

Research Article

Invasion of alien macroalgae in the Venice Lagoon, a pest or a resource?Adriano Sfriso^{1,*}, Alessandro Buosi¹, Marion Adelheid Wolf¹ and Andrea Augusto Sfriso²¹Department of Environmental Sciences, Informatics & Statistics, University Ca' Foscari, via Torino 155, 30172 Mestre (Venice), Italy²Department of Chemical and Pharmaceutical Sciences, University of Ferrara, via Borsari 46, 44121 Ferrara, ItalyAuthor e-mails: sfrisoa@unive.it (AS), alessandro.buosi@unive.it (AB), marion.wolf@unive.it (MAW), asfriso@hotmail.it (AAS)

*Corresponding author

Citation: Sfriso A, Buosi A, Wolf MA, Sfriso AA (2020) Invasion of alien macroalgae in the Venice Lagoon, a pest or a resource? *Aquatic Invasions* 15(2): 245–270, <https://doi.org/10.3391/ai.2020.15.2.03>

Received: 19 January 2019**Accepted:** 21 October 2019**Published:** 5 December 2019**Handling editor:** Carla Lambertini**Thematic editor:** Charles Martin**Copyright:** © Sfriso et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS

Abstract

Alien macroalgae, mostly invasive species, are a constant concern for coastal areas, especially in the northern Adriatic Sea where several taxa have colonized the main transitional environments. A revision of the alien macroalgae in the Venice Lagoon shows that, currently, the number of valid non-indigenous species (NIS) is 29, and this number is growing steadily. On the basis of numerous surveys carried out in the last decade the total alien standing crop (SC) was estimated to be ca. 146,534 tonnes fresh weight (fw), i.e. 32% of the total species SC (ca. 456,000 tonnes fw) measured in May–June 2014 in the whole lagoon. The most abundant species were the invasive *Agarophyton vermiculophyllum* (approx. 66,383 tonnes fw), *Agardhiella subulata* and *Hypnea cervicornis* (approx. 36,714 and 28,305 tonnes fw, respectively). These species grow mainly free-floating and usually colonize the soft substrata of the lagoon. Two other invasive species, *Sargassum muticum* and *Undaria pinnatifida*, grow mainly on the docks of Venice historical centre, therefore their distribution is significantly more limited. Recent studies have shown that *A. vermiculophyllum* in protected, eutrophic areas produced a biomass of approx. 24 kg fw m⁻² y⁻¹. This species can replace Ulvaceae with positive effects on the environment and the presence of macrofaunal taxa. Indeed, historical data analysis shows that, despite the high presence of NIS, biodiversity is increasing. In addition, *A. vermiculophyllum*, *S. muticum*, *U. pinnatifida*, *A. subulata* and *Solieria filiformis* may be promising species for phycocolloid and antioxidant or cosmetic productions.

Key words: non-indigenous species, invasive macroalgae, standing crop, transitional environments, *Agarophyton vermiculophyllum*

Introduction

Over the last 2–3 decades, the Mediterranean Sea has experienced an increasing introduction of non-indigenous species (NIS) (Zenetos et al. 2010, 2012; Petrocelli et al. 2013; Verlaque et al. 2015). In the presence of suitable ecological conditions some NIS can colonise a new environment and often naturalize (Richardson et al. 2000). Heenan et al. (1998) define “naturalized species” those that “form a wild population self-maintained by seed or vegetative reproduction or occur repeatedly in the wild”. Clement and Foster (1994) consider naturalized “the species able to be established extensively amongst native vegetation so as to appear native”. However, their presence can be limited to a few individuals or extended populations

that colonize only one area or most areas. In many cases, when they spread in more than 10 areas in the world they are considered “invasive” (Galil et al. 2014).

Depending on their abundance or trophic level, the NIS affect the autochthonous populations both directly and indirectly. Frequently, they occupy the ecological niche of native species that regress or are completely replaced. In some cases, they prey or feed on eggs and larval stages of other species as in the case of the bluefish *Pomatomus saltatrix* Linnaeus and the sea nut *Mnemiopsis leidyi* A. Agassiz. Sometimes their impact on other species or the environment is indirect as when are harvested for economic reasons. Manila clam *Ruditapes philippinarum* (Adams and Reeve) is a perfect example of indirect impact since it is an edible species of high economical value. The harvest of this species destroys the seabed, resuspends high amounts of sediments, nutrients and pollutants (Sfriso et al. 2003, 2005; Dalla Valle et al. 2003) and affects the macrofauna (Pranovi and Giovanardi 1994). As a consequence the fishing economy of the lagoons of the northern Adriatic Sea has taken advantage of this important resource, but the environmental costs are incalculable (Orel et al. 2000). However, the effects of the introduction of alien species must not be generalized. Often new introductions remain localized in small areas or integrate with native species without significant effects on biodiversity or the environment. Some species may even be of commercial interest, but it is important to know how to exploit them without damaging the environment.

Environments particularly affected by the invasion of macroalgal NIS include the transitional water systems (TWS) in the well-studied areas of the lagoon of Thau in France (Verlaque 2001; Boudouresque et al. 2011), the lagoon of Venice, the lagoons and ponds of the Po Delta and the Mar Piccolo of Taranto in Italy (Sfriso and Marchini 2014; Marchini et al. 2015; Petrocelli et al. 2013). These basins are affected by extensive anthropogenic impacts associated with the most important pathways of introduction: shellfish farming, shipping, live seafood trade and recreational boating (Occhipinti-Ambrogi et al. 2011; Petrocelli et al. 2013). The number of NIS is continuously changing, because of the constant report of new species. The update and validation of NIS records is therefore crucial to provide reliable check-lists of these species, as required by the European Community (2008).

Among NIS, macrophytes are one of the most relevant taxa, especially in commercial or tourist ports and in TWS characterized by intense aquaculture and the presence of large fish markets.

Thirty-two non-indigenous macroalgae were reported from the Italian coasts until 2009 (Occhipinti-Ambrogi et al. 2011). In 2012 the “Allochthonous Species Group” (GSA) of the Italian Society of Marine Biology (SIBM) produced a new list, containing 35 taxa: 26 Rhodophyta, 5 Ochrophyta, 3 Chlorophyta and 1 seagrass (GSA-SIBM 2012). That list included 7 species

considered invasive: *Caulerpa taxifolia* (Vahl) C. Agardh, *Caulerpa cylindracea* Sonder, *Asparagopsis armata* Harvey J.N. Norris et Fredericq, *Codium fragile* subsp. *fragile* (Suringar) Hariot, *Agarophyton vermiculophyllum* (Ohmi) Gurgel, *Sargassum muticum* (Yendo) Fensholt and *Undaria pinnatifida* (Harvey) Suringar (Zenetos et al. 2010). *Caulerpa taxifolia* and *C. cylindracea* are known to impact the environment severely. The first one is a toxic alga that significantly reduces the biodiversity of the environments it colonizes. The second one creates a dense network of stolons that hinders the presence of other species. *Codium fragile* subsp. *fragile* is scarce in the Italian coasts and does not affect the other species. Finally, *A. armata* (Kraan and Barrington 2005), *A. vermiculophyllum* (Sousa et al. 2010), *S. muticum* (Milledge and Nielsen 2016) and *U. pinnatifida* (Yamanaka and Akiyama 1993) are species that are farmed and can have interesting cosmetic, pharmaceutical, human and animal food uses and different environmental impacts.

Among the invasive species, the last 4 taxa (*C. fragile* subsp. *fragile*, *A. vermiculophyllum*, *S. muticum* and *U. pinnatifida*) are present in the Venice Lagoon, the Italian hotspot of allochthonous species introduction (Sfriso and Marchini 2014; Marchini et al. 2015). The first NIS recorded for Venice was *Codium fragile* subsp. *fragile* in 1978 (Sfriso 1987). This macroalga was first recorded in the Etang de Thau, France, by Mars (1966). In Venice it colonizes the artificial breakwaters of the lagoon inlets, the areas near the lagoon mouths and all sites characterized by high water renewal whereas inside the lagoon it is uncommon. *Sargassum muticum* and *Undaria pinnatifida*, which were recorded, for the first time, in the Etang de Thau in 1971 (Anonymous 1980) and 1980 (Pérez et al. 1984), respectively, were found in Venice in 1992 by Gargiulo et al. (1992) and by Rismondo et al. (1993). Both species grow attached to hard substrata during the cold season and can reach a biomass up to 10–15 kg fw m⁻² (Sfriso and Facca 2013). Their presence is restricted to a few areas, particularly the historic centers of Venice and Chioggia, and are of local concern because of the size they reach (on average 3–5 m). *Agarophyton vermiculophyllum* was first recorded in the Mediterranean Sea in the lagoons of the Po Delta and in the Venice Lagoon in 2008 as *Gracilaria vermiculophylla* (Sfriso et al. 2010). It was found growing attached to stones or mollusc shells, especially oyster shells, in the soft substrata of the lagoons and, also, free-floating in the water column. After few years it had become the most abundant NIS although it had colonized only protected and eutrophic areas (Sfriso et al. 2010, 2012). Other NIS which were recorded in the Venice Lagoon and have spread throughout the basin are *Agardhiella subulata* (C. Agardh) Kraft et Wynne (Curiel et al. 2005) and *Hypnea cervicornis* J. Agardh, reported as *H. flexicalulis* Y. Yamagishi and M. Masuda by Wolf et al. (2011). Both species were observed growing prevalently free-floating in the water column such as *A. vermiculophyllum* but their spread was limited and

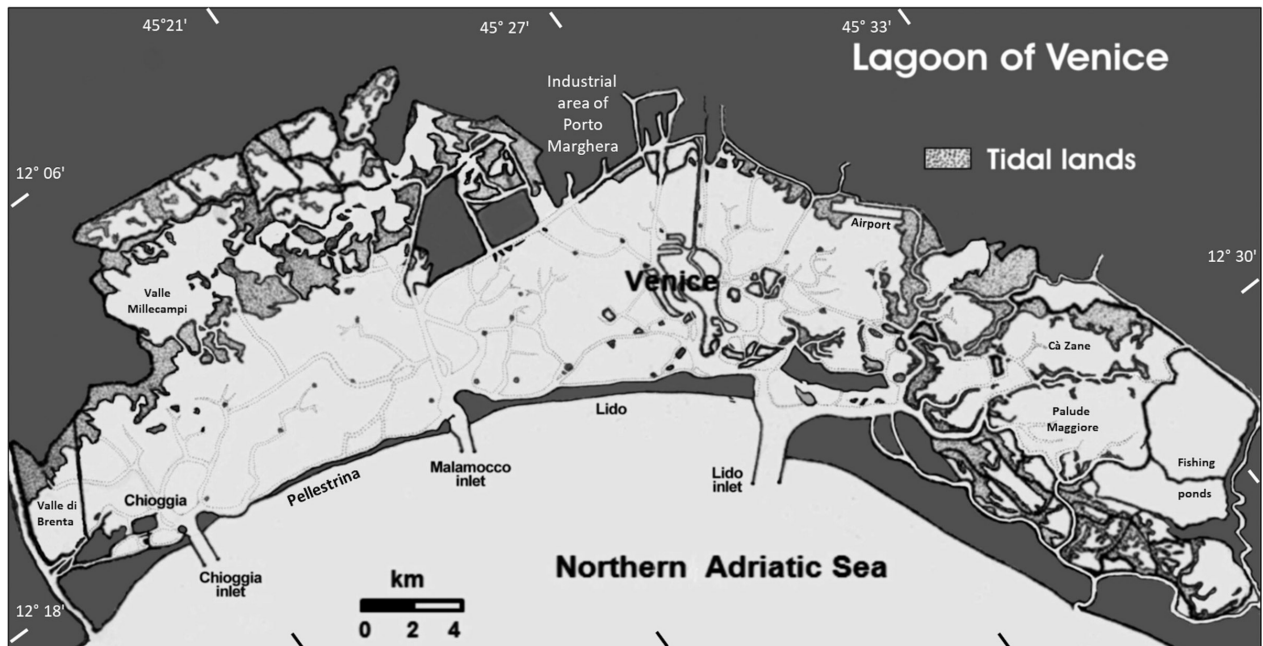


Figure 1. Map of the Venice Lagoon. Sampling was carried out in 118 (2011) and 88 (2014) soft bottom sampling sites spread in the whole lagoon. Other 35 sampling sites were monitored in 2015, 2016 and 2017 in the northern lagoon (Ca' Zane and Palude Maggiore). Moreover, in the same periods, dozens of samples were collected in the hard substrata of the islands and the jetties of the lagoon inlets (Chioggia, Malamocco and Lido).

often hindered by the fast growth of Ulvaceae or Gracilariaceae. Finally, many other species have a limited spread or biomass depending on their presence and size.

