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Chaotic and long-term trends in Berre Lagoon (Provence, France): a shift towards alien-dominated assemblages?

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Abstract

Over historical time, Berre Lagoon (SE France, NW Mediterranean Sea) had undergone various changes. These became more significant, transforming and even disruptive since the 19th century when the channel connecting the lagoon to the sea was deepened and the surrounding areas were industrialized and urbanized. Pollution and anoxic crises were major consequences. Concomitantly, many non-indigenous species (NIS) arrived in the lagoon. In recent years, climate change and freshwater input from a hydro-electric power plant have been the main drivers influencing the lagoon ecosystem. The major anoxic crisis of 2018 caused the lagoon ecosystem to collapse. In the following years, an increase in mean salinity linked with low precipitation in the regional watershed and the resulting lower freshwater input from the hydro-electric power plant caused rapid changes in ecological assemblages and favoured newly arrived NIS. An updated list of NIS and cryptogenic species (38 taxa according to the last census) is presented here. The species introduction rate has strongly increased since 2000, or at least the recognition rate. Temporal and spatial changes are discussed for major NIS in Berre Lagoon. The success of new NIS is interpreted as a consequence of the 2018 crisis, of global change and of re-marinization of the water body related to dryer periods and stricter freshwater input regulation.

Keywords: Species introduction; non-indigenous species (NIS); Berre Lagoon; Global change; anoxic crisis; climate change; coastal lagoon; Mediterranean Sea.

Introduction

Mediterranean coastal lagoons are exposed to uncontrolled species introductions as side effects of various human activities (aquaculture, shipping, etc.) (Zibrowius, 1992; Boudouresque & Verlaque, 2012). Coastal lagoons are shallower and have a smaller water body than the open sea. This results in more intense fluctuations of nutrients, salinity and temperature and an overall lower species diversity (Kjerfve, 1994). The establishment of Non-Indigenous Species (NIS) may be facilitated and their long-term impact enhanced by habitat disturbances and climate change in general (Verlaque, 2001; Boudouresque & Verlaque, 2010; Boudouresque *et al.*, 2011, 2020; Marchini *et al.*, 2015; Verlaque *et al.*, 2015; Orlando-Bonaca *et al.*, 2019; Sfriso *et al.*, 2023). In contrast with assertions based on simplistic approaches regarding species diversity and disturbances (Boudouresque, 2014), the number of species does not necessarily decline, and even may conspicuously increase (Boudouresque *et al.*, 2011; Petrocelli *et al.*, 2019; Sfriso *et al.*, 2023). NIS are identified as of concern in the European Union Marine Strategy Framework Directive (MSFD, 2008/56/EC) and considered in Descriptor 2 'non-indigenous species'; new introductions, abundance and spread, and effects on the ecosystems are criteria used to determine Good Environmental Status.

Berre Lagoon (Provence, southeast France) is a 155-km² surface-area brackish lagoon connected with the open sea (Gulf of Fos) through the Caronte Channel.

Another connection with the sea (Gulf of Marseille) for navigation was the Rove tunnel-canal opened in 1927 and obstructed by a landslide in 1963. The lagoon comprises two main parts, the larger and deeper Berre Basin (up to 9 m depth) and the smaller and shallower Vaïne Basin (up to 5 m depth) (Fig. 1). Altogether, over time, the lagoon hydrology had been marked by more progressive to more abrupt changes: (i) Connectivity with the open sea for navigation purposes had been maintained since Antiquity until, at the beginning of the 20th century, the Caronte Channel was considerably enlarged and deepened (to 9 m). The Rove tunnel-canal (see above, 1927-1963) substantially added marine inflow; (ii) Extensive industrialisation since the 1920s (petrochemical industry, international airport) and urbanization caused pollution of water, sediment, and air (Schachter, 1952; Gnerre *et al.*, 2005; Arienzo *et al.*, 2013; Austruy *et al.*, 2019; Daumalin & Gramaglia, 2020); (iii) after the commissioning of the hydro-electric power plant of Saint Chamas, in the northern part of Berre Basin, in 1966, large volumes of fresh water were injected into the brackish lagoon (Mars, 1966; Roux *et al.*, 1993).

Before these major changes, Berre Lagoon ecosystem was known to be one of the richest French Mediterranean lagoons in terms of fish abundance and species diversity (Marion, 1887; Gourret, 1907; Chevallier, 1916; Germain, 1917, Mars, 1949).

The freshwater input from the hydro-electric power plant, combined with waste-water input from industry and urbanized areas, finally caused the Berre Lagoon ecosystem to collapse (Mayot *et al.*, 2020; Rigaud *et al.*, 2021). The seagrass-dominated ecosystem shifted to unstable assemblages dominated by nitrophilous and opportunistic species (Huvé *et al.*, 1973; Bernard, 2007; Bernard *et al.*, 2007; Manté *et al.*, 2013). One of the consequences was that all fishing activities were prohibited in 1957, before being re-established only in 1994 (Bernard, 2007). Mars (1966) estimated the area covered by *Zostera marina* (L.) and *Z. noltei* Hornemann meadows at nearly 6 000 ha in 1965 for the whole lagoon. In the 1990s, continuous meadows disappeared (Pergent-Martini *et al.*, 1995), and only 1.2 ha subsisted in 2009 (Bernard *et al.*, 2013; Mayot *et al.*, 2020). Simultaneously, the freshwater plant *Stuckenia pectinata* (L.) Börner (Potamogetonaceae) became frequent as a consequence of the low salinity (≈0-20 $g.kg^{-1}$) at the time. In the 1980s, the freshwater input from the hydro-electric power plant had attained up to 6 times the volume of the lagoon per year (Bernard, 2007).

The first regulations, decided in the 1980s, aimed at reducing pollution by the petrochemical industry. In 2004, the European Commission declared that France had failed to fulfil its obligations under Articles 4 (1) and 8 of the Convention for the Protection of the Mediterranean Sea against Pollution. France was fined and forced to improve the situation by reducing and managing the freshwater input from the hydro-electric power plant. This was finally fulfilled in two steps: by application of the already existing '*Plan Barnier*' and by additional regulations decided in 2004 (Mayot *et al.*, 2013). *Stuckenia pectinata* disappeared in 2005, following a rise in salinity (>25$g.kg^{-1}$; Zaghmouri *et al.*, 2013) due to the reduction of freshwater discharges. Nevertheless, and despite initial improvements of some other parameters, the area covered by *Zostera* spp. meadows continued to decline (Bernard, 2007; Manté *et al.*, 2013). In the early 2010s, *Z. noltei* relics seemed to be on the brink of extinction (Manté *et*

