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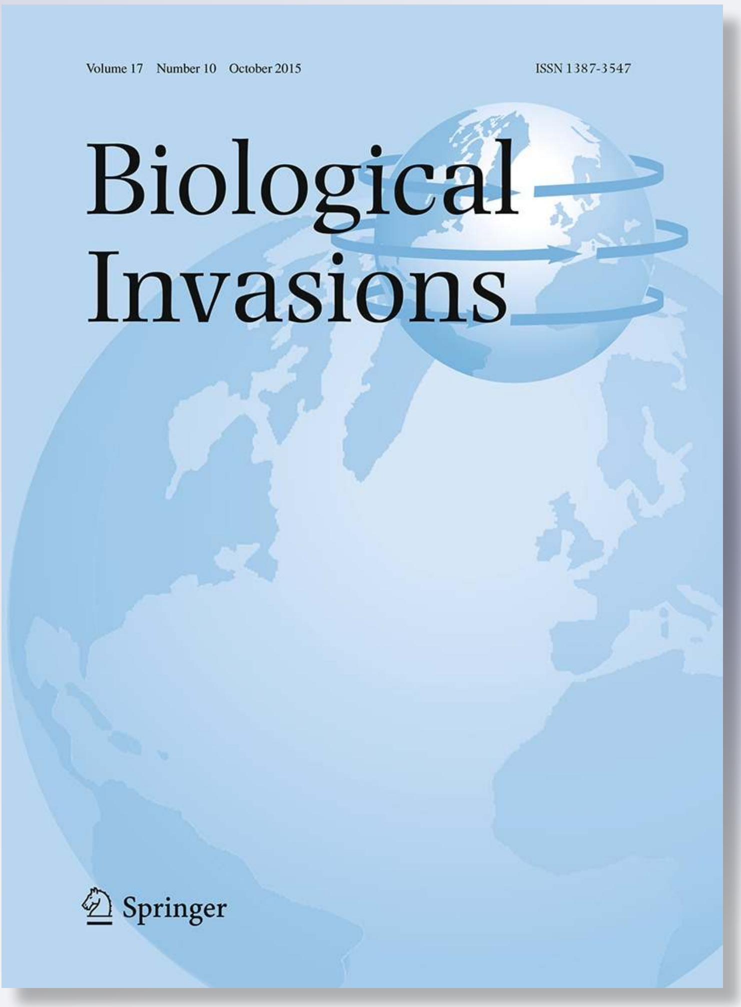

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ORIGINAL PAPER

Current status and trends of biological invasions in the Lagoon of Venice, a hotspot of marine NIS introductions in the Mediterranean Sea

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Abstract This paper provides an updated account of the occurrence and abundance of non-indigenous species (NIS) in an area of high risk of introduction: the Lagoon of Venice (Italy). This site is a known hotspot of NIS introductions within the Mediterranean Sea, hosting all the most important vectors of introduction of marine NIS—shipping, recreational boating, shellfish culture and live seafood trade. The recent literature demonstrates that the number of NIS in Venice is continuously changing, because new species are being introduced or identified, and new evidence shows either an exotic origin of species previously believed to be native, or a native origin of formerly believed "aliens", or demonstrates the cryptogenic nature of others. The number of NIS introduced in the Venetian lagoon currently totals 71, out of which 55 are established. This number exceeds those displayed by some nations like Finland, Portugal or Libya. Macroalgae are the taxonomic group with the highest number of introduced species (41 % of NIS): the most likely vector for their introduction is shellfish culture. The source region of NIS introduced to Venice is mainly represented by other Mediterranean or European sites (76 %). The Lagoon of Venice represents a sink but also a source of NIS in the Mediterranean Sea, as it is the site of first record of several NIS, which have since further spread elsewhere.

Keywords Lagoon of Venice · Non-indigenous species (NIS) · Hotspot of introduction · Shellfish culture · Sink and source

A. Marchini (✉) · J. Ferrario · A. Occhipinti-Ambrogi
Department of Earth and Environmental Sciences, University of Pavia, Via S. Epifanio 14, 27100 Pavia, Italy
e-mail: agnese.marchini@unipv.it

A. Sfriso
Department of Environmental Sciences, Informatics and Statistics, University Ca' Foscari Venezia, Calle Larga S. Marta 2137, 30123 Venice, Italy

Introduction

The global problem of the introduction and spread of non-indigenous species (NIS) is specifically addressed by the Marine Strategy Framework Directive of the European Union (European Commission 2008). Since NIS introduced by human activities may alter the biological, physical–chemical and hydromorphological features of the environment, their abundance and distribution has been included as qualitative Descriptor 2 for the determination of Good Environmental Status (GES). The European Commission Decision (European Commission 2010) set out the following criterion and indicator to be assessed in order to evaluate GES, relevant to Descriptor 2 of the MSFD:

Criterion 2.1 Abundance and state characterization of NIS, in particular of invasive species.

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Indicator 2.1.1 Trends in abundance, temporal occurrence and spatial distribution in the wild of NIS, particularly invasive NIS, notably in risk areas, in relation to the main vectors and pathways of spreading of such species.

The present work specifically addresses the abovementioned criterion and indicator, by updating the knowledge on the presence, abundance and distribution of NIS in a site of proven high invasion risk, the Lagoon of Venice (Italy, northern Adriatic Sea). The Lagoon of Venice has long been acknowledged as a hotspot of introduction of NIS (Sacchi et al. 1990; Mizzan 1999; Occhipinti-Ambrogi 2000a; Occhipinti-Ambrogi and Savini 2003; Sfriso and Curiel 2007; Sfriso et al. 2009; Occhipinti-Ambrogi et al. 2011; Marchini et al. 2013; Sfriso and Marchini 2014). This site has always featured a high concentration of most of the anthropogenic activities acknowledged as major vectors of NIS introduction: shipping, recreational boating, shellfish culture and live seafood trade (Occhipinti-Ambrogi 2000a). The strong propagation pressure caused by the action of these likely vectors of introduction combined with the local environmental conditions make the Lagoon of Venice a highly "invadable" site. In the past decades, the petrochemical industry, the excavation of deep canals to allow navigation through the lagoon, and the discharge of agricultural and domestic waste water leading to increased eutrophication have severely affected the native biota and modified the natural habitats (Occhipinti-Ambrogi 2000a). The resulting high nutrient loads and variable environmental conditions have favoured the establishment and proliferation of new opportunistic species, which have displaced declining native species and/or occupied empty ecological niches (Occhipinti-Ambrogi and Savini 2003). Furthermore, the high availability of artificial substrates is thought to supply suitable habitats for the establishment of newly-arrived species (Glasby et al. 2007; Marchini et al. 2007).

The last comprehensive account on the NIS reported from the Lagoon of Venice was provided by Occhipinti-Ambrogi (2000a). Several new published records from the Venetian lagoon have appeared since then (e.g., Wolf et al. 2011; Keppel et al. 2012; Tagliapietra et al. 2012; Sfriso et al. 2014a; Marchini et al. 2014). Partial updates of the NIS biota of Venice have been presented by Occhipinti-Ambrogi et al. (2011), Sfriso and Facca (2011), Marchini et al. (2013). The recent literature on the subject demonstrates that the number of NIS in Venice is continuously evolving, because new species are being introduced or identified, new taxonomical, biogeographical or molecular evidence shows either an exotic origin of species previously believed to be native, or a native origin of formerly known "aliens", or the cryptogenic nature of others. The continuous update, checking and validation of NIS records is therefore crucial in providing reliable and up-to-date lists of NIS, in order to meet the requirements of the Marine Strategy Directive (Ojaveer et al. 2014).

