 1980; Thomas, 1983; Azzolina, 1985; Augier and Nieri, 1987), French Riviera (Gilet, 1954; Guglielmi, 1969) and in Corsica (Picard, 1954; Gilet et al., 1954; Molinier and Molinier, 1955; Molinier, 1956, 1960; Santini, 1961; Deleuil and Molinier, 1964; Boudouresque, 1969, 1971b, 1972; Verlaque, 1975; Boudouresque and Perret, 1977; Coppejans, 1979; Clarisse, 1980–1981, 1984).

The first reports of a severe regression around a sewage outfall were documented near Marseilles in the vicinity of the untreated sewage outfall of Cortiou where the species was precisely mapped (Bellan-Santini, 1964, 1965, 1966, 1968b; Bellan and Bellan-Santini, 1972; Bellan and Pérès, 1970; Bitar, 1982). A link

Table 1

Number of historical records of *Cystoseira amentacea* from the 18th to the 21st century along the French Mediterranean coasts. HV: Herbarium vouchers, P: publications.

Century	18th		19th		20th		21st	
	HV	P	HV	P	HV	P	HV	P
Western Provence	2	0	31	4	31	37	0	1
Eastern Provence	3	0	9	1	26	45	6	9
French Riviera	0	0	41	2	41	11	60	0
Corsica	0	0	25	3	16	25	36	2
Total	5	0	106	10	114	118	102	12

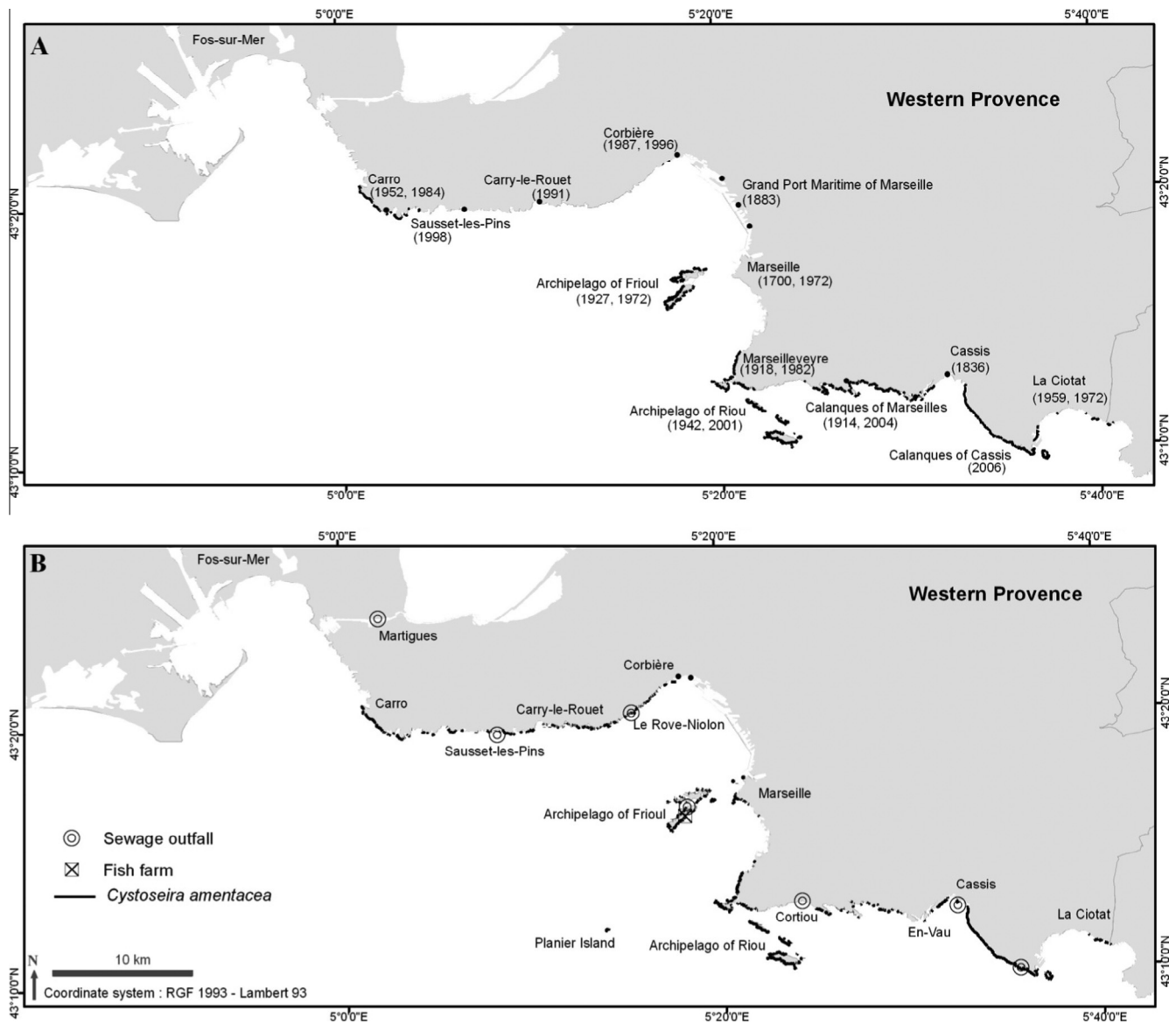


Fig. 2. Distribution of *Cystoseira amentacea* along the coastline of western Provence. Grey line: border of western Provence. (A) Historical records of *C. amentacea* (data from vouchers and literature). Only the oldest and the most recent dates have been reported. (B) Current distribution of *C. amentacea* and locations of sewage outfalls and fish farms.

between the anionic detergents and the regression of the species was hypothesised (Arnoux and Bellan-Santini, 1972). Studies and mapping of *C. amentacea* in the Gulf of Fos, impacted by a warm water outflow from a thermal power plant, the construction of one of the largest European commercial harbours and outfalls from petrochemical industries, evidenced their cumulative negative effects on the species (Desrosiers et al., 1982, 1986). A decline of *C. amentacea* on 2.4 km of shoreline was reported in the vicinity of the untreated sub-surface sewage outfall of Cap Sicié, near Toulon (Eastern Provence) (Astier, 1975; Thomas, 1983). Local depletion was reported in the vicinity of a small sewage outfall at La Madrague (Saint-Cyr-sur-Mer, Eastern Provence) (Thomas, 1983). A shift from *C. amentacea* to turf-forming algae or mussels was observed in the Gulf of Marseilles (Belsher, 1977). In contrast, a recovery of *C. amentacea* has been reported after the construction of sewage treatment plant in La Ciotat (western Provence) (Picard and Bourcier, 1975).

Mapping was undertaken in some places around the pristine Islands of Port-Cros (National Park since 1963) and Porquerolles

(Eastern Provence): *C. amentacea* was abundant and well developed, forming a more or less continuous belt (Augier et al., 1966; Augier and Boudouresque, 1967, 1969, 1970a,b, 1973, 1976; Augier, 1974, 1978, 1981, 1985). A survey (a few hundred metres) over time in the Bay of Port-Man (Port-Cros Island) showed the stability of the population over 20 years (Augier and Nieri, 1987).

Several studies of the vegetation of ports in eastern Provence first mention that small patches or isolated individuals of *C. amentacea* were able to grow on the jetties (Vignes, 1965; Bensimon et al., 1966; Carvou, 1967; Gadea, 1967; Maggi, 1967; Canamella, 1968; Carvou et al., 1968).