This paper aims to report the distribution and total standing crop (SC) of the NIS that have colonized the Venice Lagoon. The main causes of success of the most abundant species and their impact on the environment have been analysed. Particular attention has been given to the invasive species *A. vermiculophyllum*, which showed the largest expansion and the most interesting results both for the environment, preventing anoxic crises, and its abundance and commercial interest.

Materials and methods

Macrophytes were collected in the framework of some programmes carried out to assess the ecological status of the lagoon by applying the Macrophytes Quality Index (MaQI, Sfriso et al. 2014), according to the requirements of the European Water Directive 2000/60/EC.

The distribution and SC of the most common taxa in the Venice Lagoon (Figure 1) were determined by analyzing the NIS records during some surveys carried out in the soft substrata of the whole lagoon in summer and autumn 2011 (118 sites) and 2014 (88 sites). Additional data refer to the sampling of 35 sites in the North lagoon between 2015 and 2017 during the implementation of the project Life12 NAT/IT/000331 (2012) SeResto (Habitat 1150* (Coastal lagoon) recovery by SEagrass RESTORation, a new strategic approach to meet Habitat Directive (92/43/CEE) and Water Framework

Directive (2000/60/EC) objectives coordinated by our research team (www.lifenseresto.eu).

At each site, macrophyte samples were collected by scraping the bottom in a ray of 15–20 m for approx. 1m with a rake of 30 cm. The number of sub-samples depended on the variability of the macroalgae recorded in order to obtain the maximum number of species but it was never less than 6. In soft bottoms, this sampling method allowed to collect almost all the species present in the site. A comparison with the number of species collected by SCUBA divers in the same sites did not show significant differences (Sample number = 30, $p = 0.68$, $F = 0.170$, Statistica 10, StatSoft, Tulsa, USA). The dominant taxa were weighed with an electronic balance (precision ± 1 g) after a short centrifugation with a kitchen centrifuge to remove excess water. All visibly different species were fixed with a 4% formaldehyde solution and identified in laboratory with a stereoscope and a light microscope.

Specimens of dubious identification were silica gel-dried and analysed through the DNA barcoding method using different molecular markers. The plastid large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (*rbcL*) was chosen for Rhodophyta since it is one of the most commonly used markers in the analysis of these algae (Freshwater et al. 1994) whereas for Chlorophyta, the selected gene was the plastid elongation factor *tufA* according to Saunders and Kucera (2010). DNA extraction, amplification and sequencing of the chosen marker were accomplished as described in Cecere et al. (2011) and in Wolf et al. (2011, 2012, 2014, 2018). In detail, genomic DNA was extracted by using the Genomic DNA purification kit (Thermo Scientific™) for Rhodophyta samples or following the procedures outlined in Saunders and Kucera (2010) for Chlorophyta. The *rbcL* gene was amplified using the primer combination F57-R753, F577-R1381 and F577-RrbcSstart, as described by Freshwater and Rueness (1994) and the primers *tufGF4* (Saunders and Kucera 2010) and *tufAR* (Fama` et al. 2002) were employed to amplify the *tufA* gene. The PCR amplification profile followed Cecere et al. (2011) for the *rbcL* gene (initial denaturation of 2 min at 94 °C followed by 30 cycles of 40 s at 94 °C, 40 s at 50 °C and 40 s at 72 °C, with a final 5 min extension at 72 °C) and Saunders and Kucera (2010) for the *tufA* marker (initial denaturation of 4 min at 94 °C followed by 38 cycles of 1 min at 94 °C, 30 s at 45 °C and 1 min at 72 °C with a final 7 min extension at 72 °C). The amplification products were cleaned by enzymatic reaction. Sequencings of PCR products were performed on automated ABI DNA sequencers, with the same primer pairs used in the amplification reactions. The SeqMan II program from the Lasergene software package (DNASTar®, Madison, Wisconsin, USA) was used to assemble the final consensus sequences, which were then compared with other publicly available sequences using BLAST v.2.0 software (Altschul et al. 1990). The barcode sequences obtained during these studies were deposited in the International Nucleotide

Sequence Database (INSD) through the European Nucleotide Archive (ENA) platform. GenBank accession numbers are reported in Supplementary material (Table S1).

The mean biomass of each taxon was determined as the mean value of the biomass recorded at the different stations in 2011 and 2014. The estimation of the total SC was obtained by dividing the total lagoon water surface (432 km²) by the number of sites (i.e. 432 km²/118 sites and 432/88 sites).

The linear extension of hard substrata (island docks, lagoon inlets, breakwaters and rocky panels) was also sampled. On average their extension is approx. 100 km² and the mean width is ca. 3 m. The final estimation of the SC of each species is the sum of its distribution in soft and hard substrata.

On hard substrata sampling was carried out by SCUBA divers who collected all visibly different species or macroalgal assemblages. The use of a frame was in fact not adequate (Buosi and Sfriso 2017) because macroalgae are distributed differently on the bottom depending on the exposure (waves, air at low tide, depth, etc.), light availability and interferences of local disturbances such as currents and anthropogenic structures.

Results

The revision of the number of all the macroalgal taxa up to 2018 showed that the number of valid alien macroalgae, i.e. only species with unequivocal identity and non-indigenous status, is 29 (Sfriso et al. 2019a). Table S1 reports the morphological descriptions of the analyzed species whereas the biomass estimation is shown in Table 1.

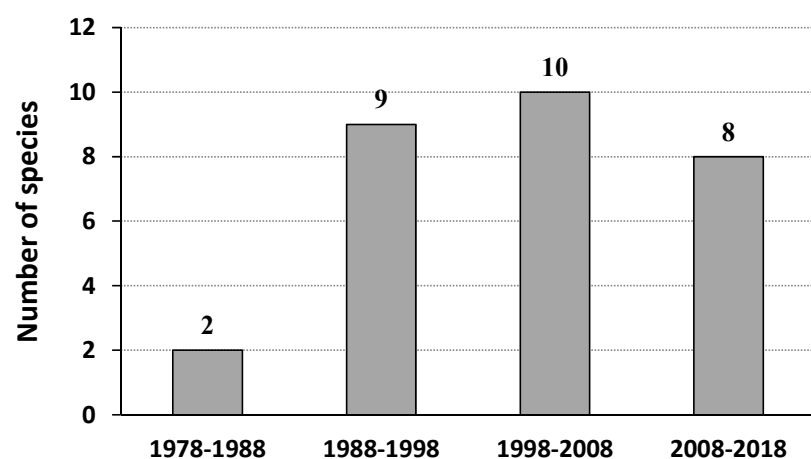
The first record was *Codium fragile* subsp. *fragile* in 1978 (Sfriso 1987), but the highest number of introductions occurred in the decades 1988–1998 and 1998–2008 (Figure 2) with 0.9 and 1.0 new introductions per year, respectively. In the decades 1988–1998 and 1998–2008 the recorded NIS were identified mainly on morphological features whereas in the decade 2008–2018 by applying the genetic-molecular analyses, a higher number of new species was discovered.

A confirmation of the progressive NIS spread in the soft bottoms of the whole lagoon can be obtained by the analysis of the species found by our research team during the campaigns carried out in 2011, 2014 (Regione Veneto et al. 2012, 2015) and 2015, 2016, 2017 in the North lagoon during the implementation of the project LIFE12/NAT/IT/000331 (2012) SeResto (www.lifeseresto.eu) (Figure 3). During the surveys in the whole lagoon, 13 NIS were recorded. On average, in 2011 they had colonized 16.5% of the 118 sampling sites and in 2014 that percentage had increased to 18% (Figure 3a).

In 2011 and 2014 the taxa recorded more frequently were *Agardhiella subulata*, which had colonized 49.7% of the sites, and the microscopic *Uronema marinum* and *Hypnea cervicornis* with 47.1% and 45.5% of the total sampling sites, respectively. The colonization of *U. marinum* in 2014

Table 1. Macroalgal NIS in Venice Lagoon and standing crop estimation.

N°	Taxon	First record	Estimated standing crop	
1	<i>Agarophyton vermiculophyllum</i> (Ohmi) Gurgel, J.N. Norris & Fredericq	2008	66383	Tonnes
2	<i>Agardhiella subulata</i> (C. Agardh) Kraft & M.J. Wynne	2003	36714	Tonnes
3	<i>Hypnea cervicornis</i> J. Agardh	2009	28305	Tonnes
4	<i>Sargassum muticum</i> (Yendo) Fensholt	1992	4825	Tonnes
5	<i>Scytosiphon dotyi</i> M. J. Wynne	1996	4775	Tonnes
6	<i>Solieria filiformis</i> (Kützing) Gabrielson	2003	3768	Tonnes
7	<i>Polysiphonia morrowii</i> Harvey	1999	517	Tonnes
8	<i>Polysiphonia schneideri</i> Stuercke & Freshwater	2017	398	Tonnes
9	<i>Ulvaria obscura</i> (Kützing) Gayral	2000	323	Tonnes
10	<i>Melanothamnus japonicus</i> (Harvey) Diaz-Tapia & Maggs	2017	272	Tonnes
11	<i>Undaria pinnatifida</i> (Harvey) Suringar	1992	143	Tonnes
12	<i>Grateloupia turuturu</i> Yamada	1989	87	Tonnes
13	<i>Uronema marinum</i> Womersley	2008	8.1	Tonnes
14	<i>Antithamnion nipponicum</i> Yamada & Inagaki	1994	3.1	Tonnes
15	<i>Codium fragile</i> subsp. <i>fragile</i> (Suringar) Hariot	1978	1.25	Tonnes
16	<i>Grateloupia yinggehaiensis</i> H.W.Wang & R.X.Luan in D.Zhao <i>et al.</i>	2008	6.6	kg
17	<i>Lomentaria hakodatensis</i> Yendo	2000	5.6	kg
18	<i>Colaconema codicola</i> (Børgesen) H.Stegenga, J.J.Bolton, & R.J.Anderson	1978	0.5	kg
19	<i>Aglaothamnion feldmanniae</i> Halos	2003	< 0.5	kg
20	<i>Botrytella parva</i> (Takamatsu) Kim	1996	+	
21	<i>Dasyisiphonia japonica</i> Yendo	1999	+	
22	<i>Pyropia yezoensis</i> (Ueda) M.S.Hwang & H.G.Choi in Sutherland <i>et al.</i>	2010	+	
23	<i>Leathesia marina</i> (Lyngbye) Decaisne	1996	+	
24	<i>Bonnemaisonia hamifera</i> Hariot	1995	+	
25	<i>Halothrix lumbricalis</i> (Kützing) Reinke	1992	+	
26	<i>Spermothamnion cymosum</i> (Harvey) De Toni	2010	+	
27	<i>Aglaothamnion halliae</i> (Collins) Aponte, D.L. Ballantine & J.N. Norris	2017	+	
28	<i>Ulva australis</i> Areschoug	2011	?	
29	<i>Ulva californica</i> Wille in F.S. Collins, Holden & Setchell	2011	?	
Total NIS standing crop			146521	Tonnes
Total macroalgal standing crop in late spring 2014			456000	Tonnes
Percentage of NIS standing crop			32	%


Figure 2. Number of macroalgal NIS introductions in the Venice Lagoon since the 1978 when the first alien species was found. Records are sorted in decades.

extended up to ca. 60.2% of the sampling sites, but its biomass was negligible. Other widespread taxa were *Solieria filiformis* (32.3%) and *Polysiphonia schneideri* Stuercke and Freshwater (17.3%) previously misidentified as *Polysiphonia denudata* (Dillwyn) Greville *ex* Harvey. The presence of other NIS was < 10% of the total sites (Figure 3b).