In the current paper, we present an updated list of NIS recorded in the Lagoon of Venice, extracted from literature surveys. Information on the date of first record, native origin, likely vectors of introduction and population status is also provided (Indicator 2.1.1 of the MSFD).

For all species unintentionally introduced, a detailed analysis of their European and Mediterranean distribution has been carried out, with reference to the timing of introductions, in order to infer the likely source region of NIS Venetian populations, as well as the likely route of secondary spread of NIS first introduced to Venice and which were then spread elsewhere via aquaculture or other vectors.

The results obtained will help to identify the current status and to predict possible future trends of NIS introduction in the Lagoon and spreading elsewhere.

Study area

The Lagoon of Venice (Fig. 1) is a microtidal lagoon of approximately 432 km^2 water surface, divided into three hydrographic basins, each of which is connected to the sea by a mouth: the northern basin (Lido mouth), the central basin, including the town of Venice and the Marghera industrial site (Malamocco mouth) and the Chioggia basin, including the town of Chioggia (Chioggia mouth). The human-induced disturbance is very intense: the hydraulic regime has been changed by the digging of deep canals, influencing the dispersal of pollutants and nutrients both inside and outside the lagoon. Industrial, urban and agricultural discharges are disposed into the lagoon, affecting water and sediment pollution (Occhipinti-Ambrogi and Savini 2003). In addition, the fishing by disruptive dredging

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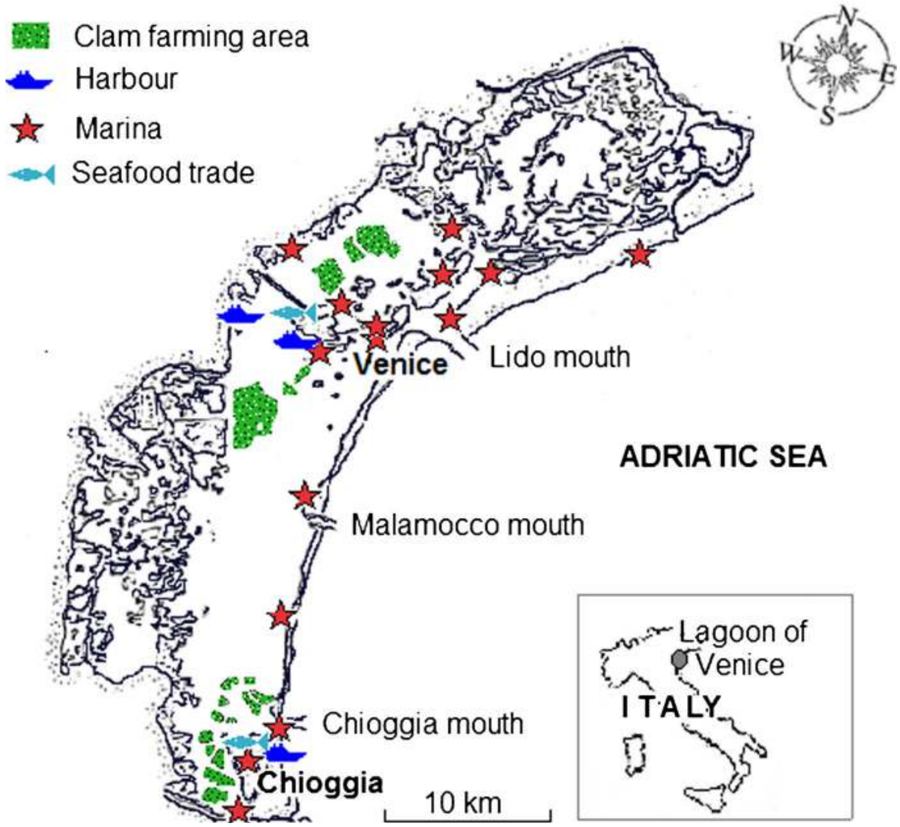

Fig. 1 The Lagoon of Venice, showing location of areas of clam farming, harbours, marinas and berths, and sites of seafood trade and processing

of the clam *Ruditapes philippinarum* (Adams and Reeve 1850), a NIS introduced in the lagoon in 1983 for economic purposes (Cesari and Pellizzato 1985a), spread nutrients (Sfriso et al. 2003) and pollutants (Masiol et al. 2014) into the whole lagoon. Sedimentation rates increased up to 16 times affecting water turbidity, sediment grain-size, macrophyte growth (Sfriso et al. 2005) and benthic macrofauna (Pranovi and Giovanardi 2004).

The Lagoon hosts two harbours, Venice and Chioggia, utilised by both international and local vessels. The harbour of Venice includes two main port areas: a commercial terminal in Marghera, accessible from the Malamocco mouth, and a passenger terminal for cruise ships, ferries and hydrofoils along the western side of Venice historical centre, accessible from the Lido mouth. The commercial terminal is one of the most important harbours in Italy, extending for an area of over 20 km^2 with 30 km of docks. The global economic crisis has affected the shipping traffic of this port, reducing the tonnage of all trade sectors from 28,176,203 in 2000 to 25,349,248 in 2012 and the number of transited vessels from 4767 in 2000 to 3745 in 2012 (Porto di Venezia 2014). The passenger terminal, with its 2,300,000 travellers per year, represents the leading Mediterranean homeport for cruise ships and the European capital of cruise lines (Comitato Cruise Venice 2014), but it also gives rise to safety and environmental concerns, being at the centre of a current economic and political debate. The modern giant cruise ships are believed to threaten the fragile historical city of Venice as their engines shake its foundations and their discharges pollute the waters. The frequent maintenance dredging of the canal used by ships would accelerate the loss of sediment from the bottom of the lagoon (Sfriso et al. 2005), further damaging the environment and the timber poles of the building foundations. For this reason, the Venice Municipality, the Veneto Region and the Italian Parliament are currently discussing the closure of this terminal. Finally, the harbour of Chioggia is mainly devoted to regional traffic (North-Adriatic area) of commercial vessels; recent proposals of development regard the activation of a

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passenger terminal for cruise lines (Porto di Chioggia 2014).

The local traffic of smaller boats, which could also play an important role in the secondary spread of NIS to nearby areas (Minchin et al. 2006; Clarke Murray et al. 2011), is also on the increase. The entire Lagoon currently hosts over 30 marinas and yacht clubs, a number that has increased in recent years from 24 marinas in 2000 to 33 in 2013. The number of moorings has increased accordingly, from 5843 in 2000 to 8427 in 2013 (Pagine Azzurre 2014). In particular, yachting is being encouraged: dedicated berths for yachts and mega-yachts have been placed in some of the most scenic areas of the city of Venice (Porto di Venezia 2014).