From 1990 to 2000, the number of scientific studies concerning *C. amentacea* decreased but was counterbalanced by the increase in the number of maps because of the demand for ecological impact studies and species inventories, as *C. amentacea* is reported as a priority habitat for the EU Natura 2000 programme (code Natura 2000: 1170-13). The species was reported as abundant in western Provence (Nieri et al., 1991; Charbonnel et al., 1993; Sinnassamy et al., 1993; Bonhomme et al., 1997, 1999; Augier et al., 1998), in

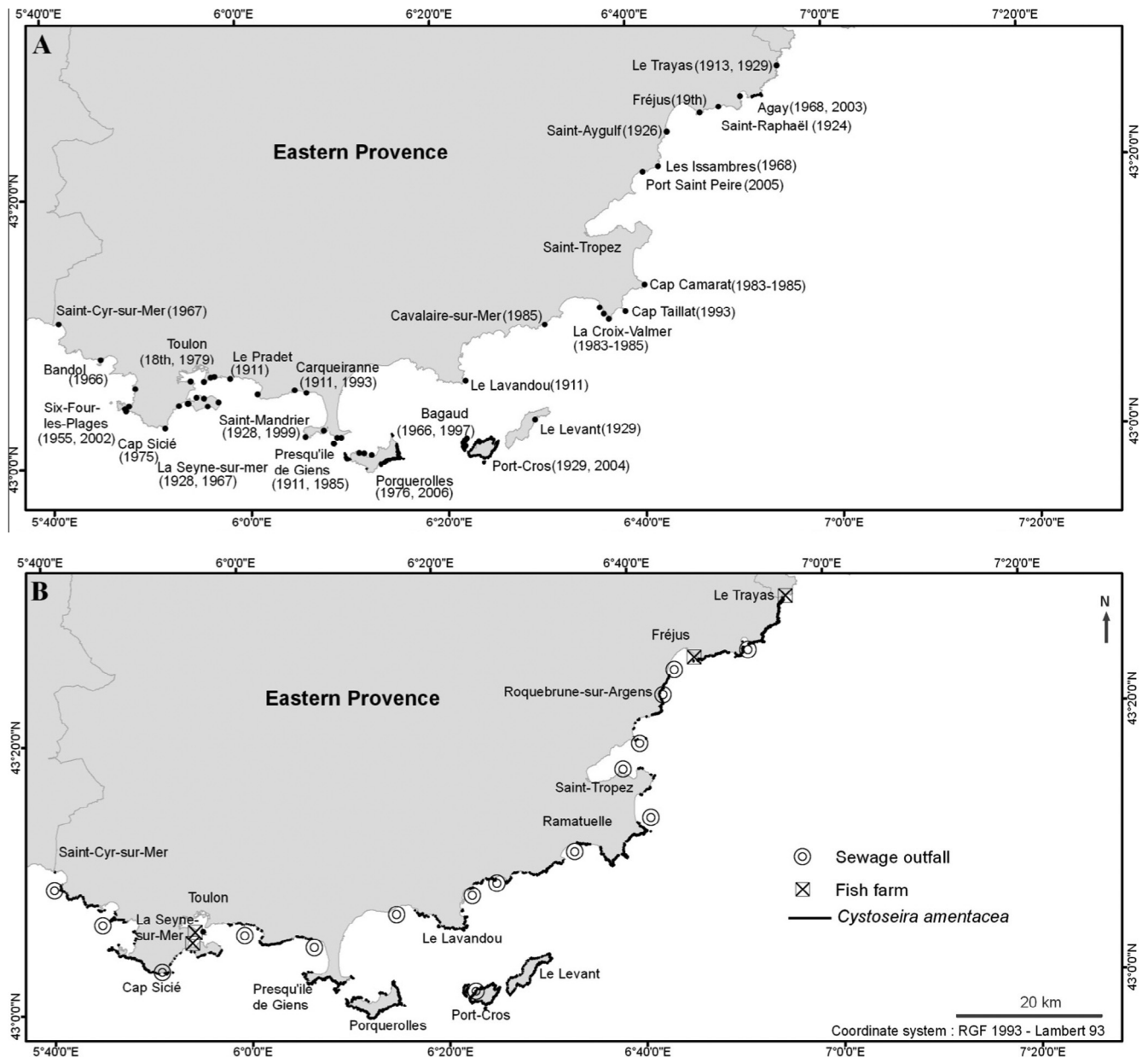


Fig. 3. Distribution of *Cystoseira amentacea* along the coastline of eastern Provence. Grey lines: borders of eastern Provence. (A) Historical records of *C. amentacea* (data from vouchers and literature). Only the oldest and the most recent dates have been reported. (B) Current distribution of *C. amentacea* and locations of sewage outfalls and fish farms.

eastern Provence (Valls et al., 1993; Augier, 1995; Francour et al., 1997; Bernard et al., 1999; Gravez et al., 1999; Meinesz et al., 2000a), on the French Riviera (Meinesz et al., 1994; Jaffrenou et al., 1996; Verlaque and Bernard, 1998) and in Corsica (Janssens, 1991; Janssens et al., 1993; Frick et al., 1996; Blachier et al., 1998; Mari et al., 1998; de Vaugelas et al., 1998; Verlaque et al., 1998; Meinesz et al., 1999).

3.1.4. 21st century

In the early 21st century, *C. amentacea* was observed as abundant in western Provence (Bonhomme et al., 2001, 2005; Cadiou et al., 2006), in eastern Provence (Bernard et al., 2001, 2002, 2004; Meinesz et al., 2001a,b,c, 2004a; Soltan, 2001; Bonhomme et al., 2004; Cottalorda et al., 2004; Ruitton et al., 2005; Gratiot et al., 2006, 2007), on the French Riviera (Meinesz et al., 2000b; Francour et al., 2003; Susini, 2006) and in Corsica (Ganteaume

et al., 2004; Meinesz et al., 2001d, 2004b; Javel et al., 2005; Ballesteros et al., 2007). Isolated individuals of *C. amentacea* have been reported on port jetties (Bernard et al., 2004; Bonhomme et al., 2005; Susini, 2006).

The survey of *C. amentacea* in the vicinity of a sewage outfall near Calvi (Corsica) and in Cortiou (Marseilles, western Provence) highlighted its decline over time (Janssens, 1991; Janssens et al., 1993; Soltan et al., 2001). A local disappearance was reported after a port enlargement at Corbières, near Marseilles (Sinnassamy et al., 1993).