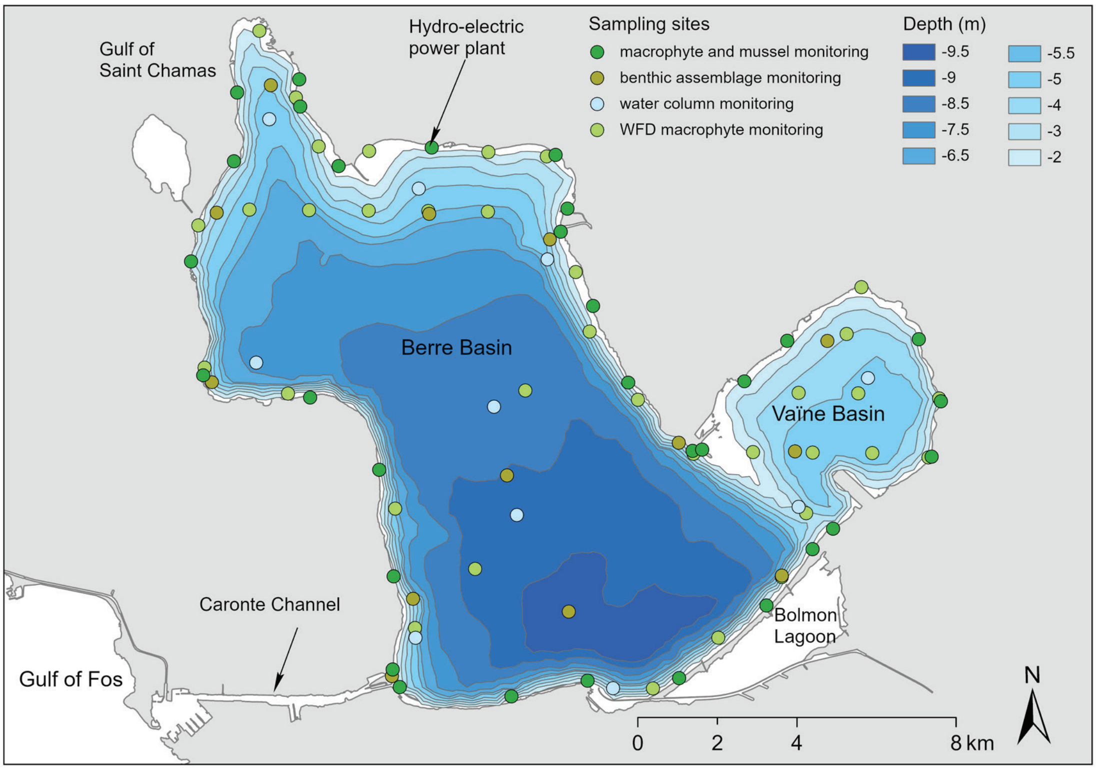

Fig. 1: Location of the sampling sites in Berre Lagoon (WFD: Water Framework Directive).

al., 2013), but then a slow recovery was observed. From 1.2 ha in 2009, the *Z. noltei* meadows increased to 18 ha in 2017. Then, 2018 was a year of unusually abundant spring rain with a notable N input (by run off), lack of wind, high summer temperatures and again unexpected freshwater input from the hydro-electric power plant in summer (Mayot *et al.*, 2020). Combined, all this had a 'cocktail effect' and produced a major anoxic crisis by water stratification that affected 93% of the lagoon area. Most benthic sessile fauna and mobile macrofauna died while *Z. noltei* meadows decreased by 60%, with 7 ha remaining in 2019 (Mayot *et al.*, 2020; Rigaud *et al.*, 2021). The following years, low rainfall and low freshwater input allowed a rapid recovery of *Z. noltei* (reaching 59.2 ha in 2024; Fig. 2).

It is self-evident that such an unstable and vulnerable ecosystem as Berre Lagoon is open to the arrival of NIS of all kinds, some proving invasive, harmful for ecosystems, the economy or human health (for definitions, see Boudouresque & Verlaque, 2012). In fact, some NIS, including invasive ones, have been known from Berre Lagoon for a long time. Here, an unprecedented update is proposed with the focus on more recent introductions of macrophytes and macrofauna and the trends observed after the 2018 anoxic crisis.

Material and Methods

Literature review

We analysed the available literature in order to list NIS, the date of their first and latest records, the potential vector(s) of introduction, their dynamics in terms of abundance and their persistence or possible collapse. To perform the literature review, articles were extracted from the 'Taxonomy and imaging Platform Macrophytes' of the Mediterranean Institute of Oceanography and from the online databases as Google Scholar, Scopus and Web of Science using the keywords 'Berre Lagoon', 'introduced species', or 'non-indigenous species'. International online species occurrence databases were also consulted: Global Biodiversity Information Facility (GBIF: www.gbif.org), Ocean Biodiversity Information System (OBIS: www.obis.org). The iNaturalist (www.inaturalist.org) research grade records were also considered. When the same species was recorded in several databases, the older record was taken into account.

Data from current monitoring

NIS data were collected from several ongoing surveys in Berre Lagoon. Monitoring of Macrophytes and Mussels (MMM) was done along 31 transects at representative sites of the lagoon every year in June-July: (i) Macrophytes (mean abundance index MAI; 1996-2024; Soltan & Francour, 2000); (ii) Mussels (MAI of *Mytilus galloprovincialis* Lamarck, 1917 and *Arcuatula senhousia* (W. H. Benson, 1842), 2006-2023). This allowed us to deduce trends in main native macrophyte populations and to detect new NIS occurrences. Along each 100 m-long transect, the cover of main macrophyte taxa was estimated using a semi-quantitative Braun-Blanquet classification (Westhoff *et al.*, 1978; quotation from 0 to 5) every 5 m. The MAI for each macrophyte group is then calculated by multiplying the occurrence (along the 20 5-m long segment) by the sum of the cover of each transect. For *M. galloprovincialis* and *A. senhousia*, another adapted quotation was used (from 0 to 6) and the cover was estimated every 10 m (10 segments per transect). The MAI is a value ranging between 0-500 and 0-600, respectively for macrophytes and mussels (see Soltan & Francour, 2000; Schohn & Astruch, 2023).

For the purposes of the European Union (EU) Water Framework Directive, the monitoring of the Ecological Quality Ratio of macrophyte communities (*Réseau de Suivi Lagunaire*, 2011) was carried out in Berre Lagoon in 2009, 2017, 2020 and 2023. Along 35 sampling sites (different from the above characterised as monitoring

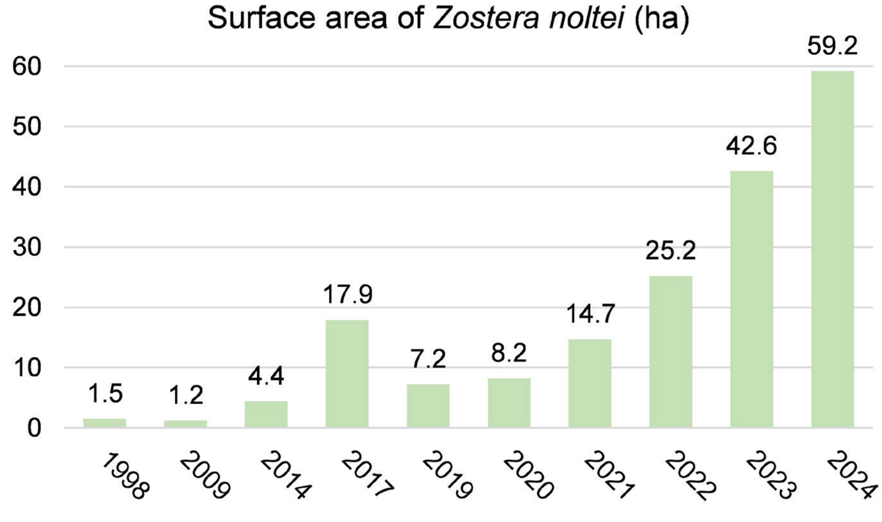

Fig. 2: Berre Lagoon. Changes in the surface area covered by *Zostera noltei* meadows (ha) in Berre Lagoon, from 1998 to 2024 (GIPREB, unpublished data).

sites), the cover of the main macrophyte species (including seagrasses) was addressed and samples were collected for identification (Schohn *et al.*, 2023).

Since 1994, the '*Groupement d'Intérêt Patrimonial pour la Réhabilitation de l'Étang de Berre*' (GIPREB), a local public Agency in charge of Berre Lagoon monitoring, management and restoration, conducts a monitoring survey on several compartments of the lagoon ecosystem, including phytoplankton (water column sampling every month, 10 sites), *Zostera* spp. meadows mapping (surface-area estimation every year since 2019 using satellite-based data and ground truth), benthic assemblages (sediment sampling every month, 13 sites).

Introduction pathways for each species were defined according to the Convention on Biological Diversity (CBD) (IUCN, 2017). Cryptogenic species (i.e., native or introduced status is uncertain, making its origin unclear; Carlton, 1996) were also considered.

