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Alien Macroalgal Rearrangement in the Soft Substrata of the Venice Lagoon (Italy): Impacts, Threats, Time and Future Trends

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Abstract: Non-native species are a concern for aquatic environments both for the ecosystem biodiversity and from the economical point of view. The Venice Lagoon is a Mediterranean hotspot of alien introductions and macroalgae are probably the most represented systematic category. For this reason, alien macroalgal distribution and variation were monitored in late spring-autumn surveys, carried out in 2011, 2014, 2018 and 2021 in the soft bottoms of the entire lagoon (87 common stations). Overall, 21 taxa were recorded; three of them (i.e., *Acanthosiphonia echinata*, *Caulacanthus okamurae*, *Osmundea oederi*) are well-established recent introductions for the lagoon, which has increased the total number of non-native species to 33. *Ulva australis*, previously reported as *Ulva laetevirens*, is the most abundant species and it is replacing *Ulva rigida*, especially in the less eutrophic areas. The invasive *Gracilariopsis vermiculophylla*, an engineering species colonizing the eutrophic choked areas especially in the central lagoon, is instead decreasing. Other abundant established taxa are now dominant components of the lagoon biomass, whereas many others are rare or have small sizes that make their biomass negligible. Overall, these species do not represent serious threats to the environment, but they rather increase biodiversity, with some of them having positive effects on ecosystem services.

Keywords: macroalgae; non-indigenous species; invasive species; *Ulva australis*; *Gracilariopsis vermiculophylla*

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1. Introduction

Allochthonous Species

Allochthonous species are one of the major environmental threats of this new millennium. The worldwide trade and commercial globalization increase has led to the spread of species, previously confined to single areas, that have colonized environments similar to the original ones by competing with the native communities and often seriously impacting the local biodiversity [1–7]. Many species have spread throughout the world and some of them have become invasive, often irreversibly changing the composition of both aquatic and terrestrial local biological communities. In some cases, the impact of non-native species (NIS) was dramatic, with the destruction of local communities and a drastic reduction of biodiversity. For example, in the 1960s the Norwegian red King Crab (*Paralithodes camtschaticus* Tilesius) was introduced into the Murmansk Fjord in Russia, from where it has spread to vast areas south of the Barents Sea, in Russian and Norwegian territorial waters [8]. This species is one of the largest crustaceans in the world and has no natural enemies or competitors; for this reason, it easily eliminates all the other benthic species and becomes the absolute master of its territory. Since *P. camtschaticus* is a species introduced for economic purposes and of high commercial value, the environmental damages have been at least partially mitigated by the strong economic return. The same situation occurred with the introduction of the clam *Ruditapes philippinarum* Adams and Reeve in many European lagoons [9,10], where the fishing of these mollusks has created serious environmental damages, leading also to a drastic reduction of the native species [11,12].

In other cases, the accidental introduction of NIS has led to both environmental and economic damages. The catfish *Silurus glanis* Linnaeus, the largest European fish species native to western Asia and Eastern Europe, was introduced to Western Europe [13,14] for sport fishing and aquaculture and it had strong adverse impacts on the native fish communities [15]. Similarly, the introduction of *Mnemiopsis leidyi* A. Agassiz and *Callinectes sapidus* Rathbun had a drastic impact on Mediterranean fish species. *M. leidyi* is a voracious zooplanktivore ctenophore; in the early 1980s, it was introduced into the Black Sea basin from the northern European coastal waters and, in 2009, it invaded the Mediterranean coasts, triggering massive blooms with abrupt decreases in zooplankton, ichthyoplankton, and fisheries [16]. The blue crab *C. sapidus* is native to the western Atlantic, from Nova Scotia (Canada) to Argentina, and it has recently spread along the Mediterranean coasts [17,18] by ballast waters, with direct and indirect impacts on benthic communities and local fishery. In the last years, this crab has completely colonized the Po Delta lagoons and it is currently also colonizing the Venice Lagoon.

About macrophytes, in these last decades, many non-native macroalgae have invaded the hard and soft substrata of marine coasts, strongly affecting the native vegetation [3,6]. *Caulerpa taxolia* (Valh) C. Agardh is a harmful and extremely invasive macroalga that since 1992 had infested tens of thousands of ha in the Mediterranean Sea, favored by the mild water temperatures and the absence of predators. *C. taxolia* has been included in the list of the 100 most harmful invasive alien species in the world.

However, the highest number of NIS was mostly introduced in some Mediterranean transitional water systems, such as the lagoon of Thau [19–21], the lagoon of Venice [22,23] and the Mar Piccolo of Taranto [24,25].

The lagoon of Venice (Italy) is a site of proven high invasion risk and it is acknowledged as a hotspot of NIS introductions [22,23,26]. Many anthropogenic activities, such as commercial and touristic traffic, the presence of wholesale fish markets, and the intense activity of shellfish farming, are vectors of continuous and multiple introductions.

Indeed, in 2019, before the COVID-19 epidemiological emergency, Venice and Chioggia ports had a traffic of 3723 commercial ships (gross tonnage: 79,368,374 tonnes) and 497 tourist ships (1.6 million passengers) [27]. In this context, allochthonous species can be easily introduced by ship hull fouling or with ballast waters. In addition, in the Venice Lagoon two large wholesale fish markets are present, one at Chioggia and the other at the historical center of Venice, and they import a great part of the products from abroad. These fish and shellfish products are often packed with fresh macroalgae that, at the end of the market day, are downloaded into the canals. Finally, a wide area (ranging from approx. 3500 ha, in 2006, to 1725 ha, in 2018) was licensed for the farming of the introduced clam *Ruditapes philippinarum* Adam and Reeve [28]. A minor part of the seeds needed for clam farming is collected from the lagoon and from the mouth of Brenta, Adige and Po Delta rivers, but the majority is bought from abroad, especially from the hatcheries in the Pacific coasts of the United States [29]. Besides clam seeds, juveniles or germlings of non-native species can arrive in the lagoon and colonize this new environment.