3.2. Field data

C. amentacea is very common along the whole of the rocky coasts of Provence, French Riviera and Corsica. The species is present along 377 km (scale 1:2500) from Menton (Italian border) to

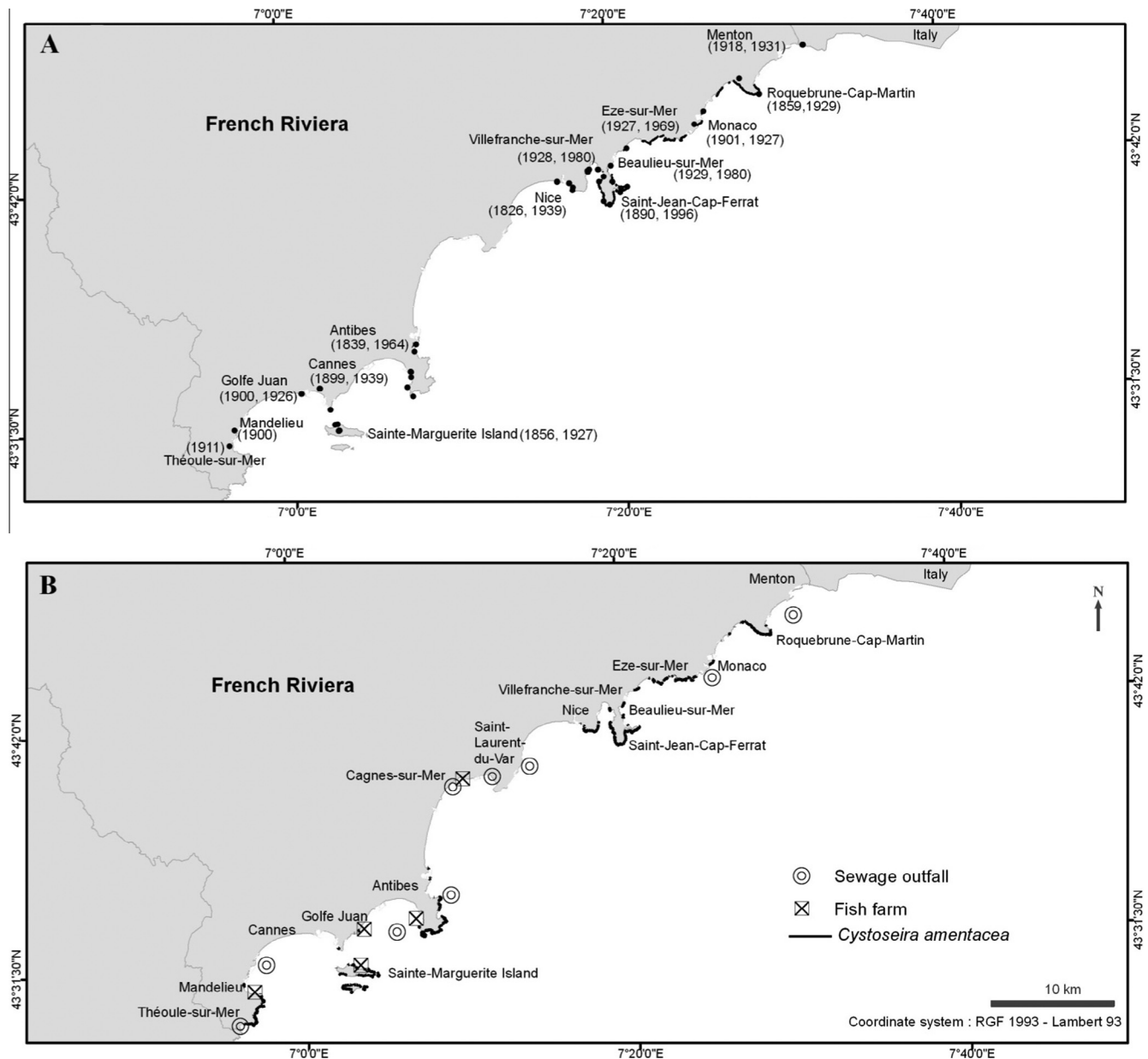


Fig. 4. Distribution of *Cystoseira amentacea* along the coastline of the French Riviera. Grey lines: borders of French Riviera. (A) Historical records of *C. amentacea* (data from vouchers and literature). Only the oldest and the most recent dates have been reported. (B) Current distribution of *C. amentacea* and locations of sewage outfalls and fish farms.

Bonnieu Cove, in the Gulf of Fos. In Corsica, the species is spread along 748 km (scale 1:2500). It is absent from the sandy eastern coast of Corsica, from Bastia to Sulenzara, due to the lack of suitable hard substrates.

Most of the populations constitute patchy to continuous belts, with high variation according to the area. Populations are more extensive and more abundant in eastern Provence and Corsica than in other areas (Table 2).

In western Provence, *C. amentacea* occupies only 45 km, i.e. 23% of the hard substrates (Table 2, Fig. 2B), because part of the coast is unsuitable for its development, with high cliffs shading the shore, vertical substrate and overhanging rocks. Furthermore, the northern part of the Marseilles region is directly under the cumulative impact of different human activities. Thus, even when substrates are favourable for the development of *C. amentacea*, the populations are sparsely distributed, outcompeted by large stands of

M. galloprovincialis and *Corallina* spp. The southern part of the city is under the influence of its sewage outlet and *C. amentacea* is lacking over 6.5 km in the vicinity of the outfall (Cortiou), being replaced by mussel beds and *Corallina* spp. assemblages (Fig. 2B).

In eastern Provence, where the coast is more favourable to the development of the species, cliffs are rarer and the region is less urbanised than western Provence, *C. amentacea* is very abundant and occupies 288 km: 72% of the available hard substrate (Table 2, Fig. 3B). The possible influence of the only large city (Toulon) is counterbalanced by its geographical position within a semi-enclosed bay. Near the outfall of the Cape Sicié sewage outlet, *C. amentacea* is reduced to isolated individuals or small patches over 500 m, while *Corallina* spp. assemblages are dominant.

On the French Riviera (including the Principality of Monaco), the species occupies 44 km: 42% of the available hard substrates (Table 2, Fig. 4B). Despite the profound changes that have occurred