Besides intensive shipping and boating, the Lagoon of Venice is also highly exposed to another globally acknowledged vector of NIS introduction: shellfish culture (Minchin 2007; Mineur et al. 2007; Haydar and Wolff 2011). Venice was the leading European site of clam production (Boscolo-Brusà et al. 2013), with 4500 ha devoted to shellfish farms, managed by 497 licensed operators, out of which 253 are in the Chioggia basin (Provincia di Venezia 2014). Most farms rear the Indo-Pacific Manila clam, *R. philippinarum*, which achieved a record production of about 40,000 tonnes yr^{-1} between 1995 and 2000 (Sfriso et al. 2014b). Subsequently, the overexploitation of the free-access fishery, due to indiscriminate exploitation of natural beds, illegal collecting, use of high-impacting harvest gears, lack of efficient programming schedules and inadequate management of nursery areas, caused a strong decline in productivity which decreased to ca. 2000 t $year^{-1}$ in 2012. Since the late '90s (Orel et al. 2000), local authorities have been regulating clam culture activities using techniques based on wild spat harvesting and seeding in licensed culture areas. The availability and quality of wild *R. philippinarum* stocks are the limiting factors for the development of clam culture: farmers are facing the decline of the seed stocks and are often obliged to buy Manila clam seeds from abroad. The amount of seeds imported from foreign hatcheries in 2013 was over 451,000 kg (Provincia di Venezia 2014). The Lagoon of Venice also represents a site of oyster and mussel farming, exporting mollusc juveniles to other Italian farming sites, especially those in Liguria and Sardinia—Western Mediterranean region (Prioli 2008).

The two main urban centres of the Lagoon, Chioggia and Venice, also host facilities for seafood trade and processing, where loading and unloading of live seafood takes place directly on the docks, very close to the lagoon waters (Ferrario et al. 2013). Furthermore, residues of sales of the fish markets are often thrown into the Lagoon canals at the end of the day (Sfriso and Marchini 2014). It has been shown that about 20 edible species of exotic origin are regularly traded live for fish markets and processed near the lagoon canals, and might be accidentally released in the wild. The analysis of their biological and ecological traits showed that they are euryecious species, able to grow on every kind of substrate, to thrive in low salinity and to endure a broad spectrum of water temperatures (Ferrario et al. 2013). Other non-commercial NIS, such as macroalgae used as packaging material for bivalves sold in the fish market, are also likely to be accidentally released in the lagoon waters (Sfriso and Marchini 2014).

Materials and methods

Lists of exotic species from the Lagoon of Venice were obtained from the works of Mizzan (1999) and Occhipinti-Ambrogi (2000a). The scientific literature was surveyed to update the lists with more recent records, as well as to validate the non-indigenous status of the species. The species listed as "valid NIS" are only those with unequivocal identity and non-indigenous status. Consequently, cryptogenic species, or species with uncertain identity (i.e. suspected misidentifications, species complexes, etc.) were excluded. Population status of each species was assessed on the basis of literature data and personal observations using the following categories: established—common (having colonised large areas of the lagoon), established—rare (occurring in restricted areas of the lagoon), not established. Spread ability was assumed as proxy for population size, therefore 'established—common' NIS are considered having high abundance in the lagoon.

In order to identify the most successful "international invaders" that are present in the Lagoon of Venice, the updated list of NIS was compared with the lists provided by Galil et al. (2014) of "widespread NIS". Galil et al. (2014) defined "widespread NIS" as

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those species that have been recorded in 10 or more countries in European Seas, whereas "post-1990 widespread NIS" are species that have been recorded in 5 or more countries since 1990.

The following possible vectors of introduction were assigned to each NIS: "culture", "vessels", "culture, vessels", "other vectors". With the exception of documented intentional introductions for shellfish culture, the vectors of introduction are rarely identified from direct evidence; in most cases, they are inferred from knowledge on the habitat preference and biological traits of a species (Galil et al. 2014). In cases where more than one vector might have operated, as often is the case in the Lagoon of Venice, the introduction is referred to as polyvectic (e.g. "culture, vessels"). Data on the year of first record of all NIS in the Lagoon of Venice, combined with their likely vector of introduction, allowed us to visualize the timeline of introductions in relation to the vectors.

A regression analysis was carried out to estimate the trend of increase in the number of NIS, using the curve estimation tool of the SPSS 13.0 statistical software. The analysis was performed on the total set of NIS and on subsets composed by the established NIS, as well as NIS introduced by culture and by vessels. Furthermore, the dataset was split into two time frames, in order to estimate "historical introductions" and "modern introductions" separately. We set the separation point at year 1966, when the first intentional introduction of the Pacific oyster *Crassostrea gigas* (Thunberg 1793) occurred. Besides witnessing the beginning of importation of exotic shellfish for aquaculture, the 1960s also roughly represent the starting point for the intensification of both shipping traffic and research effort in Venice. Therefore, it is reasonable to foresee a change of slope in the rate of NIS records since that decade.

For all species unintentionally introduced, we performed a more detailed literature analysis, with the aim of reconstructing their introduction history in the context of the Mediterranean Sea (MED) and Western European Margins (WEM, Galil et al. 2014), including the Iberian coast, Celtic Seas, North Sea, Skagerrak, Norwegian Sea, Barents Sea, and the Iceland shelf. The year of first record of a NIS in a location does not always correspond to the real time of its introduction, especially in the case of small-sized species that might have been disregarded or misidentified for a long time (e.g. Marchini et al. 2014; Sfriso et al. 2014a). However, in the absence of more solid evidence, in this work the locality where a NIS was first spotted (i.e. other European/Mediterranean localities) is assumed to represent the first introduction event of that species in WEM, MED. A comparative analysis of first-record years between Venice and other Mediterranean and Western European locations was then performed, resulting in the identification of NIS that have:

(a) arrived in the Lagoon of Venice after having already been introduced to other Mediterranean or Western European sites;
(b) arrived in the Lagoon of Venice first, and then spread to other Mediterranean or Western European sites.

The results of this comparison allowed us to make inferences on (a) the presumable source region of Venice NIS, and (b) the role of Venice as a source region for NIS that have further spread elsewhere in the MED and WEM. Years of first records in other Mediterranean and European countries were extracted from AquaNIS, an on-line information system for aquatic NIS from coastal environments of Europe and adjacent regions (Olenin et al. 2014).

Results

The literature survey allowed us to update the number of NIS introduced in the Lagoon of Venice, resulting in 71 species: 29 macroalgae, 13 molluscs, 13 crustaceans, 4 annelid worms, 4 cnidarians, 4 tunicates, 3 bryozoans, and 1 pycnogonid (Table 1). Only 3 NIS were intentionally introduced for culture purposes: the Manila clam *R. philippinarum*, the Pacific oyster *C. gigas*, and the rock oyster *Saccostrea glomerata* (Gould 1850).

Only a few species of the present inventory are documented as "not established" NIS: this category includes the rock oyster *S. glomerata,* now being extinct after unsuccessful culture experiments, and species represented by single or a few specimens only recorded once or a few times, i.e. *Callinectes danae* Smith 1869, *Callinectes sapidus* Rathbun 1896, *Charybdis (Charybdis) lucifera* (Fabricius 1798), *Cuthona perca* (Er. Marcus 1958), and *Haminoea japonica* Pilsbry 1895. Conversely, 55 NIS have found favourable environmental conditions for survival and reproduction, thus generating established populations

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Table 1 List of NIS in the Lagoon of Venice, ordered by year of first record; W = "widespread NIS", PW = "post-1990 widespread NIS" sensu Galil et al. (2014); MED = first Mediterranean record; EU = first European record. Population status categories: EC = established, common; ER = established, rare; NE = not established; U = unknown