Among these NIS, macroalgae represent the most abundant new entries [22,26,30]. New species, already present in the Mediterranean Sea or of allochthonous origin, are reported almost every year ([30–32] and references therein). The new species establishment is favored by the high availability of artificial substrata, such as the city docks, the stone bank reinforcements of islands and tidal lands, and the surfaced and submerged breakwaters [33–35]. Therefore, the number of introductions is continuously increasing and their record is due to the high number of macrophyte studies performed in the lagoon. In addition, molecular studies contribute to discovering cryptic species, previously confused with the native ones, and to solving taxonomically difficult issues. For example, *Carradoriella denudata* (Dillwyn) Savoie and G.W. Saunders and *Caulacanthus ustulatus* (Turner) Kützing] are now identified with *Kapraunia schneideri* (Stuercke and Freshwater) Savoie and G. W Saunders ([30] and references therein) and *Caulacanthus okamurae* Yamada [32], respectively.

This study deals with the spatial distribution and temporal changes of macroalgal NIS that have colonized the soft substrata of the whole Venice Lagoon between 2011 and 2021, with the aim of highlighting which species have had the highest spread or, vice versa, which ones have regressed after a rapid colonization, even if still part of the current flora. For each investigated population, information is given about the first record, introduction vector, origin, impact, status, and future development of the species.

In addition, the updated amount of macroalgal NIS present on the Venice Lagoon soft and hard substrata is provided, with particular attention to cryptic species and to taxa that, before molecular analyses or nomenclatural adjustments, were believed to be native to this environment.

2. Materials and Methods

2.1. Study Area

The lagoon of Venice (Figure 1), with a surface of approx. 549 km^2, is the largest Transitional Water System (TWS) of the Mediterranean Sea.

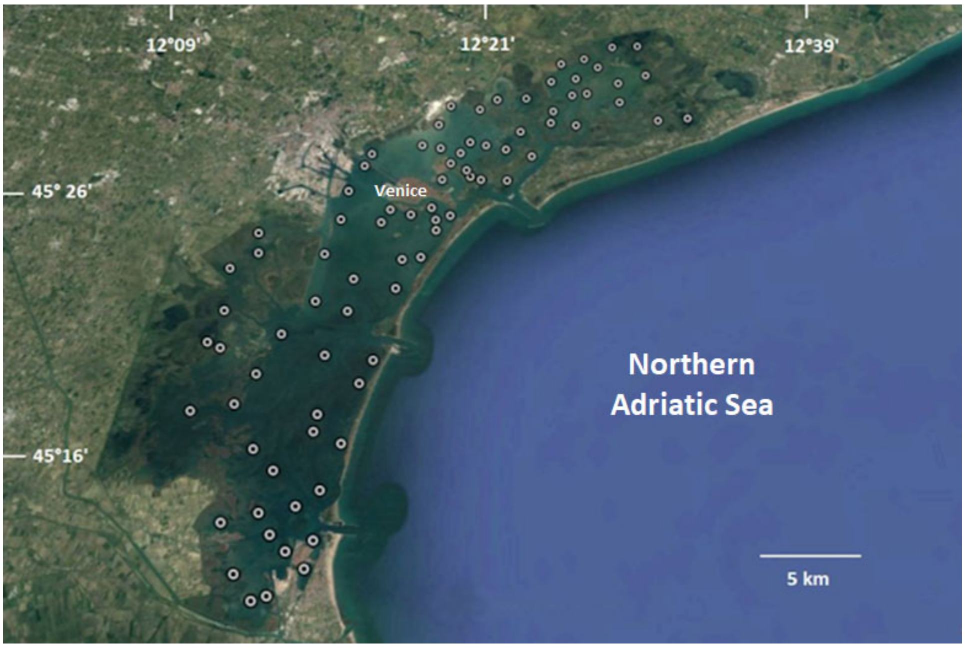

Figure 1. Map of the Venice Lagoon. White circles represent the 87 sampling stations, distributed in the entire lagoon.

The mean depth is progressively increasing; in fact, it was approx. 0.5 m before the 18th century during the Serenissima Republic of Venice, while currently, it is about 1.2 m, recorded after the construction of long jetties at the three lagoon inlets (Malamocco, in 1806–1872; Lido, in 1882–1910; Chioggia, in 1911–1933) and deep canals (Vittorio Emanuele III, in 1920–1925, and Malamocco-Marghera, in 1964–1968), built to allow oil tankers to reach directly the petrochemical refineries of Marghera [36]. Water exchange occurs with the sea throughout three large (600–900 m) and deep (12–16 m) inlets (Lido, Malamocco, Chioggia) and it accounts on average for 60% of total water reservoir every 12 h. Due to the high water exchange, the lagoon has a high resilience. Currently, areas previously affected by high seaweed production (in the 1970s–1980s) or by intense clam activities (in 1990s and 2000s) are improving; this is due to the declining of the trophic level [37] and clam production [38].

At present, the lagoon is composed of a high number of different habitats ranging from heavily marinized areas, closed to the lagoon inlets and the largest canals, to choked areas, where water renewal occurs after 30–40 days [39]. Recently, Sfriso et al. (2017) [40] reported that the Venice Lagoon is representative of almost all the ecological conditions recorded in the biggest Italian lagoons (i.e., Grado-Marano, Po Delta, Comacchio Valleys, Pialassa della Baiona, Lesina, Varano, Orbetello), which account for approx. 78% of the Italian transitional lagoons and ponds (1088 km^2 on a total of 1398 km^2).