Results

Updated list of introduced species

On the basis of the available literature, collected data and long-term monitoring, an updated list of NIS and cryptogenic species is proposed (Table 1). A total of 38 species, including 33 considered as NIS and 5 as cryptogenic were recorded: 9 macrophyte species (1 Chlorophyta, 6 Rhodophyta and 2 Ochrophyta); 5 Chordata (Ascidians), 4 Annelida, 3 Bryozoa, 2 Cnidaria, 1 Ctenophora, 8 Arthropoda (Crustacea) and 6 Mollusca (Gastropoda and Bivalva). Twenty-two out of 38 species are considered as well established. While 0 to 3 new NIS were recorded per decade until the 1990s, 9, 4 and 13 were recorded in the 2000s, 2010s and 2020s, respectively (Fig. 3). The primary introduction pathways are dominated by Transport-Stowaway mechanisms, such as ballast water and fouling, and Escape from Confinement, particularly through shellfish transfer, which involve 34 out of 38 species. For three species, the pathways remain unknown, while one species, *Ruditapes philippinarum* (A. Adams & Reeve, 1850), was intentionally released into the wild through shellfish transfer activities.

Trends of selected NIS

Non-indigenous macrophytes

Gracilaria vermiculophylla (Ohmi) Papenfuss was recorded for the first time in Berre Lagoon in 2015. Its frequency (number of records compared to the total number of study sites), yearly assessed since 2016 along the 31 transects (MMM), was mostly around 55-58%, with lower values in 2019 (42%) and 2020 (35%) (Fig. 4). It

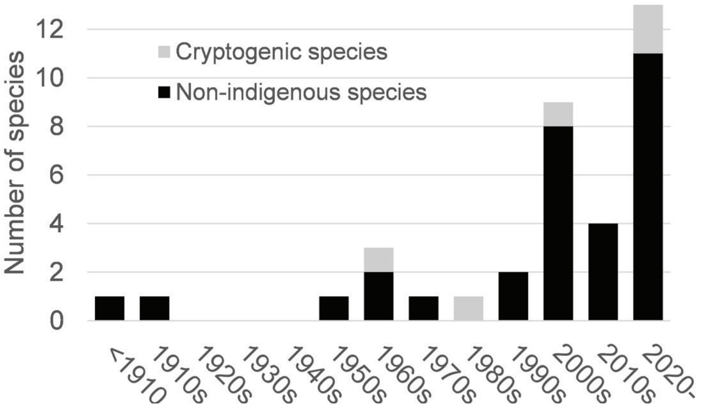

Fig. 3: Number of new NIS and cryptogenic species recorded in Berre Lagoon per decade. Only 36 among the 38 species are considered here, information about the first record of the two others is lacking.

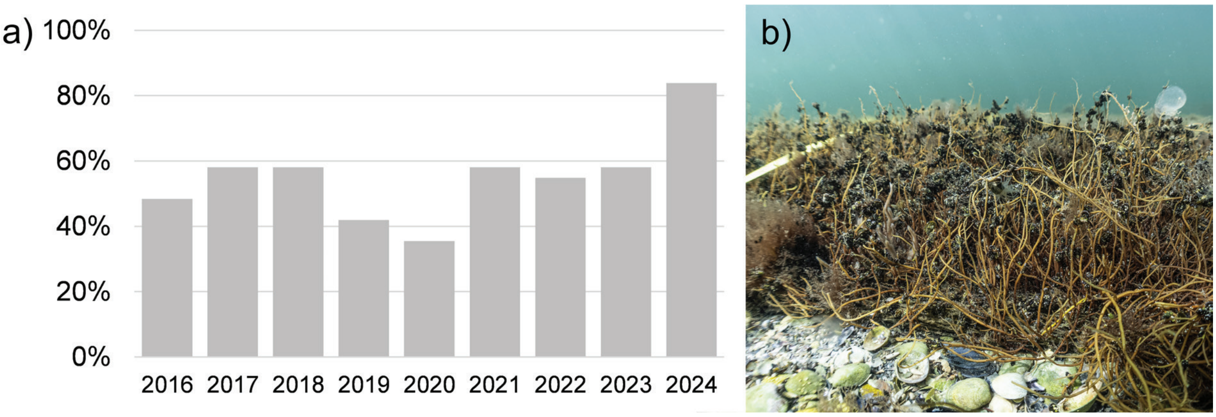

Fig. 4: a) Patterns of change in *Gracilaria vermiculophylla* occurrence (% of the 31 sites where the species was present, see MMM) between 2016 and 2024 in Berre Lagoon. b) *G. vermiculophylla* observed in 2023 in Berre Lagoon (©Patrick Astruch).

Table 1. List of Non-Indigenous Species (NIS) in Berre Lagoon, date of first and last records in the lagoon, population status categories (EC = established, common; ER = established, rare; NE = non-established; U = unknown, primary origin (putative secondary origin), putative vector to Berre, reference, (Pers. Obs.: FA: Frédéric André; HZ: Helmut Zibrowius; MV: Marc Verlaque; NM: Nicolas Mayot; PA: Patrick Astruch; PB: Pascal Bazile; TT: Thierry Thibaut). See Appendix 1 for species authorities. *: *M. harveyi* and *M. japonicus* are two closely related Pacific species. The species level identification requires molecular analyses. Pathways (IUCN, 2017): RN: Release in Nature; EC: Escape from Confinement; TS: Transport-Stowaway; BW: Ballast Waters; F: Fouling; ST: Shellfish Transfer; OF: Oyster farming; FB: Fishing bait.

Kingdom	Phylum	Species	First record	Last record	Population status	Origin (secondary)	Pathways	References
Archaeplastida	**Viridiplantae**	*Codium fragile* subsp. *fragile* (Suringar) Hariot	1950s	2024	EC	Pacific	TS (BW, F)	Feldmann (1956), PA, MV
	Rhodophyta	*Gracilaria vermiculophylla* (Ohmi) Papenfuss	2015	2024	EC	NW Pacific, SE Asia (NE Atlantic, Venice Lagoon)	TS (BW, F), EC (ST from Venice Lagoon)	TT
		Dasya sessilis Yamada	2022	2023	EC	NW Pacific, SE Asia (Thau Lagoon)	EC (ST from Thau Lagoon), TS (F)	MV, PA
		Grateloupia turuturu Yamada	2023	2023	NE	SE Asia, SW Pacific (Thau Lagoon)	EC (ST from Thau Lagoon), TS (F)	MV, PA
		Melanothamnus harveyi (Bailey) Díaz-Tapia & Maggs	2005	2024	EC	Pacific (NE Atlantic)	TS (BW, F)	MV
		Polysiphonia morrowii Harvey	2023	2023	ER	Pacific (Thau Lagoon)	TS (BW, F)	MV
		Yendoa hakodatensis (Yendo) C.C.Santos, Lyra & J.M.C.Nunes	2023	2023	EC	Northwestern Pacific (Thau Lagoon?)	EC (ST from Thau Lagoon), TS (F)	MV, PA
Stramenopiles	**Ochrophyta**	*Colpomenia peregrina* Sauvageau	2000s	2024	EC	NE Pacific	EC (ST)	MV
		Rugulopteryx okamurae (E.Y.Dawson) I.K.Hwang, W.J.Lee & H.S.Kim	2023	2023	NE (Caronte channel)	NW Pacific (Thau Lagoon)	TS (transfer from fishing boats, F)	PA
Opisthochonta	**Chordata**	*Botrylloides diegensis* Ritter & Forsyth, 1917	2021	2023	U	NE Pacific	TS (BW)	FA., iNaturalist
		Botrylloides violaceus Oka, 1927	2021	2023	U	NW Pacific	TS (BW)	FA, iNaturalist
		Microcosmus squamiger Michaelsen, 1927	1981 (Nice), 2021 (Berre Lagoon)	2021	ER (Caronte channel)	Australasia	TS (F)	Monniot (1981), FA, iNaturalist

