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ORIGINAL ARTICLE

# Toward the first documented extinction of a marine macroalga in the Mediterranean Sea?

**Emmanuelle Descourvières[1,2] · Vinko Bandelj[2,3] · Adriano Sfriso[4] · Martina Orlando-Bonaca[5] · Vesna Mačić[6] · Ljiljana Iveša[7] · Silvija Kipson[8] · Edi Gljušćić[7] · Claudio Battelli[9] · Isabella Moro[10,11] · Cosimo Solidoro[2,3] · Annalisa Falace[1,2]**

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## Abstract

*Fucus virsoides* is a glacial relict-species endemic to the Adriatic that was widespread from northern Italy to southern Albania. In recent decades, however, it has suffered an alarming decline. In this study, all available records were reviewed to reconstruct its historical and current occurrence and to investigate the possible causes of its decline. Comprehensive mapping revealed a continuing decline with a significant shift, leaving only about 20 fragmented populations. While the species is already classified as critically endangered in Albania, *F. virsoides* could be considered functionally extinct in Istria (Croatia), critically threatened with extinction in Italy and Montenegro and locally extinct in Slovenia. The status of the species in the rest of Croatia is still unclear. The remaining populations are located in areas characterised by low temperatures, low salinity and high nutrient concentrations. Long-term analyses of these key abiotic factors revealed profound changes that suggest a link to the species' decline. This study provides a thorough assessment of the overall status of *F. virsoides* and argues for its inclusion on the IUCN Red List. Immediate conservation measures are needed for the long-term survival of this species.

**Keywords** *Fucus virsoides* · Adriatic Sea · Endangered species · Distribution

## Introduction

*Fucus* species (Fucales, Phaeophyceae) are intertidal canopy-forming algae widely distributed on temperate and cold rocky coasts (Lüning 1990; Chapman 1995). They provide crucial ecosystem services (Wernberg and Filbee-Dexter 2019), by enhancing habitat complexity (Kautsky et al. 1992; Boaden 1996; Fredriksen et al. 2005) and species diversity (e.g. Aneer et al. 1983; Duffy and Hay 1991; Borg et al. 1997). In addition, *Fucus* spp. are a source of bioactive components that are of interest to the pharmaceutical, food, and cosmetics industries (Catarino et al. 2018 and references therein).

*Fucus virsoides* J. Agardh is the only representative of the genus in the Mediterranean and endemic to the Adriatic (Linardić 1949; Giaccone and Pignatti 1967). Its occurrence

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✉ Annalisa Falace
falace@units.it

[1] Department Life Sciences, University of Trieste, Trieste, Italy

[2] National Institute of Oceanography and Applied Geophysics - OGS, Trieste, Italy

[3] National Biodiversity Future Center - NBFC, Palermo, Italy

[4] Department of Environmental Sciences, Informatics and Statistics (DAIS), University Ca' Foscari Venice, Mestre, Italy

[5] Marine Biology Station Piran, National Institute of Biology, Piran, Slovenia

[6] Institute of Marine Biology, University of Montenegro, Kotor, Montenegro

[7] Ruder Bošković Institute, Center for Marine Research, Rovinj, Croatia

[8] SEAFAN - Marine Research and Consultancy, Zagreb, Croatia

[9] Frane, Marušič 4, Izola, Slovenia

[10] Department of Biology, University of Padova, Padua, Italy

[11] Department of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn, Naples, Italy

has been interpreted as a glacial relict (Munda 1972), extending from northwestern Italy to southern Albania (Linardić 1949; Kashta 1992; Mačić 2006). The occurrence of *F. virsoides* in the Mediterranean region appears to be the result of geographical isolation, fostering speciation through long-term isolated reproduction. This likely occurred after the initial migration of the genus during the Pleistocene glacial events, followed by isolation after the last glaciation (Serrão et al. 1999). This explanation is supported by the possible presence of the Atlantic *Fucus vesiculosus* Linnaeus in the northwestern Mediterranean from the Last Glacial Maximum to the mid-Holocene (Assis et al. 2014).

The distribution of *F. virsoides* is controlled by environmental factors such as substrate type and orientation (Vukovič 1982; Lipizer et al. 1995; Battelli 2002, 2013, 2016a; Rindi and Battelli 2005; Orlando-Bonaca et al. 2013), wave exposure (Munda 1972; Lipizer et al. 1995; Orlando-Bonaca et al. 2013), and salinity (Vouk 1938; Linardić 1949; Giaccone and Pignatti 1967; Munda 1972; Orlando-Bonaca et al. 2013). It is naturally exposed to variable conditions, such as desiccation, changes in water and air temperature, salinity, light (i.e. quality, quantity, UV-radiation), wave action and nutrient supply (Pignatti 1962; Giaccone and Pignatti 1967; Munda 1972; Dethier and Williams 2008; Lamote et al. 2012; Battelli 2013). In addition, it is highly exposed to human pressure (Vukovič 1980, 1982; Munda 1993a, 1993b, 2000; Lipizer et al. 1995; Battelli 2002; Lipej et al. 2004, 2006; Rindi and Battelli 2005; Falace et al. 2010, 2018; Orlando-Bonaca et al. 2013; Gerdol et al. 2020).