In order to determine the ecological status of the entire lagoon and in agreement with the European Water Directive (WFD 2000/60/EC), the Regional Agency for the Environmental Prevention and Protection of Veneto (ARPAV) has funded several projects to monitor the biological composition of macrophytes, fish fauna, benthic macrofauna and phytoplankton. Macrophytes (macroalgae and aquatic angiosperms) were monitored by our research team in 2011 (118 stations), 2014, 2018, 2021 (88 stations, Figure 1), and the ecological status was recorded by applying the Macrophyte Quality Index (MaQI) [41]. Eighty-seven stations were common to the 4 annual surveys and all the macroalgal NIS recorded in those years were compared to understand the distribution and time changes.

2.2. Macrophyte Sampling

During the annual surveys, macroalgae were sampled in late spring–early summer and in autumn, in the 87 stations shown in Figure 1. At each station, six subsamples of macroalgae were collected in the soft bottoms, with a rake crawling onto the bottom for approx. one meter on a surface of 20 × 20 m [41]. Macroalgal samples, representative of all visible species, were fixed in water and a 4% formaldehyde solution for morphological analyses. Some cryptic taxa were also dried in silica gel for molecular analyses based on the DNA barcoding method [30–32].

2.3. Molecular Analyses

The DNA was extracted from fragments of selected silica-dried specimens using the Genomic DNA purification kit (Thermo Scientific™). Different molecular markers were chosen based on the taxa to which the selected specimens had been morphologically attributed; for example, the *rbc*L-5P gene fragment (about 700 bp) or a longer portion of the *rbc*L gene (about 1290 bp) was generally used for members of the phylum Rhodophyta, while a portion of the SSU rDNA gene (about 700 bp) was employed for some specimens belonging to the phylum Chlorophyta. The chosen molecular markers, the specific primers used, and the employed amplification conditions are reported in the corresponding references [30–32]. The produced amplicons were cleaned with the HT ExoSAP-IT (Applied Biosystems™) and, successively, sequenced at the Eurofins Genomics Sequencing Service (Germany). The final consensus sequences were assembled with the software GeneStudio (http://genestudio.com, last accessed on 10 February 2020). The obtained sequences were compared with those present in the INSDC (International Nucleotide Sequence Database Collaboration) archives using the BLAST tool, available on the USA National Centre for Biotechnology Information (NCBI) web server (http://www.ncbi.nlm.nih.gov, last accessed on 10 February 2020), and finally deposited in the INSDC archives (for sequence accession numbers see the corresponding references [30–32]).

3. Results

During spring and autumn surveys carried out in 2011, 2014, 2018 and 2021 in the 87 stations, an overall total of 21 NIS was recorded (Table 1). On average, eight species were present in more than 10 stations, eight between 1 and 7 stations, whereas the remaining five species were recorded only occasionally.

The most abundant NIS was the Chlorophycea *Ulva australis* Areschoug, recorded in 51–74 stations (on average: 63 stations, 72% of the total) (Table 1, Figure 2). This NIS showed a slight increase from 2011 to 2021.

Table 1. Number of non-indigenous macroalgae recorded in the lagoon surveys carried out in 2011, 2014, 2018, and 2021 on the soft substrata of 87 common stations spread over the entire lagoon.

Alien Species in Soft Substrata of the Venice Lagoon															
N°	Alien Species	First Record in Venice		Number of Stations					% of Stations					Standing Crop 2014 (Sfriso et al., 2020) [30]	
		Study	Probable date	2011	2014	2018	2021	Mean	2011	2014	2018	2021	Mean		
1	*U. australis*	2011	<2007	51	64	61	74	63	59	74	70	85	72	unknown	
2	*A. subulata*	2003	2003	38	44	52	47	45	44	51	60	54	52	36,714	tonnes FWT
3	*H. cervicornis*	2011	2009	42	35	47	46	43	48	40	54	53	49	28,305	tonnes FWT
4	*U. marinum*	2014	2008	27	53	40	43	41	31	61	46	49	47	8.1	tonnes FWT
5	*S. filiformis*	2005	2003	26	29	19	20	24	30	33	22	23	27	3768	tonnes FWT
6	*K. schneideri*	2018	<2007	17	14	43	12	22	20	16	49	14	25	398	tonnes FWT
7	*A. echinata*	2019	2014	0	0	34	45	20	0	0	39	52	23	0	
8	*G. vermiculophylla*	2008	2008	11	21	8	5	11	13	24	9.2	5.7	13	66,383	tonnes FWT
9	*C. okamurae*	2020	2014	0	8	9	12	7	0.0	9.2	10	13.8	8.3	0	
10	*U.obscura*	2002	2000	3	10	1	11	6	3.4	11.5	1.1	12.6	7.2	323	tonnes FWT
11	*M. japonicus*	2018	1998	9	8	4	3	6	10	9.2	4.6	3.4	6.9	272	tonnes FWT
12	*O. oederi*	2021	2014	0	2	8	11	5	0	2.3	9.2	12.6	6.0	0	
13	*A. halliae*	2018	2016	0	0	8	10	5	0	0	9.2	11.5	5.2	<0.5	kg FWT
14	*S. muticum*	1992	1992	0	2	4	7	3	0	2.3	4.6	8.0	3.7	4825	tonnes FWT
15	*P. morrowii*	2001	1999	3	0	0	5	2	3.4	0	0.0	5.7	2.3	517	tonnes FWT
16	*A. nipponicum*	1996	1994	2	1	1	1	1	2.3	1.1	1.1	1.1	1.4	3.1	tonnes FWT
17	*D. japonica*	2005	1999	0	0	0	3	0.8	0	0	0	3.4	0.9	+	
18	*S. cymosum*	2013	2010	0	2	0	0	0.5	0	2.3	0	0	0.6	+	
19	*S. dotyi*	1996	1996	0	0	0	2	0.5	0	0	0	2.3	0.6	4775	tonnes FWT
20	*C. fragile*	1987	1978	0	0	1	0	0.3	0	0	1.1	0	0.3	1.25	tonnes FWT
21	*G. turuturu*	1993	1989	0	1	0	0	0.3	0	1.1	0	0	0.3	87	tonnes FWT