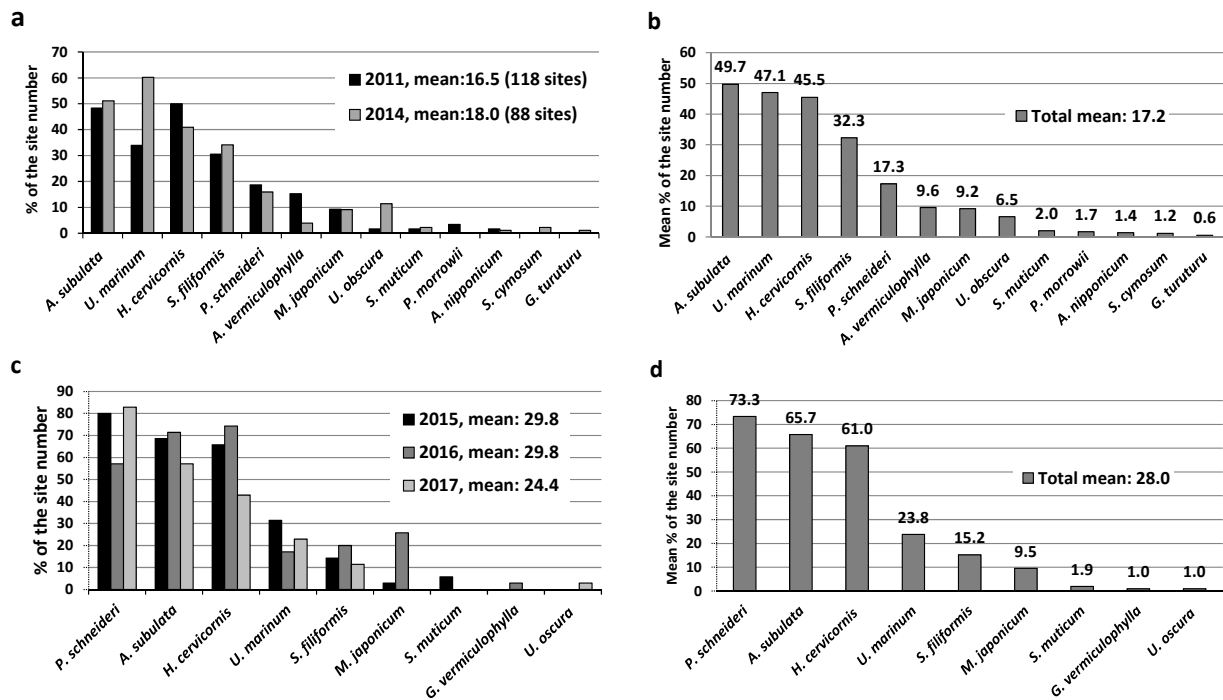


Figure 3. Percentage of sites colonized by macroalgal NIS: a, b) in the whole lagoon during the surveys of 2011 and 2014; c, d) in the northern lagoon during the surveys of 2015, 2016 and 2017.

Additional information on the colonization ability of NIS in the lagoon was provided by the monitoring of choked areas such as the northern region of the North basin (Ca' Zane and Palude Maggiore, Figure 1). There, 9 NIS were recorded with a spread ranging from 24.4 to 29.9% of the 35 sampling sites (Figure 3c), although the area is clearly separated from the rest of the lagoon by islands and tidal lands. In those areas the most widespread species were *P. schneideri* (on average 73.3%), *A. subulata* (65.7%) and *H. cervicornis* (61.0%). *Uronema maritimum* (23.8%) and *S. filiformis* (15.2%) were also common, whereas the other species were rare (Figure 3d).

The list of the 29 NIS that colonize the lagoon is ranked according to their SC. Three taxa: *P. schneideri*, *Melanothamnus japonicus* (Bailey) Díaz-Tapia and Maggs and *Aglaothamnion halliae* (Collins) Aponte, D.L. Ballantine and J.N. Norris are new records for the Mediterranean Sea (Wolf et al. 2018). The first two species: *P. schneideri* and *M. japonicus*, formerly misidentified as *P. denudata* and *M. harvey* (Bailoey) Díaz-Tapia and Maggs, have spread almost over the whole lagoon. *Aglaothamnion halliae* is rare and was recorded only occasionally in a limited area of the northern historical centre of Venice.

In the whole lagoon (water surface approx. 432 km²), the total alien SC was estimated to be ca. 146,521 tonnes fw (Table 1). *Agarophyton vermiculophyllum* accounted for 45.3% of the total alien SC (Figure 4). Five other taxa with a SC > 1% (i.e. 1465 tonnes) were: *A. subulata* (25.1%), *H. cervicornis* (19.3%), *S. muticum* (3.29%), *S. dotyi* (3.26%) and *S. filiformis* (2.57%). These 6 taxa accounted for approx. 98.8% of the total alien SC (Figure 4). Another 9 taxa displayed a remarkable SC, ranging from 1.25 to 517 tonnes fw, although

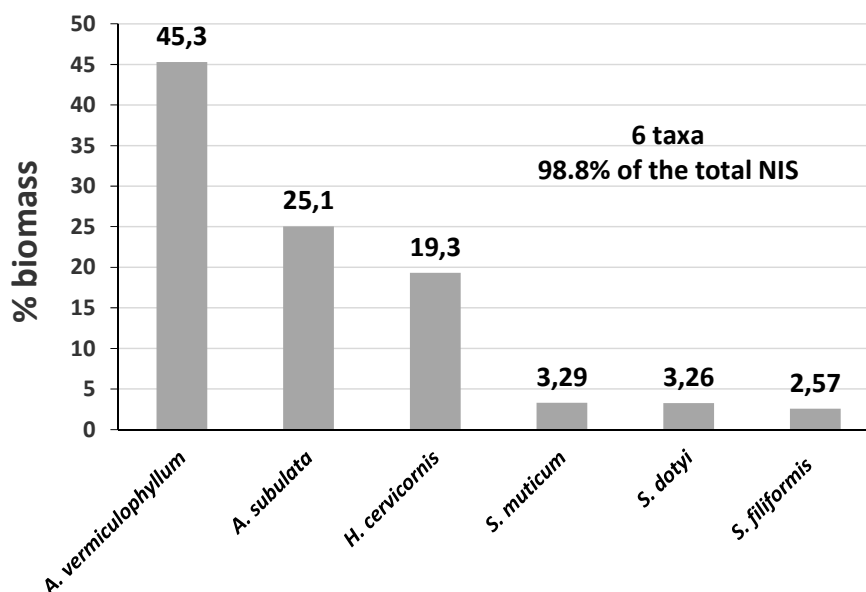


Figure 4. Percent biomass of the most abundant macroalgal NIS in the Venice Lagoon.

Table 2. Temporal trend of the number of macroalgae in the Venice Lagoon.

Taxa	Schiffner and Vatova 1938	Pignatti 1962	Sfriso 1987	Solazzi et al. 1991	Sfriso and La Rocca 2005	Sfriso and Curiel 2007	Sfriso et al. 2019a
	Number						
Chlorophyceae	38	21	38	38	62	71	84
Rhodophyceae	83	77	53	43	109	148	179
Fucophyceae	19	18	16	15	43	56	59
Xanthophyceae	1	0	1	1	1	2	1
Total	141	116	108	97	215	277	323

these values represent a low percentage when compared to the total NIS biomass. Two taxa; *Grateloupia yinggehaiensis* H.W. Wang et R.X. Luan and *Lomentaria hakodatensis* Yendo were rare species as well as *Colaconema codicola* (Børgesen) H. Stegenga, J.J. Bolton, and R.J. Anderson. Their SC ranged between 0.5 and 6.6 kg. Nine species were sampled only occasionally (SC < 0.5 kg fw or negligible). Finally, the last two taxa, *Ulva australis* Areschoug and *Ulva californica* Wille in F.S. Collins, Holden and Setchell, had a SC that cannot be easily quantified because of their difficult identification on a morphological basis.

However, despite the fact that the NIS standing crop was approx. 32% of that of the macroalgae of the entire lagoon (Table 1), macroalgal biodiversity is increasing (Table 2). Data on the number of macroalgal taxa have been available since the end of the 1930s. Schiffner and Vatova (1938) reported a macroalgal check-list that, after the nomenclature revision, accounted for 141 taxa. In subsequent years the number of taxa decreased due to eutrophication and nuisance macroalgal proliferation (Pignatti 1962; Sfriso 1987; Solazzi et al. 1991). It increased again since the end of the 1990s when the abnormal macroalgal biomass of nuisance macroalgae collapsed (Sfriso and Marcomini 1996; Sfriso and Facca 2007). Currently the number of macroalgal taxa is 323 (Sfriso et al. 2019a) (Table 2).



Figure 5. Images of the 6 most abundant macroalgal NIS recorded in the Venice Lagoon: 1) *Agarophyton vermiculophyllum* and medullar cells with the broad walls; 2) *Agardhiella subulata*; 3) *Hypnea cervicornis* and axis cross-section; 4) *Sargassum muticum* and sub-spherical pneumatocysts; 5) *Scytosiphon dotyi* and cross-section of a filament with plurilocular sporocysts; 6) *Solieria filiformis* and the stoloniferous basal region. All photos were provided courtesy of Adriano Sfriso.

The 29 macroalgal taxa and their corresponding SC are listed below. Images of all species are shown in Figures 5, 6, 7.

1. *Agarophyton vermiculophyllum* (Ohmi) Papenfuss (Figure 5.1) was one of the last introductions (Sfriso et al. 2010, as *Gracilaria vermiculophylla*) but it is also the NIS which had the highest SC (ca. 66,383 tonnes fw, Table 1), although it had colonized only the choked areas of the lagoon where water was turbid and eutrophic. The occupied lagoon area is ca. 84.7 km² (19.6% of the total lagoon water surface). In those areas it was the dominant species and in some cases it reached 8–10 kg fw m⁻² but its mean SC could be estimated in ca. 784 g fw m⁻².

2. *Agardhiella subulata* (C. Agardh) Kraft and Wynne (Figure 5.2) was first found by Curiel et al. (2003). This species had spread over a wide lagoon area showing a total SC of 36,714 tonnes fw (Table 1). Differently from *A. vermiculophyllum*, this macroalga usually grows attached to hard substrata, nevertheless it had colonized almost half of the lagoon surface (i.e. ca. 215 km²). The taxon was found mainly in turbid areas where it was often associated to *A. vermiculophyllum*. Its estimated SC was ca. 171 g fw m⁻².

3. *Hypnea cervicornis* J. Agardh (Figure 5.3) was the 3rd most abundant species. It was recorded for the first time by Wolf et al. (2011) as *Hypnea flexicaulis* Y. Yamagishi and M. Masuda. It grew prevalently free-floating with an estimated SC of ca. 28,305 tonnes fw. Its populations covered a surface of ca. 197 km² with a mean SC of ca. 144 g fw m⁻².

4. *Sargassum muticum* (Yendo) Fensholt (Figure 5.4) the 4th species in terms of SC, was found in the lagoon by Gargiulo et al. (1992). It grew over ca. 70 km of linear hard substrata around the docks of Venice, Chioggia, Pellestrina, Lido, other small islands and the breakwaters that protect the lagoon inlets. In addition, scattered thalli had colonised a surface of ca. 9.5 km² of oyster banks at west and south-west of the historical centre of Venice. Overall, the estimated SC was ca. 4,825 tonnes fw, with a mean biomass of ca. 10 kg fw m⁻² in hard substrata. It was the largest species present in the lagoon. On average, the thalli were 3–5 m long, but they could reach 8 m in deeper waters (Sfriso and Facca 2013).

5. *Scytosiphon dotyi* M.J. Wynne (Figure 5.5) was first recorded by Curiel et al. (1996). It is another very abundant Phaeophyceae with a total SC of ca. 4,775 tonnes fw. It colonized the hard substrata of islands, breakwaters and docks (ca. 100 km) with a mean SC of ca. 75 g fw m⁻², but it also colonized ca. 216 km², about half of the lagoon water surface. In this case, the biomass was much lower, ca. 21.5 g fw m⁻². This species was present only in winter and early spring.

6. *Solieria filiformis* (Kützing) P.W. Gabrielson (Figure 5.6) found by Curiel et al. (2005), covered ca. 140 km² with a mean SC of ca. 27 g fw m⁻² accounting for ca. 3,768 tonnes fw. It grew free-floating in the soft bottoms and was frequently associated with *A. vermiculophyllum* and *A. subulata*.

7. *Polysiphonia morrowii* Harvey (Figure 6.7) is a very abundant species particularly in late winter and spring. It was recorded for the first time by Curiel et al. (2001). It colonized the hard substrata of islands, breakwaters and the city docks along a linear surface of ca. 100 km² with a mean SC of 590 g fw m⁻² but it was present in other 7.3 km² of the lagoon surface where it had a mean SC of ca. 46.5 g fw m⁻². Overall, we estimated a total SC of ca. 517 tonnes fw.