In recent decades, *F. virsoides* has suffered an alarming decline (Munda 1979, 1982; Falace 2000; Falace and Bressan 2003; Mačić 2006; Falace et al. 2010, 2018; Orlando-Bonaca et al. 2013; Battelli 2016a) and has therefore been included in the "*List of Endangered or Threatened Species*" of the Barcelona Convention (amended Annex II of the Protocol on Specially Protected Areas and Biological Diversity in the Mediterranean, UNEP 2019).

*Fucus* populations are declining due to a combination of multiple impacts (e.g. Vogt and Schramm 1991; Martínez et al. 2012; Nicastro et al. 2013; Mota et al. 2015; Riera et al. 2015), affecting their ecological and physiological performance, with cascading effects on productivity and ecosystem services (Altieri et al. 2007; Assis et al. 2014; Casado-Amezúa et al. 2019). The loss of *F. virsoides* has been linked to pollution (Munda 1982, 1991, 1993a; Falace et al. 2018; Gerdol et al. 2020), habitat fragmentation (Mačić 2006; Falace et al. 2010; Orlando-Bonaca et al. 2013; Pavičić-Hamer et al. 2016) and climate change (Boero and Bonsdorff 2007; Boero et al. 2008; Munda 2008). Numerous concurrent changes in the physical, chemical and ecological properties of the Adriatic have occurred, including oligotrophication (Mozetič et al. 2010) and surface temperature warming (Giani et al. 2012; Grilli et al. 2020), with changes in biodiversity, including macroalgal structure and function (Falace et al. 2010), shifts in fisheries productivity (Fortibuoni et al. 2017) and invasive species introduction (Malej et al. 2017; Sfriso et al. 2020).

Due to its ecological value as part of the natural heritage in several countries, *F. virsoides* needs the highest protection status. Therefore, there is an urgent need to assess the status of this species in order to develop appropriate management and conservation (Falace et al. 2010).

The aims of the present work were: 1) to review all available historical and current distribution data, as these are highly fragmented, and 2) to discuss the likely causes of the decline and propose appropriate management measures to prevent the extinction of the species.

## Materials and methods

### Geographical area

The Adriatic is a semi-enclosed basin in the northernmost part of the Mediterranean Sea, bordered from west to south-east by Italy, Slovenia, Croatia, Bosnia and Herzegovina, Montenegro and Albania. It exhibits pronounced longitudinal and transverse asymmetries in its geomorphology, bathymetry, and hydrology (Artegiani et al. 1997; Totti et al. 2019), resulting in a biogeographical subdivision into three sub-basins (Artegiani et al. 1997) (Fig. S1).

The northern sub-basin is very shallow (average depth 35 m) and is influenced by the largest Adriatic freshwater inflows (Cushman-Rosin et al. 2001), 50% of which originate from the Po (Penna et al. 2004). The middle sub-basin has an average depth 140 m (Zavatarelli et al. 1998), while the southern sub-basin is characterized by a depression, the South Adriatic Pit, with a depth of over 1200 m, and extends to the Strait of Otranto, through which it is connected to the Ionian Sea. Here the saltier and warmer water from the Ionian Sea mixes with the fresher and colder water from the Adriatic. The western coast is characterised by sand and gentle slopes, while the eastern coast, which is more irregular, has rocky substrates, steep slopes, and numerous islands (Russo and Artegiani 1996).

The Adriatic is influenced by dynamic meteorological conditions (Cushman-Roisin et al. 2001), including strong winds such as the dry, cold and strong Bora wind. It generates upwelling along the eastern coast, providing cold and nutrient-rich water (Rachev and Purini 2001). Through heat loss and evaporation, this polar continental air mass also contributes to the formation of dense water (Vilibić and Supić 2005). In addition, the Adriatic is considered a dilution basin due to the freshwater imbalance, which is influenced by freshwater runoff (Raicich 1996). Salinity shows

an increasing north–south gradient, while temperature and nutrient concentrations generally show a decreasing trend. The tides are among the highest in the Mediterranean, with higher amplitudes in the northern sub-basin (ca. 90 cm) than in the central and southern sub-basins (ca. 20–30 cm) (Tsimplis et al. 1995; Marcos et al. 2009; Battelli 2016b).

In recent decades, the Adriatic coast has undergone significant anthropogenic changes due to socio-economic activities, which have led to changes in coastal marine ecosystems.

### Data collection

All available scientific articles, proceedings, and reports on *F. virsoides* were analysed. Two online scientific databases, *Scopus* and *Web of Science*, as other digital archives (e.g. Macroalgal Herbarium Consortium Portal-https://macroalgae.org/portal/), repositories, and unpublished data were consulted. Past and current locations of *F. virsoides* were geolocated and then analysed using QGIS (QGIS.org 2023).

Annual and seasonal average values of Sea Surface Temperature (SST), salinity, dissolved inorganic nitrogen [DIN = sum of ammonium, nitrite and nitrate] and phosphorus [DIP = dissolved inorganic phosphorus] were downloaded from the European Marine Observation and Data Network (EMODnet—https://emodnet.ec.europa.eu/en) *in-situ* dataset (Tab. S1). The data were trimmed to a narrow strip along the coast (from the coastline to 20—40 km offshore) and focused on the surface (0—1 m). To check for increasing or decreasing linear trends in the time data series of the coastal and surface strips for all four environmental parameters, we calculated linear regressions from 1990 to 2021 and from 1993 to 2017 for physical and chemical parameters, respectively, using the Python package statsmodels (Seabold and Perktold 2010).