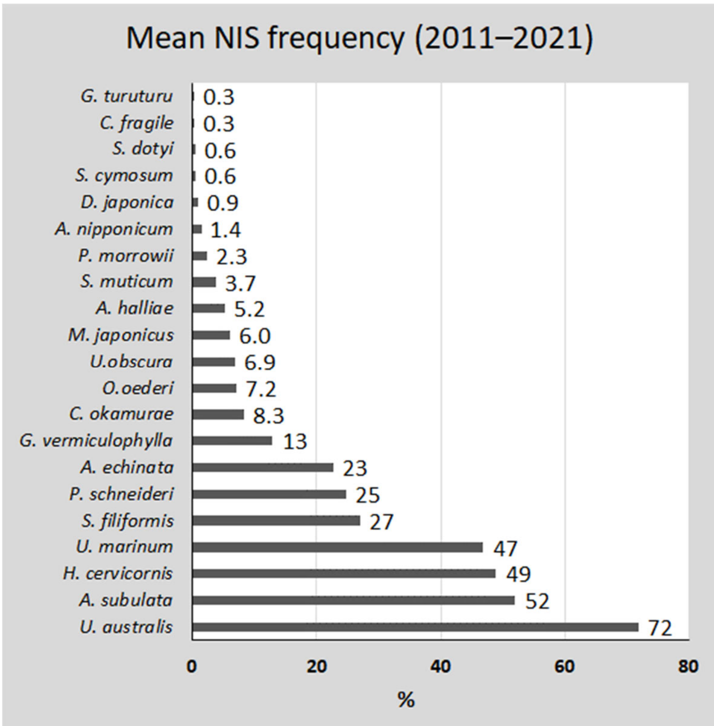

Figure 2. Frequency of the 21 macroalgal non-indigenous species (NIS) in the soft substrata of 87 Venice Lagoon stations.

The Rhodophyceae *Agardhiella subulata* (C. Agardh) Kraft *et* M. J. Wynne and *Hypnea cervicornis* J. Agardh were recorded on average in 45 (52%) and 43 (49%) stations, both increasing until 2018 and slightly decreasing in 2021.

Uronema marinum Womersley, a microscopic Chlorophycea that grows epiphytic on larger macroalgae such as the Gracilariaceae and the Cladophoraceae, was the fourth most abundant species recorded in 27–53 stations (on average: 41 stations, 47% of the total).

Four NIS (i.e., *Solieria filiformis* (Kützing) P. W. Gabrielson, *Krapaunia schneideri*, *Acanthosiphonia echinata* (Harvey) Savoie and G.W. Saunders and *Gracilariopsis vermiculophylla* Ohmi) were reported on average in 11–24 stations (13–27% of the total).

Acanthosiphonia echinata was identified in the Venice Lagoon by molecular analyses only in 2018 [31]. Indeed, this species was absent in 2011 and 2014 but was first recorded in 2018 in 34 stations (39%) and increased up to 45 stations (52%) in 2021.

Conversely, *Gracilariopsis vermiculophylla* and *Solieria filiformis* (Kützing) P.W. Gabrielson, after their highest spread recorded in 2014 (21 and 29 stations, i.e., 24–33% of the total), progressively decreased to 5–20 stations (5.7–23%). *Krapaunia schneideri* showed a peak in 2018 (43 stations, i.e., 49% of the total), whereas in the other years it ranged between 12 and 17 stations (14–20%).

The Chlorophycea *Ulvaria obscura* (Kützing) P. Gayral *ex* Bliding (mean value 7.2%), the Phaeophyceaea *Sargassum muticum* (Yendo) Fensholt (mean value: 3.7%) and six different rhodophycean species had mean frequencies ranging from 1.4 to 8.3% (Table 1).

Caulacanthus okamurae (mean value 8.3%) was very common on hard substrata and colonized also shells or wooden poles, especially in the mesolittoral waters.

Osmundea oederi (Gunnerus) G. Furnari was recorded since 2014 as *Osmundea truncata* (Kützing) K.W. Nam and Maggs and, in the following years, its frequency progressively increased up to 12.6%. This species grows mainly attached to the bivalve *Pinna nobilis* Linnaeus or in shells of oysters or other mollusks.

Melanothamnus japonicus (Harvey) Díaz-Tapia and Maggs showed the highest abundance in 2011 (10%) and decreased to 3.4% in 2021.

Aglaothamnion halliae (Collins) Aponte, D.L. Ballantine and J.N. Norris was first reported in the lagoon in 2017 by molecular analyses ([30] and references therein) and showed a mean frequency of 5.2%. During the surveys of 2018 and 2021, this NIS was found in eight (9.2%) and 10 (11.5%) stations, respectively.

