Research Article

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Range expansion of some non-indigenous seaweeds along the coasts of Brittany – English Channel

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Abstract: Non-indigenous seaweed species have been introduced to the coasts of Brittany, France for decades, with an increasing arrival rate since the 1970s due to both the introduction of the Pacific oyster and increased maritime traffic. In this study, seven species of red macroalgae originating from the Pacific Ocean were found in new locations around the coasts of Brittany between 2018 and 2022. The seaweed species belong to four different orders: Ceramiales (*Antithamnion hubbsii*, *Polysiphonia morrowii*, and *Symphyocladiella dendroidea*), Halymeniales (including *Pachymeniopsis lanceolata* and *Polyopes lancifolius*), Rhodymeniales (*Botryocladia wrightii*), and Gigartinales (*Solieria* sp.). The dispersal mode and putative invasive potential of each species were examined, and the species were described in terms of their macroscopic and microscopic appearance and habitat. These finds result from a combination of citizen science and long-term monitoring. Used together, these two approaches can aid in the detection of these species on other European coasts and in understanding their dispersion.

Keywords: Brittany; maritime traffic; non-indigenous species; oyster farming; Rhodophyta.

1 Introduction

The North-East Atlantic Ocean has a high diversity of seaweed species, with approximately 1400 species identified (Guiry 2001). This diversity is considered high when compared to other regions of the world (Kerswell 2006). Atlantic France, among other European locations such as Ireland, southern England and Spain, is considered as a hot-spot of seaweed species richness (Burel et al. 2019a; Tittley 2002). Brittany in western France, is a particularly rich area for seaweed species, with about 650 species reported (Dizerbo and Herpe 2007). The high diversity in this region is attributed to a variety of factors such as a range of habitats (Croguennec et al. 2011), a large tidal range (between 4 m and almost 15 m), and the biogeographic transition between the Lusitanian province and the Boreal province (Couceiro et al. 2013). However, it is considered that about 7 % of all these species (about 50 taxa) are non-indigenous species (Burel et al. 2019a).

Non-indigenous species (NIS) are defined as species that have arrived outside their native range, either accidentally or deliberately aided by human activities (Massé et al. 2023; Nunes et al. 2014; Thomsen et al. 2016). The macroalgal flora of Brittany has a long history of incrementation by macroalgal NIS (Goulletquer et al. 2002; Mineur et al. 2012). Several have been introduced for decades, like *Melanothamnus harveyi* (Bailey) Díaz-Tapia *et* Maggs in 1832 (Thuret and Bornet 1878, as *P. insidiosa*) or *Colpomenia peregrina* Sauvageau in the Gulf of Morbihan in 1905 (Fabre-Domergue 1906, as *C. sinuosa*). Both species continue to be regularly found on these coasts. New non-indigenous species have been detected in Brittany almost every year since the middle of the 20th century (Cabioc'h et al. 1997; Cabioc'h and Magne 1987; Le Roux 2008, 2018; Mineur et al. 2010; Rio and Cabioc'h 1988). There has been a significant increase in the arrival rate of non-indigenous species in Brittany since the 1970s due to both the introduction of *Magallana gigas* (formerly *Crassostrea gigas*) Thunberg (Mineur et al. 2014) and the increase in maritime traffic (Galil et al. 2008).

Some NIS remain currently only known to exist in their original location of introduction like *Chondracanthus chamissoi* (C. Agardh) Kützing (Mineur et al. 2012, as *Chondracanthus* sp.). On the contrary, other NIS are considered as invasive because they have negative ecological or socio-

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economic impacts through their spread and proliferation (Boudouresque and Verlaque 2002). *Sargassum muticum* (Yendo) Fensholt and *Undaria pinnatifida* (Harvey) Suringar are commonly documented examples of invasive macroalgae on European coasts. These two large brown macroalgae are long-term introduced macroalgal species on the western coasts of Europe and noticeably in Brittany (Dizerbo 1989; Floc'h et al. 1996), that are found at least from Norway to Portugal/Morocco (Critchley et al. 1983; Minchin and Nunn 2014; Sabour et al. 2013; Schiller et al. 2018). The invasive character of successful macroalgal introductions, *i.e.* active proliferation of an allochthonous species, is not always certain, even though largely observed for *Caulacanthus okamurae* Yamada (Le Duff et al. 2008, as *C. ustulatus*).