Taxon	Species			Year of first record		Native origin	Likely vector	Population status	References
Molluscs	*Littorina saxatilis* (Olivi 1792)			1792	MED	NE Atlantic	Vessels	EC	Olivi (1792)
Crustaceans	*Amphibalanus eburneus* (Gould 1841)	as *Balanus eburneus*		Nineteenth century		NW Atlantic	Vessels	EC	Relini (1969)
Cnidarians	*Diadumene lineata* (Verrill 1869)	as *Haliplanella luciae*		1925	MED	NW Pacific	Vessels	EC	Pax (1925)
Annelid worms	*Ficopomatus enigmaticus* (Fauvel 1923)	as *Mercierella enigmatica*	W	1934		Southern Ocean	Vessels	EC	Fauvel (1938)
Annelid worms	*Hydroides dianthus* (Verrill 1873)		W	1934		W Atlantic	Vessels	EC	Fauvel (1938)
Annelid worms	*Hydroides elegans* (Haswell 1883)		W	1934		SW Pacific	Vessels	EC	Fauvel (1938)
Bryozoans	*Zoobotryon verticillatum* (Delle Chiaje 1822)	misidentified as an algae	W	1937		Tropical E Atlantic	Vessels	ER	Neviani (1937)
Crustaceans	*Callinectes sapidus* Rathbun 1896		W	1949	MED	W Atlantic	Vessels	NE	Mizzan (1993)
Molluscs	*Crassostrea gigas* (Thunberg 1793)	as *Gryphaea* sp.	W	1966		NW Pacific	Culture (Intentional)	EC	Matta (1969)
Tunicates	*Styela plicata* (Lesueur 1823)			1971		SE Asia	Vessels	EC	Brunetti (1979)
Tunicates	*Perophora multiclathrata* (Sluiter, 1904)	as *Perophora viridis*		1973		Cosmopolitan	Vessels	U	Brunetti and Menin (1977)
Molluscs	*Anadara kagoshimensis* (Tokunaga 1906)	as *Scapharca inaequivalvis*		1976		NW Pacific	Vessels	EC	Mizzan (1999)
Molluscs	*Cuthona perca* (Er. Marcus 1958)			1976	EU	Indo Pacific	Vessels	NE	Perrone (1995)
Macroalgae	*Codium fragile fragile* (Suringar) Hariot	as *C. fragile*, *C. fragile tomentosoides*	W	1978		NW Pacific	Culture	EC	Sfriso (1987)
Macroalgae	*Colaconema codicola* (Børgesen) H. Stegenga, J.J. Bolton and R.J. Anderson			1978		Subcosmopolitan	Culture	U	Sfriso et al. (2002)
Cnidarians	*Garveia franciscana* (Torrey 1902)			1978	MED	Indo Pacific	Vessels	ER	Morri (1982)
Pycnogonids	*Ammothea hilgendorfi* (Böhm 1879)			1979	MED	Indo Pacific	Vessels	ER	Krapp and Sconfietti (1983)
Macroalgae	*Antithamnionella elegans* (Berthold) J.H. Price and D.M. John			1980		Atlantic	Unknown	ER	Sfriso (1987)
Crustaceans	*Callinectes danae* Smith 1869			1981	EU	W Atlantic	Vessels	NE	Mizzan (1993)

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Table 1 continued

Taxon	Species			Year of first record		Native origin	Likely vector	Population status	References
Crustaceans	*Paracerceis sculpta* (Holmes 1904)			1981		Pantropical	Culture, Vessels	U	Forniz and Sconfietti (1983)
Molluscs	*Rapana venosa* (Valenciennes 1846)			1981		NW Pacific	Vessels	ER	Cesari and Pellizzato (1985b)
Bryozoans	*Tricellaria inopinata* (d'Hondt and Occhipinti-Ambrogi 1985)		W	1982	EU	Indo Pacific	Culture, Vessels	EC	d'Hondt and Occhipinti Ambrogi (1985)
Molluscs	*Ruditapes philippinarum* (Adams and Reeve 1850)	as *Tapes philippinarum*	W	1983		Indo Pacific	Culture (Intentional)	EC	Cesari and Pellizzato (1985a)
Molluscs	*Saccostrea glomerata* (Gould 1850)	as *S. commercialis*		1984		SW Pacific	Culture (Intentional)	NE	Cesari and Pellizzato (1985a)
Molluscs	*Bursatella leachii* Blainville 1817	as *B. leachi leachi*	W	1985		Circumtropical	Suez Canal, Vessels	ER/U	Cesari et al. (1986)
Macroalgae	*Grateloupia turuturu* Yamada	as *G. doryphora*		1989		SE Pacific	Culture	EC	Tolomio (1993)
Crustaceans	*Acartia (Acanthacartia) tonsa* Dana 1849	as *Acartia tonsa*	W	1992		Pantropical	Culture, Vessels	EC	Camatti et al. (2000)
Crustaceans	*Dyspanopeus sayi* (Smith 1869)			1992	MED	NW Atlantic	Culture, Vessels	EC	Froglia and Speranza (1993)
Macroalgae	*Halothrix lumbricalis* (Kützing) Reinke			1992		Circumboreal	Unknown	U	Gargiulo et al. (2000)
Molluscs	*Haminoea japonica* Pilsbry 1895	as *H. callidegenita*		1992	EU	NW Pacific	Culture	NE	Alvarez et al. (1993)
Macroalgae	*Sargassum muticum* (Yendo) Fensholt		W	1992		Atlantic, Pacific	Culture	EC	Gargiulo et al. (1992)
Macroalgae	*Undaria pinnatifida* (Harvey) Suringar			1992		Atlantic, Pacific	Culture	EC	Rismondo et al. (1993)
Molluscs	*Xenostrobus securis* (Lamarck 1819)			1992	EU	Pacific	Culture, Vessels	ER	Sabelli and Speranza (1994)
Tunicates	*Botrylloides violaceus* Oka 1927		PW	1993	EU	Pacific	Culture	EC	Zaniolo et al. (1998)
Bryozoans	*Celleporella carolinensis* Ryland 1979			1993	EU	W Atlantic	Vessels	U	Occhipinti-Ambrogi and d'Hondt (1995–1996)
Cnidarians	*Diadumene cincta* Stephenson 1925			1993		NE Atlantic	Suez Canal, Vessels	EC	Birkemeyer (1995–1996)
Macroalgae	*Antithamnion hubbsii* E.Y. Dawson	as *A. pectinatum*		1994		Atlantic, Indian	Culture, Vessels	EC	Curiel et al. (1996a)