The red alga *Polysiphonia morrowii* is very abundant in hard substrata in spring, whereas this species is rare in soft substrata. Indeed, it was averagely present only in 2.3% of the total stations. The species *Sargassum muticum* is very abundant on hard substrata during the cold season, whereas it almost disappears in summer. During our surveys, it was recorded attached to oyster shells with an increasing frequency in 0–8.0% of the total stations. *Antithamnion nipponicum* Yamada and Inagaki was the last macroalga showing a mean presence higher than 1% (i.e., 1.4%).

The other five NIS were recorded with mean frequencies ranging from 0.3 to 0.9%. These species are usually attached to hard substrata and, occasionally, to shells, stones, or wooden poles, and some of them can be very abundant, such as *Scytosiphon dotyi* M.J. Wynne, *Grateloupia turuturu* Yamada, and *Codium fragile* (Suringar) Hariot.

Figure 3 shows the temporal trend of each species from 2011 to 2021. *Ulva australis*, *Acanthosiphonia echinata*, *Caulacanthus okamurae*, *Osmundea oederi*, *Aglaothamnoin halliae,* and *Sargassum muticum* were characterized by a clear increasing trend, even if *U. australis* and *S. muticum* had been already present in the lagoon for many years. *Melanothamnus japonicum* showed a progressive inverse trend, whereas the other species had minor changes or were recorded only occasionally.

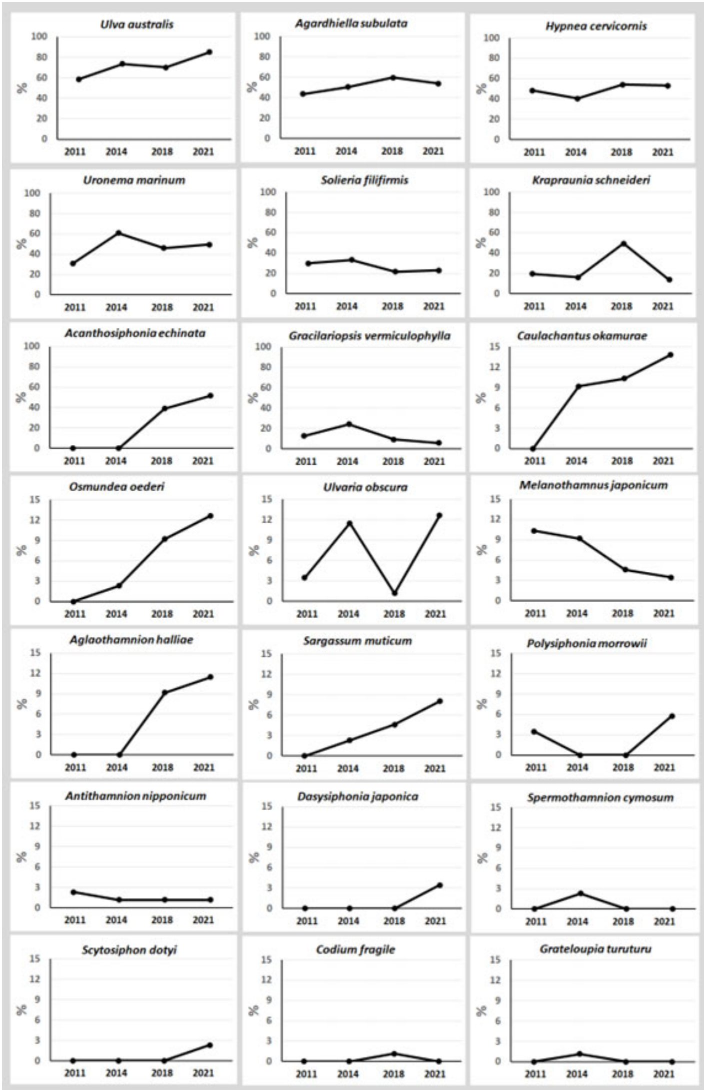

Figure 3. Per cent trends of the 21 macroalgal non-indigenous species (NIS) in the 87 stations monitored in 2011, 2014, 2018, and 2021.

4. Discussion

The lagoon of Venice is the second hot spot of macroalgal NIS in the Mediterranean Sea, just behind the lagoon of Thau in [19–21], with the most recent allochthonous species list updated by Sfriso et al. (2020) [30]. In this study, the total standing crop of each species has also been determined by considering both the soft and hard substrata of the entire lagoon. Overall, 29 taxa have been listed and their biomass has been calculated to be ca. 1/3 of the total macroalgal biomass present in the lagoon.

In particular, considering the soft substrata of the 87 surveyed stations, 21 taxa have been recorded and some of them are new species, recently identified by molecular (i.e., *Acanthosiphonia echinata* [31], *Caulacanthus okamurae* [32]), or morphological analyses (i.e., *Osmundea oederi* (Gunnerus) G. Furnari).