The usual vectors of primary introductions into coastal waters (*i.e.* initial introduction of a NIS outside the native range) include 1. Shellfish aquaculture, especially spat transport (Murray et al. 2020), 2. Marine traffic, through ballast release and fouling (Molnar et al. 2008) and 3. Aquarium trade (Vranken et al. 2018). In addition, secondary introduction (*i.e.* progression from the location of its primary introduction to other areas within the same region) may be performed step by step, or through additional human activities. Examples of NIS that have undergone prominent secondary introduction include *Sargassum muticum* and *Grateloupia turuturu* (Stiger-Pouvreau and Thouzeau 2015).

Seaweeds are increasingly being studied by biodiversity citizen science monitoring (Brodie et al. 2022) and this appears particularly pertinent for exotic species (Díaz-Tapia et al. 2020). In the present study, using both Citizen Science and long-term monitoring program, seven red macroalgal NIS originating from the Pacific Ocean are reported in new locations along the coasts of Brittany for the period 2018–2022. Detailed descriptions and illustrations are provided, including their macroscopic and microscopic appearance and their habitat. For each species, the potential dispersal mode and invasive potential are detailed. This information will help to identify these species in other parts of Europe and better understand their spread.

2 Materials and methods

Between 2018 and 2022, a total of 45 sites were visited: 21 during macroalgal habitat monitoring, 24 during citizen science programs or field courses in phycology (Figure 1). The 21 sites were initially chosen to best represent macroalgae-dominated rocky shores along the coast of Brittany *i.e.* the most luxuriant and the largest number of Phaeophyceae belts. Macroalgal habitat monitoring was performed by the authors based at the Laboratory of Environmental Marine Sciences (LEMAR) and the Observatory of Sciences of the Universe (OSU). Macroalgal monitoring programs include (1) the Réseau Benthique (REBENT) which is a program that was initiated in 2004 in Brittany, and aims to assess the biodiversity of coastal benthic communities, (2) the Water Framework Directive (WFD), an European Union directive which initiated monitoring in 2007, aiming to assess and improve the quality of water bodies, including coastal waters, and (3) the Marine Strategy Framework Directive (MSFD), another European Union directive which started monitoring in 2018, with the aim of achieving and maintaining a high environmental status of European marine habitats. Supplementary Table S1 provides specific information on the monitoring activities and corresponding site locations. The 24 citizen science program/field courses sites were chosen to simply fill in the gaps between the 21 sites described above, or simply for their proximity to the University.

In Brittany, rocky shores are highly influenced by the tide, resulting in a vertical zonation of macroalgal species, and particularly, Phaeophyceae: there can be up to six zones from the top to the bottom of the shore either dominated or co-dominated by (1) *Pelvetia canaliculata*, (2) *Fucus spiralis*, (3) *Ascophyllum nodosum* – *Fucus vesiculosus*, (4) *Fucus serratus*, (5) *Himanthalia elongata* – *Bifurcaria bifurcata*, (6) *Laminaria digitata*. The monitoring sites were sampled using a plastic grid (1.65 × 1.65 m) composed of 25 quadrats of 33 × 33 cm. Three sampling spots are analyzed for each Phaeophyceae-dominated community, and there were up to 18 sampling spots per site depending on the number of zones. More information about the sampling method is provided in Burel et al. (2019b). In addition to those found within the quadrats, any non-native species that were visible outside of the quadrats were also recorded.

The primary objective of citizen science programs and field courses in phycology was to carry out a comprehensive inventory species richness of each site. Therefore, the method used involved wandering around and searching for the relevant habitats. The main citizen science program considered in the present study is the OBCE (Observatoire Breton du Changement sur les Estrans, Hily et al. 2022), a project that is supported by multiple local associations (Bretagne Vivante – SEPNB, Vivarmor Nature). Initiated in 2018, this initiative aims at involving the public in the collection of scientific data and the exploration of coastal diversity. Participants are trained to identify various species, which are then aggregated and validated by an expert.