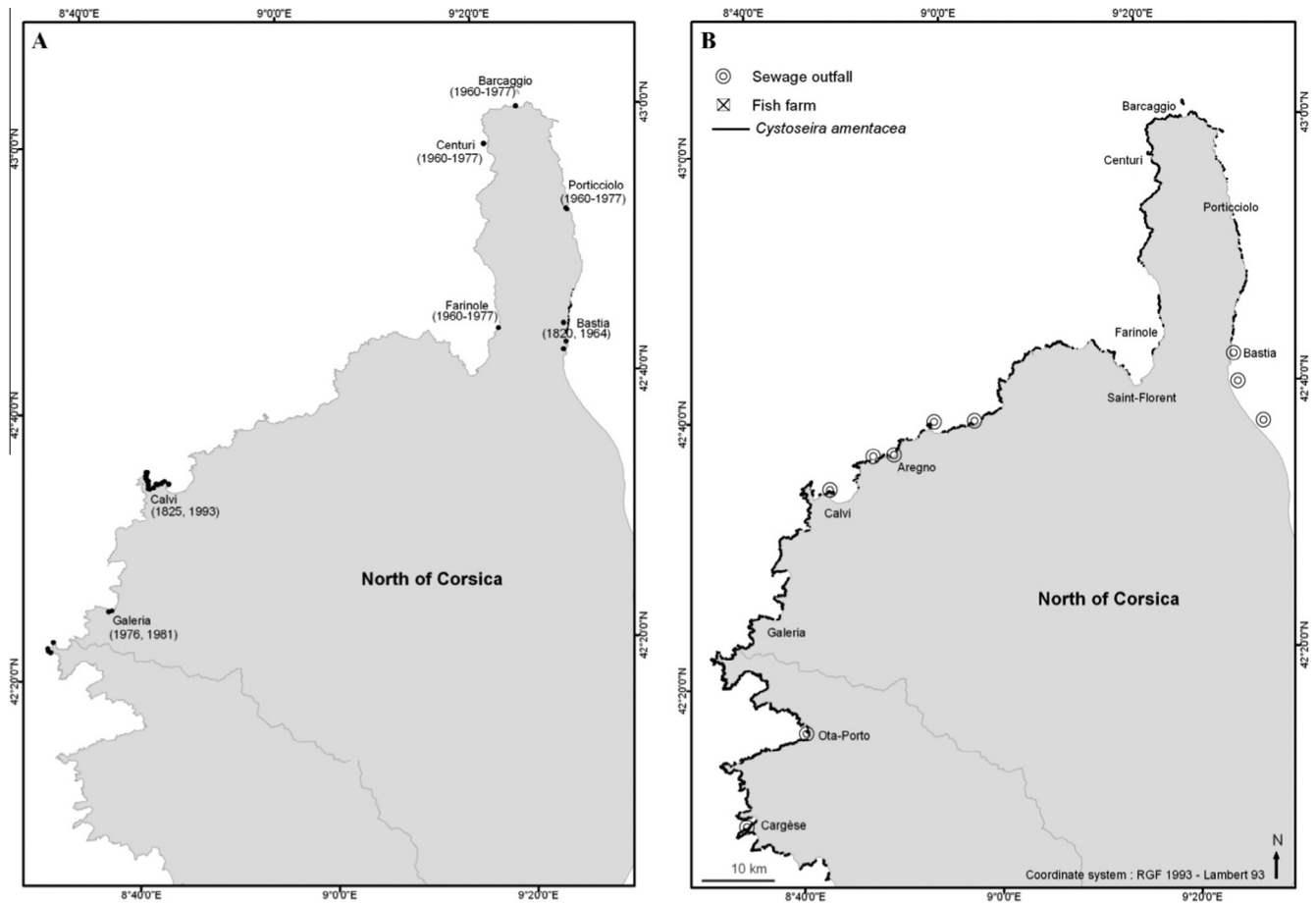


Fig. 5. Distribution of *Cystoseira amentacea* along the coastline of northern Corsica. Grey line: border of northern Corsica. (A) Historical records of *C. amentacea* (data from vouchers and literature). Only the oldest and the most recent dates have been reported. (B) Current distribution of *C. amentacea* and locations of sewage outfalls.

along this coast (coastal development, land reclamations, building of a number of ports and marinas) *C. amentacea* is still abundant on all the suitable substrates; the populations are mainly constituted by a continuous belt. Populations are isolated from each other by wide beaches and mostly located around the capes and islands. In the vicinity of the ports, and off the main cities (Cannes, Antibes, Nice, Villefranche-sur-Mer, Saint-Jean-Cap-Ferrat), *Corallina* spp. assemblages dominate. At Monaco, where 87% of the coast has been completely artificialized, a few patches remain; they are located off the Oceanographic Museum, on the last natural rocky substrates of the Principality.

C. amentacea is very abundant in Corsica, especially on the west coast where the populations are the most highly developed. On the east coast, *C. amentacea* is found along the entire rocky coast but populations are more fragmented (Table 2, Fig. 5B and Fig. 6B). Close to Bastia, Ajaccio and Calvi, *C. amentacea* is less abundant and is replaced to a greater or lesser extent by *Corallina* spp. assemblages.

3.3. Impact of sewage outfalls

We analysed the abundance of each dominant species or functional group around 20 sewage outfalls. Each sewage outfall is a particular case, depending on location on the coast, depth, effluent flow, date of setting up, type of treatment and frequency of untreated release events during heavy rains. Field observations clearly showed a relationship between the benthic assemblages

and the existence of an outfall at Cortiou (Fig. 2B) and Cape Sicié (Fig. 3B), the two studied sewage treatment plants with the highest outflow. In addition, the treated effluent is released at the sea surface and 6 m depth, respectively. (Fig. 7, Table 3). Overall, this pattern is confirmed by the two-dimensional nMDS ordination (Fig. 7), although not statistically significant (PERMANOVA; Table 3). However, a significant difference is evidenced if only two classes of sewage volume (below and above 10000 m³ d⁻¹, respectively) are considered (results not shown).

3.4. Impact of fish farms

Like for the sewage outfalls, each fish farm is a particular case, according to the production, the food used (data not available) and the exposure to hydrodynamism. There is no clear relationship between the presence of a fish farm and the abundance of species and functional groups (*Corallina* spp., *C. amentacea*, *M. galloprovincialis*, turf algae), either from the field evidence and from statistical analyses (Fig. 8, Table 4).

3.5. Impact of ports

We analysed the impact of 193 ports, according to their surface area. During field surveys, an effect of the vicinity of the port on the abundance of each dominant species or functional group on the hard substrates was obvious. In the vicinity of ports, especially medium and large ones, *C. amentacea* is absent or only present as isolated individuals and patches, to the advantage of