Other NIS represent species already present in the lagoon, but previously indicated with different taxonomic names, such as the species *Ulva australis* whose origin is not well-known. The last classification of this species derives from numerous taxonomic revisions or misapplied names of laminar taxa, formerly cited as *Ulva lactuca* Linnaeus, *Ulva rigida* C. Agardh, *Ulva pertusa* Kjellman, and *Ulva laetevirens*, which also includes numerous forms and varieties [42]. Based on a study by Phillips (1988) [43] regarding the southern Australian and European *Ulva* species, Furnari et al. (1999, 2003) [44,45] temporarily assigned all the Mediterranean *U. rigida* records to *U. laetevirens*, pending taxon revision. Successively, Sfriso (2010) [46] suggested the coexistence of both *Ulva rigida* and *Ulva laetevirens,* based on the morphological differences in the thallus basal region, and showed that *Ulva laetevirens* was more abundant in areas where nutrient levels were low. Later, for the first time, Manghisi et al. (2011) [47] reported the presence of *Ulva pertusa* in the lagoon of Venice by morphological and reproductive observations, whereas a molecular study by Wolf et al. (2012) [48] on *Ulva* biodiversity recorded the presence of both *Ulva pertusa* and *Ulva rigida*. Almost simultaneously, Coucerio et al. (2011) [49] demonstrated that *U. pertusa* and *U. australis* are conspecific and Kraft et al. (2010) [50] confirmed that *U. rigida* and *U. australis* are two distinct species. However, in Womersley (1984) [51] and in Guiry and Guiry (2023) [42], *U. laetevirens* was synonymized with *Ulva australis*. Consequently, *U. australis* presence in the Venice Lagoon dates back before 2007 [52] and, with the reduction of the basin trophic status [40], this species is progressively replacing *U. rigida,* which grows better in eutrophic waters [46]. In light of this new nomenclatural change, *U. australis* has become the most common NIS in the Venice Lagoon. In fact, it was recorded from 59% (2011) to 85% (2021) of the considered stations, with an increasing trend probably due to the reduction of the lagoon trophic conditions [37], also confirmed by the reduction of *U. rigida* records (54% in 2011, 47% in 2014, 36% in 2018 and 33% in 2021).

Gracilariopsis vermiculophylla, a highly invasive species introduced from Virginia by oyster and other mollusk import [53–55], is the most abundant NIS reported by Sfriso et al. (2020) [30], reaching a standing crop of approx. 66,383 tonnes on a fresh weight basis (FWT) (Table 1). This species was first recorded in 2008 as *Gracilaria vermiculophylla* (Ohmi) Papenfuss both in some lagoons and ponds of the Po Delta and in eutrophic and choked areas of the central Venice Lagoon basin, where it has rapidly become the most abundant NIS in the following years. *G. vermiculophylla* mainly grows free-floating on bottoms characterized by fine sediments and can reach biomasses of 8–10 kg $FWTm^{-2}$. Its highest spread occurred in 2014, with the colonization of 21 stations, but it progressively reduced its presence (5 stations only) in the following years, with a biomass rarely exceeding 2–3 kg $FWTm^{-2}$.

Agardhiella subulata and *Hypnea cervicornis* are other two free-floating species, probably introduced by aquaculture; the first one of pantropical origin, was first recorded by Curiel et al. (2003) [56] and the second one, native from Korea, was identified as *H. flexicaulis* Y. Yamagishi and M. Masuda by molecular analyses ([30] and references therein). Both species have colonized the entire lagoon and therefore they can be considered invasive to this basin. They have been recorded on average in 45 (52% of the total) and 43 (49%) stations, respectively, confirming that they represent very widespread and well-established NIS both on soft and hard substrata of the lagoon. Both species showed the highest distribution in 2018 and decreased slightly during the following year, probably because of unfavorable meteorological conditions.

Solieria filiformis is another abundant free-floating species of Atlantic origin (3768 FWT tonnes in 2014 [30]). It was first recorded in the Venice Lagoon by Curiel et al. (2005) [57] and reached the maximum distribution in 2014 (29 stations). As the two previous NIS, it is a well-established species, present in the whole lagoon, which preferentially colonizes choked areas characterized by fine sediments.

Surprisingly, the fourth most common species is *Uronema marinum,* a very small taxon epiphytic on larger macroalgae and native to Australian waters. The biomass of this NIS was estimated to be approx. 8.1 tonnes FWT in 2014 [30], when it showed the highest spread (61% of the total stations), almost doubling the values recorded in 2011 (31%). In 2018 and 2021, *U. marinum* distribution was quite similar, since it colonized 54% and 53% of the considered stations, respectively. However, this species showed negligible biomass due its microscopic size, being characterized by filaments approx. 100–300 (500) µm long and 8–12 (15) µm wide, composed of 3–20 (30) subcylindrical cells, more elongated (1.5–4 times) and wider in the distal portion ([30] and references therein). *U. marinum* filaments colonize mostly choked areas, where they can be single or isolated or form dense hairlike covers, especially on macroalgal species of Gracilariaceae, Solieriaceae, and Cladophoraceae.

Polysiphonia morrowii, *Melanothamnus japonicum*, *Kapraunia schneideri* and *Acanthosiphonia echinata* are polysiphonous taxa growing on hard substrata. *P. morrowii* is a well-established cosmopolitan species, first recorded in 1999 by Curiel et al. (2001) [58] and now spread in the whole lagoon. It is very abundant during the spring season, in docks of Venice historical center and islands and in the breakwaters along the main canals (517 tonnes in 2014 [30]), while, during late spring-early summer, it has been recorded only occasionally in 2.3% of the stations.

Melanothamnus japonicus, introduced with aquaculture from Japan, Korea, and British Columbia, was first reported in the Mediterranean Sea in 2018 ([30] and references therein). However, this species was misidentified with *M. harveyi* (Bailey) Díaz-Tapia and Maggs, previously recorded in the Venice Lagoon as *Polysiphonia harvey* Bailey since 1998 [59]. *M. japonicus* has shown a decreasing trend from 2011 (9 stations) to 2021 (3 stations).

Kapraunia schneideri, also introduced with aquaculture from North Carolina (USA), was first reported in 2018 as *Polysiphonia schneideri* Stuercke and Freshwater ([30] and references therein). However, it was present in the lagoon also in the past when it was misidentified with *Polysiphonia denudata* (Dillwyn) Greville *ex* Harvey in Hooke. This NIS showed a peak in 2018, when it colonized 43 stations (49% of the total), whereas it has been recorded only in 12–17 stations during the other surveys.