## Results

A total of 558 records documenting the presence of *F. virsoides* were gathered from the nineteenth century until 2023 (Figs. S2a, b; Tab. S2). The historical and current occurrences of *F. virsoides* along the Adriatic coasts are illustrated in Fig. 1a, b. Current occurrences refer to observations from 2020 onward, unless extinction was detected thereafter. References for the occurrence of *F. virsoides* are in the supplementary materials (Table S3).

### Historical and current distribution of *F. virsoides*

**Italy** *F. virsoides* was reported between 1941 and 1946 only in the Venice Lagoon (Zanardini 1841) and on the Riviera del Conero (Pierpaoli 1946; Linardić 1949). As noted by Solazzi (1966–1967), the species disappeared from the Riviera del Conero, so that the Venice Lagoon represents the limit of its distribution on the Italian coast.

Until the early 2000s, it was found both in the Venice Lagoon and in the coastal marine waters of Lido and Pellestrina. Between 1941 and 2004, *F. virsoides* was reported

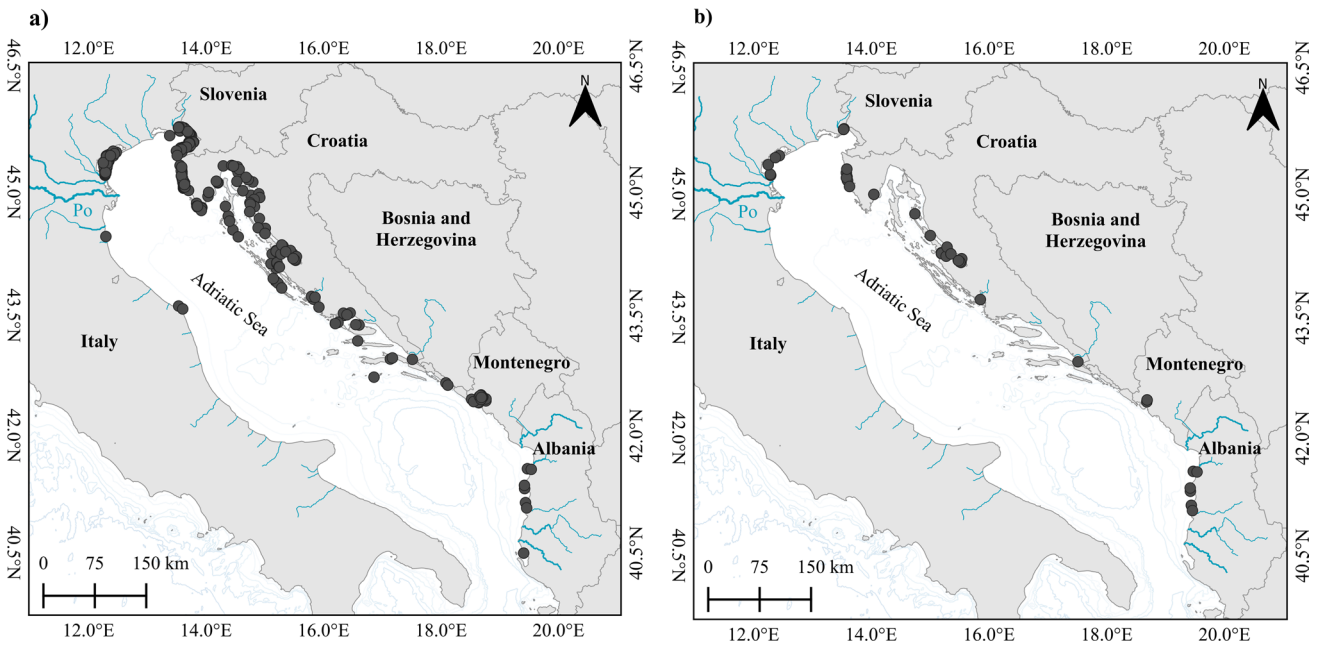


**Fig. 1** Historical (**a**) and current (**b**) known populations of *Fucus virsoides* in the Adriatic Sea

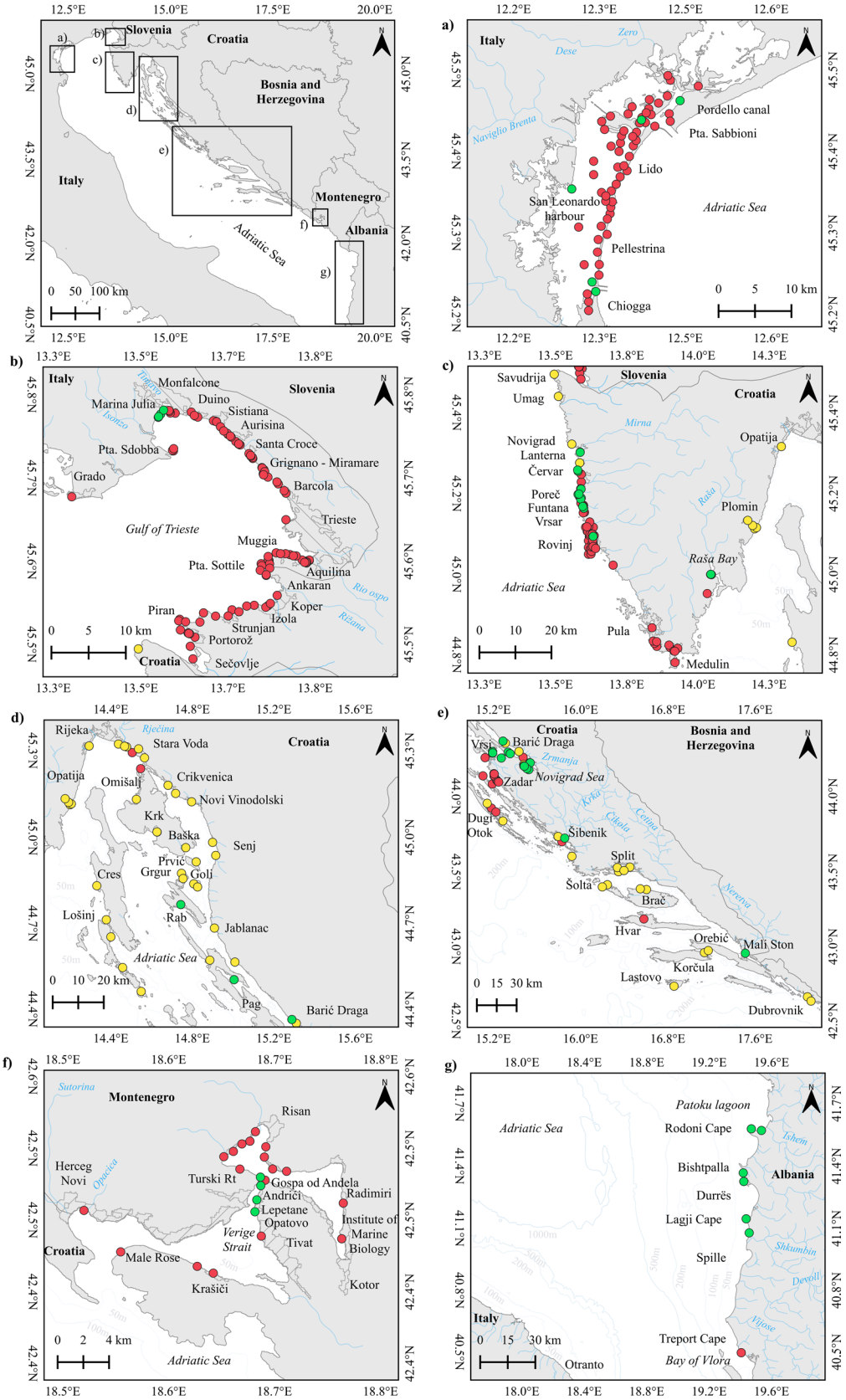


**Fig. 2** *Fucus virsoides* in the Venice Lagoon (**a**), in the Gulf of Trieste (Italy) (**b**), in Istria (**c**), in Kvarner (**d**), in Dalmatia (Croatia) (**e**), in the Boka Kotorska Bay (Montenegro) (**f**) and in Albania (**g**). Green points = present in historical sites; red points = extinct in historical sites, yellow points = a historical site with no current assessment; the grey hatched areas are coastal towns

by many authors (approx. 30 papers) (Sfriso and Curiel 2007). In the following years, *Fucus* disappeared from the coastal waters (panels and lagoon jetties), but it was still very common in the lagoon (Fig. 2a). Here it colonized with dense populations most of the banks of Punta Sabbioni, Lido, Pellestrina, Chioggia and all the small islands in the lagoon, including some embankments and heavily polluted internal canals of the historic centre of Venice. The decline of *Fucus* in the lagoon was observed in 2015–16, when it disappeared almost everywhere. As of 2024, there are only a few remaining populations, mostly in areas protected by direct wave action and influenced by high water renewal that prevents extremely high temperatures (e.g. in the San Leonardo harbour in the central lagoon and in the Pordelio canal near Treporti at Punta Sabbioni in the northern lagoon (Fig. S2c)). In the past, the seawater temperatures were colder in winter and many freezing water events were recorded (Fig. S2d). Camuffo et al. (2017) reconstructed freezing water events in the Venice Lagoon during the last 1400 years. Between 2012 and 2015, frozen water was only occasionally detected in some salt marshes and canals. In the following years until today, the water temperature in January–February hardly fell below 4–5 °C. At the same time, the rapid decline of *F. virsoides* began.