Continued

Table 1 continued

Kingdom	Phylum	Species	First record	Last record	Population status	Origin (secondary)	Pathways	References
		Molgula manhattensis (De Kay, 1843)	<2007	2023	EC	NW Atlantic, cryptogenic	TS (BW)	FA, iNaturalist
		Styela plicata (Lesueur, 1823)	<2004	2023	U	NW Pacific - (Thau Lagoon)	TS (F)	FA
	Annelida	*Alitta succinea* (Leuckart, 1847)	<1990	2023	EC	NW Atlantic, cryptogenic	EC (OF, FB), TS (F, BW)	FA, NM
		Ficopomatus enigmaticus (Fauvel, 1923)	1910s	2024	EC	Cosmopolitan	TS (BW, F)	Fauvel (1923)
		Hydroides dianthus (Verrill, 1873)	1960s	?	U	Cryptogenic	TS (BW)	Bellan (1964), Zibrowius (1971)
		Pseudopolydora paucibranchiata (Okuda, 1937)	?	2023	EC	NW Pacific Ocean - cosmopolitan	?	FA, iNaturalist
	Bryozoa	*Amathia verticillata* (delle Chiaje, 1822)	2021	2023	U	W Atlantic-Caribbean Sea, cryptogenic	TS (F)	FA, iNaturalist (Caronte channel)
		Bugulina stolonifera (Ryland, 1960)	2023	2023	EC	Cryptogenic	?	FA, iNaturalist
		Tricellaria inopinata d'Hondt & Occhipinti Ambrogi, 1985	2023	2023	U	NE Pacific - cosmopolitan	TS (BW)	FA, iNaturalist, GBIF
	Cnidaria	*Gonionemus vertens* A. Agassiz, 1862	2016	2023	EC	North Pacific, north Atlantic and Arctic	TS (BW), EC (ST)	Marchessaux et al. (2017)
		Diadumene lineata (Verrill, 1869)	? (1971 in the Mediterranean)	2023	EC	NW Pacific - cosmopolitan	TS (F)	FA, iNaturalist, GBIF
	Ctenophora	*Mnemiopsis leidyi* A. Agassiz, 1865	2000	2024	EC	NW Atlantic -USA (Cosmopolitan)	TS (BW)	Delpy et al. (2012); Marchessaux et al. (2021, 2023)
	Arthropoda (Crustacea)	*Acartia (Acanthacartia) tonsa* Dana, 1849-1852	1966	?	EC	Cosmopolitan	TS (BW)	Gaudy & Vinas (1985)
		Amphibalanus eburneus (Gould, 1841)	1990	2023	U	NE Atlantic	TS (F)	Stora et al. (1995); FA

Continued

Table 1 continued

Kingdom	Phylum	Species	First record	Last record	Population status	Origin (secondary)	Pathways	References
		Amphibalanus amphitrite (Darwin, 1854)	Antiquity	2023	U	Indo-Pacific	TS (F)	FA
		Ampithoe valida S.I. Smith, 1873	2003	?	U	NW Atlantic	TS (F)	Faasse (2015)
		Callinectes sapidus Rathbun, 1896	1962	2024	ER	W Atlantic	TS (BW)	NM, Veyssière et al. (2022)
		Caprella scaura Templeton, 1836	2021 (Berre), 1999 (Venice Lagoon)	2023	EC	W Indian	?	FA, iNaturalist, GBIF
		Pseudodiaptomus marinus Sato, 1913	2008	?	U	Indo-Pacific	TS (BW)	Delpy et al. (2012)
		Rhithropanopeus harrisii (Gould, 1841)	2000	2024	EC	NW Atlantic	TS (BW)	Noël (2001)
	Mollusca (Gastropoda)	*Haloa japonica* (Pilsbry, 1895)	2021	2023	EC	NW Pacific - (Europe & NE Pacific)	TS (BW)	FA, iNaturalist, GBIF
		Rapana venosa (Valenciennes, 1846)	2015	2024	EC	Eastern Asia (Black Sea)	EC (ST), TS (BW, F)	PA, PB, Goulletquer (2016)
	Mollusca (Bivalvia)	*Arcuatula senhousia* (W. H. Benson, 1842)	2005	2024	EC	NW Pacific	TS (BW, F)	PA, HZ
		Magallana gigas (Thunberg, 1793)	1970s?	2024	U (channel of Caronte)	NW Pacific (Thau Lagoon)	EC (ST)	PA
		Mya arenaria Linnaeus, 1758	1990	2023	EC	Arctic and North Atlantic	TS (BW, F)	Stora et al. (1995); Porcheddu et al. (2002); Zibrowius (2002)
		Ruditapes philippinarum (A. Adams & Reeve, 1850)	2013	2024	EC	SE Asia (Venice Lagoon, Arcachon Bay?)	RN (ST)	Mahé et al. (2020, 2022)

was mainly located in the most confined areas (Gulf of Saint-Chamas, Vaïne Basin), far from the connection to the open sea. In 2024, it was located on 26 of the 31 transects (84%).

Codium fragile subsp. *fragile* (Suringar) Hariot was introduced into the Mediterranean in the 1940s and later into Berre Lagoon (Riouall, 1972). In 2018, before the anoxic crisis, its occurrence in the lagoon was low and mainly located in the vicinity of the Caronte Channel, close to the open sea. Following the 2018 anoxic crisis, *C. fragile* abundance and number of records were at their lowest in 2019, then increased, particularly in 2022 and 2023, when the species occurred in almost all the shallow sites of the Lagoon (Fig. 5a) before decreasing in 2024 (Fig. 5c).

In the summer of 2022 and 2023, three new macrophyte NIS were observed: *Dasya sessilis* Yamada, *Grateloupia turuturu* Yamada, and *Yendoa hakodatensis* (Yendo) C.C. Santos, Lyra & J.M.C. Nunes (synonym *Lomentaria hakodatensis* Yendo, 1920) (Figs 6a, 6b, 6c). The first records of *D. sessilis* were in June 2022 at a few sites along the northern shore. Its occurrence and abundance increased in 2023 and 2024. The first records of *G. turuturu* were in June 2023, its occurrence was low. The first records of *Y. hakodatensis* were from June 2023 in several localities. Sometimes it was associated with *Centroceras gasparrinii* (Meneghini) Kützing, a native species on the increase since 2022.

Rugulopteryx okamurae (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim has been spreading since 2016 in western Provence (Ruitton *et al.*, 2021) and is known in the neighbouring area of the Gulf of Fos. Only one specimen has been recorded in June 2023 at 3 m depth on muddy substrate at the vicinity of the Caronte Channel.

Non-indigenous macrofauna

Arcuatula senhousia is now present all around the lagoon (Fig. 7a). This bivalve from the northwestern Pacific was recognized for the first time in Berre Lagoon in early April 2006 along the Jaï beach (southwestern part of the lagoon), in only 0.2-0.3 m depth. It was already abundant, attached to various other shells, in particular to *Mytilus galloprovincialis*, its native competitor, and also formed carpets. *Arcuatula senhousia* seems to have surpassed another native mussel, *Mytilaster marioni* (Locard, 1889). In the following months of 2006, dense carpets were found elsewhere, at various depths (1-7 m). This shows that *A. senhousia* probably had been present