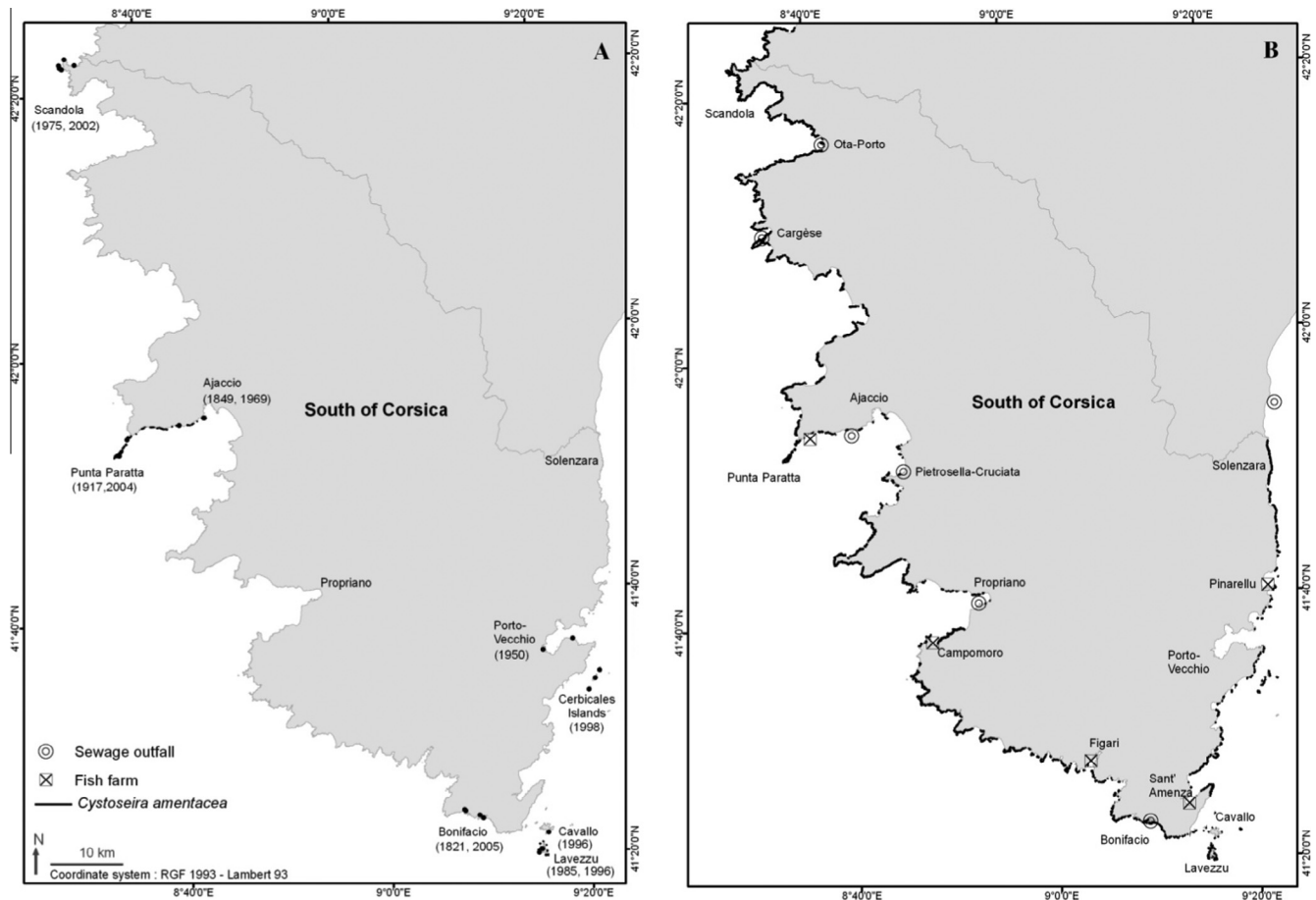


Fig. 6. Distribution of *Cystoseira amentacea* along the coastline of southern Corsica. Grey line: border of southern Corsica. (A) Historical records of *C. amentacea* (data from vouchers and literature). Only the oldest and the most recent dates have been reported. (B) Current distribution of *C. amentacea* and locations of sewage outfalls and fish farms.

Table 2

Structure of *Cystoseira amentacea* population divided into 6 categories along the French Mediterranean coasts (% of hard substrates). C0: absence, C1: Rare scattered plants, C2: Abundant scattered plants, C3: Abundant patches of dense stands, C4: Almost continuous belt, C5: Continuous belt. Shore length: cumulative length (measured on a 1:2500 map) of the coast colonised by C1–C5 *C. amentacea*.

	C0	C1	C2	C3	C4	C5	Shore length (km)
Western Provence	77.05	2.16	4.45	5.38	5.40	5.56	45
Eastern Provence	27.59	0.77	3.40	11.66	13.10	43.48	288
French Riviera	57.51	0.91	2.12	5.67	6.54	27.24	44
Corsica	34.14	1.06	6.70	29.99	15.87	12.23	748
Total (France)	38.60	1.11	5.48	22.02	13.63	19.17	1125

Corallina spp. This effect is confirmed by statistical analyses (Fig. 9, Tables 5 and 6).

3.6. Development of *Cystoseira amentacea* on man-made structures

We found 41 sites with *C. amentacea* growing on man-made structures: 25 on harbour jetties and the others on breakwaters, groynes, pontoons and artificial platforms (Supplementary material Table S8). Its presence was limited to isolated individuals or small patches. The largest population was observed along 293 m of the jetty at Frioul Island port (Marseilles). In the immediate vicinity (<100 m) of these populations, natural populations were found, constituting putative source populations. However, on the breakwater enclosing the Bay of Toulon, we found isolated individuals up to 3320 m distant from the nearest natural population. Similar observations were made at Marseilles (Corbières, Digue

des Catalans). Most of jetties have been rebuilt at least once since their construction; this is not the case of the segment of the Toulon breakwater that harbours *C. amentacea*, which dates from 1880. Overall, the populations established on man-made structures represent a diminutive cumulative length (2.74 km), compared to the total length of artificial habitats (116.53 km), *Corallina* spp. assemblages being widely dominant.

3.7. Comparison between historical and current maps

The current maps exhibit extensive and numerous areas occupied by *C. amentacea* that were not mentioned in the historical maps. This does not mean a progression of the species distribution, but rather emphasises the vast lack of knowledge and the lacunae in the previous mappings. Here, we only compare reliable historical maps with current distribution (Table 7).

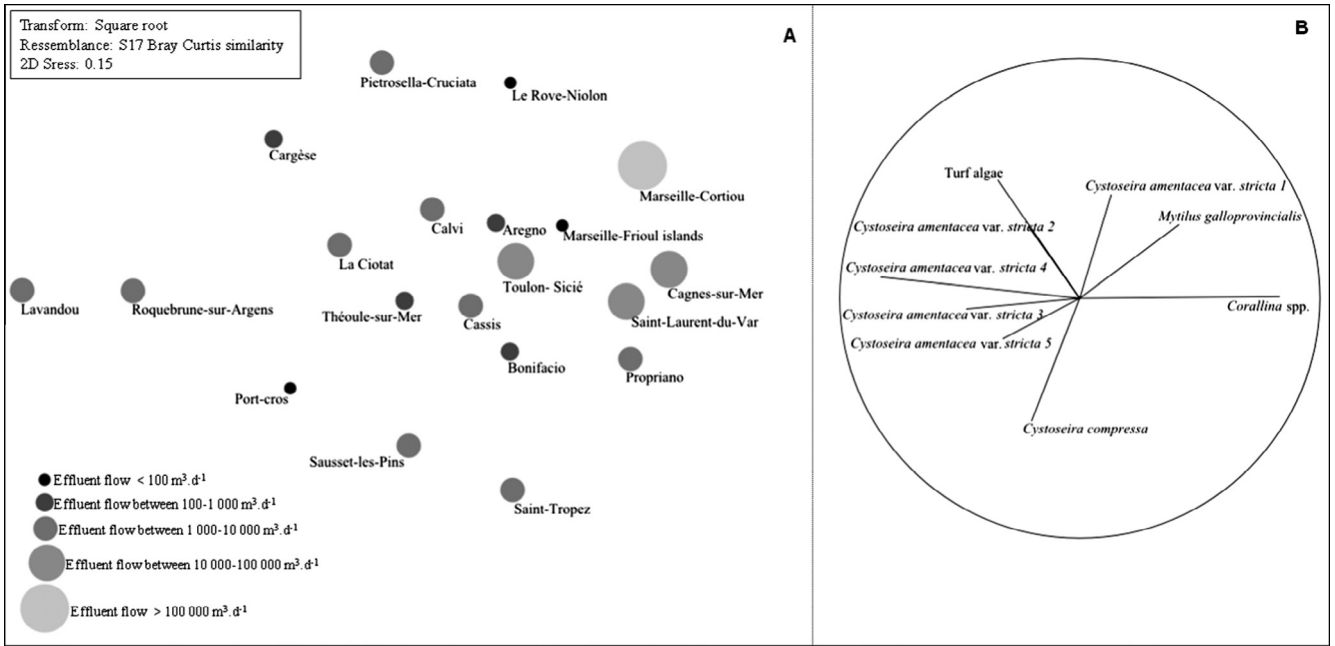


Fig. 7. (A) Two-dimensional nMDS ordination plot on abundance of each dominant species or functional group near each outfall according to their mean effluent flow. The grouping of the major sewage treatment plants) on the right seems to show an effect of the effluent volume. (B) Correlation vectors on taxa of interest (Spearman). The opposition of long vectors (*Cystoseira amantacea* 4 and *Corallina* spp.) also seems to reflect an effect of sewage volume. 2D stress: 0.15.

Table 3

Permutation multivariate analysis of variance (PERMANOVA) on square root transformation of abundance of each dominant species or functional group of each sewage outfall, according to the effluent flow, using S17 Bray Curtis similarity.