For the Italian coasts of the Gulf of Trieste (Fig. 2b), most of the data come from Linardić (1949), Pollesello et al. (1992), Osterc and Stibilj (2008), Lipizer et al. (1995), Falace et al. (2010) and Orlando-Bonaca et al. (2013). Lipizer et al. (1995) investigated the distribution of *F. virsoides* from Punta Sdobba (Gorizia) to Punta Sottile (Muggia). Dense belts were reported for Punta Sdobba, Marina Julia, Monfalcone, Costa dei Barbari (Aurisina), Ginestre (Aurisina), Aquilinia, Muggia, and Punta Sottile with discontinuous belts at Duino, Sistiana, Filtri di Aurisina (Aurisina), Santa Croce, Grignano, Miramare, San Bartolomeo (Muggia) and Rio Ospo (Muggia) and scattered patches at Canovella degli Zoppoli (Aurisina) and Cedas (Trieste) in areas with high ecological, physical and chemical variability. In 2009, Orlando-Bonaca et al. (2013) produced a high-resolution Geographic Information System database using visual census methods to determine the presence and abundance of *F. virsoides*, including the geomorphology of the substrate along the Italian and Slovenian coasts of the Gulf of Trieste. On the Italian side of the Gulf, continuous or almost continuous belts were observed from Duino to Punta Sottile. However, no thalli were found in the harbors of Sistiana, San Rocco (Muggia) and San Bartolomeo (Muggia). From Sistiana to Trieste, of the 12 populations recorded, 10 were located inside marinas or small artificial shelters and two were directly exposed to the open sea. The longest populations were found along the rocky coast in Duino and Muggia near freshwater inlets with muddy seabed.

In 2017 (Falace et al. 2018; Gerdol et al. 2020), the last populations of *F. virsoides* were found only on the Italian coast of the Gulf of Trieste on the artificial substrate of Marina Julia (Monfalcone). This site is influenced by the estuaries of the Isonzo and Timavo rivers and receives direct freshwater inflow from the protected Natura 2000 Site Cavana di Monfalcone.

**Slovenia** The occurrence of *F. virsoides* along the Slovenian coast has been well documented over time (Herbario Lugduno-Batavo; Schiffner Algae marinae; Accurti 1858; Linardić 1949; Štirn 1965; Vukovič 1980, 1982; Munda 1991, 1993a, 1993b; Alberti and Battelli 2002; Battelli 2002; Battelli and Alberti 2003; Lipej et al. 2004; Osterc and Stibilj 2008, 2012; Orlando-Bonaca et al. 2013, Battelli 2016a) and several maps have been produced (Štirn 1965; Vukovič 1982; Lipej et al. 2004; Orlando-Bonaca et al. 2013; Battelli 2016a) (Fig. 2b).

In 2009, Orlando-Bonaca et al. (2013) documented continuous populations over a length of 2.33 km between Koper and Izola, populations in the marina of Izola, and populations at Sečovlje extending over 2.78 km within the Sečovlje Salina Nature Park. However, no populations were observed in the Ankaran, Strunjan and Piran areas.

Battelli (2016a) found spatial and quantitative variability in the distribution of *F. virsoides*, recorded from the Ankaran to Sečovlje areas until the summer of 2010. Continuous and almost continuous belts were found in Izola and San Simon (Izola), abundant patches from Porporela harbour (Koper) to Viližan Bay (Izola) and Cape Madona (Piran), while rare to scattered thalli were observed from Sv. Jerney Bay to Sv. Katarina (Ankaran), from Cape Kane (Strunjan) to Fiesa–Madona (Piran), and from Bernardin (Piran) to the Sečovlje Salina Nature Park (Sečovlje). In autumn 2010, a drastic decline in *F. virsoides* populations was observed, leading to the almost complete disappearance of the population. As a result, only rare and scattered individuals were found at Viližan Bay (Izola) by 2014, and in Pirat Bernardin (Portorož) by 2015. This marked the disappearance of the last *F. virsoides* population in Slovenia. Coinciding with the decline of *Fucus*, Battelli (2016a) recorded a massive increase in the macro-grazer *Patella caerulea* Linnaeus, 1758. No new individuals of *F. virsoides* have been observed in Slovenia since 2015.

**Croatia** Due to the extensive coastline (6,278 km, determined at a scale of 1:25000), of which 4,398 km are accounted for by 1,246 islands and islets (Duplančić Leder et al. 2004; Lincke et al. 2020), the accurate mapping of the distribution of *F. virsoides* for the entire Croatian coastline is lacking. From 1886 to the present, sporadic localizations have been recorded (Herbar der Zoologisch-Botanischen Gesellschaft in Wien; Herbarium von Anton Hansgirg; W. Migula, Cryptogamae Germaniae, Austriae et Helvetiae exsiccatae Fasc; Schiffner Algae marinae; Herbier F. Magne;

Linardić 1949; Čmelik and Morovć 1950; Gessner 1969; Munda 1969; Zavodnik 1965, 1967a, 1967b, 1973, 1977; Gessner and Hammer 1971; Munda 1972, 1973, 2000; Pelivan and Lutkić 1994; Zavodnik et al. 2002, 2005; Battelli and Alberti 2003; Osterc and Stibil 2008; Jakl et al. 2008; Čelig 2010; Koletić et al. 2011; Hanžek et al. 2012; Najdek-Dragić et al. 2014; Kučinar 2014; Gljušćić 2016; Pavičić-Hamer et al. 2016; Miočić-Stosic et al. 2020; Antolić et al. 2021; Cvitković et al. 2021; Dobrinčić et al. 2021, 2022; Jerković et al. 2021; Banožić et al. 2022; Gljušćić et al. 2023; Cikoš et al. 2023), often only with the names of nearby towns.