8. *Polysiphonia schneideri* Stuercke and Freshwater (Figure 6.8) was recently identified through molecular analyses (Wolf et al. 2018). This species had been in the lagoon for many years but misidentified as *Polysiphonia*

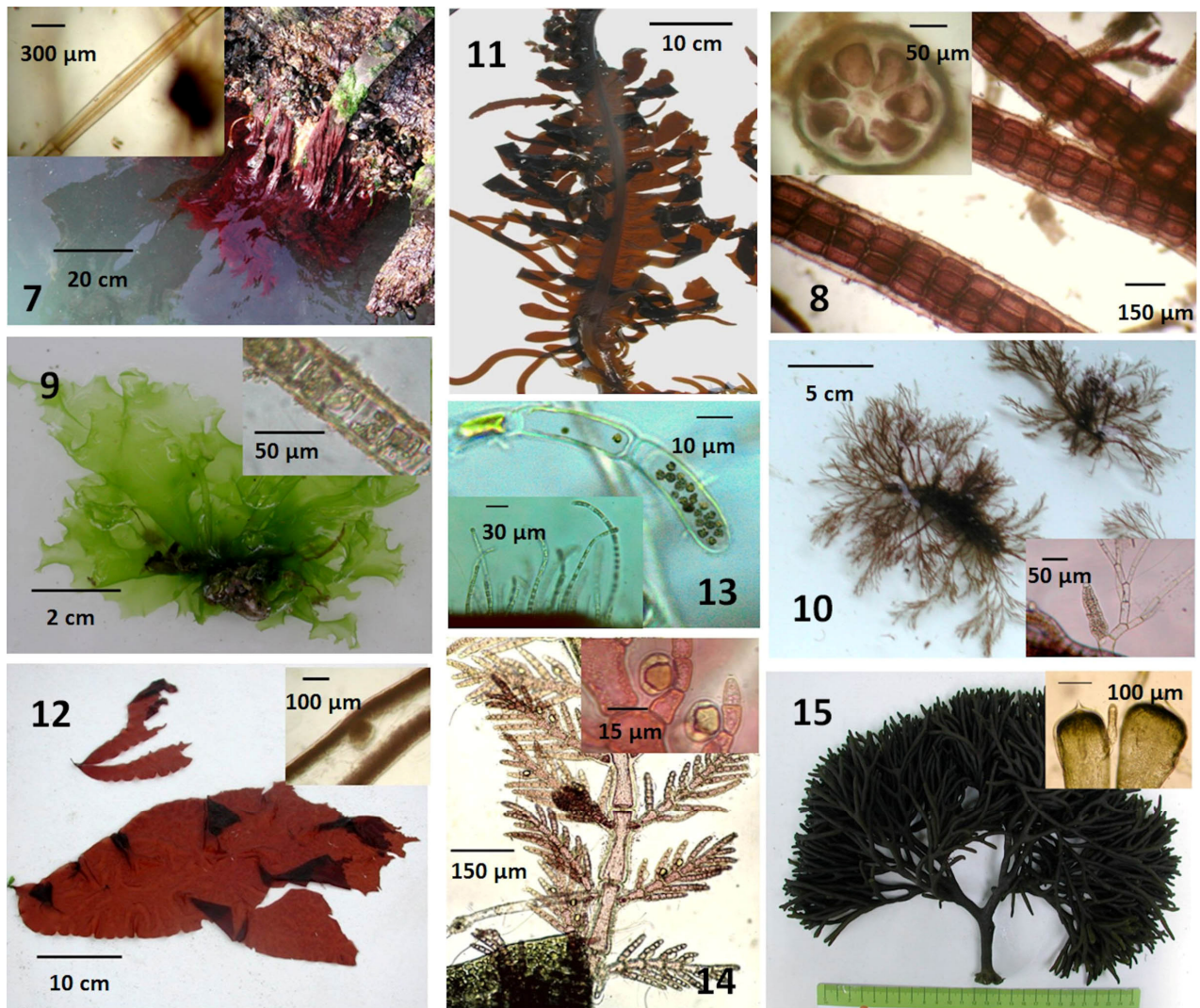


Figure 6. Images of 9 NIS with a biomass ranging from > 1 to hundreds of tonnes: 7) *Polysiphonia morrowii* and some long periaxial cells; 8) *Polysiphonia schneideri* and a cross-section highlighting the number of periaxial cells; 9) *Ulvaria obscura* with a cross-section of the blade; 10) *Melanothamnus japonicus* and a spermatangial branch formed at the first dichotomy of a modified trichoblast with 1–2 sterile apical cells; 11) *Undaria pinnatifida*; 12) *Grateloupia turuturu* with a cystocarp sunken in the medullar part of the blade; 13) *Uronema marinum* and apical cell with several zooids; 14) *Antithamnion nipponicum* highlighting globular-elliptic gland cells; 15) *Codium fragile* subsp. *fragile* with utricles characterized by conical tips. All photos were provided courtesy of Adriano Sfriso.

denudata (Dillwyn) Greville *ex* Harvey in Hooker. It was very common in the lagoon and covered ca. 77.7 km² of soft substrata with ca. 4.24 g m⁻² and 100 linear km of artificial rock substrata with ca. 230 g m⁻², for a total SC of ca. 398 tonnes fw.

9. *Ulvaria obscura* (Kützing) Gayral (Figure 6.9) was first recorded by Sfriso et al. (2002) as *Monostroma obscurum* (Kützing) J. Agardh. That species was very common and showed a highly variable SC in different years. It usually grows attached to mollusc shells, but under favourable conditions this macroalga can form free-floating biomasses, especially between the shoots of the seagrasses *Zostera marina* Linnaeus and *Cymodocea nodosa* (Ucria) Ascherson. During the samplings of 2011 and 2014, we observed that it had covered ca. 29.3 km² with a mean SC of ca. 11.0 g fw m⁻². Overall, the total estimated SC was ca. 323 tonnes fw.

10. *Melanothamnus japonicus* (Bailey) Díaz-Tapia and Maggs (Figure 6.10) is also a new record for the Mediterranean Sea (Wolf et al. 2018). It had been misidentified as *Melanothamnus harveyi* (Bailey) Díaz-Tapia and Maggs in Díaz-Tapia *et al.*, a species reported for the Venice Lagoon since 1998 as *Polysiphonia harveyi* Bailey (Bellemo et al. 1999). On the whole, *M. japonicus* covered 39.7 km² of soft substrata with ca. 5.25 g m⁻² fw and 100 linear km of artificial rock substrata with ca. 210 g m⁻², for a total SC of ca. 272 tonnes fw. The presence of the cryptic species *M. harveyi* was not confirmed for the Venice Lagoon, as reported in Wolf et al. (2018). Additional surveys are necessary to understand if both species are present before excluding *M. harveyi* definitively.

11. *Undaria pinnatifida* (Harvey) Suringar (Figure 6.11) that dates back to 1992 (Rismondo et al. 1993) displayed a SC of ca. 143 tonnes fw. It grew strongly attached by thick rhizoids (haptera) to docks and dams along the canals of the historical centre of Venice, Chioggia and Lido where hydrodynamic and nutrient availability were high. Small patches were also present on oyster banks for a total surface of ca. 1 ha around the National Electricity Authority (ENEL) pylons, in front of the Industrial areas of Porto-Marghera. This species was not present in the breakwaters of the lagoon inlets or in areas with low concentrations of nutrients.

12. *Grateloupia turuturu* Yamada et al. (Figure 6.12) was first recorded in 1989 as *Grateloupia doryphora* (Tolomio 1993). The surveys carried out in 2011 and 2014 reported that it had colonised ca. 2.6 km² of soft bottom with a mean SC of 46.5 g m⁻² fw, accounting for ca. 87 tonnes. This species formed abundant populations on the docks of the historical centre of Venice and other islands but its SC was hardly higher than 60 g fw m⁻². Overall, the total estimated SC was ca. 87 tonnes fw.

13. *Uronema marinum* Womersley (Figure 6.13) is the smallest NIS species. The first record was in 2008 in the Venice Lagoon, the lagoons of the Po Delta and in Pialassa della Baiona in the Emilia-Romagna Region (Sfriso et al. 2014). It was never recorded in other lagoons or marine coasts of the Mediterranean Sea. *Uronema marinum* was found in ca. 203 km² (47.1% of the examined stations), especially in stagnant and eutrophic areas rich in orthophosphates. In those areas it formed dense populations, that covered larger macroalgae almost completely. Scattered filaments were also present near the lagoon inlets, but they were mostly attached to floating thalli of Gracilariaceae and Solieriaceae coming from the inner areas. Due to the microscopic size of the species, an estimation of its SC was very difficult. However, we estimated a mean SC of ca. 0.04 g fw m⁻², accounting for ca. 8.1 tonnes fw.

14. *Codium fragile* subsp. *fragile* (Suringar) Hariot (Figure 6.14) was first recorded in 1978 by Sfriso (1987). It is a species considered invasive or “widespread NIS” because it had been recorded in the European Seas of 10 or more countries (Galil et al. 2014). However, the spread of this species

was not successful in the lagoon of Venice, where it colonized only the breakwaters of some islands for a total extension of ca. 4.0 km and a mean SC of ca. 62.5 g fw m⁻², accounting for ca. 1,250 kg fw.

15. *Antithamnion nipponicum* Yamada and Inagaki (Figure 6.15) recorded in 1994 by Curiel et al. (1996) was very common along the sea coastline, but it was rare in the lagoon. In fact, it was found only in ca. 6.13 km², ca. 1.42% of the entire lagoon sampled in 2011 and 2014. The species is a small epiphyte that presented a mean SC of ca. 3.07 tonnes fw.

16. *Grateloupia yinggehaiensis* H.W. Wang and R.X. Luan in D. Zhao et al. (Figure 7.16) is a thin ribbon-like macroalga that was first recorded in 2008 in the Brentella canal, which is affected by the warm water discharges from the cooling system of Fusina hydroelectric power plant (Wolf et al. 2014). This species, which had never been recorded in other Mediterranean lagoons, had colonized only ca. 200 m of the canal banks with a mean SC of ca. 33 g fw m⁻², accounting for ca. 6.6 kg fw overall.

17. *Lomentaria hakodatensis* Yendo (Figure 7.17) similarly to *G. yinggehaiensis*, is a species that was found only in a very restricted lagoon area, ca. 120 m of linear docks, at Chioggia near the wholesale fish market. Its SC was ca. 47 g fw m⁻² and accounted for a total SC of 5.6 kg fw. It was first recorded in 2000 by Curiel et al. (2006).

18. *Colaconema codicola* (Børgesen) H. Stegenga, J.J. Bolton, and R.J. Anderson (Figure 7.18) is a small species that grew as epiphyte on *C. fragile* subsp. *fragile* and therefore was found in the same lagoon areas. Its first record dates back to 1978 (Sfriso and Marchini 2014). It is a common species but its estimated SC was ca. 0.5 kg fw.

In addition to those common species, 9 rare macroalgae were recorded during our surveys:

19. *Botrytella parva* (Takamatsu) Kim (Figure 7.19) was recorded in 1996 as *Sorocarpus* sp. by Curiel et al. (1999). Later it was found many times in the North-East area of the historical centre of Venice. The gross morphology of the thalli is very similar to that of many other Ectocarpales and its identification is very difficult.

20. *Dasysiphonia japonica* (Yendo) H.-S.Kim (Figure 7.20) was first recorded in the sea coasts of Lido in 1999 by Sfriso and La Rocca (2005) as *Dasya* sp. Later, a few samples were recorded in the lagoon side of the breakwaters of Lido and Malamocco inlets, but its presence was very rare.