Source	df	SS	MS	Pseudo-F	P (perm)	Perms	P (MC)
Effluent flow	4	11 760	2940.1	1.2559	0.194	999	0.254
Residual	15	35 114	2340.9				
Total	19	46874					

Table 4

Permutation multivariate analysis of variance (PERMANOVA) on square root transformation of abundance of each dominant species or functional group of each fish farm, according to the distance from the coast, using S17 Bray Curtis similarity.

Source	df	SS	MS	Pseudo-F	P (perm)	Perms	P (MC)
Distance	2	6324.8	3162.4	0.79519	0.748	78	0.632
Residual	10	39769	3976.9				
Total	12	46094					

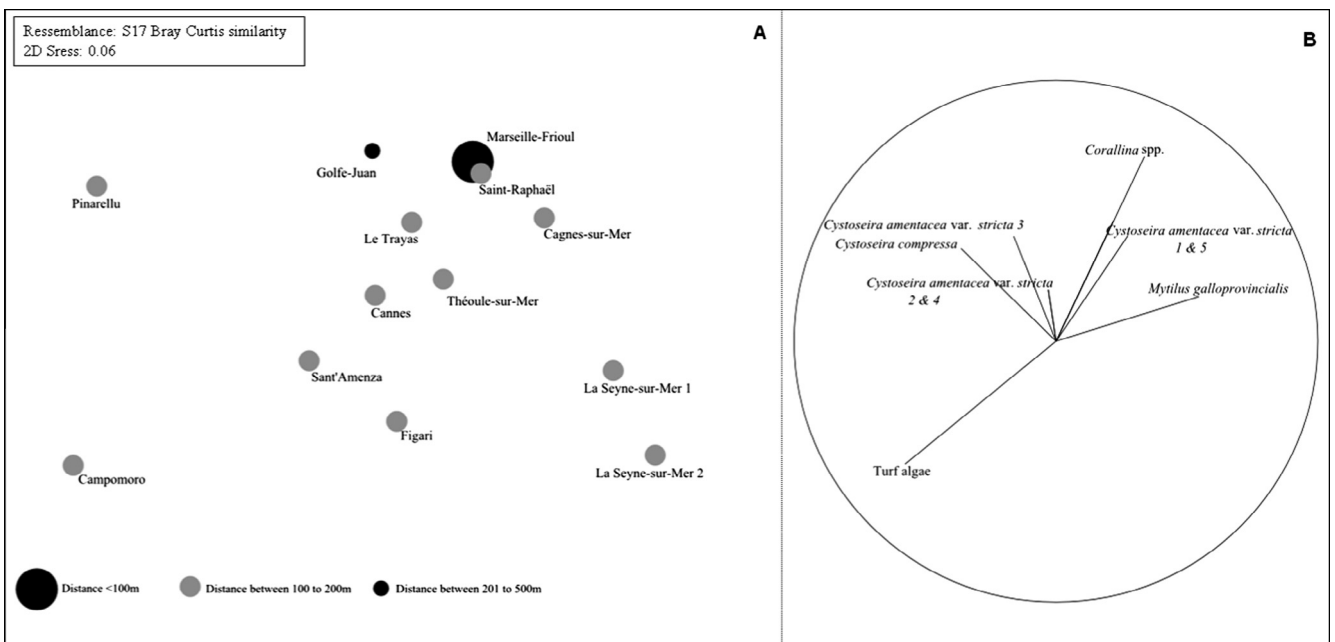


Fig. 8. (A) Two-dimensional nMDS ordination plot on abundance of each dominant species or functional group near each fish farm, according to the distance from the coast. (B) correlation vectors on taxa and functional groups of interest (Spearman); 2D stress: 0.06.

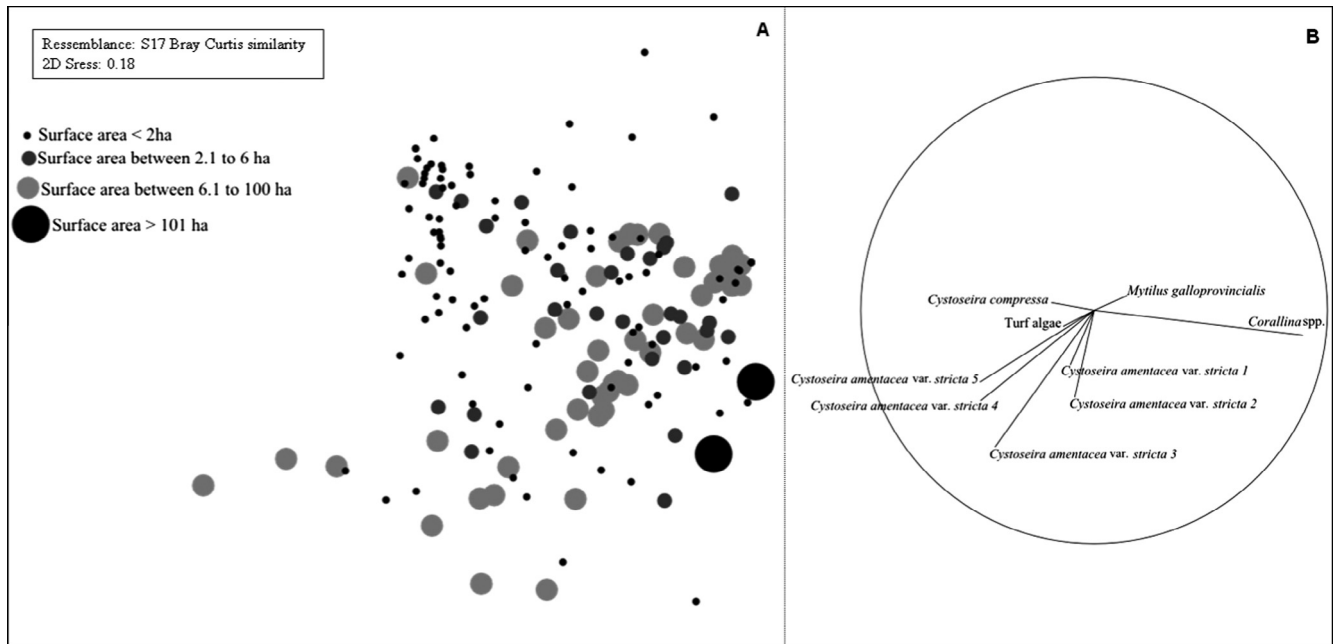


Fig. 9. (A) Two-dimensional nMDS ordinations plot on abundance of each dominant species or functional group near each port, according to its surface area. The dispersion of the smallest ports reflects their low impact, in contrast with larger ones. (B) Correlation vectors on taxa of interest (Spearman); the opposition of long vectors (*Cystoseira amentacea* 3, 4 and 5 and *Corallina* spp.) reflects the port effect. 2D stress: 0.18.

Table 5
Permutation multivariate analysis of variance (PERMANOVA) on square root transformation of abundance of each dominant species or functional group, regarding each surface area of port, using S17 Bray Curtis similarities: small port ≤ 2 ha; middle port = 2.1–6 ha; large port = 6.1–100 ha; very large port ≥ 101 ha.

Source	df	SS	MS	Pseudo-F	P (perm)	Perms	P(MC)
Surface area	3	55927	18642	7.6304	0.001	997	0.001
Residual	189	4.6176E5	2443.2				
Total	192	5.1769E5					

Table 6
Pair-wise comparison on square root transformation of abundance of each dominant species or functional group, regarding each surface area of port, using S17 Bray Curtis similarities: small port ≤ 2 ha; medium sized port = 2.1–6 ha; large port = 6.1–100 ha; very large port ≥ 101 ha.