When a NIS species was found in a new location, the habitat was first thoroughly described, with a description of other species living nearby, and pictures were taken on site. When possible, several complete samples were collected in plastic storage bags for further identification in the laboratory. These samples were kept in a freezer until they could be examined. Anatomical characteristics and reproductive features (when present) were observed using binocular magnifier and microscopy. Microscopic photographs and drawings were then made. Specimens were finally preserved on paper by drying and are currently kept in the herbarium of the European Institute for Marine Studies, located in Plouzané, France.

3 Results and discussion

From 2018 to 2022, a comprehensive survey was conducted resulting in the identification of 216 species. Out of these, 172 species were identified during the monitoring of macroalgal

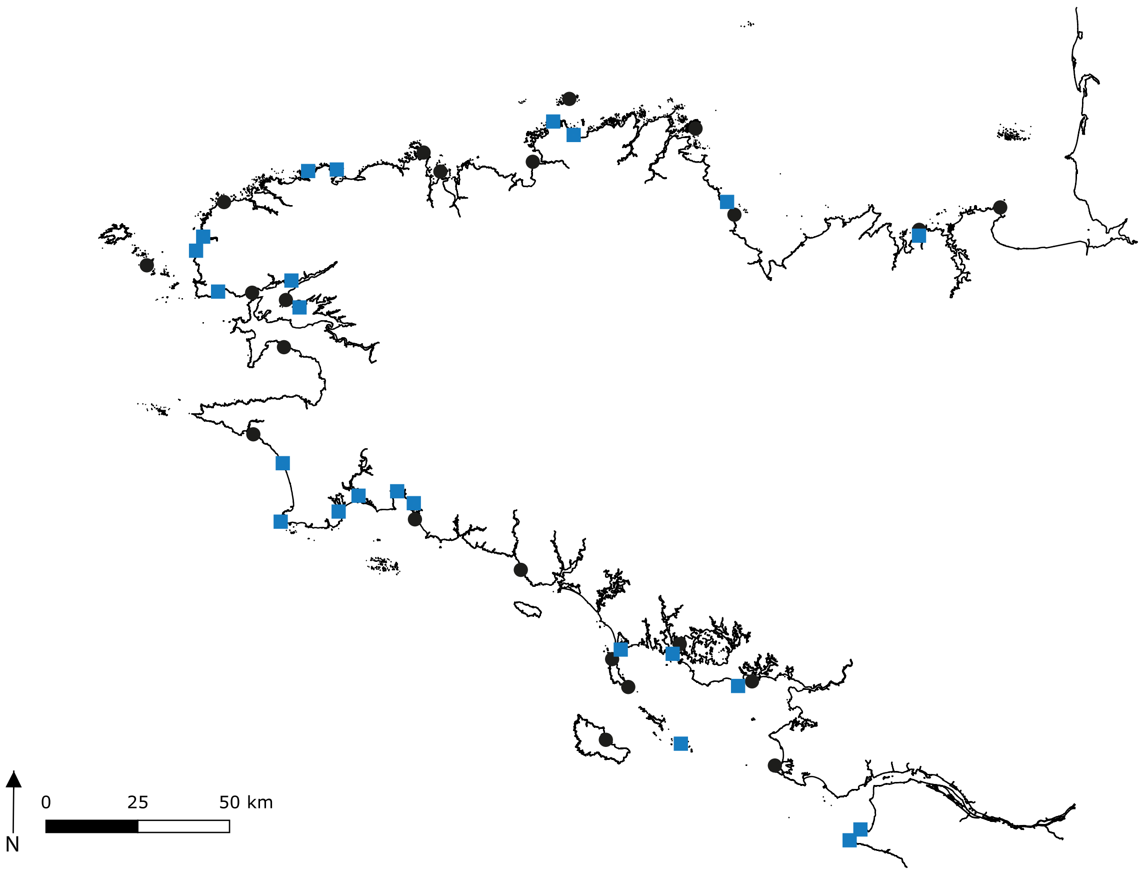

Figure 1: Map of Brittany showing the sites examined during the study, ca. 2018–2022. Blue squares represent sites visited during the citizen science program or during courses at the university, black dots represent sites visited during the monitoring program.

habitats, and 161 species were identified through the citizen science program, with 116 species being common to both. Of the 216 macroalgal species observed, seven Rhodophyta have shown a recent (2018–2022) extension of their range (Table 1 and Figure 2). These species will be described individually, followed by a general discussion.