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Table 1 continued

Taxon	Species			Year of first record		Native origin	Likely vector	Population status	References
Crustaceans	*Caprella scaura* Templeton 1836 sensu lato		W, PW	1994	EU	Indo Pacific	Culture, Vessels	EC	Mizzan (1999)
Macroalgae	*Antithamnionella spirographidis* (Schiffner) E.M. Wollaston			1995		Indo Pacific	Culture, Vessels	EC	Curiel et al. (1996b)
Macroalgae	*Bonnemaisonia hamifera* Hariot		W	1995		Indo Pacific	Culture, Vessels	EC	Curiel et al. (1996b)
Macroalgae	*Botrytella parva* (Takamatsu) H.-S. Kim	as *Sorocarpus* sp.		1996	EU	NE Pacific	Culture	EC	Curiel et al. (1999)
Macroalgae	*Leathesia marina* (Lyngbye) Decaisne			1996		Atlantic, Pacific	Culture	ER	Bellemo et al. (1999)
Macroalgae	*Scytosiphon dotyi* M.J. Wynne			1996		Circumboreal	Culture	EC	Curiel et al. (1996b)
Macroalgae	*Neosiphonia harveyi* (J.W. Bailey) M.-S. Kim, H.-G. Choi, Guiry & G.W. Saunders		W	1998		NW Pacific	Culture	EC	Bellemo et al. (1999)
Macroalgae	*Heterosiphonia japonica* Yendo	as *Dasyopsis spinella*	W	1999		NW Pacific	Culture	EC	Sfriso et al. (2002)
Annelid worms	*Ophryotrocha japonica* Paxton and Åkesson 2010			1999	EU	Pacific	Vessels	U	Simonini (2002)
Macroalgae	*Polysiphonia morrowii* Harvey			1999	EU	Cosmopolitan	Culture	EC	Curiel et al. (2002)
Molluscs	*Anadara transversa* (Say 1822)	as *Anadara demiri*		2000		W Atlantic	Culture, Vessels	EC	Mizzan (2002)
Macroalgae	*Lomentaria hakodatensis* Yendo			2000		Pacific	Culture, Vessels	EC	Curiel et al. (2006)
Macroalgae	*Ulvaria obscura* (Kützing) P. Gayral ex C. Bliding	as *Monostroma obscurum*		2000		Circumboreal	Culture	EC	Sfriso et al. (2002)
Molluscs	*Arcuatula senhousia* (Benson in Cantor 1842)	as *Musculista senhousia*		2001		SW Pacific	Culture	EC	Mizzan (2002)
Crustaceans	*Rhithropanopeus harrisii* (Gould 1841)		W	2002		NW Atlantic	Culture, Vessels	EC	Mizzan (2005)
Macroalgae	*Agardhiella subulata* (C. Agardh) Kraft and M.J. Wynne			2003		Pantropical	Culture	EC	Curiel et al. (2005)
Macroalgae	*Aglaothamnion feldmanniae* Halos			2003		NE Atlantic	Vessels	ER	Curiel et al. (2003)
Macroalgae	*Solieria filiformis* (Kützing) P.W. Gabrielson			2003		Atlantic	Culture, Vessels	EC	Curiel et al. (2005)
Crustaceans	*Eriocheir sinensis* H. Milne Edwards 1853		W	2005		NW Pacific	Live food trade	NE/ER	Mizzan (2005)

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Table 1 continued

Taxon	Species			Year of first record		Native origin	Likely vector	Population status	References
Crustaceans	*Paranthura japonica* Richardson 1909			2005	MED	NW Pacific	Culture	EC	Marchini et al. (2014)
Crustaceans	*Charybdis (Charybdis) lucifera* (Fabricius 1798)			2006	EU	Indo Pacific	Vessels	NE	Mizzan and Vianello (2008–2009)
Macroalgae	*Gracilaria vermiculophylla* (Ohmi) Papenfuss		W, PW	2008		NW Pacific	Culture	EC	Sfriso et al. (2010)
Macroalgae	*Grateloupia yinggehaiensis* H.W. Wang and R.X. Luan			2008	EU	Indo Pacific	Culture	ER	Wolf et al. (2014)
Macroalgae	*Uronema marinum* Womersley			2008		SW Pacific	Culture	EC	Sfriso et al. (2014a)
Macroalgae	*Hypnea flexicaulis* Y. Yamagishi and M. Masuda			2009	EU	Indo Pacific	Culture, Vessels	EC	Wolf et al. (2011)
Molluscs	*Polycera hedgpethi* Er. Marcus 1964			2009		NE Pacific	Culture, Vessels	ER	Keppel et al. (2012)
Tunicates	*Didemnum vexillum* Kott 2002		PW	2010	MED	SW Pacific	Culture, Vessels	EC	Tagliapietra et al. (2012)
Macroalgae	*Pyropia yezoensis* (Ueda) M.S. Hwang and H.G. Choi			2010		N Pacific	Culture	ER	Armeli-Minicante (2013a)
Macroalgae	*Spermothamnion cymosum* (Harvey) De Toni			2010	EU	SW Pacific	Unknown	ER	Armeli-Minicante (2013b)
Macroalgae	*Ulva californica* Wille			2011	MED	W Pacific	Culture, Vessels	EC	Wolf et al. (2012)
Macroalgae	*Ulva australis* Areschoug	as *U. pertusa*		2011		Indo Pacific	Culture, Vessels	ER	Manghisi et al. (2011)
Crustaceans	*Ianiropsis serricaudis* Gurjanova 1936			2012	MED	NW Pacific	Culture, Vessels	EC	Marchini et al. (2015)
Crustaceans	*Palaemon macrodactylus* Rathbun 1902			2012		W Pacific	Vessels	U	Cavraro et al. (2014)
Cnidarians	*Pelagia benovici* Piraino, Aglieri, Scorrano and Boero 2014			2013	EU	Unknown	Vessels	U	Piraino et al. (2014)

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that in many cases have managed to colonise large areas of the basin (established—common: 59 % of the whole dataset).

Twenty-two NIS present in the Lagoon of Venice are "widespread NIS" on the European scale, i.e. either NIS recorded in 10 or more countries in European seas or recorded in 5 or more countries since 1990 (the latter case is called "post-1990 widespread NIS"). The first set includes 19 species (Table 1), with 2 species being also "post-1990 widespread NIS": the amphipod *Caprella scaura* Templeton 1836 (first European record: Lagoon of Venice, 1994) and the Rhodophycea *Gracilaria vermiculophylla* (Ohmi) Papenfuss (first European record: Oosterschelde delta, Netherlands, 1994). Three more NIS, the decapod *Palaemon macrodactylus* Rathbun 1902 and the ascidians *Botrylloides violaceus* Oka 1927 and *Didemnum vexillum* Kott 2002, present in Europe since 1999, 1993 and 1998, respectively, have spread to five or more countries and are therefore considered "post-1990 widespread NIS". The records of *B. violaceous* and *D. vexillum* in the Lagoon of Venice represent the first ones for Europe and the Mediterranean, respectively.

The recorded introduction events range from the fifteenth century, the supposed time of entry for the gastropod *Littorina saxatilis* (Olivi 1792), to November 2013, when a new jellyfish species, *Pelagia benovici* Piraino, Aglieri, Scorrano and Boero 2014, was observed for the first time. The number of introductions has steadily increased over the decades (Fig. 2a), both for all NIS and established NIS, following an exponential-like trend. However, regression analysis for all NIS shows that the exponential model matches the observed data only approximately ($R^2 = 0.835$) (Table 2). A best-fitting model is obtained if the dataset is split into two time frames, one including "historical introduction events" (before 1966) and the other including "modern introduction events" (after 1966). The linear regression model shows a very good fit especially in the second time frame ($R^2 = 0.980$). The slope of this linear trend is rather steep: 1.47, meaning almost 3 new NIS every 2 years. As regards established NIS, the exponential model shows a good fit in all cases (whole time frame: $R^2 = 0.822$ and second time frame $R^2 = 0.986$).

The Pacific region is the native area for the majority of NIS recorded in Venice (about 37 %), followed by the Atlantic region (20 %) and Indo-Pacific region (about 17 %). The vector responsible for the highest number of introductions is "culture", alone (34 %) or combined with shipping ("culture, vessels": 28 %). Figure 2b clearly shows that culture-associated NIS have started to appear in the 1970's, after the introduction of the Pacific oyster, and have dramatically increased in the following decades. Shipping traffic has also provided a relevant contribution to NIS introductions in Venice (31 %), representing the most important vector up until the past decade (Fig. 2b). Regression analysis shows that both vectors have followed an exponential trend of NIS increase (Table 2), higher for culture ($b_1 = 0.074$) than for vessels ($b_1 = 0.010$).