Pair-wise tests	t	P (perm)	Number of perms	P (Monte Carlo)
Large port/middle port	1.8478	0.01	999	0.02
Large port/small port	4.1901	0.001	999	0.001
Large port/very large port	1.6623	0.039	613	0.027
Medium sized port/small port	2.185	0.002	999	0.004
Medium sized port/very large port	1.8518	0.01	477	0.012
Small port/very large port	1.738	0.008	876	0.015

The comparison of the historical maps with the current maps, within exactly the same areas, shows that, in most cases, only small changes occurred, -3.8% to 4.4% (overall: -0.2%) (Table 7: non-bold lines). These slight differences (positive or negative) between historical and current maps probably result from differences in mapping techniques and accuracy of positioning of the historical maps. Considering these biases, these results reflect a remarkable stability over 1–5 decades. In contrast, a conspicuous decline occurred in 4 areas (Table 7: bold lines). The possible causes and biases for this decline are discussed below.

4. Discussion

For the first time, *C. amentacea* has been exhaustively mapped at a very large scale (1:2500), over 1832 km of its distribution area where hard substrates, putatively favourable to its dwelling, are present. It occurs along 1125 km of coast, from discontinuous

populations (isolated individuals) to continuous belts; the continuous and almost continuous belts are found along 369 km of shoreline. Thus, a general view of its current distribution in the French Mediterranean Sea is now available. This distribution has been compared with a comprehensive analysis of all available historical data from literature, grey literature and herbarium vouchers since 1700.

Most authors have emphasised the dramatic decline of species of the genus *Cystoseira* throughout the Mediterranean Sea (e.g. Munda, 1974, 1982, 1993; Boudouresque, 2003; Thibaut et al., 2005; Devescovi and Ivesa, 2007; Airoldi et al., 2008; Falace et al., 2010; Mačić et al., 2010; Frascchetti et al., 2011; Giakoumi et al., 2012; Sala et al., 2012; Bianchi et al., 2014; Templado, 2014). It is the case, in particular, for *C. amentacea* (e.g. Bellan-Santini, 1963, 1964, 1966, 1968b; Arnoux and Bellan-Santini, 1972; Bellan and Bellan-Santini, 1972; Belsher and Boudouresque, 1976; Clarisse, 1980–1981, 1984; Boudouresque

Table 7

Comparison of the length (in m) of shoreline occupied by *Cystoseira amentacea* in the past (various periods) and today, where reliable historical maps are available. Bold: conspicuous decline.

Source	Location	Historical	Current	Difference (%)
Ollivier (1929)	Between Eze-sur-Mer and Cap Martin	13269	9977	–24.8
Guglielmi (1969)	Beaulieu-sur-Mer and Saint-Jean-Cap-Ferrat	10425	7311	–29.9
Meinesz et al. (2000b)	Coastline of Nice	2369	2279	–3.8
Bonhomme et al. (2004)	Cap Dramont corniche d'Anthéor, Saint-Raphaël	7333	7356	0.3
Augier and Boudouresque (1967)	Bay of La Palud, Port-Cros Island	689	709	2.9
Augier and Boudouresque (1970b)	Bay of Port-Man, Port-Cros Island	1571	1577	0.4
Augier and Boudouresque (1976)	Port-Cros Island (part)	10453	10537	0.8
Meinesz et al. (2000a, 2001a,b, 2004a) and Cottalorda et al. (2004)	All mapped areas of Port-Cros Island	19107	19296	1.0
Meinesz et al. (2001c)	Bagaud Island	6211	6120	–1.5
Augier (1978)	Bon Renaud Cove, Porquerolles Island	113	118	4.4
Augier (1981)	Port-Fay Cove, Porquerolles Island	554	555	0.2
Augier (1995)	Gorges du Loup Cove, Porquerolles Island	271	279	3.0
Gratiot et al. (2006)	Porquerolles Island (part)	12625	12614	–0.1
Picard and Bourcier (1975)	La Ciotat	5689	5610	–1.4
Bellan-Santini (1966)	Calanques of Marseilles	17465	8051	–53.9
Soltan (2001)	Calanques of Marseilles	13154	8051	–38.8
Cadiou et al. (2006)	Cassis, between Canaille Cape and Grand Caunet Cape	7528	7479	–0.7
Clarisse (1980–1981, 1984)	Between punta Revellata and the harbour of Calvi	7056	5801	–17.8
Blachier et al. (1998)	Between punta Cappicciolu and punta Sperone	6011	5826	–3.1

et al., 1990; Soltan et al., 2001; Boudouresque, 2003; Susini, 2006; Susini et al., 2007). This worrying trend resulted in the listing of *C. amentacea* under the Berne Convention, the Barcelona Convention and Habitat of Community Interest in the UE (Micheli et al., 2013).

We were therefore expecting a severe decline of *C. amentacea*, as reported for *C. mediterranea* along the French Catalonian coast (Thibaut et al., 2005), at least in Provence and French Riviera, in relation with the increase in human pressure (population, summer touristic frequentation, coastal development and leisure boating). Since the last decades of the 20th century, the increase in marine habitat losses (275 ports, 144 land reclamations, 458 groynes and jetties) has been dramatic (Meinesz et al., 2013). As regard the pollution, it has conspicuously increased over the investigated period, especially during the 20th century (Serrano et al., 2011) and its decline in the study area, following the construction of sewage treatment plants, is too recent (1980–1990s) to have been likely to reverse the trend (Soltan et al., 2001; Thibaut et al., 2005).

In fact, among most of the precise locations where historical specimens were reported, we found the species present at the same sites; in some cases, when the abundance was indicated, it proved to be unchanged. In the Gulf of Fos (western Provence), which harbours one of the largest French port and industrial facilities (petrochemical and chemical industries, oil refineries, steelworks, power plant, etc.), the distribution of *C. amentacea* has remained unchanged since 1975 (Fig. 2B), but populations are now more fragmented and are in competition with mussel beds (Desrosiers et al., 1982, 1986) whereas industrial activities and perturbations have clearly increased over the past 40 years. Only 4 locations presented a conspicuous decline of *C. amentacea* populations between historical and current data (Table 7): the Calanques of Marseilles (Western Provence), between Eze-sur-Mer and Cap Martin, between Beaulieu-sur-Mer and Saint-Jean-Cap-Ferrat (French Riviera) and between Punta Revellata and the harbour of Calvi (Corsica). Ollivier (1929) mapped the species between Eze-sur-Mer and Cap Martin, including the Principality of Monaco. The 24.8% loss can be related to well-documented events, such as the near-total artificialisation of the coastline, especially at Monaco (between 1963 and 2002), where artificialisation encompasses 87% of the coastline (Meinesz et al., 2013). This loss, and its rate of development, is therefore convincing. The 29.9% loss observed between Beaulieu-sur-Mer and Saint-Jean-Cap-Ferrat is based upon a map of Guglielmi (1969). This map is highly reliable and the causes of the loss well identified: enlargement of the

coastal road at Beaulieu-sur-Mer (~1975), building of the port of Beaulieu-sur-Mer (1969), enlargement of the Saint-Jean-Cap-Ferrat port (1972), land reclamation of Le Lido (Saint-Jean-Cap-Ferrat, ~1998) (Meinesz et al., 2013). In Corsica, a similar decline trend has been documented between Punta A Rivillata (La Revellata) and the harbour of Calvi (–17.8%, Clarisse, 1980–1981, 1984), where the impact of a sewage outfall has been suspected (Janssens, 1991).