Finally, *Acanthosiphonia echinata* is a NIS introduced with aquaculture from the western Atlantic [31] and it represents a new entry in the lagoon, where it has been reported only since 2014. Indeed, it can be easily determined also morphologically by the numerous scar cells and cicatrigenous branches arising from them. As expected for a new entry, *A. echinata* has rapidly spread in the lagoon, colonizing 34 and 45 stations in 2018 and 2021, respectively.

Aglaothamnion halliae ([30] and references therein) (introduced from Florida), *Caulachantus okamurae* [32] (of Indo/western Pacific origin) and *Osmundea oederi* (from the Atlantic) are other recently reported species. *C. okamurae* and *O. oederi* have been present in the lagoon at least since 2014, but they were misidentified with *Caulachantus ustulatus* (Turner) Kützing and *Osmundea truncata* (Kützing) K.W. Nam and Maggs, respectively, two species included in the Venetian flora for several years [52]. *Aglaothamnion halliae* is a new entry, recorded since 2016 ([30] and references therein), whose distribution is rare and restricted to eutrophic and chocked areas, especially in the central lagoon. It was recorded in 8 (2018) and 10 (2021) stations, but its biomass is negligible since it is a small species attached to larger macroalgae or shells.

Antithamnion nipponicum and *Spermothamnion cymosum* are two small species only occasionally sampled as epiphytes on larger taxa. *A. nipponicum*, introduced from Atlantic/Indian regions by aquaculture activities, was reported in the lagoon in 1994 as *A. pectinatum* (Montagne) Brauner [60]. It is a cryptic species, reported also as *A. hubbsii* E.Y. Dawson, which is present only occasionally attached to the basal region of many larger macroalgae. Athanasiadis (2009) [61] recognized *A. hubbsii* as a distinct species from *A. nipponicum*, although some recent authors [62] put the two species in synonymy.

Spermothamnion cymosum, an SW Pacific species whose introduction vector is unknown, was recorded in 2010 at the Certosa island, near the historical center of Venice, by Armeli-Minicante (2013) [63]. In the following years, some occasional samples were found only in the same restricted area and, during the four lagoon surveys, it was found in two stations in 2014.

Scytosiphon dotyi M.J. Wynne is a circumboreal Phaeophycea, introduced with aquaculture and first recorded by Curiel et al. (1996) [60] in 1996. In late winter-early spring, this species rapidly colonized the hard and soft substrata of the lagoon, reaching a standing crop of 4775 tonnes FWT in 2014 [30]. In the following years, as other cold-adapted Phaeophyceae, *S. dotyi* has rapidly declined and now it colonizes mostly the hard substrata with a very low biomass. In our surveys its presence was negligible.

The Chlorophycea *Ulvaria oscura* is a very variable established species, firstly recorded in 2000 ([30] and references therein) as *Monostroma obscurum* (Kützing) J. Agardh. This is a circumboreal species, introduced with aquaculture, which usually grows within the seagrass prairies. It was relatively common in 2014 and 2021, especially in the stations colonized by *Cymodocea nodosa* (Ucria) Ascherson and *Zostera marina* Linnaeus, where it developed extensive blooms in some years. Indeed, in 2014 the standing crop of *U. obscura* in the lagoon was estimated to be approx. 323 tonnes FWT and was represented by small and rare thalli growing at the base of plant shoots.

Sargassum muticum (Yendo) Fensholt is an Atlantic cold-adapted species, introduced with aquaculture and first recorded in the lagoon by Gargiulo et al. (1992) [64]. This species is the biggest macroalga present in the lagoon, with thalli on average 3–5 m long but that can reach 8 m in deeper waters [30]. *S. muticum* mostly grows on Venice and Chioggia docks, almost completely covering the bigger canals of these cities, with concern for the residents as thalli extend up to 20–30 m from the borders. In our surveys, *S. muticum* was recorded only occasionally, because samplings mainly occurred in the warm season, when this brown seaweed was in quiescence.

Dasysiphonia japonica (Yendo) H.-S. Kim is a red algal species, introduced from NW Pacific with aquaculture, which colonizes areas of high ecological value. It was first reported from the Lido Sea coasts in 1999 as *Dasya* sp. ([30] and references therein) and, in 2021, it was recorded only in three stations. *D. japonica* is rather rare in the lagoon soft bottoms, while it mainly grows on hard substrata of the most marinized areas and along the marine coasts.

Finally, *Grateloupia turuturu* Yamada and *Codium fragile* (Suringar) Hariot are other two species very common on Venice Lagoon hard substrata. *G. turuturu,* present in the lagoon since 1989, was recorded as *Grateloupia doryphora* (Montagne) M. Howe by Tolomio (1993) [65]. It is a cold-adapted species from SE Pacific, introduced through aquaculture, which mostly colonizes the eutrophic docks of the cities of Venice, Chioggia, and the Lido Island. Therefore, this NIS is difficult to find during late spring and autumn surveys. Among the taxa reported in Table 1, *Codium fragile* is the first alien macroalga recorded in the Venice Lagoon, and it was introduced from NW Pacific through aquaculture activities. Similar to *G. vermiculophylla* and *Sargassum muticum,* it is an invasive species since it was reported from at least ten other areas worldwide according to Galil et al. (2014) [66]. However, its distribution on Venice Lagoon hard substrata is rare, with global biomass estimated to be only approx. 1.25 tonnes FWT in 2014 [30] and is only occasionally sampled in one station in 2018, during our surveys.