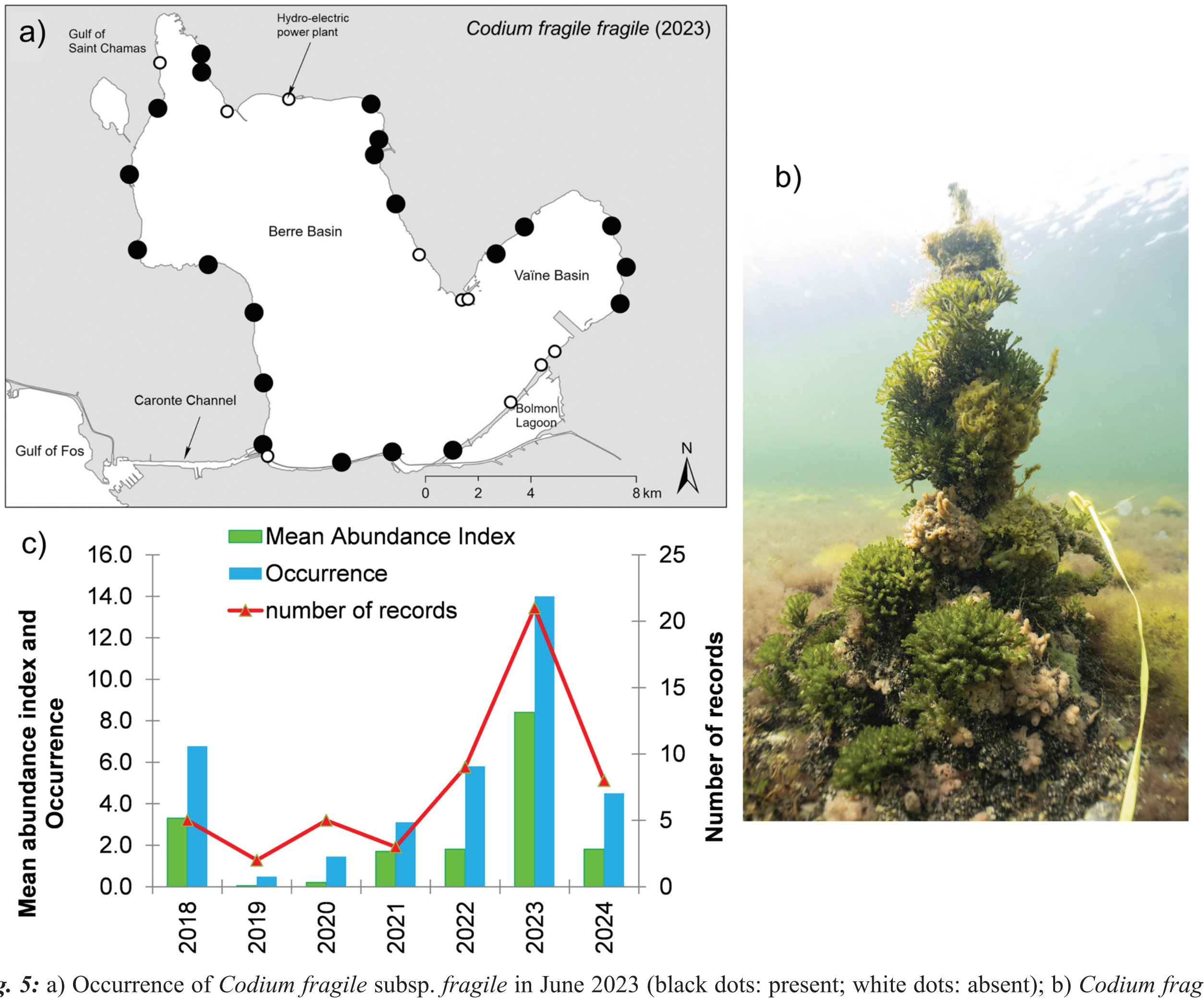

Fig. 5: a) Occurrence of *Codium fragile* subsp. *fragile* in June 2023 (black dots: present; white dots: absent); b) *Codium fragile* subsp. *fragile* colonizing a macrowaste (Berre Lagoon, ©Thomas Schohn). c) Mean abundance index, occurrence, and number of records (along the 31 transects from MMM) of *C. fragile* subsp. *fragile* in Berre Lagoon from 2018 to 2024.

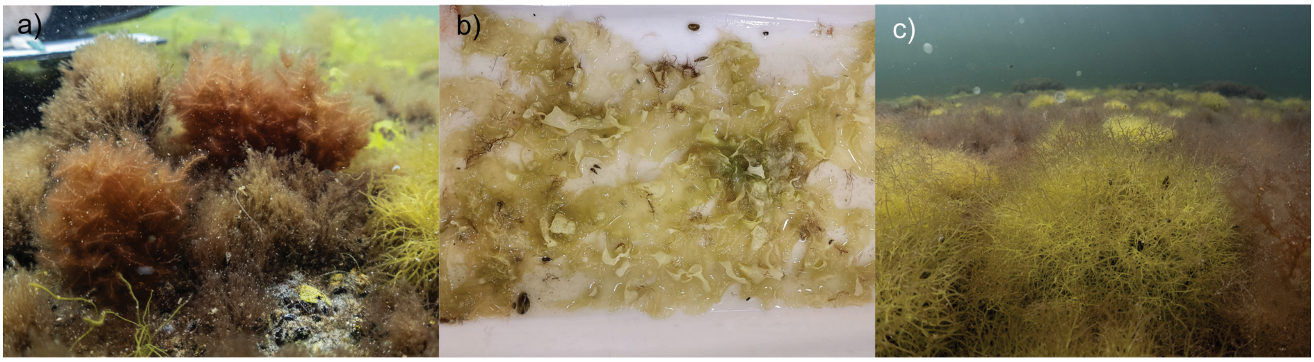

Fig. 6: Non-indigenous macrophytes observed in Berre Lagoon: a) *Dasya sessilis. b) Grateloupia turuturu; c) Yendoa hakodatensis,* here associated with *Centroceras gasparrinii* (©Thomas Schohn).

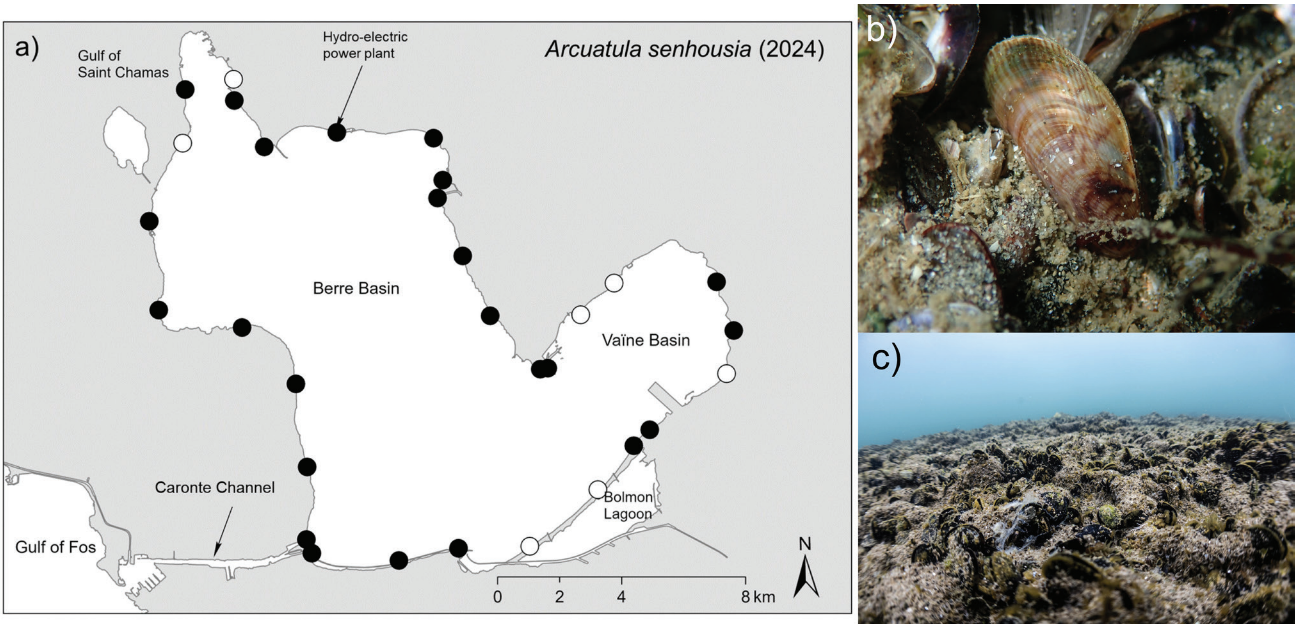

Fig. 7: a) Location of *Arcuatula senhousia* along the 31 transects from MMM during June 2023 survey (black dots: present; white dots: absent); b) *A. senhousia* individual ©Frédéric André; c) '*Carpet'* of *A. senhousia* spreading on *Mytilus galloprovincialis* bank (©Thomas Schohn).

in the lagoon for a few years already. A decrease in abundance was recorded after the 2018 crisis, with a minimum in 2022. Then a new increase was observed in 2023 and 2024, reaching a mean abundance index closer to *M. galloprovincialis* (Fig. 8).