21. *Pyropia yezoensis* (Ueda) M.S. Hwang and H.G. Choi in Sutherland et al. (Figure 7.21) was recorded in 2010 in the historical centre of Venice (Armeli-Minicante 2013a). After this first record, *P. yezoensis* was never found again in the lagoon. This can be due to the difficulty of distinguishing this species from similar taxa such as *P. elongata* (Kylin) Neefus et J. Brodie and *Pyropia olivii* (Orfanidis, Neefus et T.L. Bray) J. Brodie et Neefus, now *Pyropia koreana* (M.S. Hwang and I.K.Lee) M.S. Hwang,

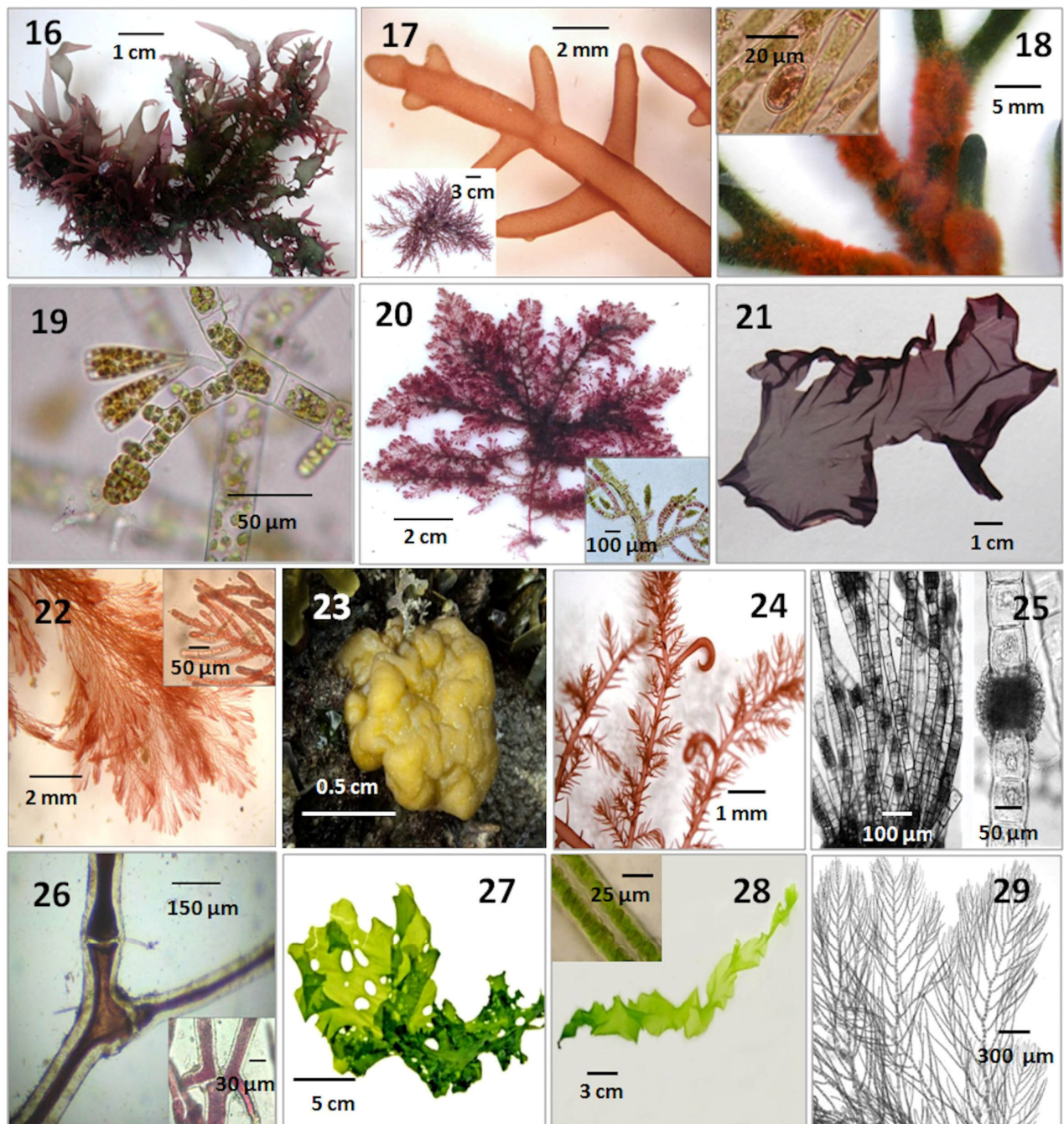


Figure 7. Images of the other 14 NIS with a negligible biomass: 16) *Grateloupia yinggehaiensis*; 17) *Lomentaria hakodatensis*; 18) *Colaconema codicola* with a typical monosporangium; 19) *Botrytella parva* with several discoidal plastids and an apical plurilocular sporangium; 20) *Dasysiphonia japonica* and tetrasporangial stichidia, born on pseudolateral branches; 21) *Pyropia yezoensis*; 22) *Aglaothamnion feldmanniae* and apical distichous-alternate branches, arranged on a plane; 23) *Leathesia marina*; 24) *Bonnemaisonia hamifera*; 25) *Halothrix lumbricalis*; 26) *Spermiothamnion cymosum*, detail of branching and rhizoids at the base of the cells; 27) *Ulva australis*; 28) *Ulva californica* and cross-section of the median region; 29) *Aglaothamnion halliae*. Photos 16, 17, 18, 19, 20, 22, 23, 24, 26, 27, 28, were provided courtesy of Adriano Sfriso. Photo 21, courtesy of Armeli-Minicante (2013a); photo 25, courtesy of Fletcher (1987); photo 29 courtesy of Wolf et al. 2018).

H.G.Choi Y.S.OH and I.K, Lee, which are very common and abundant in the lagoon.

22. *Aglaothamnion feldmanniae* Halos (Figure 7.22) was recorded for the first time in 2003 by Curiel et al. (2003). That species was reported to grow in the benthos around the city of Chioggia, but it was not present

anywhere else in the lagoon. Therefore, it must be considered very rare and with a negligible SC.

23. *Leathesia marina* (Lyngbye) Decaisne (Figure 7.23) was recorded in 1996 by Bellemo et al. (1999). This species was found rarely and its SC is not quantifiable.

24. *Bonnemaisonia hamifera* Hariot (Figure 7.24) was first recorded in 1995 by Curiel et al. (1996). Later, it was occasionally reported by the same authors, but in 40 years we have never recorded this species again during our surveys in the lagoon.

25. *Halothrix lumbricalis* (Kützing) Reinke (Figure 7.25) was reported only in 1992 by Gargiulo et al. (2000). It is a very small species with a negligible SC and after 1992 was never found again.

26. *Spermothamnion cymosum* (Harvey) De Toni (Figure 7.26) was first recorded in the Mediterranean Sea in 2010 at the Certosa island in the historical centre of Venice (Armeli-Minicante 2013b). In that place it was common, but its SC was negligible (< 0.5 kg fw).

27. *Ulva australis* Areschoug (Figure 7.27) was first recorded in 2011 by Manghisi et al. (2011) and identified through molecular analyses as *Ulva pertusa* Kjellman by Wolf et al. (2012). However, its morphology is very similar to other Ulvaceae such as *U. rigida* C. Agardh and *U. laetevirens* Areschoug, for this reason its identification is difficult and its distribution in the lagoon is unknown.

28. *Ulva californica* Wille in F.S. Collins, Holden and Setchell (Figure 7.28) is distinguishable from the widespread *U. linza* Linnaeus. *Ulva californica* was first reported for the Mediterranean Sea by Wolf et al. (2012) based on the molecular analyses of some specimens collected in the lagoon of Venice. Later, there were no other reports of this species in the lagoon and its distribution is unknown.

29. *Aglaothamnion halliae* (Collins) Aponte, D.L. Ballantine and J.N. Norris (Figure 7.29) was a small species found, for the first time in the Mediterranean Sea in 2017 near the trans-lagoon bridge that connects Venice to the mainland (Wolf et al. 2018). Its distribution seemed limited to the area of the first record and its SC was negligible.

Discussion

The Venice Lagoon hosts a higher number of NIS compared to other Italian transitional water systems. That number is very similar to the records found in the Thau Lagoon (France) (Verlaque 2001), and many new species are continuously being recorded (Marchini et al. 2015; Sfriso et al. 2019a). Across the entire lagoon, *A. vermiculophyllum* is the most abundant species, accounting for ca. 45.3% (i.e. 66,383 tonnes fw) of the total NIS SC. This percentage rises to 89.7% (i.e. 131,402 tonnes fw) when *A. subulata* and *H. cervicornis* SC are added (Table 1). All three species

grow attached to the hard substrata and detach from the bottom to colonize large areas of the lagoon by free-floating. Another three NIS, two of which grow attached to hard substrata (*Sargassum muticum* and *Scytosiphon dotyi*) and one prevalently free-floating (*Solieria filiformis*), increase the NIS SC to 98.8% of the total. All the other species are negligible even if some of them show a biomass on the order of hundreds of tonnes. Among them *Undaria pinnatifida* is particularly interesting because it is in association with *Sargassum muticum*. In late winter and spring, both species colonize the hard substrata of the historical centre of Venice and cause significant problems to navigation. However, their SC is insignificant (< 1%) when it is compared with other algae such as *Ulva rigida* and *Ulva laetevirens* that used to colonize the lagoon (Sfriso and Facca 2007). At the end of their life cycle, these macroalgae detach from the hard substrata but they are not a real inconvenience for people because their decomposition is slow. In contrast, Ulvaceae decompose very quickly and trigger extensive anoxic crises leading to the death of the benthic and fish fauna and the emission of stinking or toxic substances such as hydrogen sulphide (Sfriso 1987).

Two more new entries for the Mediterranean Sea, *Polysiphonia schneideri* and *Melanothamnus japonicus* (Wolf et al. 2018), formerly misidentified as *P. denudata* and *M. harveyi*, respectively, have a very similar morphology and showed a significant SC (398 and 272 tonnes, respectively). The presence of *M. harveyi* and *P. denudata* has not yet been confirmed, although several samples have been analyzed (Wolf et al. 2018).

The quick spread of NIS was confirmed during the surveys in the soft substrata of the whole lagoon in 2011 and 2014 and in 35 choked lagoon sites of the northern lagoon in the framework of the project Life12 NAT/IT/000331 (2012) SeResto during 2015–2017 (Bonometto et al. 2017; www.lifeseresto.eu). The highest percentage of colonization was in protected areas, between 24.4 and 29.8 % of the sampling sites, but it decreased to only 16.5–18.0% of the sites of the whole lagoon (Figure 3), even if the number of species was higher. It is interesting to note that in the protected areas of the northern lagoon the presence of *A. vermiculophyllum* was sporadic because waters were clear and oligotrophic (www.lifeseresto.eu).

Agarophyton vermiculophyllum, *Sargassum muticum*, *Undaria pinnatifida* and *Codium fragile* subsp. *fragile*, are 4 widespread NIS which Galil et al. (2014) defined “invasive” because they had been recorded in 10 or more countries. Among them, only the first three species are widespread in the lagoon and *A. vermiculophyllum* is confirmed to be the most invasive one (Figure 8). This species which was first recorded in the western part of the industrial area of Porto Marghera in May 2008, in few years had colonized a great part of the choked areas with biomasses up to 8–10 kg fw m⁻². The most probable introduction vector was the importation of oysters and clam seeds from other European countries (Marchini et al. 2015). The Venice

Lagoon is in fact characterized by extensive shellfish farming activities largely based on the aquaculture of *Ruditapes philippinarum* Adams and Reeve and *Cassostrea gigas* Thunberg. In 2011, *A. vermiculophyllum* spread also in Valle Millecampi and Valle di Brenta in the southern lagoon, and some samples were also recorded near Venice airport in the northern basin. In 2014 the species established stable populations in almost all the choked areas of the lagoon, except the northernmost sites where water is clear and oligotrophic as recorded in 2011 (Facca et al. 2014) and 2014 (Sfriso et al. 2019a). These results confirm the fast-spreading trend of *A. vermiculophyllum*, that was reported for other countries in Northern Europe where, in the early 2000s it had been introduced with the importation of oysters from Virginia (USA) (Rueness 2005; Thomsen et al. 2005, 2007). In 2014, the spread of *A. vermiculophyllum* was particularly massive in the northern side of the bridge that connects Venice to the mainland (Figure 8). There, this species almost completely replaced *U. rigida*, due to the high concentration of phycocyanin which gives it a black color (black *Gracilaria*) and allows its growth in turbid environments that are prohibitive for other species. Its rapid spread in 2014 and the following years and the replacing of *U. rigida* prevented the anoxic crisis that in 2013 affected the area by causing the decomposition of approx. 10,000 tonnes fw of biomass in a few days. The anoxic crisis causing the death of the fish and benthic macrofauna and the release of nauseating smell of sulphides occurred on the night of the Redeemer Feast that Venetians celebrate on boats, compromising the festivities (Bastianini et al. 2013). Contrary to the Ulvaceae, that rapidly collapse when water temperature exceeds 25–26 °C, *A. vermiculophyllum* survives at temperatures higher than 30 °C. Under extreme temperatures its decomposition is very slow and doesn't trigger anoxic events. Because of its resistance to high temperatures and no danger of anoxic crises in the areas it populates, *A. vermiculophyllum* is probably the first record of a NIS whose introduction showed a positive effect on the environment. Moreover, the measurements of relative growth rates (RGRs), biomass production, agar, protein and antioxidant yields of *A. vermiculophyllum* carried out in the choked areas of the lagoon showed that this species could be a very interesting commercial resource for industrial applications. The annual biomass yield ranged from 12.8 kg fw m⁻² in turbid waters to 22.0 kg fw m⁻² in clear waters (Sfriso and Sfriso 2017; Sfriso et al. 2017a). In moderately turbid waters, the production of *A. vermiculophyllum* was similar to that of *Ulva rigida*, but in very turbid areas it was the only macroalga able to grow. The potential agar yield was estimated in 0.66–1.14 kg m⁻² (Sfriso et al. 2017a) whereas the mean production of proteins was ca. 0.4 kg m⁻² (Sfriso et al. 2017b). This abundant species showed also a high concentration of antioxidants such as phycoerythrin, phycocyanin and allophycocyanin. In particular, the concentration of phycoerythrin, one of the most fluorescent compounds

used to highlight small cancer nodes at the beginning of their formation is up to $> 2 \text{ mg g}^{-1} \text{ fw}$ with a production of $17\text{--}27 \text{ g m}^{-2} \text{ y}^{-1}$ (Sfriso et al. 2018). In addition, all these compounds have effective anti-aging properties and antioxidant effects approx. 2–10 times higher than vitamin C (Sonani et al. 2014).