The comparison of years of first record between Venice and other Mediterranean and Western European sites was performed on the unintentionally introduced NIS (therefore excluding *C. gigas*, *R. philippinarum* and *S. glomerata*). Two more species were also excluded: the "historical" NIS *Amphibalanus eburneus* (Gould 1841), because it was impossible to define the precise timing of its introduction in Venice and elsewhere, and the polychaete *Ophryotrocha japonica* Paxton and Åkesson 2010, because it was found at the same time in Venice as well as in other Italian harbours and lagoons (Simonini 2002). Within the 66 remaining NIS, 41 were already known from other localities in the MED and/or WEM, while for 25 of them Venice represents the site of first Mediterranean record. The latter group also includes 15 first European records. As regards the first records of the 41 NIS already known in the MED or WEM, 28 had first been recorded in the MED, out of which 13 were in France (Lagoon of Thau area). 23 more NIS had been previously seen in the WEM (Fig. 3). It means that the likely source region of the majority (77 %) of Venice populations of NIS are other European sites, with France playing a prominent role.

As regards the 25 NIS whose first Mediterranean record was in Venice, 11 have not (yet) spread anywhere else in the Mediterranean region while 14 were found elsewhere in the Mediterranean right after the Venetian record, and 5 also in the WEM (Fig. 4; Table 3). The most noteworthy cases include the Indo Pacific bryozoan *Tricellaria inopinata* d'Hondt and Occhipinti-Ambrogi (1985), which was a species new to science when it was discovered in Venice for the first time, and is now a very common species in many Mediterranean and European harbours as far as the

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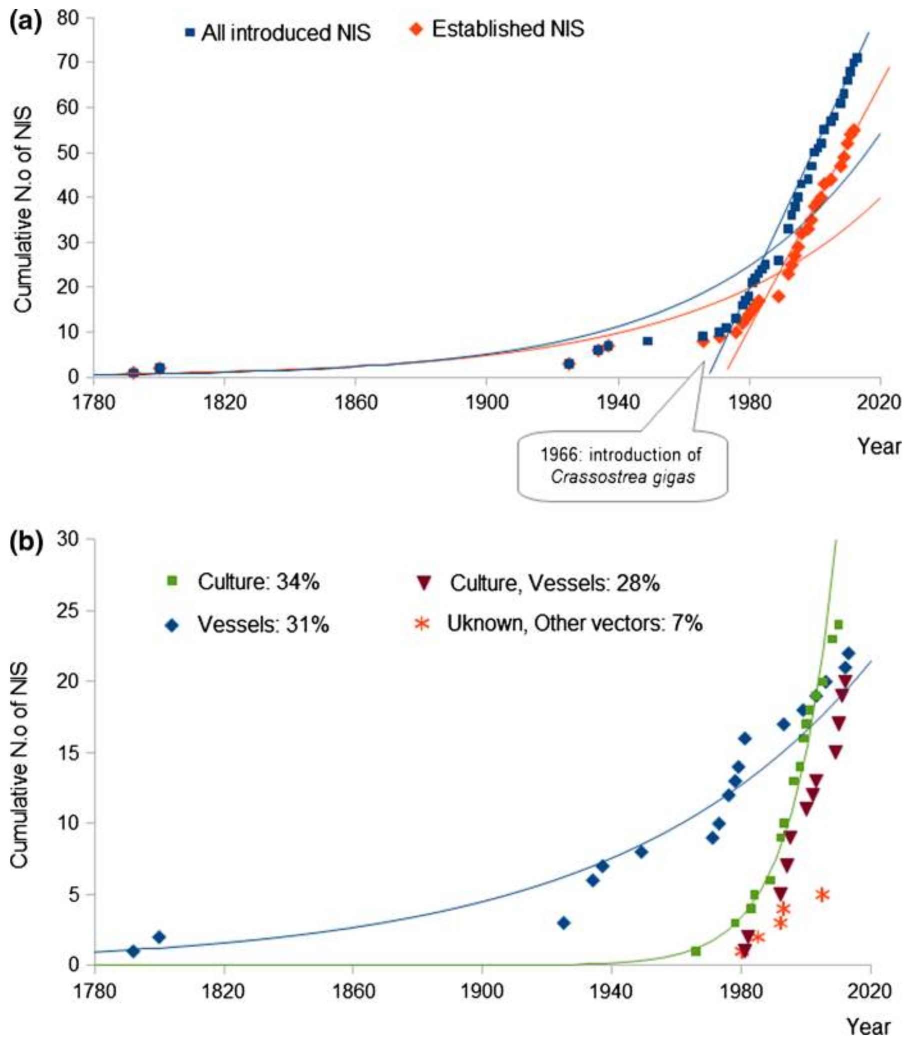

Fig. 2 Cumulative number of NIS introductions in the Lagoon of Venice, based on year of first record of each NIS in the Lagoon. **a** All NIS and established NIS. **b** All NIS classified by their main vectors of introduction. Regression equations are shown in Table 2

North Sea (Johnson et al. 2012), and the above mentioned amphipod *C. scaura*, first spotted in Venice in 1994 and now known in 10 countries including the Atlantic coasts of Spain and Portugal, up to Macaronesia (Ros et al. 2014).

Discussion

The current number (71) of marine and brackish NIS recorded in the Lagoon of Venice is strikingly high: all the Baltic countries, and several other countries in the WEM and MED display fewer NIS than Venice alone (Galil et al. 2014). Therefore Venice confirms its reputation of hotspot of introduction in Italy (Occhipinti-Ambrogi 2000a; Occhipinti-Ambrogi et al. 2011), and equals other globally acknowledged hotspots of introductions of marine NIS in the world, like the Bay of Biscay (Goulletquer et al. 2002) and the Wadden Sea (Buschbaum et al. 2012) in the NE Atlantic, or the San Francisco Bay (Ranasinghe et al. 2005) and Puget Sound (Wonham and Carlton 2005) in the NE Pacific. In the MED, the known hotspots of introduction are the Levantine coasts of the Eastern Mediterranean region (Galil 2006, 2007) and the Lagoon of Thau in France, Western Mediterranean (Boudouresque et al. 2011). Whilst the former mainly hosts NIS of Erythrean origin entering through the Suez Canal, and the latter hosts NIS of North-Western Pacific origin, namely hitch-hickers of the Japanese oyster, Venice is a “melting pot” of non-indigenous biota. In fact, the populations introduced to the Italian Lagoon

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Table 2 Results of regression analysis: best-fit models are shown

Data set	Time-frame	N	Regression model	b_0	Standard error	b_1	Standard error	R^2	Significance level
All NIS	Whole	38	Exponential	3.334E−016	0	0.20	0.002	0.835	***
All NIS	Before 1966	6	Exponential	1.31E−008	0	0.10	0.02	0.835	*
All NIS	After 1966	32	Linear	−2890.658	77.096	1.470	0.039	0.980	***
Established NIS	Whole	32	Exponential	1.799E−014	0	0.17	0.001	0.822	***
Established NIS	Before 1966	5	Exponential	4.197E−008	0	0.10	0.03	0.806	*
Established NIS	After 1966	27	Exponential	1.217E−038	0	0.045	0.001	0.986	***
All NIS introduced by culture	Whole	16	Exponential	4.54E−064	0	0.074	0.003	0.978	***
All NIS introduced by vessels	Whole	18	Exponential	8.287E−011	0	0.01	0.001	0.921	***

Linear model: $Y = b_0 + b_1X$; exponential model: $Y = b_0 \exp(b_1X)$

Significance level: * $p < 0.05$; ** $p > 0.005$; *** $p < 0.001$

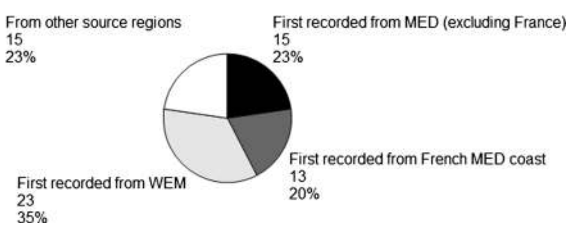

Fig. 3 Location of first European record of NIS introduced to the Lagoon of Venice. "Other source regions" may include the native region of a NIS or other world regions where the NIS has been introduced. Data refer to NIS unintentionally introduced