Most historical records focus on the Istrian peninsula (northern Adriatic) (Fig. 2c). From the 19$^{th}$ to the beginning of the twentieth century, *F. virsoides* was abundant and widespread in this region (Linardić 1949; Munda 2000; Battelli and Alberti 2003) with records in Umag, Novigrad, Poreč, Pula, Medulin, and numerous records around Rovinj. Subsequently, populations were found around Novigrad, Červar, Poreč, Funtana, Vrsar, Medulin, and Trget (Čelig 2010; Kučinar 2014; Gljušćić 2016; Gljušćić et al. 2023). In the last three decades, the decline of *F. virsoides* has been noted along the Istrian coast and the first regressions were reported by Zavodnik (1967a) and Munda (1972, 1973, 1980). Gljušćić et al. (2023) comprehensively mapped the Istrian coast and found further declines through comparisons with historical data. They documented a local extinction in southern Istria (Figs. S2e,f), characterised by the disappearance of continuous belts in the Medulin area, followed by a disappearance in the Rovinj area in 2016, while at the same time previously unrecorded populations were recorded in the Poreč area. In the period 2021–2023, there were still some small remnant settlements from Červar to Vrsar, and one settlement was located in Lanterna, and in Uvala Blaž (Raša Bay, near Trget) (Gljušćić et al. 2023). Of these, only the settlements in Lanterna, Bijela uvala (Funtana) and Uvala Blaž (Raša Bay) are currently preserved, as a result of further degradation as well as stochastic events (grazing, weather events, damage caused by coastal wreckage and moving substrate).

Outside the Istrian peninsula (Figs. 2d, e), only a limited number of localised and sporadic observations have been made along the entire mainland and islands coast. In addition, most historical sites were surveyed only once, making it impossible to determine the long-term distribution patterns. During this study, isolated patches were observed on Pag Island, Ražanac, Rab and in Barić Draga, populations already listed by Linardić (1949). Previously unrecorded isolated populations were found in Mali Ston Bay (Miočić-Stosic et al. 2020), Lastovo Island (Jakl et al. 2008), Vrsi and Šibenik. Moderately abundant patches in the Posedarje area (Novigrad Sea), first documented in 2011 (Hanžek et al. 2012), have persisted and have been extensively sampled for scientific experiments (Cvitković et al. 2021; Dobrinčić et al. 2021, 2022; Jerković et al. 2021; Banožić et al. 2022; Cikoš et al. 2023). The most extensively documented disappearance took place in the Zadar region, where a population observed in 2011 (Hanžek et al. 2012) disappeared by 2023, as well as populations recorded by Linardić (1949) on the nearby islands Ugljan and Dugi Otok. Moreover, in the Kvarner region, more specifically in Omišalj (Krk) and Stara Voda (Rijeka), the populations observed until 2021 were also no longer present by 2023. *F. virsoides* recorded by Linardić (1949) in Starigrad (the Hvar Island) seems also to disappear by 2011 (Koletić et al. 2011).

**Montenegro** The first record of *F. virsoides* in the Boka Kotorska Bay (southern Adriatic) in Montenegro dates back to 1949 (Linardić 1949). Later, Solazzi (1971) identified two localities in the Kotor Bay (Radimiri and Institute of Marine Biology), both of which had disappeared by 2003 (Mačić 2006). Between 2003 and 2004, Mačić (2006) investigated the distribution of *F. virsoides* and recorded a further 16 sites, 2 of which had disappeared by 2005 (Krašići, in the Tivat Bay and Gospa od Andela, in Kotor Bay). Most of the recorded sites were located in Risan Bay, while other populations were observed in the Verige strait, Krašiči (Tivat Bay) and Male Rose (Herceg Novi Bay). During this study, *F. virsoides* was not found at most of the historical locations. Only remnant populations were found in the shallow waters of the narrow Verige Strait (Opatovo, Lepetane, Andrići, Turski Rt), characterized by low temperature and salinity due to freshwater input, rocky substrate, and sheltered habitat (Fig. 2f). The observed decline was attributed to habitat destruction, eutrophication, and cumulative concurrent abiotic changes.

**Albania** In Albania, historical and current records were extremely rare. Kashta (1987, 1992) documented the occurrence of *F. virsoides* in Albania and identified Treport Cape in the Bay of Vlora as the southern limit of its distribution range. However, after 1994, Kashta (1995–1996) reported its disappearance from the Bay of Vlora, which was confirmed by Blanfuné et al. (2016) in 2003. Recently, as part of a Marine Protected Area Gap Analysis (UNEP/MAP-SPA/RAC-PAP/RAC et al. 2021), the presence or absence of *F. virsoides* was recorded along the Albanian coast and 3 populations of *F. virsoides* were observed from the Patoku Lagoon to Spille, which may now represent the new southernmost limit of its distribution range (Fig. 2g). According to the Albanian Red List (Decision of the Council of Ministers 2013), the status of *F. virsoides* along the Albanian coast is critically endangered

## Long-term environmental data collection and analysis

From 1990 to 2021, the SST along the Adriatic coasts, from the Venice Lagoon to the Bay of Vlora (southern Albania),

showed a significant increase (the slope of the linear trend $m = 0.011$ °C $a^{-1}$; $p < 0.05$) (Fig. S3). The strongest increase was observed in winter ($m = 0.042$ °C $a^{-1}$; $p < 0.05$) (Fig. S4). In addition to the documented temperature gradient from north to south, the warming also showed a gradient in intensity. The southern sub-basin showed a stronger warming ($m = 0.018$ °C $a^{-1}$; $p < 0.05$), as did the central sub-basin ($m = 0.017$ °C $a^{-1}$; $p < 0.05$). In contrast, for the northern sub-basin, the warming linear trend is not significant if computed over this period ($m = 0.002$ °C $a^{-1}$; $p > 0.05$) (Fig. S3).