3.1 *Antithamnion hubbsii* E.Y. Dawson 1962

The filamentous *Antithamnion hubbsii* is a Ceramiaceae originating from the Pacific Ocean. This species has been the subject of nomenclatural and typification problems and the type locality is still discussed between Japan and Baja California, Mexico (Athanasiadis 2016; Cho et al. 2005). In Europe, *A. hubbsii* was first found in the Mediterranean Sea in 1988 in the Thau Lagoon, France, as *Antithamnion nipponicum* Yamada *et* Inagaki, and then in 1994 in Venice Lagoon, Italy, as *A. pectinatum* (Montagne) Brauner in Athanasiadis *et* Tittley (Curiel et al. 1996). It was probably introduced *via* oysters transfers, as already reported for many seaweed species in both lagoons (Sfriso and Curiel 2007; Verlaque 2001). It was then reported as *A. nipponicum* in the Atlantic Ocean, firstly in 2004 in the South Basque country (Secilla et al. 2007), and secondly in 2007 in Norway (Rueness et al. 2007). The first specimen on the coasts of France was found in 2011 in the North Basque country, probably arriving *via* marginal colonization (Bárbara and Díaz-Tapia 2012). Its finding on pontoons in the Gulf of Morbihan, Brittany in 2017 (Le Roux 2018), then in the marinas of Brest in 2018, of Bénodet and Concarneau in 2020 and of Perros-Guirec in 2022 (this study), rather suggests a mode of propagation *via* maritime traffic. Fouling has also been suspected to explain the progression of the species in the English Channel and its probable spread northward (Baldock 2020). Specimens sampled during this study were only found attached to floating pontoons mainly during spring and summer, or epiphytic on various red macroalgae, *Fucus* spp. and *Ulva* spp. Like other *Antithamnion* species, thalli of *A. hubbsii* are characterized by uniseriate, ecorticate filaments with typical opposite ramifications and secondary ramification (Figure 3c). The larger specimens were up to 2.5 cm high (Figure 3a), but usually around 1 cm (Figure 3b). Specimens grow characteristic refringent glandular cells on

Table 1: Details of the sampling locations, periods and collector for each surveyed site.

Species	Location	Period	Collectors[a]
Antithamnion hubbsii	Brest	17.05.18	TB, MH, MLD
	Concarneau	22.05.20	MH
	Bénodet	14.07.20	MH
	Perros-Guirec	04.03.22	TB
Botryocladia wrightii	Préfailles	20.04.19	DC, TP
	Saint Briac sur Mer	30.09.19	FG, MC
	Tréveneuc	14.03.20	GK
	Locmariaquer	17.09.20	TB, NB
	La Plaine-sur-Mer	02.02.22	DC, TP
Pachymeniopsis lanceolata	Sarzeau	23.09.20	TB
Polyopes lancifolius	Saint-Pierre-Quiberon	08.05.20	ALR
	Bréhat	28.08.21	TB, GB
	Carantec	08.10.21	TB, EAG
	Trégastel	16.05.22	FG, MC
Polysiphonia morowii	Brest	17.05.18	TB, MH, MLD
	Loctudy	01.09.19	TB
	Plougastel-Daoulas	11.02.20	TB
	Plougonvelin	12.02.20	TB
	Plouzané	17.11.20	TB
	Crozon	13.01.21	TB
	Ploudalmézeau	03.03.22	MH
Solieria sp.	Hoedic	27.09.22	NB
Symphyocladiella dendroidea	Brest	17.05.18	TB, MH, MLD
	Bénodet	14.07.20	MH
	Loctudy	07.02.21	MH
	Concarneau	14.02.21	MH
	La Forêt-Fouesnant	14.02.21	MH
	Perros-Guirec	04.03.22	TB

[a]ALR, Auguste Le Roux; DC, Dominique Chagneau; FG, Florence Gully; GB, Guillaume Bridier; GK, Gaël Kervarec; MC, Marc Cochu; MH, Mathieu Helias; MLD, Michel Le Duff; NB, Nathalie Bourgougnon; TB, Thomas Burel; TP, Thierry Poissonnet.

basal cells of the lateral branches (Figure 3e). Fertile thalli were observed in the Marina of Brest, developing tetrasporangia replacing adaxial branchlets (55–70 µm × 40–55 µm, Figure 3d). As it can be easily confused with other *Antithamnion* spp., a diagram of the branching patterns of the five *Antithamnion* species is shown in Figure 4.