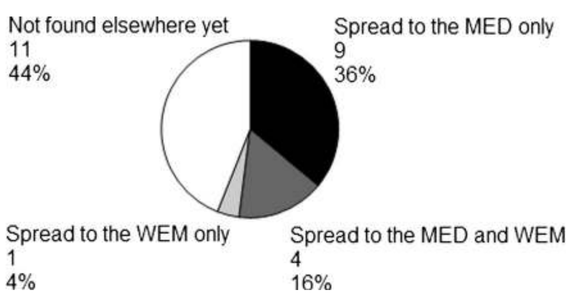

Fig. 4 Supposed secondary spread of NIS introduced to the Lagoon of Venice as first Mediterranean record. Data refer to NIS unintentionally introduced

are native to tropical, subtropical and temperate regions from oceans all over the world (Table 1), resulting from the combination of multiple vectors of introduction operating in this site. Furthermore, the Lagoon hosts species with a salinity preference range varying from oligohaline—e.g. *Ficopomatus enigmaticus*, *Garveia franciscana* (Torrey 1902), *Xenostrobus securis* (Lamarck 1819) to euhaline—e.g. *Anadara transversa* (Say 1822). The variety of habitats situated in the Lagoon of Venice enables a variety of organisms with different requirements and ranges of environmental tolerance to establish themselves there: indeed, this is one of the characteristics of "invader friendly site" (Zaiko et al. 2007). The high rate of establishment success of the NIS reported from Venice (see Table 1, species labelled as EC or ER) indicates, as already documented by Occhipinti-Ambrogi (2000a), that the Lagoon of Venice presents a combination of conditions that have contributed to its high invasion rate: strong natural and human-induced disturbance, high propagule pressure, interaction of multiple vectors.

The updated inventory of NIS in the Lagoon of Venice has more than doubled the number of NIS presented in the previous comprehensive review by Occhipinti-Ambrogi (2000a), which included "only" 30 species. Besides the 28 new NIS discovered after the publication of that inventory, the non-indigenous status of a few species has changed. Four species listed in the former account are now excluded, because they have been shown to be either cryptogenic or of uncertain identity. This set includes 3 macroalgae and 1 crustacean: *Ectocarpus siliculosus* var. *hiemalis* (P.L. Crouan and H.M. Crouan) Gallardo, suspected cryptogenic; *Punctaria tenuissima* (C. Agardh) Greville, possibly conspecific with *P. latifolia* Greville (Kersen 2012); *Radicilingua thysanorhizans* (Holmes) Papenfuss, excluded following Ribera Siguan (2002); *Elasmopus pectenicrus* (Bate 1862), whose status of

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Table 3 Secondary spread of unintentionally introduced NIS whose first Mediterranean or European record has occurred in Venice

Species first recorded in Venice and not known from elsewhere in the Mediterranean Sea	
Ammothea hilgendorfi (Böhm 1879)	
Callinectes danae Smith 1869	
Celleporella carolinensis Ryland 1979	
Charybdis (Charybdis) lucifera (Fabricius 1798)	
Cuthona perca (Er. Marcus 1958)	
Hypnea flexicaulis Y. Yamagishi and M. Masuda	
Ianiropsis serricaudis Gurjanova, 1936	
Grateloupia yinggehaiensis H.W. Wang and R.X. Luan	
Spermothamnion cymosum (Harvey) De Toni	
Pelagia benovici Piraino, Aglieri, Scorrano and Boero 2014	(First record in the whole North Adriatic region, including Venice)
Ulva californica Wille	
Species first recorded in Venice and having subsequently been observed elsewhere (MED = Mediterranean Sea; WEM = Western European Margins)	
Botrylloides violaceus Oka 1927	WEM
Botrytella parva (Takamatsu) H.-S. Kim	MED
Callinectes sapidus Rathbun 1896	MED
Caprella scaura Templeton 1836 sensu lato	MED, WEM
Diadumene lineata (Verrill 1869)	MED
Didemnum vexillum Kott 2002	MED
Dyspanopeus sayi (Smith 1869)	MED
Garveia franciscana (Torrey 1902)	MED
Haminoea japonica Pilsbry 1895	MED
Littorina saxatilis (Olivi 1792)	MED
Paranthura japonica Richardson 1909	MED
Polysiphonia morrowii Harvey	MED, WEM
Tricellaria inopinata d'Hondt and Occhipinti-Ambrogi (1985)	MED, WEM
Xenostrobus securis (Lamarck 1819)	MED, WEM

"Lessepsian migrant" has been recently questioned (Christodoulou et al. 2013). *Grateloupia doryphora* (Montagne) M.A. Howe and *Sorocarpus* sp., listed by Occhipinti-Ambrogi (2000a), were instead misidentifications of *Grateloupia turuturu* Yamada and *Botrytella parva* (Takamatsu) H.S. Kim, respectively.

Conversely, the current inventory includes species first recorded a long time ago, whose non-indigenous status has been recently proven in the literature, but were not included by Occhipinti-Ambrogi (2000a) because they were formerly considered native or cryptogenic: they correspond to the definition of "pseudo-indigenous" species (Carlton 2009). This is the case of the marine snail *L. saxatilis*, whose Venetian population underwent mitochondrial DNA analysis (Panova et al. 2011). All the individuals from Venice were shown to share the same haplotype, with higher affinity to populations from the British Isles and Sweden than with southern Mediterranean populations. Consequently, the hypothesis of a relic of a wider Pleistocene distribution was rejected, revealing the human-mediated introduction of *L. saxatilis* from the WEM, probably due to merchant galleys of the Venetian Republic in the fifteenth century. *L. saxatilis* therefore represents the oldest marine NIS known in Venice, and indeed in the whole MED. In the Lagoon of Venice *L. saxatilis* can be found under and on rocks and in crevices at tidal level (Crocetta et al. 2013). Another very old record of a pseudo-indigenous species is the cosmopolitan barnacle *A. eburneus*,

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which the recent literature considers as native to the NW Atlantic and introduced by vessels elsewhere (Carlton et al. 2011). Besides these "historical" NIS, 15 additional NIS, introduced to Venice between 1924 and 1999, were not listed in the account of Occhipinti-Ambrogi (2000a). The list includes: the macroalgae *Antithamnionella elegans* (Berthold) J.H. Price and D.M. John, *Antithamnionella spirographidis* (Schiffner) E.M. Wollaston, *Bonnemaisonia hamifera*, *Codium fragile* subsp. *fragile*, *Colaconema codicola* (Børgesen) H. Stegenga, J.J. Bolton and R.J. Anderson, *Halothrix lumbricalis* (Kützing) Reinke, *Leathesia marina* (Lyngbye) Decaisne, *Scytosiphon dotyi* M.J. Wynne; the cnidarian *Diadumene lineata* (Verrill 1869); the molluscs *Cuthona perca* (Er. Marcus 1958) and *Haminoea japonica* Pilsbry 1895; the copepod crustacean *Acartia* (*Acanthacartia*) *tonsa*, the bryozoan *Zoobotryon verticillatum* (Delle Chiaje 1822), and the ascidians *Perophora multiclathrata* (Sluiter 1904) and *Styela plicata* (Lesueur 1823). These species were not recognized as NIS at the time of their first finding, thus representing other cases of pseudo-indigenous species, either because of misidentification or perhaps because they were believed to be native.