On the contrary, *Sargassum muticum* and *Undaria pinnatifida* have a negative impact on the environment because of the floating biomasses displaced by currents (*S. muticum*) and the long thalli (*S. muticum* and *U. pinnatifida*) attached to the docks of the historical centre of Venice and islands hinder the navigation of small boats (Sfriso and Facca 2013). However, from an economical point of view these two taxa could be a relevant resource for their alginate content. These phycocolloids, have gelling properties similar to agar-agar and are used as thickeners and stabilizers in the food, pharmaceutical and cosmetic industries. In addition, *S. muticum* is rich in phenolic compounds that have shown excellent qualities as antioxidants when extracted at temperatures below $40 \text{ }^{\circ}\text{C}$ (Le Lann et al. 2008; Sabeena Farvin and Jacobsen 2013). Phlorotannins are an important fraction of these polyphenols. Their half-life in the human body reaches 12 hrs while terrestrial polyphenols' 30–180 minutes (Namvar et al. 2013). The antioxidant effects of these compounds act in synergy with α - γ tocopherols and carotenoids (Sabeena Farvin and Jacobsen 2013). *Undaria pinnatifida* is also widely used in the eastern countries for soup preparations and contains fucosan, a pigment used in cosmetics whose action has shown effects on the suppression of weight gain and the improvement of lipid metabolism (Jeon et al. 2010). These species have also anti-inflammatory, anti-obesity, anti-cancer and UV-preventive properties (Milledge and Nielsen 2016).

High concentrations of phycocolloids are present also in the NIS *Agardhiella subulata* and *Solieria filiformis* which could be a precious source of carrageenans (Murano et al. 1997; Toffanin et al. 1997). Indeed, carrageenans are widely used as thickening, gelling and stabilizing agents in pharmaceutical, cosmetic, printing and textile compounds (Campo et al. 2009; Robledo and Freile-Pellegrin 2010).

In China, South Korea, Japan, the Philippines and Malaysia currently, ca. 1 M tonnes of algae are collected each year for the extraction of polysaccharides, with a phycocolloid production reaching 55,000 tonnes y^{-1} , which means a market value of 585 Mln US\$ (213 M US \$ from the production of alginates, 132 Mln US\$ from agar and 240 Ml US\$ from carrageenan (Hugh 2003)) and a mean income of 10,600 US\$ $\text{tonne}^{-1} \text{ y}^{-1}$. However, Europe has a significant cultural deficit in the area of algae (with the exception of Ireland and Iceland, which traditionally consume certain types of algae) and only lately Governments have begun to favour the development of this market. The Regulation EU 2015/2283 on “novel foods” and the Legislative Decree 152/2006, which integrates and updates

the previous environmental standards, have led to the transformation of the algal biomass from special waste into resource, encouraging its collection, sale and marketing. Therefore, the presence of species of high economical value, notwithstanding their status of alien species, should be reconsidered also because the species that are really dangerous for the Venice Lagoon are Ulvaceae and Cladophoraceae for the serious environmental impacts they can trigger (Sfriso 1987; Ménesguen 2018). The other NIS (Table 1) instead, due to their ecological behaviour or low SC, have a negligible impact on the ecological status of the lagoon and, in general, their presence has enriched the biodiversity of the environment. In fact, the biomass of nuisance macroalgae in 2014 was approx. 10% of that recorded in 1980 before the introduction of the first NIS (Sfriso and Facca 2007; Sfriso et al. 2019b) and the decline of Ulvaceae (Sfriso and Marcomini 1996). Moreover, the number of total macroalgal taxa in the lagoon had shown a decreasing trend in the period from 1938, when the first complete check-list was produced, until 1991 (97 taxa) when Ulvaceae proliferated (Table 2). In the following years, when the biomass decreased, the number of taxa increased remarkably (up to 323 taxa in 2018), although the NIS introduction (Sfriso et al. 2019a). In fact, many dominant NIS are seasonal or naturalized species growing along with native species. The only NIS that showed a strong spatial competition with native species was *A. vermiculophyllum* for its ability to adapt in choked, turbid and nutrient-enriched environments and replace Ulvaceae. The presence of this species doesn't trigger anoxic crises and is associated to a high benthic biodiversity: small fish such as *Aphanius fasciatus* Valenciennes a species present in the IUCN *Red List* of Threatened Species, Version 2019.2, many other commercial fish such as *Zosterisessor ophiocephalus* Pallas and *Atherina boyeri* Risso typical of TWS of the Adriatic Sea and various species of shrimps. The same high biodiversity, that in the presence of Ulvaceae was hampered by anoxic crises, was also recorded by Nyberg et al. (2009) and Ramus et al. (2017) along the coasts of northern Europe and Virginia. Nyberg and coauthors found 92 taxa associated with *A. vermiculophyllum*, especially Malacostraca, Gastropoda and Florideophyceae. The diversity of the associated taxa was not affected by *A. vermiculophyllum* biomass. In Virginia and Sweden animal abundances were positively correlated with the biomass of algae and plants associated with *A. vermiculophyllum*. Moreover, Ramus et al. (2017) found that in the absence of native habitat formers, such as naked sediment or the areas colonised by Ulvaceae in the Italian TWS, those NIS had an overall positive, density-dependent impact across a diverse set of ecosystem processes (e.g., abundance and richness of nursery areas). Their work supports the idea that where native foundation species are lost, invasive habitat formers may be considered a source of valuable ecosystem functions.

Conclusions

This paper gives an overview of alien species that have invaded the Venice Lagoon since the 1978. The list has been updated with the most recent nomenclature (Guiry and Guiry 2019) and the record of three new species: *Polysiphonia schneideri*, *Malanothamnus japonicus* and *Aglaothamnion halliae* which had never been reported before in the Mediterranean Sea. *P. schneideri* and *M. japonicus* were present in the lagoon, but they had been misidentified as other morphologically similar species (*P. denudata* and *M. harvey*, respectively). The presence of these cryptic species is now confirmed, not only in Venice Lagoon but also in the Mediterranean Sea. Moreover, an estimate of the SC of the NIS which colonise the lagoon has been carried out for the first time after extensive monitoring surveys in the soft and hard bottoms of this basin. Among the 29 NIS present in the lagoon three: *A. vermiculophyllum*, *A. subulata* and *H. cervicornis*, are the most widespread species, they account for 89.7% of the total NIS SC of ca. 131,402 tonnes fw. Three additional species, *S. muticum*, *S. dotyi* and *S. filiformis*, increases the NIS SC to 98.8% of the total alien species which corresponds to ca. 1/3 of the total macroalgal SC of the lagoon.

Contrary to other NIS that often threaten biodiversity and human well-being, such as the recent introduction of the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865, which is a pest for eggs and larvae and the marine biodiversity, the introduction of these macroalgae had positive effects and biodiversity is steadily increasing (Sfriso et al. 2019a). Moreover, many species are rich in precious substances useful for the food, cosmetic and pharmaceutical sectors. In the future, those important commercial compounds could be extracted from those NIS instead of being imported from Asian countries. Finally, the colonization and naturalization of *A. vermiculophyllum*, a species that grows in eutrophic and turbid waters, has confirmed the positive impact on the other taxa and the whole environment as reported by other researchers (Nyberg et al. 2009; Ramus et al. 2017) for Northern Europe. Indeed, *A. vermiculophyllum* is able to replace Ulvaceae and does not trigger anoxic events and the death of fish and macrofauna.

Acknowledgements

The authors thank Dr. Orietta Zucchetta for reviewing the English language and are grateful to the anonymous referees and Dr. Carla Lambertini for useful suggestions and further English adaptations to improve the manuscript.

References

- Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. *Journal of Molecular Biology* 215: 403–410, [https://doi.org/10.1016/S0022-2836\(05\)80360-2](https://doi.org/10.1016/S0022-2836(05)80360-2)
- Anonymous (1980) Activit  de l'Institut des P ches en 1979. Principales actions en mati re de cultures marines. Science & P che [Main actions in marine farming. Science & Fishing]. *Bulletin de l'Istitut des P ches Maritimes* 306: 1–39

- Armeli-Minicante S (2013a) *Pyropia yezoensis* (Ueda) M.S. Hwang et H.G. Choi: Prima segnalazione in Adriatico. *Bollettino del Museo di Storia Naturale di Venezia* 64: 141–142
- Armeli-Minicante S (2013b) *Spermothamnion cymosum* (Harvey) De Toni. Prima segnalazione della specie in Adriatico [First report of the species in the Adriatic]. *Bollettino del Museo di Storia Naturale di Venezia* 64: 143–144
- Bastianini M, Brenardi-Aubry F, Acri F, Braga F, Facca C, Sfriso A, Finotto S (2013) The Redentore fish die-off in the Lagoon of Venice: an integrated view. Società Botanica Italiana, Gruppo di Algologia, Riunione Scientifica Annuale, Venezia, 18-19 Ottobre, 32 pp
- Bellemo G, Curiel D, Marzocchi M, Iuri M, Pavan M, Vecchiato N, Scattolin M (1999) Aggiornamento di nuove specie algali per la laguna di Venezia [Update of new algal species for the Venice lagoon]. *Lavori della Società Veneziana di Scienze Naturali* 24: 55–66
- Bonometto A, Buosi A, Facca C, Ponis E, Sfriso A. (2017) Habitat 1150* (Coastal lagoon) recovery by SEagrass RESTORation. A strategic approach to meet HD & WFD objectives. Deliverable D.1.2. Monitoring of aquatic angiosperms. 3rd year monitoring report, 35 pp
- Boudouresque C-F, Klein J, Ruitton S, Verlaque M (2011) Biological invasion: the Thau Lagoon, a Japanese biological island in the Mediterranean Sea. In: Ceccaldi HJ, Dekeyser I, Girault M, Stora G (eds), *Global change: mankind-marine environment interactions*. Springer Science, Dordrecht, pp 151–156, https://doi.org/10.1007/978-90-481-8630-3_27
- Buosi A, Sfriso A (2017) Macrophyte assemblage composition as a simple tool to assess global change in coastal areas. Freshwater impacts and climatic changes. *Science of the Total Environment* 605–606: 559–568, <https://doi.org/10.1016/j.scitotenv.2017.06.196>
- Campo VL, Kawano DF, Silva DB, Carvalho I (2009) Carrageenans: Biological properties, chemical modifications and structural analysis - a review. *Carbohydrate Polymers* 77: 167–180, <https://doi.org/10.1016/j.carbpol.2009.01.020>
- Cecere E, Moro I, Wolf MA, Petrocelli A, Verlaque M, Sfriso A (2011) The introduced seaweed *Grateloupia tururturu* (Rhodophyta, Halymeniales) in two Mediterranean transitional water systems. *Botanica Marina* 54: 23–33, <https://doi.org/10.1515/bot.2011.009>
- Clement EJ, Foster MC (1994) *Alien plants of the British Isles*. Botanical Society of the British Isles, London, 580 pp
- Curiel D, Bellemo G, Marzocchi M (1996) New records of marine algae in the Lagoon of Venice. *Plant Biosystems* 130: 352, <https://doi.org/10.1080/11263509609439592>
- Curiel D, Bellemo G, Iuri M, Marzocchi M, Scattolin M (1999) First report of the genus *Sorocarpus* Pringsheim (Fucophyceae, Ectocarpaceae) in the Mediterranean. *Botanica Marina* 42: 7–10, <https://doi.org/10.1515/BOT.1999.002>
- Curiel D, Bellemo G, La Rocca B, Scattolin M, Marzocchi M (2001) Note su specie algali nuove per la laguna di Venezia [Notes on algal species new to the Venice lagoon]. *Lavori Società Veneta di Scienze Naturali* 26: 101–102
- Curiel D, Bellemo G, Scattolin M, La Rocca B, Marzocchi M (2003) Ritrovamento in laguna di Venezia di specie algali nuove per l'Adriatico e rare per il Mediterraneo [Discovery in the Venice lagoon of algal species new to the Adriatic Sea and rare for the Mediterranean Sea]. *Informatore Botanico Italiano* 35: 7–11
- Curiel D, Bellemo G, Checchin E, Dri C, Miotti C, Marzocchi M (2005) Segnalazione di nuove macroalghe per la laguna di Venezia [Reporting of new macroalgae for the Venice lagoon]. *Lavori Società Veneziana di Scienze Naturali* 30: 41–44
- Curiel D, Bellemo G, Scattolin M (2006) First report of *Lomentaria hakodatensis* (Lomentariaceae, Rhodophyta) from the lagoon of Venice (Adriatic Sea, Mediterranean). *Acta Adriatica* 47(1): 65–72
- Dalla Valle M, Marcomini A, Sfriso A, Sweetman AJ, Kevin CJ (2003) Estimation of PCDD/F distribution and fluxes in the Venice lagoon, Italy. *Chemosphere* 51: 603–616, [https://doi.org/10.1016/S0045-6535\(03\)00048-1](https://doi.org/10.1016/S0045-6535(03)00048-1)
- European Community (2008) Regulation 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). *Official Journal of the European Communities* 164: 19–40
- European Community (2015) Regulation 2015/2283 of the European Parliament and of the Council of 25 November 2015 on novel foods. *Official Journal of the European Communities* L327/1
- Facca C, Ceoldo S, Pellegrino N, Sfriso A (2014) Natural recovery and planned intervention in coastal wetlands: Venice Lagoon (Northern Adriatic Sea, Italy) as a case study. *The Scientific World Journal* 2014: 1–16, <https://doi.org/10.1155/2014/968618>
- Fama' P, Wysor B, Kooistra W, Zuccarello GC (2002) Molecular phylogeny of the genus *Caulerpa* (Caulerpales, Chlorophyta) inferred from chloroplast tufA gene. *Journal of Phycology* 38: 1040–1050, <https://doi.org/10.1046/j.1529-8817.2002.t01-1-01237.x>
- Fletcher RL (1987) *Seaweeds of the British Isles: Fucophyceae (Phaeophyceae)*. HMSO, Rowland Phototypesetting, Suffolk, England, 359 pp.