Since the 2000s, the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 was observed in coastal lagoons along the Mediterranean coast of France, from Berre Lagoon in the east to Bages-Sigean Lagoon in the west (Marchessaux & Belloni 2021). In Berre Lagoon, the abundance pattern of *M. leidyi* shows a significant temporal variability. A study conducted from 2010 to 2017 (Marchessaux *et al.*, 2020) found that the average abundance ranged from 1 to 2 individuals per m^3, with a peak abundance of 940 individuals per m^3 recorded once in the Vaïne basin.

Gonionemus vertens A. Agassiz, 1862 is a small (up to 2-3 cm) hydromedusa native of the northwestern Pacific accidentally carried to various parts of the Atlantic (USA, Argentina, western Europe, Baltic Sea) and also the Mediterranean. In Berre Lagoon, it was detected in 2015 in the Vaïne basin, with a bloom close to *Z. noltei* meadows, its typical habitat there (Marchessaux *et al.* 2017). Since then, it has been observed annually, but not quantified (authors pers. comm.).

The Blue Crab *Callinectes sapidus* Rathbun, 1896, native to the western Atlantic where it always has been fished commercially, is now widely present in European seas and throughout the Mediterranean. In Berre Lagoon, the first specimen was collected in 1962 and first documented as 'Zibrowius pers. comm.' in Galil *et al.* (2002). It is summarily mentioned also in Veyssière *et al.* (2022). In fact, for the Mediterranean this was an early record, but the specimen in question, already correctly identified in 1962, was rediscovered only in 1993. It had been stored away and forgotten at Station Marine d'Endoume (Marseille) before finally being deposited at Muséum National d'Histoire Naturelle (Paris). Compared to other areas in the Mediterranean Sea, the abundance of *C. sapidus* in Berre Lagoon has remained low (Mancinelli *et al.*, 2017). However, since the end of 2023 and particularly since summer 2024, local fishermen report that their catches increased, with up to 8 000 individuals caught per month in autumn 2024 (GIPREB unpublished data).

Rapana venosa (Valenciennes, 1846) is a large gastropod native to the northwestern Pacific, spreading in several areas in the world (Harding & Mann, 1999) and

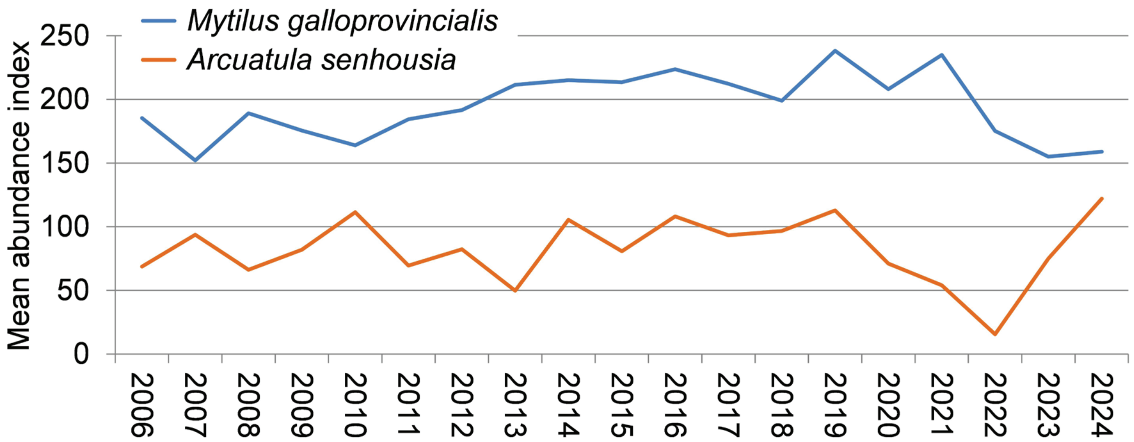

Fig. 8: Mean abundance index of the native *Mytilus galloprovincialis* (blue) and the introduced *Arcuatula senhousia* (orange) from 2006 to 2024 (from MMM).

known in Berre Lagoon since 2015 (Pascal Bazile, pers. comm.). While only few individuals and clutches were observed in 2022 (Fig. 9b), a spectacular abundance was detected in 2023 and 2024, the species being present in 52 and 58% of the transects (MMM). It was present almost all around the lagoon, except in the Vaïne basin (Fig. 9a).

Ruditapes philippinarum is a bivalve native of the northwestern Pacific which has become a notable fisheries resource in Berre Lagoon. After the 2018 anoxic crisis, its abundance increased enormously. In less than 3 years, the estimated biomass has increased from 130 to > 3 000 metric tons. *R. philippinarum* has colonized all soft substrates, from near the surface to 4 m depth. The density can reach > 2 000 individuals per m² (Mahé *et al.*, 2020, 2022). Since 2018, the fishery is regulated in order to guarantee a sustainable level (Fig. 10).

Seven more macrofauna NIS and cryptogenic species have been recognized for the first time in Berre Lagoon since 2020: the ascidians *Botrylloides diegensis* Ritter & Forsyth, 1917 and *B. violaceus* Oka, 1927, the cryptogenic bryozoans *Amathia verticillata* (delle Chiaje, 1822) and *Bugulina stolonifera* (Ryland, 1960) and the cosmopolite *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985, the amphipod *Caprella scaura* Templeton, 1836 and the gastropod *Haloa japonica* (Pilsbry, 1895) (Fig. 11).

Discussion

Our review identified 38 NIS and cryptogenic species in Berre Lagoon. This list is not exhaustive, considering issues of taxonomy (e.g., Polychaeta, see Zibrowius, 2002).

For instance, the serpulid *Hydroides dianthus* (Verrill, 1873), previously identified as an introduced species in several Mediterranean lagoons and harbours originating from the western Atlantic (USA) (Zibrowius, 1971; Bi-

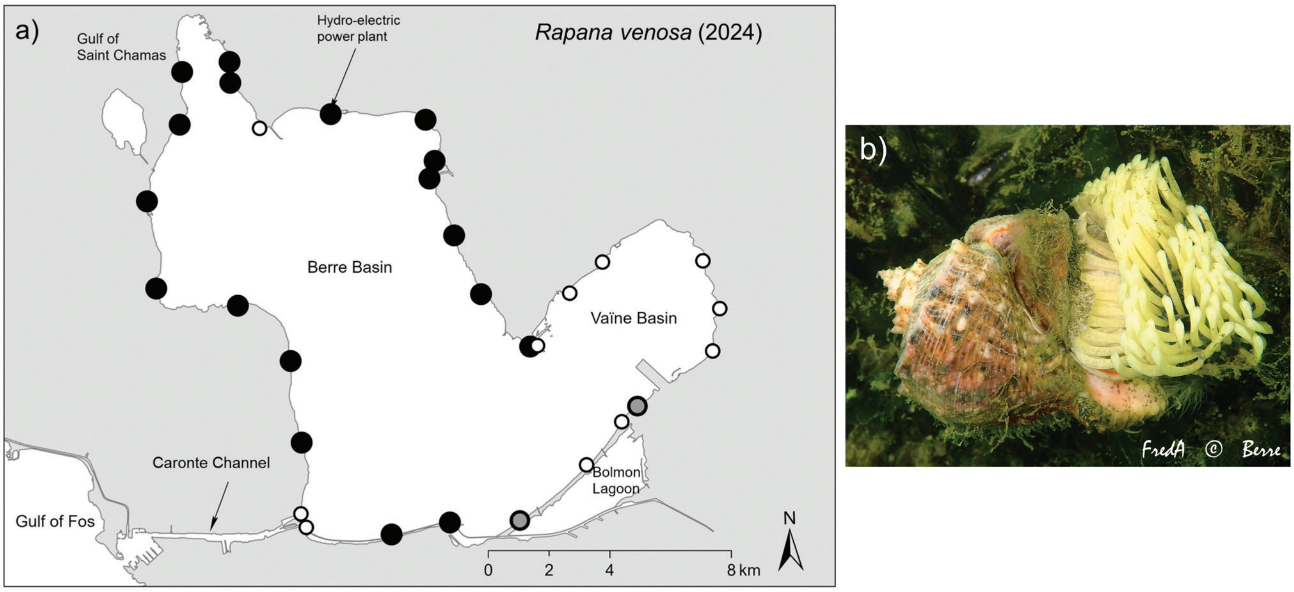

Fig. 9: a) Location of *Rapana venosa* along the 31 transects from MMM during June 2024 survey (black dots: present; grey dots: absent but already observed; white dots: absent). b) *R. venosa* close to its clutch of eggs (©Frédéric André).