Amongst the 28 "new NIS" of the Lagoon of Venice, i.e. those recorded after the publication of Occhipinti-Ambrogi (2000a), 57 % is composed of macroalgae. This high percentage is not only due to the likelihood of this taxon to be unintentionally transported during shellfish transfers (Mineur et al. 2007), but also to the intensive research it has been a subject of recently (Sfriso and Curiel 2007; Sfriso et al. 2009). In particular, recent molecular tools have allowed scientists to identify cryptic species of non-indigenous origin, such as the red algae *G. vermiculophylla* (Sfriso et al. 2010), *Hypnea flexicaulis* Y. Yamagishi and M. Masuda (Wolf et al. 2011), *Grateloupia yinggehaiensis* (Wolf et al. 2014), *Spermothamnion cymosum* (Harvey) De Toni (Armeli-Minicante 2013b), and the green algae *Ulva australis* Areschoug (Manghisi et al. 2011), *Ulva californica* Wille (Wolf et al. 2012) and *Uronema marinum* Womersley (Sfriso et al. 2014a).

Recent pan-European studies have shown that "vessels" are the most important vectors of introduction for marine NIS in Europe, with the exception of the Eastern Mediterranean region, where the most important route is the Suez Canal (Katsanevakis et al. 2013; Galil et al. 2014). However, the relative importance of the vector "culture" is remarkably higher in a few countries, especially France (Galil et al. 2014), where the renowned oyster-culture activity has caused the unintentional introduction of several species of Pacific origin (Goulletquer et al. 2002; Mineur et al. 2007; Boudouresque et al. 2011).

The contribution of single vectors in Venice is similar to that exhibited by France, with a number of culture-associated NIS reaching and even exceeding the number of those introduced by vessels. The results of our survey suggest that the Lagoon of Thau in France, termed «a Japanese biological island in the Mediterranean Sea» by Boudouresque et al. (2011), is the likely source origin for 13 NIS reported in Venice. Furthermore, the Lagoon of Venice itself represents a likely NIS source region for other Mediterranean culture sites, e.g. the Po Delta Lagoon and Pialassa della Baiona pond in the North-Adriatic Sea; the Lagoon of Olbia in the Tyrrhenian Sea; the Mar Piccolo of Taranto in the Ionian Sea. All these Italian sites share with Venice a number of NIS whose records have often occurred after the Venetian one (Cecere et al. 2000, 2011; Doneddu 2011; Lodola et al. 2012; Petrocelli et al. 2013; Sfriso et al. 2010, 2012, 2014c). The continuous import/export of live bivalves for farming among these culture sites is likely to have facilitated the spread of several populations of Pacific origin, following a stepping stone colonization process, in which Venice has played the role of sink and source of NIS. A likely route for culture-associated introduction is: first introduction to French shellfish farms (or other shellfish farms in western Europe), then secondary introduction to Venice, then further spread from Venice to other Mediterranean sites. This is the route of invasion suggested by Marchini et al. (2014) for the isopod *Paranthura japonica* Richardson 1909, but it also applies to other cases such as the macroalgae *G. turuturu*, *Heterosiphonia japonica* Yendo, *Undaria pinnatifida* (Harvey) Suringar. For several species, the vector "culture" might have operated in combination with shipping, recreational boating, live food trade, transport on floatsam, in a combination of causes that is difficult to disentangle and control, in a locality where all these vectors operate intensively.

Generally, the introduction of NIS is negatively perceived because of potential adverse interactions with native species, as well as potential threats to

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biodiversity and ecosystem functions (Vilà et al. 2009; Simberloff 2011; Strayer 2012). However, not all NIS in the Lagoon of Venice have produced negative effects, and a few of them have brought positive changes. For example, the intentionally introduced clam *R. philippinarum* has greatly benefited the economy of the area, although a shortsighted resource management (catching systems) has led to significant environmental damage, by disrupting sediment texture, killing the benthic infauna (Pranovi and Giovanardi 2004) and resuspending high amounts of fine sediments, which has affected primary producers and the entire food chain (Sfriso et al. 2005). In confined areas of the Lagoon, the substitution of native species (the green algae *Ulva rigida* C. Agardh and *Ulva laetevirens* Areschoug) with the introduced red algae *G. vermiculophylla* has locally reduced eutrophication effects. As observed in spring 2014 by one of the authors (AS), *G. vermiculophylla* resists to high temperatures (up to 32–33 °C) and water turbidity much more than laminar Ulvaceae (which collapse at 27–28 °C), thus avoiding anoxic crises. Moreover, the latter species as well as other NIS, such as *U. pinnatifida* and *Sargassum muticum* (Yendo) Fensholt, may have interesting biomedical, cosmetic, food and technological uses (Sfriso and Marchini 2014).

The linear increase in the number of introduced species observed for all NIS and for established NIS suggests alarming future scenarios. If the upward trend observed after 1966 continues in the next few years, and no action is taken to prevent new introductions, the cumulative number of introductions is expected to almost double by 2050 at the rate of 1.47 new NIS per year. It must be also taken into account that, according to global climate change scenarios and relative models (Umgiesser et al. 2014), the increase of temperature in the Lagoon of Venice is expected to be even higher than the one found offshore in the Adriatic sea, and this might affect the phenomenon of NIS introductions. In particular, the Lagoon might become a more suitable habitat for the colonisation of species of tropical-subtropical affinity that have already established in the Mediterranean Sea, like the numerous immigrants entered via Suez Canal (Galil et al. 2014), some of which are now spreading northward in the Adriatic Sea (Dulčić et al. 2013; Sulić Šprem et al. 2014). Furthermore, thermophilic NIS, already established but usually restricted to limited areas of the lagoon affected by thermal pollution, such as the thermophilic *G. yinggehaiensis* and *Z. verticillatum*, currently common at the "Fusina" station, near the industrial area of Marghera (Occhipinti-Ambrogi 2000b; Wolf et al. 2014), might further spread and generate impacts. For example, *Z. verticillatum*, due to its outstanding reproductive potential, ability of attaching to a large variety of natural and artificial substrates and to host several associated non-indigenous invertebrates, is considered a high nuisance NIS (Ryland 1965; Gosset et al. 2004; Farrapeira 2011), whose further spread in the Lagoon of Venice might cause ecologic and economic impacts.

The continuous input of exotic biota and particularly of successful invaders in such a "sink and source" site constitutes a threat to the marine ecosystem not only on a local scale, but also at the Mediterranean and European level. We stress the fact that legislative action is urgently needed in order to reverse the observed trends and contain further dispersion of the NIS already introduced.

Conclusion

The number of NIS in the Lagoon of Venice has dramatically increased, from 30 known NIS in 2000 to 71 in the current inventory. The continuous input of exotic biota has seriously modified the Lagoon environment, although not all NIS have affected the environment negatively. In some cases, the Lagoon has represented the starting point of further invasion phenomena at Mediterranean and European level. Notwithstanding this and the commitments of the European legislation, the issue of marine invasions has not yet been dealt with from a management point of view. Since eradication of already established NIS is virtually impossible, appropriate preventive management of vectors of introduction and efficient monitoring performed by specialised research staff should be urgently planned. Furthermore, awareness raising campaigns should be promoted, in order to inform and involve the civil population (including boaters, clam farmers, employees of the shipping lines and live food trade sectors), who in many cases might be directly responsible for unintentional introductions through careless procedures.

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