Mean annual surface salinity increased ($m = 0.012$ psu $a^{-1}$; $p < 0.05$) (Fig. S5), and this increase was constant across seasons (± 0.001 SD) (Fig. S6). In addition to the documented salinity gradient from north to south, a slight gradient of salinity increase in the opposite direction was observed, with a faster increase in the northern ($m = 0.014$ psu $a^{-1}$; $p < 0.05$) than in the central ($m = 0.011$ psu $a^{-1}$; $p < 0.05$) and southern ($m = 0.009$ psu $a^{-1}$; $p < 0.05$) sub-basins (Fig. S5).

From 1993 to 2017, a general increase in the average annual DIN concentration was observed along the Adriatic coast ($m = 1.94E\text{-}04$ µM $a^{-1}$; $p < 0.05$). Specifically, an increase was recorded from 1993 to 2003, followed by a subsequent decrease until 2017, the last year available in the EMODnet dataset (Fig. S7, S8). This trend is similar in all seasons and sub-basins. However, concentrations were highest in winter and lowest in summer, and both the northern and southern sub-basins had higher concentrations than the central sub-basin (Fig. S9).

The average annual DIP concentration showed a slight increase along the Adriatic coast ($m = 2.39E\text{-}6$ µM $a^{-1}$; $p < 0.05$) (Figs. S7, S10). All seasons showed similar concentration ranges, but significant increases were observed in winter, summer and autumn, but not in spring (Fig. S11). Furthermore, only the southern sub-basin showed a significant increase ($m = 1.24E\text{-}5$ µM $a^{-1}$; $p < 0.05$) (Fig. S10).

In the northern sub-basin, we observed significant differences in nutrient concentrations between the west coast (from the Venice Lagoon to Grado) and the east coast (from Grado to Šibenik) (Fig. 12). On the west coast, the trend in DIN and DIP concentrations was similar to that on the Adriatic coast from northern Italy to southern Albania (Figs. S8, S10), albeit with higher concentrations. On the east coast, however, the DIN concentration increased as on the Adriatic coast, while the DIP concentration decreased ($m = -2.49E\text{-}6$ µM $a^{-1}$; $p < 0.05$). In particular, a significant decrease was recorded in the Gulf of Trieste ($m = -8.89E\text{-}6$ µM $a^{-1}$; $p < 0.05$), which decreased from 0.09 ± 0.01 µM in 1993 to 0.025 ± 0.005 µM in 2017, accompanied by a decrease in DIN concentration ($m = -8.27E\text{-}5$ µM $a^{-1}$; $p < 0.05$) (Fig. 12). This decrease led to an increase in the N:P ratio from 40 in 1993 to 102 in 2017 in the Gulf of Trieste, compared to the Adriatic coasts, where the N:P ratio changed from 16 to 41 (Fig. S7).

## Discussion

The present study provides the first comprehensive distribution of *F. virsoides* in its range, the Adriatic Sea. The investigation of historical data allowed the reconstruction of long-term changes showing a strong decline to about 20 remaining populations. As *F. virsoides* no longer forms contiguous belts, it can be considered functionally extinct in Istria (Croatia). In Italy and Montenegro, it is threatened with extinction. In Albania, it was classified as critically endangered in 2013, while it is already extinct in Slovenia. The current status of *F. virsoides* in the remaining regions of Croatia (Kvarner and Dalmatia) is still elusive. Population assessments have primarily relied on the CARLIT method (Ballesteros et al. 2007). However, a significant proportion of these regions, around 65%, have not been studied recently, resulting in a lack of data. Although the identification of some recent, small populations in Croatia is noteworthy, this does not indicate an expansion of the range, but rather highlights gaps in the historical data.

While declines of *F. virsoides* have been documented in certain regions since 1970 (Zavodnik 1967a; Munda 1972, 1973, 1980; Orlando-Bonaca et al. 2013; Battelli 2016a; Rindi et al. 2019, 2020; Gljušćić et al. 2023), recognisable regime shifts were observed especially between 2010 and 2016 (Falace et al. 2010; Battelli 2016a; Gljušćić et al. 2023). Located in the coldest regions of the Mediterranean, the Adriatic has historically served as a refuge for *F. virsoides*. However, a variety of anthropogenic stressors (e.g. habitat destruction, pollution, overgrazing) exacerbated by climate change, have significantly reduced the species' range.