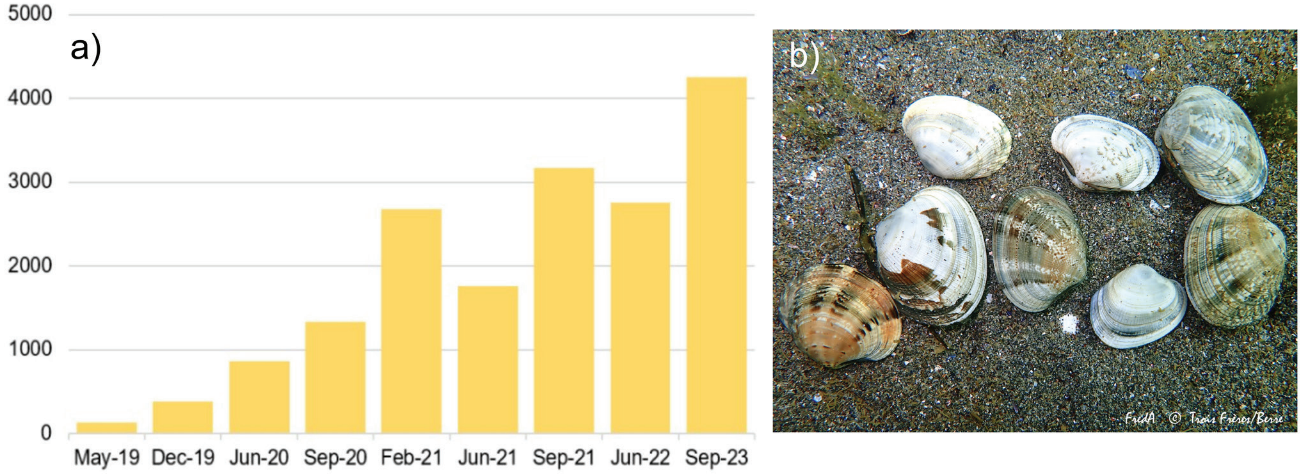

Fig. 10: a) Estimated stock (in tons) of *Ruditapes philippinarum* in Berre Lagoon from May 2019 to September 2023 (GIPREB, unpublished data); b) several *R. philippinarum* on fine sands (©Frédéric André).

Fig. 11: a) *Haloa japonica*; b) *Caprella scaura*; c) *Botrylloides diegensis* (©Frédéric André).

anchi, 1981), has been reconsidered based on a recent DNA-based study. This study suggests a Mediterranean origin, with Mediterranean populations exhibiting greater molecular diversity (Sun *et al.*, 2017; Langeneck *et al.*, 2020). This being so, the spread of a native species from geologically recent Mediterranean coastal lagoons to the open coasts and estuaries of the western Atlantic appears unlikely. In addition, a later presentation (Kupriyanova *et al.*, 2023) concluded that the situation '*is not yet clear to draw firm conclusions*', admitting that there are other lines of evidence contradicting this. In our study, we classified *H. dianthus* as a cryptogenic species in Berre Lagoon rather than a NIS, despite its first record in the 1960s (Bellan, 1964), while its true origin remains unclear (HZ disagrees on this point).

Here, we focused on species involved in habitat structure and main trophic compartments (primary producers, filter-feeders, carnivores, etc.), which may have an impact on the ecosystem functioning of the lagoon. Most of the species listed here have occurred in the lagoon for decades but recent new records, particularly in 2022 and 2023, show a trend toward an increase in the species introduction rate. The following species deserve special attention:

(i) *Gracilaria vermiculophylla* is recognized as one of the most invasive Rhodophyta species in the Northern Hemisphere (Zi-Min & Lopez-Bautista, 2014). Its rapid growth, tolerance to diverse environmental conditions, and ability to outcompete native species pose significant risks to estuarine and lagoon ecosystems. In Berre Lagoon, its current spread remains limited in terms of abundance. But, as known in other areas, it has the potential to alter nutrient dynamics and disrupt community structures and diversity. The species' capacity to form dense mats may also impede the growth of native seagrasses and associated macrofauna, thus further threatening ecosystem stability (Zi-Min & Lopez-Bautista, 2014). At the same time, *G. vermiculophylla* can act as a new primary producer, habitat-forming and providing abundant food resources (Davoult *et al.*, 2017).

(ii) The record of *Rugulopteryx okamurae* in Berre Lagoon consists of a single individual observed in June 2023, along with occasional sightings in the Caronte Channel. The species is already established and abundant in nearby areas (Gulf of Fos and Bay of Marseille - Ruitton *et al.*, 2021; Borriglione *et al.*, 2024) where its impact on benthic communities has been well documented. Its presence in Berre Lagoon warrants careful monitoring.

(iii) The ctenophore *Mnemiopsis leidyi* is native to estuaries and coastal waters in the American Atlantic, from Chesapeake Bay to the Gulf of Mexico and Argentina (Shiganova *et al.*, 2019). Dispersed elsewhere by ballast water, *M. leidyi* became a top marine NIS feared as a zooplankton and fish larvae predator (Lowe *et al.* 2007). Imported in ballast water from the Gulf of Mexico in 1982, it has had a high economic impact in the Black Sea over the years (Shiganova, 1998). By now *M. leidyi* is widely present in the western and eastern Mediterranean basins

(Fuentes *et al.* 2010; Shiganova *et al.*, 2019; Badreddine *et al.*, 2020). In Mediterranean lagoons, *M. leidyi* now has a severe ecological and economic impact because of its high predation capacities on zooplankton communities (e.g., copepods, fish larvae) and also on benthic species (e.g., amphipods) (Marchessaux *et al.*, 2021a, 2021b). Its abundance varies over the year, with distinct blooms. Being the most abundant gelatinous organism in Berre Lagoon, *M. leidyi* has also become a nuisance to fisheries by deteriorating the caught fish and causing additional labour needed for cleaning clogged nets. Altogether, the economic loss is estimated to represent 50% of the annual revenue (Marchessaux *et al.*, 2023a).

(iv) *G. vertens* has a powerful sting, that can cause various degrees of pain and even anaphylactic shock (Pigulevsky & Michaleff, 1969). The hands of fisherman are exposed to severe burns (Marchessaux *et al.*, 2023a). So far, the species and its painful effects remained essentially confined to the Vaïne basin. It mainly thrives during hot summer periods and its density is variable. A comprehensive quantitative and spatial survey is essential to mitigate and address potential risks for lagoon users.

(v) In Berre Lagoon, *Arcuatula senhousia* typically constitutes dense carpets fixing the sediment, as this has been described in the literature based on observations made elsewhere (e.g., Takenaka *et al.*, 2018). Despite interannual changes, *A. senhousia* abundance is stable in the long term, never surpassing the native *Mytilis galloprovincialis*.

(vi) The abundance of *Rapana venosa* in Berre Lagoon has significantly increased in recent years. *R. venosa* preys on the native *Mytilus galloprovincialis* and the introduced *Ruditapes philippinarum* (Hu *et al.*, 2016; Berov *et al.*, 2020). The high availability of both prey species is likely to have facilitated its spread which should be monitored in the future.

(vii) *Callinectes sapidus* is now spreading spectacularly in Berre Lagoon. This suggests that the population had grown in an environment with suitable salinity (Marchessaux *et al*., 2024). Consequences on the ecosystem functioning of the lagoon are expected to be significant as observed in other locations in the Mediterranean Sea (Marchessaux *et al.*, 2023b): predation on *R. philippinarum* and fish juveniles, degradation of fishing gear (e.g., trammel nets, fyke nets).