- Freshwater DW, Rueness J (1994) Phylogenetic relationships of some European *Gelidium* (Gelidiales, Rhodophyta) species, based on rbcL nucleotide sequence analysis. *Phycologia* 33: 187–194, <https://doi.org/10.2216/i0031-8884-33-3-187.1>
- Freshwater DW, Fredericq S, Butler BS, Hommersand MH, Chase MW (1994) A gene phylogeny of the red algae (Rhodophyta) based on plastid rbcL. *Proceedings of the National Academy of Sciences* 91: 7281–7285, <https://doi.org/10.1073/pnas.91.15.7281>
- Galil BS, Marchini A, Occhipinti-Ambrogi A, Gollasch S, Minchin D, Narščiū A, Ojaveer H, Olenin S (2014) International arrivals: widespread bioinvasions in European seas. *Ecology and Evolution* 26: 152–171, <https://doi.org/10.1080/03949370.2014.897651>
- Gargiulo MG, De Masi F, Tripodi G (1992) *Sargassum muticum* (Yendo) Fensholt (Phaeophyta, Fucales) is spreading in the Lagoon of Venice (Northern Adriatic Sea). *Plant Biosystems* 126: 259
- Gargiulo MG, De Masi F, Tripodi G (2000) Problemi nomenclaturali, tassonomici e ambientali relativi alle macroalghe della laguna di Venezia [Nomenclatural, taxonomic and environmental problems related to the macroalgae of the Venice lagoon. In: Istituto Veneto di Scienze, Lettere ed Arti (ed), La Ricerca Scientifica per Venezia. Il progetto Sistema Lagunare Veneziano, Vol. II. La Garangola, Padova, pp 1116–1135
- GSA-SIBM (2012) Alien Species in Italian Seas, version 1.2. <http://www.sibm.it> (accessed 8 March 2014)
- Guiry MD, Guiry GM (2019) AlgaeBase. National University of Ireland, Galway. <http://www.algaebase.org> (accessed 23 July 2019)
- Heenan PB, Breitwieser I, Glenny DS, deLange PJ, Brownsey PJ (1998) Checklist of dicotyledons and pteridophytes naturalised or casual in New Zealand: additional records 1994–96. *New Zealand Journal of Botany* 36: 155–162, <https://doi.org/10.1080/0028825X.1998.9512556>
- Hugh DJM (2003) A guide to seaweed industry. FAO Fisheries Technical Paper, 441, Rome, pp 1–7
- Jeon SM, Kim HJ, Woo MN, Lee MK, Shin YC, Park YB, Choi MS (2010) Fucoxanthin-rich seaweed extract suppresses body weight gain and improves lipid metabolism in high-fat-fed C57BL/6J mice. *Biotechnology Journal* 5: 961–969, <https://doi.org/10.1002/biot.201000215>
- Kraan S, Barrington KA (2005) Commercial farming of *Asparagopsis armata* (Bonnemaisoniaceae, Rhodophyta) in Ireland, maintenance of an introduced species? *Journal of Applied Phycology* 17: 103–110, <https://doi.org/10.1007/s10811-005-2799-5>
- Le Lann K, Jégou C, Stiger-Pouvreau V (2008) Effect of different conditioning treatments on total phenolic content and antioxidant activities in two Sargassacean species: Comparison of the frondose *Sargassum muticum* (Yendo) Fensholt and the cylindrical *Bifurcaria bifurcata* R. Ross. *Phycological Research* 56: 238–245, <https://doi.org/10.1111/j.1440-1835.2008.00505.x>
- Life12 NAT/IT/000331 (2012) SeResto (Habitat 1150* (Coastal lagoon) recovery by SEagrass RESTORation, a new strategic approach to meet Habitat Directive (92/43/CEE) and Water Framework Directive (2000/60/EC). <http://www.lifeseresto.eu> (accessed 20 March 2018)
- Manghisi A, Armeli Minicante S, Bertuccio C, Morabito M, Torricelli P, Genovese G (2011) A cryptic alien seaweed spreading in Mediterranean coastal lagoons. *Transitional Waters Bulletin* 5(1): 1–7
- Marchini A, Ferrario J, Sfriso A, Occhipinti-Ambrogi A (2015) Current status and trends of biological invasions in the Lagoon of Venice, a hotspot of marine NIS introductions in the Mediterranean Sea. *Biological Invasions* 17: 2943–2962, <https://doi.org/10.1007/s10530-015-0922-3>
- Mars P (1996) Recherches sur quelques étangs du littoral méditerranéen français et sur leurs faunes malacologiques. *Vie & Milieu* 20 supplement: 1–359
- Ménesguen A (2018) Les marées vertes. 40 clés pour comprendre. Édition Quae RD 10. Versailles, France, 120 pp
- Milledge JJ, Nielsen BV (2016) High-value products from macroalgae: the potential uses of the invasive brown seaweed, *Sargassum muticum*. *Reviews in Environmental Science and Bio/Technology* 15: 67–88, <https://doi.org/10.1007/s11157-015-9381-7>
- Murano E, Toffanin R, Cecere E, Rizzo R, Knutsen SH (1997) Investigation of the carrageenans extracted from *Solieria filiformis* and *Agardhiella subulata* from Mar Piccolo, Taranto. *Marine Chemistry* 58: 319–325, [https://doi.org/10.1016/S0304-4203\(97\)00058-3](https://doi.org/10.1016/S0304-4203(97)00058-3)
- Namvar F, Mohamad R, Baharara J, Zafar-Balanejad S, Fargahi F, Rahman HS (2013) Antioxidant, Antiproliferative, and Antiangiogenesis Effects of Polyphenol-Rich Seaweed (*Sargassum muticum*). *BioMed Research International* 2013: 604787, <https://doi.org/10.1155/2013/604787>
- Nyberg CD, Thomsen MS, Wallentinus I (2009) Flora and fauna associated with the introduced red alga *Gracilaria vermiculophylla*. *European Journal of Phycology* 44: 395–403, <https://doi.org/10.1080/09670260802592808>
- Occhipinti-Ambrogi A, Marchini A, Cantone G, Castelli A, Chimenz C, Cormaci M, Frogliola C, Furnari G, Gambi MC, Giaccone G, Giangrande A, Gravili C, Mastrototaro F, Mazziotti C, Orsi-Relini L, Piraino S (2011) Alien species along the Italian coasts: an overview. *Biological Invasions* 13: 215–237, <https://doi.org/10.1007/s10530-010-9803-y>

- Orel G, Boatto V, Sfriso A, Pellizzato M (2000) Piano per la gestione delle risorse alieutiche delle lagune della Provincia di Venezia [Plan for the management of fishery resources in the lagoons of the Province of Venice]. Provincia di Venezia, SannioPrint, Benevento, Italy, 102 pp
- Pignatti S (1962) Associazioni di alghe marine sulla costa Veneziana [Associations of marine algae on the Venetian coast]. *Memorie dell'Istituto Veneto di Scienze, Lettere ed Arti* 32: 1–134
- Pérez R, Kaas R, Barbaroux O (1984) Culture expérimentale de l'algue *Undaria pinnatifida* sur les côtes de France. *Science & Pêche, Bulletin de l'Institut des Pêches Maritimes* 343: 3–15
- Petrocelli A, Cecere E, Verlaque M (2013) Alien marine macrophytes in transitional water systems: new entries and reappearances in a Mediterranean coastal basin. *Biological Invasion Records* 2: 177–184, <https://doi.org/10.3391/bir.2013.2.3.01>
- Pranovi F, Giovanardi O (1994) The impact of hydraulic dredging for short-necked clams, *Tapes* spp., on an infaunal community in the lagoon of Venice. *Scientia Marina* 58: 345–353
- Ramus AP, Silliman RB, Thomsen MS, Long ZT (2017) An invasive foundation species enhances multifunctionality in a coastal ecosystem. *PNAS* 114: 8580–8585, <https://doi.org/10.1073/pnas.1700353114>
- Regione Veneto, ARPAV, CORILA (2012) Monitoring plan of the Venice lagoon water bodies aimed at the definition of the ecological status under Directive 2000/60/EC. Line 2: Monitoring of the Biological Quality Element “Macrophytes”. Final Report, 30 pp. + 10 tables [in Italian]
- Regione Veneto, ARPAV, CORILA (2015) Monitoring plan of the Venice lagoon aimed at the definition of the ecological status under Directive 2000/60/EC (Legislative decree N. 152/2006 s.m.i.). 2nd monitoring cycle, period 2013–2015. EQB: Macrophytes. Final Report, 33 pp. + 7 tables [in Italian]
- Richardson DM, Pysek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107, <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Rismondo A, Volpe S, Curiel D, Solazzi A (1993) Segnalazione di *Undaria pinnatifida* (Harvey) Suringar a Chioggia (Laguna Veneta) [Reporting of *Undaria pinnatifida* (Harvey) Suringar in Chioggia (Venetian Lagoon)]. *Lavori Società Veneta di Scienze Naturali* 18: 328–330
- Robledo D, Freile-Pelegrin Y (2010) Prospects for the cultivation of economically important carrageenophytes in Southeast Mexico. *Journal of Applied Phycology* 3: 127–134, <https://doi.org/10.1007/s10811-010-9585-8>
- Rueness J (2005) Life history and molecular sequences of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta), a new introduction to European waters. *Phycologia* 44: 120–128, [https://doi.org/10.2216/0031-8884\(2005\)44\[120:LHAMSO\]2.0.CO;2](https://doi.org/10.2216/0031-8884(2005)44[120:LHAMSO]2.0.CO;2)
- Sabeena Farvin KH, Jacobsen C (2013) Phenolic compounds and antioxidant activities of selected species of seaweeds from Danish coast. *Food Chemistry* 138: 1670–1681, <https://doi.org/10.1016/j.foodchem.2012.10.078>
- Saunders GW, Kucera H (2010) An evaluation of rbcL, tufA, UPA, LSU and ITS as DNA barcode markers for the marine green macroalgae. *Cryptogamie Algologie* 31: 487–528
- Schiffner C, Vatova A (1938) Le alghe della Laguna: Chlorophyceae, Phaeophyceae, Rhodophyceae, Myxophyceae [The algae of the lagoon: Chlorophyceae, Phaeophyceae, Rhodophyceae, Myxophyceae]. In: Minio M (ed), *La Laguna di Venezia*, Vol. 3, pp 1–250
- Sfriso A (1987) Flora and vertical distribution of macroalgae in the lagoon of Venice: a comparison with previous studies. *Plant Biosystems* 121: 69–85, <https://doi.org/10.1080/11263508709431647>
- Sfriso A, Curiel D (2007) Check-list of marine seaweeds recorded in the last 20 years in Venice lagoon and a comparison with the previous records. *Botanica Marina* 50: 22–58, <https://doi.org/10.1515/BOT.2007.004>
- Sfriso A, Facca C (2007) Distribution and production of macrophytes in the lagoon of Venice. Comparison of actual and past abundance. *Hydrobiologia* 577: 71–85, <https://doi.org/10.1007/s10750-006-0418-3>
- Sfriso A, Facca C (2013) Annual growth and environmental relationships of the invasive species *Sargassum muticum* and *Undaria pinnatifida* in the lagoon of Venice. *Estuarine Coastal and Shelf Science* 129: 162–172, <https://doi.org/10.1016/j.ecss.2013.05.031>
- Sfriso A, La Rocca B (2005) Aggiornamento di taxa macroalgali nei litorali e nei bassofondali della laguna di Venezia [Update of macroalgal taxa in the coasts and in the shallow waters of the Venice lagoon]. *Lavori - Società Veneziana di Scienze Naturali* 30: 45–58
- Sfriso A, Marchini A (2014) Updating of non-indigenous macroalgae in the Italian Coasts. New introductions and cryptic species. *Biologia Marina Mediterranea* 21(1): 60–69
- Sfriso A, Marcomini A (1996) Decline of *Ulva* growth in the lagoon of Venice. *Bioresource Technology* 58: 299–307, [https://doi.org/10.1016/S0960-8524\(96\)00120-4](https://doi.org/10.1016/S0960-8524(96)00120-4)
- Sfriso AA, Sfriso A (2017) In situ biomass production of Gracilariaceae and *Ulva rigida*: The Venice Lagoon as study case. *Botanica Marina Special Issue: Phycomorph* 60: 1–13, <https://doi.org/10.1515/bot-2016-0061>