Taking into account the 29 macroalgal NIS reported by Sfriso et al. (2020) [30] until 2014, the new records of *Acanthosiphonia echinata*, *Caulacanthus okamurae*, *Osmundea oederi,* and the recent determination of *Neopyropia koreana* (M.S. Hwang and I.K. Lee) L.-E. Yang and J. Brodie (previously reported as *Pyropia olivii* (Orfanidis, Neefus and T.L. Bray) J. Brodie and Neefus), the number of NIS in the Venice Lagoon increased from 29 to 33 taxa in 2021. This number is higher than that recently reported for the Mar Piccolo of Taranto (i.e., 15 NIS [24]), but lower than that recorded in the Lagoon of Thau (i.e., 58 NIS, [21]). However, despite the negative reputation that non-native species generally have among researchers [1–3,20–22,66–69], an evaluation of their environmental impact should be made of species by species.

Luckily, the macroalgal NIS recorded in the Venice Lagoon have not had significant negative impacts on the other species, and, in general, they have increased the macrophyte biodiversity. Indeed, despite the increasing NIS introduction, in 2018 the number of macroalgae in the lagoon reached up to 323 taxa [30] and aquatic angiosperms almost doubled their cover and production in comparison to 2003 [70].

In addition, some taxa have positive effects on the environment or could have important applications. In the Venice Lagoon, *G. vermiculophylla* has replaced Ulvacean taxa in the most turbid and eutrophic areas, due to the high concentration of phycocyanin that gives it a black color (black *Gracilaria*) and to its high resistance to high temperatures, this species has reduced the possible occurrence of hypo-anoxic crises ([30] and references therein). In fact, *G. vermiculophylla* withstands high water temperatures without decomposing, contrarily to the laminar Ulvaceae that degrade already at 25–26 °C. *G. vermiculophylla* is also a pioneer species [71–73], because it colonizes naked bottoms where water turbidity hampers the presence of other macroalgae. Along the coasts of Virginia and North Europe, Nyberg et al. (2009) [71] found that *G. vermiculophylla* beds favored the presence of a high number of hypo-epibenthic taxa, such as Gastropods and Bivalves, whose abundance was positively correlated with the macroalgal biomass. Ramus et al. (2017) [72] reported that, in the presence of turbid waters, this NIS had an overall positive density-dependent impact on many ecosystem services, especially creating nursery areas for many fish and crustaceans. Similarly, a study by Wood and Lipcius (2022) [73] carried out in Chesapeake Bay reported that *G. vermiculophylla* may provide a nursery habitat where eelgrass *Zostera marina* has been extirpated.

In addition, although the reproduction, cultivation, transport, purchase, sale, use, exchange, possession, and release of invasive NIS is generally prohibited by the European Union [74] and subsequent additions, *G. vermiculophylla* is rich in precious substances, useful for the food, cosmetic and pharmaceutical sectors, which should be seriously considered.

Conversely, other NIS species can locally create obstacles to small-scale navigation, such as the invasive *S. muticum*, which mainly colonizes the docks of Venice and Chioggia and some oyster beds in shallow waters. However, *S. muticum* is a cold-adapted species that disappears almost completely in June, leaving only the basal part of 10–15 cm.

The other NIS reported in Table 1 have a negligible impact on the lagoon environment and usually are mixed or seasonally alternate with native species, although many of them are seasonally very spread and abundant. The only potentially dangerous species for the environment is *Ulva australis*, which is strongly invasive in the TWS of the northern Adriatic Sea and is replacing *Ulva rigida* in areas with relatively low trophic levels. However, *U. australis* has a biomass significantly lower compared to that recorded for *U. rigida* in the past [70] and cases of hypo-anoxic conditions, due to its decomposition, are becoming more and more rare.

Finally, some NIS colonize only areas characterized by high ecological conditions and are good indicators of pristine or almost pristine environments, such as in the case of *Dasysiphonia japonica* and *Osmundea oederi*. Both these species grow on hard substrata, perfectly integrated with the other species, in areas characterized by high water renewal, especially near the lagoon mouths. While *D. japonica* is quite rare, *O. oederi* is more common and is found mostly attached to the shells of *Pinna nobilis* Linnaeus within the prairies of *Cymodocea nodosa.* These species can therefore be considered a biodiversity enrichment, without representing any environmental threat.

5. Conclusions

Although the Venice Lagoon has one of the highest numbers of alien macroalgal species worldwide, these NIS have no significant impacts on the local flora, which shows an increasing number of species and a greater diffusion of aquatic angiosperms. Most NIS are widespread in a large part of the lagoon, together with the native species, and do not cause any environmental damage other than a local or temporary reduction of biomass. Some others, such as *G. vermiculophylla*, *Solieria filiformis,* and *Agardhiella subulata,* colonize very turbid areas, where even the Ulvaceae are not able to survive; this avoids recurrent anoxic crises and creates a suitable substrate for the colonization by fish and benthic species, which cannot survive in bare environments. Also, the increasing replacement of *U. rigida* by *U. laetevirens*, which colonizes preferentially less eutrophic environments and has lower biomass, is reducing the risk of hypo-anoxic crises. The most recent introductions of *A. echinata*, *C. okamurae,* and *O. oederi* do not affect these considerations. Also, we expect that future introductions of further macroalgal NIS will not have significant environmental and economic impacts on the Venice Lagoon, contrarily to what happened with the introduction of alien animal species (such as the ctenophore *Mnemiopsis leidyi,* the bivalve *Ruditapes* *philippinarum* and the crab *Callinectes sapidus*) that strongly affected the presence of local fish species and caused a significant damage to the local fishing economy.

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