The greatest loss has been documented in the vicinity of the Cortiou sewage outfall at Marseilles (western Provence), the largest French Mediterranean city and one of the largest cities of the whole Mediterranean Sea, where a steady decrease of *C. amentacea* has apparently occurred since the 1960s (Bellan-Santini, 1966; Soltan, 2001; Soltan et al., 2001). The loss, with reference to the 1960s hypothetical baseline, would be 39% in the early 2000s (Soltan, 2001) and 54% (present work). However, the validity of the baseline can be questioned; Bellan-Santini (1966, 1968b) mapped the species in some places where its presence is unlikely, due to unsuitable habitats such as beaches, protected coves, under overhanging rocks, on cliffs and on *Lithophyllum byssoides* (Lamarck) Foslé rims. We therefore suspect an overestimation of the rate of loss since the 1960s. In any case, the 1960s do not constitute a reliable baseline since pollution in the Marseilles area was already worrying in the late 19th century, when the Cortiou sewage outfall was constructed (Marion, 1883), and in the first half of the 20th century (Berner, 1931). Nevertheless, the loss continued after 2000 and the unbiased map of Soltan (2001), which is unexpected due to the construction of a sewage treatment plant in 1987 and the improvement of the treatment process in 2007, for the largest discharge of sewage along the French coasts (1 630 000 population equivalent). The reason could lie in the fact that the outfall flow is extremely high (192 000–233 000 m³ d^{–1}), and located at sea level, it gives rise to a large plume of freshwater drifting at the sea surface (low salinity is known to have a negative effect on some species of Fucales, Zavodnik, 1975), and it is dumped without any treatment during the occasional heavy rains.

Our results confirm that *C. amentacea* is able to colonise man-made structures (we found the species at 41 sites). These populations cannot be perennial since the structures (rocks, concrete blocks, etc.) can be replaced from time to time; this is the probably the case in many ports (French Riviera and eastern Provence) where all the previously reported sightings were not observed again after the enlargement of the port (Ollivier, 1929;

Bensimon et al., 1966; Carvou, 1967; Gadea, 1967; Maggi, 1967; Canamella, 1968; Carvou et al., 1968; Vignes, 1968; Susini, 2006). In the Mediterranean, among the Fucales, only *C. compressa* was commonly observed on dykes (Susini, 2006) and, in the Adriatic *Fucus virsoides* J. Agardh is also able to grow on man-made substrates (Mačić, 2006), whereas in the Atlantic *Fucus* spp. are commonly observed on man-made substrates. The observation of *C. amentacea* on relatively recent man-made substrates (less than 40 years) and relatively distant from the nearest natural population invalidates the hypothesis of Mangialajo et al. (2012) suggesting very slow colonisation, step by step, by eggs disseminated over less than few dozen cm from the source population. Possible dispersion mechanisms, able to account for our results, involve the sea bird *Larus cachinnans* Pallas 1811 (Bartoli et al., 1997) and drifting fragments (e.g. Raphélis specimens in Herbarium Général, MU; drift specimens on French Riviera beaches).

When disturbed, *C. amentacea* is replaced by *Corallina* spp, the mussel *M. galloprovincialis* and/or *C. compressa*. This phenomenon has been extensively documented; the fast growing *Corallina* spp. take the place of *C. amentacea* while mussels prevent the recruitment of *C. amentacea* (Berner, 1931; Desrosiers et al., 1982, 1986; Bulleri et al., 2002). A number of authors (Bellan and Bellan-Santini, 1972; Kautsky et al., 1992) have reported increments of mussels in polluted waters, particularly in the vicinity of domestic outfalls. Similarly, an increase in mussel populations has been related to algal stand declines in Great Britain and the Baltic Sea (Kautsky et al., 1992). Lastly, *C. compressa* is a tolerant opportunistic fast growing species, replacing *C. amentacea* when disturbed (Mangialajo et al., 2012). Loss of *C. amentacea* reduces the species diversity (point diversity, as defined by Boudouresque (2011) from 133 species in *C. amentacea* stands in pristine waters, 108 species in *C. elongata* stands and 76 species in mussel beds in polluted sites (Bellan and Bellan-Santini, 1972). Competition between rhodophytes and fucoids is a common feature worldwide (Worm and Chapman, 1996). In Asturias (Spain), coastal development and pollution on rocky coast result in long term changes, with the decline of *Fucus* and *Laminaria* in favour of *Gelidium* sp. (Fernandez and Niell, 1982). In the Atlantic, *C. tamarascifolia*, *C. baccata* (S.G. Gmelin) P.C. Silva and *Bifurcaria bifurcata* R. Ross forests have been replaced by turf algae in Abra Bilbao Bay (Biscayne Gulf) under a pollution gradient (Díez et al., 1999, 2009). Overall, the replacement of *C. amentacea* by *Corallina* spp., mussel beds and/or *C. compressa* can be interpreted as a phase shift from a canopy stage to a less structured stage (turf), inducing simplification of the zonation pattern, as reported when fucoids have been lost (Munda, 1980, 1993; Tewari and Joshi, 1988; Fairweather, 1990; Rueness and Fredriksen, 1991).

To date, *C. amentacea* has been regarded as a species very sensitive to human impact, e.g. pollution, coastal development and land reclamations. It was thought to have become relatively rare in the highly man-impacted north-western Mediterranean and therefore benefits from a protection status. Undoubtedly, our results confirm a positive correlation between the decline of the species and the vicinity of medium-sized and large ports; as regards the sewage outfalls, such a correlation only concerns very large outfalls flowing at the sea surface, such as that at Marseilles; finally, no relation may be observed between *C. amentacea* and fish farms. The species has a low nitrogen uptake rate (Orlandi et al., 2014) that could protect the species from non-permanent nitrogen pollution. However, at the scale of the French Mediterranean coasts (Provence, French Riviera and Corsica), this impact seems limited. The comparison of 14 accurate maps produced in the past (1967 through 2006) with current maps, under a variety of human pressure, along 81 km of coastline, failed to evidence any general trend (only 0.02% of difference). Loss is concentrated in 4 areas near Marseilles (Provence), Nice-Monaco (French Riviera) and Calvi (Corsica): from 75 km (1929–1984; may

be a slight overestimation) to 47 km (currently) of coastline. Overall, at the scale of the study area, *C. amentacea* extends along 1125 km, with long stretches of near-continuous to continuous belts. Although the sensitivity of the species to human impact is confirmed, its resilience may be higher than previously thought.

A large amount of historical data, in the form of rarely available old publications, grey literature and herbarium vouchers, do exist, although frequently neglected by authors. Taking into account these data makes it possible to reduce the sliding baseline syndrome, i.e., in the absence of any benchmark, the acceptance of an already degraded environment or of a hypothetically exaggerated degraded one, as the reference, i.e. the baseline. The reconstruction of historical data performed here demonstrates its feasibility, usefulness and efficiency. In addition, the accurate mapping of the current distribution of *C. amentacea* (2008–2011) will allow future comparisons.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.marpolbul.2014.09.043>.

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