- Sfriso A, La Rocca B, Godini E (2002) Inventario di taxa macroalgali in tre aree della laguna di Venezia a differente livello di trofia [Inventory of macroalgal taxa in three areas of the Venice lagoon at different trophic levels]. *Lavori Società Veneta di Scienze Naturali* 27: 85–99
- Sfriso A, Facca C, Ceoldo S, Silvestri S, Ghetti PF (2003) Role of macroalgal biomass and clam fishing on spatial and temporal changes in N and P sedimentary pools in the central part of the Venice lagoon. *Oceanologica Acta* 26/1: 3–13, [https://doi.org/10.1016/S0399-1784\(02\)00008-7](https://doi.org/10.1016/S0399-1784(02)00008-7)
- Sfriso A, Facca C, Marcomini A (2005) Sedimentation rates and erosion processes in the lagoon of Venice. *Environment International* 31: 983–992, <https://doi.org/10.1016/j.envint.2005.05.008>
- Sfriso A, Maistro S, Andreoli C, Moro I (2010) First record of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta) in the Po Delta lagoons, Mediterranean Sea (Italy). *Journal of Phycology* 46: 1024–1027, <https://doi.org/10.1111/j.1529-8817.2010.00893.x>
- Sfriso A, Wolf MA, Maistro S, Sciuto K, Moro I (2012) Spreading and autoecology of the invasive species *Gracilaria vermiculophylla* Gracilariales, Rhodophyta) in the lagoons of the north-western Adriatic Sea (Mediterranean Sea, Italy). *Estuarine Coastal and Shelf Science* 114: 192–198, <https://doi.org/10.1016/j.ecss.2012.07.024>
- Sfriso A, Buosi A, Sfriso AA (2014) On the occurrence of *Uronema marinum* Womersley (Chaetophorales, Chlorophyta) in the north-western lagoons of the Adriatic Sea, Mediterranean Sea (Italy). *Mediterranean Marine Science* 15: 101–105, <https://doi.org/10.12681/mms.517>
- Sfriso A, Buosi A, Tomio Y, Wolf MA, Juhmani AS, Sfriso AA (2019a) Macroalgae in the lagoon of Venice: long-term changes, alien taxa and environmental impact. 7th European Phycological Congress, 25-30 August, Zagabria, p 95
- Sfriso A, Buosi A, Mistri M, Munari C, Franzoi P, Sfriso AA (2019b) Long-term changes of the trophic status in transitional ecosystems of the northern Adriatic Sea, key parameters and future expectations: The lagoon of Venice as a study case. In: Mazzocchi MG, Capotondi L, Freppaz M, Lugliè A, Campanaro A (eds), Italian Long-Term Ecological Research for understanding ecosystem diversity and functioning. Case studies from aquatic, terrestrial and transitional domains. *Nature Conservation* 34: 193–215, <https://doi.org/10.3897/natureconservation.34.30473>
- Sfriso AA, Gallo M, Baldi F (2017a) Seasonal variation and yield of sulfated polysaccharides in seaweeds from the Venice Lagoon. *Botanica Marina Special Issue: Phycomorph* 60: 339–349, <https://doi.org/10.1515/bot-2016-0063>
- Sfriso AA, Gallo M, Baldi F (2017b) Seaweed protein production in the Venice Lagoon: Seasonal variations in *Ulva rigida*, and three Gracilariaceae. *Biologia Marina Mediterranea* 24(1): 86–87
- Sfriso AA, Gallo M, Baldi F (2018) Phycoerythrin productivity and diversity from five red macroalgae. *Journal of Applied Phycology* 30: 2523–2531, <https://doi.org/10.1007/s10811-018-1440-3>
- Solazzi A, Orel G, Chiozzotto E, Scattolin M, Curiel D, Grim F, Aleffi F, Del Piero D, Vatta P (1991) Le alghe della Laguna di Venezia [The algae of the Venice lagoon]. Vol. 1. Venezia, 119 pp
- Sonani RR, Singh NK, Kumar J, Thakar D, Madamwar D (2014) Concurrent purification and antioxidant activity of phycobiliproteins from *Lyngbya* sp. A09DM: An antioxidant and anti-aging potential of phycoerythrin in *Caenorhabditis elegans*. *Process Biochemistry* 49: 1757–1766, <https://doi.org/10.1016/j.procbio.2014.06.022>
- Sousa AMM, Sereno AM, Hilliou L, Gonçalves PM (2010) Biodegradable Agar Extracted from *Gracilaria vermiculophylla*: Film Properties and Application to Edible Coating. *Materials Science Forum* 636–637: 739–744, <https://doi.org/10.4028/www.scientific.net/MSF.636-637.739>
- Thomsen MS, Gurgel CFD, Fredericq S, McGlathery KJ (2005) *Gracilaria vermiculophylla* (Rhodophyta, Gracilariales) in Hog Island Bay, Virginia: a cryptic alien and invasive macroalga and taxonomic correction. *Journal of Phycology* 42: 139–141, <https://doi.org/10.1111/j.1529-8817.2006.00160.x>
- Thomsen MS, Staehr PA, Nyberg CD, Schwaerter S, Krause-Jensen D, Silliman BR (2007) *Gracilaria vermiculophylla* (Ohmi) Papenfuss, 1967 (Rhodophyta, Gracilariaceae) in northern Europe, with emphasis on Danish conditions, and what to expect in the future. *Aquatic Invasions* 2: 83–94, <https://doi.org/10.3391/ai.2007.2.2.1>
- Toffanin R, Cecere E, Rizzo R, Knutsen SH (1997) Investigation of the carrageenans extracted from *Solieria filiformis* and *Agardhiella subulata* from Mar Piccolo, Taranto. *Marine Chemistry* 58: 319–325, [https://doi.org/10.1016/S0304-4203\(97\)00058-3](https://doi.org/10.1016/S0304-4203(97)00058-3)
- Tolomio C (1993) Prima segnalazione di *Grateloupia doryphora* (Mont.) Howe (Rhodophyceae) nella laguna di Venezia [First record of *Grateloupia doryphora* (Mont.) Howe (Rhodophyceae) in the Venice lagoon]. *Lavori della Società Veneziana di Scienze Naturali* 18: 215–220
- Verlaque M (2001) Check-list of the macroalgae of Thau lagoon (Hérault, France): a hot spot of marine species introduction in Europe. *Oceanologica Acta* 24: 29–49, [https://doi.org/10.1016/S0399-1784\(00\)01127-0](https://doi.org/10.1016/S0399-1784(00)01127-0)

- Verlaque M, Ruitton S, Mineur F, Boudouresque CF (2015) CIESM Atlas of Exotic Species in the Mediterranean. Vol 4. Macrophytes. CIESM Publishers, Monaco, pp 364
- Wolf MA, Sfriso A, Andreoli C, Moro I (2011) The presence of exotic *Hypnea flexicaulis* (Rhodophyta) in the Mediterranean Sea as indicated by morphology, rbcL and cox1 analyses. *Aquatic Botany* 95: 55–58, <https://doi.org/10.1016/j.aquabot.2011.02.009>
- Wolf MA, Sciuto K, Andreoli C, Moro I (2012) *Ulva* (Chlorophyta, Ulvales) biodiversity in the North Adriatic Sea (Mediterranean, Italy): cryptic species and new introductions. *Journal of Phycology* 48: 1510–1521, <https://doi.org/10.1111/jpy.12005>
- Wolf MA, Sfriso A, Moro I (2014) Thermal pollution and settlement of new tropical alien species: the case of *Grateloupia yinggehaiensis* (Rhodophyta) in the Venice Lagoon. *Estuarine Coastal and Shelf Science* 147: 11–16, <https://doi.org/10.1016/j.ecss.2014.05.020>
- Wolf MA, Buosi A, Juhmani ASF, Sfriso A (2018) Shellfish import and hull fouling as vectors for new red algal introductions in the Venice Lagoon. *Estuarine Coastal and Shelf Science* 215: 30–38, <https://doi.org/10.1016/j.ecss.2018.09.028>
- Yamanaka R, Akiyama K (1993) Cultivation and utilization of *Undaria pinnatifida* (wakame) as food. *Journal of Applied Phycology* 5: 249, <https://doi.org/10.1007/BF00004026>
- Zenetos A, Gofas S, Verlaque M, Cinar M, García Raso E, Bianchi CN, Morri C, Azzurro E, Bilecenoglu M, Frogia C, Siokou I, Violanti D, Sfriso A, San Martín N, Giangrande A, Katağan T, Ballesteros E, Ramos-Esplá A, Mastrototaro F, Ocaña O, Zingone A, Gambi MC, Streftaris N (2010) Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution. *Mediterranean Marine Science* 11: 381–493, <https://doi.org/10.12681/mms.87>
- Zenetos A, Gofas S, Morri C, Rosso A, Violanti D, Garcia Raso JE, Cinar ME, Almogi-Labin A, Ates AS, Azzurro E, Ballesteros E, Bianchi CN, Bilecenoglu M, Gambi MC, Giangrande A, Gravili C, Hyams-Kaphzan O, Karachle V, Katsanevakis S, Lipej L, Mastrototaro F, Mineur F, Pancucci-Papadopoulou MA, Ramos Esplá A, Salas C, San Martin G, Sfriso A, Streftaris N, Verlaque M (2012) Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Patterns in introduction trends and pathways. *Mediterranean Marine Science* 13: 312–336, <https://doi.org/10.12681/mms.327>

Supplementary material

The following supplementary material is available for this article:

Figure S1. First record of *Agarophyton vermiculophyllum* in the Venice Lagoon in late spring 2008 (Sfriso et al. 2010) and spread in the choked areas of the whole lagoon in 2011 and 2014.

Table S1. Macroalgal NIS in Venice Lagoon, taxon description.

Table S2. Records of *Agarophyton vermiculophyllum* in the Venice Lagoon in 2008, 2011 and 2014.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2020/Supplements/AI_2020_Sfriso_etal_SupplementaryTables.xlsx

http://www.reabic.net/aquaticinvasions/2020/Supplements/AI_2020_Sfriso_etal_SupplementaryFigure.pdf