The extant populations primarily inhabit regions bordering freshwater inputs, characterized by lower temperatures and salinity (e.g. Marina Julia, the surroundings of Novigrad and Poreč, Funtana, Trget, Barić Draga, the Novigrad Sea, Vrsi, Šibenik, Mali Ston Bay). They also thrive in lagoons, such as the Venice Lagoon, and in enclosed seas and bays with freshwater inflow (e.g. Novigrad Sea, Mali Ston Bay and Boka Kotorska Bay). Both temperature and salinity have been identified as critical factors for the occurrence of *Fucus* (e.g. Vouk 1938; Linardić 1949; Giaccone and Pignatti 1967; Munda 1972; Mačić 2006). Linardić (1949) defines *F. virsoides* as a micro-euryhaline and micro-eurythermal species whose optimum skewed towards the minimum values.

Over the last three decades, both sea surface temperature and salinity along the Adriatic have experienced an upward trend. While *Fucus* species are known for their resilience to

extreme thermal conditions, making them relatively robust compared to other infralittoral macrophytes (e.g. Saha et al. 2020), the rise in winter temperatures, a critical period for the vegetative and generative development of *F. virsoides* (Linardić, 1949), may significantly affect its physiological functioning and overall survival. The increased salinity, particularly noticeable in the northern sub-basin, is attributed to the reduced outflow from the northern tributaries and the Po River (Tsimplis et al. 2008; Cozzi and Giani 2011), which not only affects the nutrient balance but also influences the structure and dynamics of the marine ecosystem (Cozzi and Giani 2011). Orlando-Bonaca et al. (2013) suggested that the proximity of *F. virsoides* to freshwater inflows could also be the result of limited grazing pressure, particularly by limpets (Arrontes et al. 2004).

Nitrogen (N) and phosphorus (P) are essential for the growth of macroalgae (Harrison and Hurd 2001). Despite the increase in DIN values in all sub-basins, a significant increase in DIP values can only be observed in the southern sub-basin. Overall, DIP concentrations in the northern and central sub-basins exhibit a lower trend than in their southern counterparts. This pattern is influenced by Italian legislation to control nutrient pollution, with a focus on phosphorus regulation (Marchetti et al. 1989; Palmeri et al. 2005). On the Adriatic coasts, N enrichment resulted in a rise in the N:P ratio from 30:1 to 41:1, exceeding the critical threshold of 30:1 indicating phosphorus limitation (Atkinson and Smith 1983). Notably, in the Gulf of Trieste, the N:P ratio increased from 31:1 to 102:1. Interestingly, nutrient stresses do not appear to affect the functional traits of *F. virsoides* (author's unpublished data), but these nutrients could play a positive role during stressful events and possibly mitigate the associated detrimental effects, as indicated by Gerdol et al. (2020).

During this study, we observed dense recruits on previously bare artificial substrates in Marina Julia (Monfalcone Bay) (Figs. S2g, S2h), underscoring the high recovery potential of *F. virsoides*, as documented in prior studies (Hanel 2002; Zavodnik et al. 2002; Iveša and Djakovac 2015). The same was recently observed in Bijela Uvala (Funtana-Poreč), where the population experienced a sharp decline by the dumping of allochthonous pebbles from the artificial beaches. Indeed, the genus *Fucus* exhibits remarkable expansion potential (Williams and Smith 2007) with high phenotypic plasticity and rapid ecotypic selection (Wahl et al. 2011). By adapting to dynamic and unstable intertidal environments coupled with life history traits such as an effective reproductive capability and rapid growth, *F. virsoides* exhibits characteristics akin to an *r-strategist* (MacArthur and Wilson 2001). The species expends considerable energy on reproduction and contributes to increased fitness through high fecundity (production of numerous zygotes), a short generation time and hermaphroditism. Following Grime's CSR strategies in plant ecology (Grime 1974, 1977, 2001), *F. virsoides* could be classified as a ruderal strategist (R). This categorization is justified by its reproductive investment, which allows recovery following disturbance. However, the strong anthropogenic pressure at the land-sea interface leads to changes in the coastline and irreversible habitat destruction.

As a glacial relict endemic to the Adriatic (Munda 1972), *F. virsoides* possesses a unique genetic heritage and evolutionary history trajectory. However, the identification of only a few fragmented populations suggests a scenario of limited genetic connectivity, possibly leading to inbreeding and reduced genetic diversity and adaptability to changing environmental conditions, thus increasing the risk of extinction.

In the broader context of biodiversity conservation, this study serves as a comprehensive assessment of the overall status of *F. virsoides*. This taxon is highly threatened with extinction in the wild due to declining population sizes and fragmented habitats, but has not yet been assessed ("*Not Evaluated*") by the International Union for Conservation of Nature (IUCN). However, based on the categories and criteria of the IUCN Red List (IUCN 2024), we strongly advocate classifying *F. virsoides* as "*Critically Endangered*" due to the existing high risk of extinction. This classification emphasizes the urgent need for immediate conservation initiatives and effective management measures to ensure the long-term survival and resilience of the species.

The long-term environmental data analysis presented here reveals significant spatio-temporal changes that suggest possible correlations with the decline of *F. virsoides*. However, it must be recognized that while this analysis provides compelling insights, it's not sufficient to conclusively demonstrate causality. Further research on the influence of single and multiple stressors and their complex interactions on the ecophysiology of *F. virsoides* is crucial to gain a deeper understanding of the factors driving its loss, and then develop effective nature-based solutions in time to prevent its extinction.

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