The recent increase in new records since the 2000s does not necessarily mean that these species arrived quite recently. The increase in records of NIS could also be due to greater sampling and monitoring efforts and raised awareness of recreational naturalist divers of specific taxonomic groups. For some species the pattern and date of introduction into the Mediterranean is well documented (e.g., *Rugulopteryx okamurae*, see Ruitton *et al.*, 2021; Borriglione *et al.*, 2024; *Ruditapes philippinarum*, see Mahé *et al.*, 2022). For many others the actual introduction probably happened well before they were first noticed (e.g., *Microcosmus squamiger*, *Botrylloides* spp.).

Recent freshwater input regulation of the hydro-electric power plant and dry periods favour marinization of the lagoon. The mean salinity was 15-25 g.kg^{-1} before 2018 and 17-32 g.kg^{-1} since 2022, the highest value ever recorded since the hydro-electric power plant started working in 1965 (GIPREB, unpublished data; Fig. 12). Water clarity is increasing, and reduced water stratification is preventing shallow anoxia (GIPREB unpublished data). The consequences for Berre Lagoon functioning are diverse: (i) resilience and spreading of the ecosystem-engineer seagrass *Zostera noltei*, (ii) increasing occurrence of marine teleost fish (e.g., *Mullus surmuletus* L., 1758, *Diplodus sargus* L., 1758), and cephalopods (e.g., *Octopus vulgaris* Cuvier, 1797) in catches by fishermen, and (iii) relatively stable environmental factors (e.g., eutrophication; GIPREB unpublished data). In 2023, monitoring of macrophyte assemblages for WFD purposes showed that the ecological quality of the water body had improved as indicated by the abundance and diversity of key taxa (e.g. *Zostera noltei*) (Fig. 2; unpublished data). These more suitable environmental conditions are likely to favour the new NIS that arrived after the 2000s and in particular after the 2018 anoxia crisis.

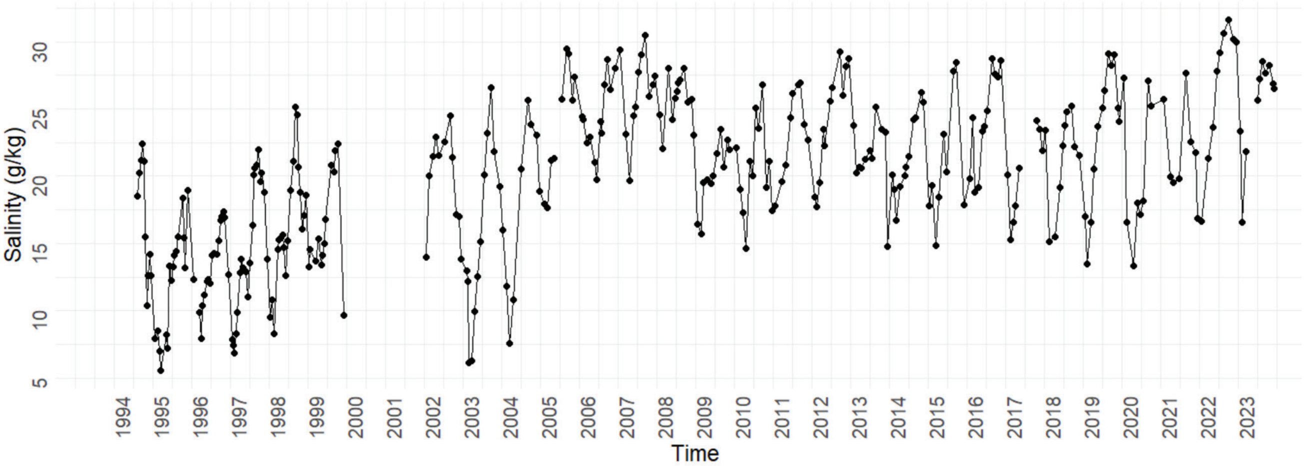

Fig. 12: Mean monthly salinity (g.kg^{-1}) at 13 sites all over Berre Lagoon between the surface and 1 m depth (GIPREB unpublished data)

Despite this recent improvement, marine heat waves (MHW) likely to occur in future summers will maintain the risk of new anoxic crises. Even with a higher mean salinity and a reduced stratification of the water column, the current dynamics of the lagoon ecosystem remain fragile and vulnerable. Nevertheless, during summer 2022, with the most severe MHWs ever observed in the northwestern Mediterranean Sea (Marullo *et al.*, 2023; Boudouresque *et al.*, 2024), no anoxia was noticed in Berre Lagoon. The dry spring and summer seasons and the low freshwater input from the hydro-electric power plant have undoubtedly prevented a critical water stratification.

Recent new NIS records in Berre Lagoon, particularly those of *Grateloupia turuturu, Yendoa hakodatensis* and *Rugulopteryx okamurae* are likely secondary introductions from the neighbouring Thau Lagoon (Gulf of Lion, France), a well-known hotspot of NIS introductions due to shellfish aquaculture (Verlaque, 2001; Verlaque *et al.*, 2007, 2015). We may speculate that the situation in Berre Lagoon (9 taxa of non-native macrophytes) is evolving towards a situation similar to that in Thau Lagoon (58 taxa of non-native macrophytes).

The main pathways of species introduction into Berre Lagoon are simple spreading from neighbouring areas, shipping in general (possibly responsible for long-distance dispersal known as ‘saltation’), transit of fishing and oyster farming boats and possibly unauthorized introductions of brown algae from Thau Lagoon for ‘restoration’ purposes (M. Verlaque, anonymous testimony) (see Boudouresque & Sempéré, 2017, for dispersal). By the end of the years 2000, the feasibility of oyster farming was considered, taking into account freshwater input regulation and an expected increase in salinity. The project was abandoned and the lagoon was spared from a potential source of additional introductions. However, other accidental or deliberate introductions may have occurred when seafood (e.g. shellfish, sea urchins) from Thau Lagoon was immersed near shore for stabulation (and maybe even with the intention of acclimatisation) by restaurants and by individual consumers. Indeed, similar factors are known from Venice Lagoon, another Mediterranean NIS hotspot and source of dispersal (Pranovi *et al.*, 2006; Marchini *et al.*, 2015).

Berre Lagoon is a model in terms of ecosystem collapse and resilience processes. The management plan (*Contrat d’Étang*) aims at restoring 1 500 ha of *Zostera* spp. meadows, (where the initial cover was >6000 ha) as a significant step towards a more balanced ecosystem (Bernard *et al.*, 2007, Aronson *et al.*, 2012; Grisel, 2013). The recent enforcement of freshwater input regulations (since 2023, no inputs are allowed between April and September) is intended to achieve a more stable and higher salinity, another management objective. Despite the presence of some recently arrived NIS, a more balanced ecosystem is expected to more successfully face climate change-related stressors. Provided that the dynamics of these new NIS does not turn into invasive, their presence in Berre Lagoon may even prove advantageous for the new ecosystem functioning. For example, *Gracilaria vermiculophylla* is known to be harmful when overgrowing and drifting (van Ginneken & De Vries, 2018). However, being more resistant to higher temperatures than the native *Ulva rigida* C. Agardh, 1823, it will be more efficient in limiting eutrophication (Marchini *et al.*, 2015). Since 2018, large stocks of *Ruditapes philippinarum* are the resources of new fisheries (Mahé *et al.*, 2022). The more recent proliferation of *Rapana venosa*, a species exploited in the Black Sea (Janssen *et al.*, 2014), also suggests regulated harvesting. To fishermen it would provide a new substantial resource, as a counterpart to preserving native and vulnerable fish stocks, such as *Anguilla anguilla* (L., 1758), *Dicentrarchus labrax* (L., 1758), *Sparus aurata* (L., 1758).

The present study evidenced a trend of an increase in species introduction since the 2000s, Further monitoring will provide warning of the possible arrival of potential new NIS, and identify vectors with a view to controlling them as part of appropriate management of the partly repaired and improved ecosystem.

Acknowledgements

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