3.2 *Botryocladia wrightii* (Harvey) W.E. Schmidt, D.L. Ballantine *et* Fredericq 2017

Botryocladia wrightii is a Rhodymeniaceae originating from the North-West Pacific, initially described from Japan by Harvey in 1860 as *Halosaccion wrightii*. It was first found outside its native distribution area in 1978 in the Thau Lagoon as *Chrysymenia wrightii* Harvey (Ben Maiz 1986). *Botryocladia wrightii* was found in 2005 in the North-East Atlantic (Galicia, North-West Spain) under the name *Chrysymenia wrightii* (Bárbara et al. 2008). It was discovered in the Gulf of Morbihan in 2010 (Le Roux 2018) and reached the coasts of England in 2013 (Bunker 2014). All specimens found in this study were collected in the lower part of the intertidal zone with a deposit of sand. This species develops a tubular hollow thallus, somewhat gelatinous, more or less cylindrical, with a color from golden orange to purplish (Figure 5a). The largest sampled specimens were up to 20 cm, with main axes up to 0.6 cm wide (Figure 5b). The thallus is attached to the substratum by a discoid holdfast and shows numerous branches with an irregular branching pattern. In transverse section, the center of the thallus appears hollow with a cortex consisting of small cortical cells and large subcortical cells (Figure 5c). Cystocarpic plants were found in Tréveneuc (Figure 5d). When present, cystocarps (up to 1000 µm) are numerous and protrude all over the thallus. Specimens of *B. wrightii* can be confused with the native *Dumontia contorta* (S. G. Gmelin) Ruprecht, but differ in the branching pattern, the inner structure of the thallus and the arrangement of cystocarps.

3.3 *Pachymeniopsis lanceolata* (Okamura) Yamada *ex* Kawabata 1954

Pachymeniopsis lanceolata was originally described from Japan, as *Aeodes lanceolata* Okamura, and is native to Japan (Okamura 1934; Yoshida et al. 2015), China (Liu 2008) and Korea (Lee and Kang 2001). The species was reported in various locations in the Pacific Ocean outside of its natural range through the last decades, such as California (Aguilar-Rosas et al. 2010), Mexico (Pedroche and Sentíes 2020) or New Zealand (D'Archino and Zuccarello 2021). The first European occurrence for *P. lanceolata* was detected in French waters in the Thau Lagoon (Verlaque et al. 2005, as *Grateloupia lanceolata*) and it was later found in the Gulf of Morbihan (Le Roux 2018). In August 2020, specimens were collected outside the Gulf of Morbihan on the shore at Penvins, Sarzeau. Individual thalli grew up to 30–40 cm, with a dark to purplish-red color (Figure 6b). The color turns a distinctive green when aging. Thalli are characterized by the large foliose palmate frond (regularly wider than 10 cm) attenuated at the base (cuneate base, see Figure 6a). The texture is much more coriaceous and never soft as it is in *Grateloupia turuturu*. The thickness of the blade is up to 800 µm with a compact cortex and medulla (Figure 6c). Locally *P. lanceolata* can be misidentified with the introduced *G. turuturu*. The latter species is much more linear, and as shown above, both texture and thickness are good criteria. One has to be vigilant though, as both species were commonly found

Figure 2: Distribution range of seven non-indigenous Rhodophyta in Brittany in 2023. Circles: previous records (from Geoffroy et al. 2016; Le Roux 2018), stars: new records (this study). For each species, the first date of introduction in Brittany (always in the Gulf of Morbihan) is indicated on the map (Le Roux 2018 and pers. comm.).

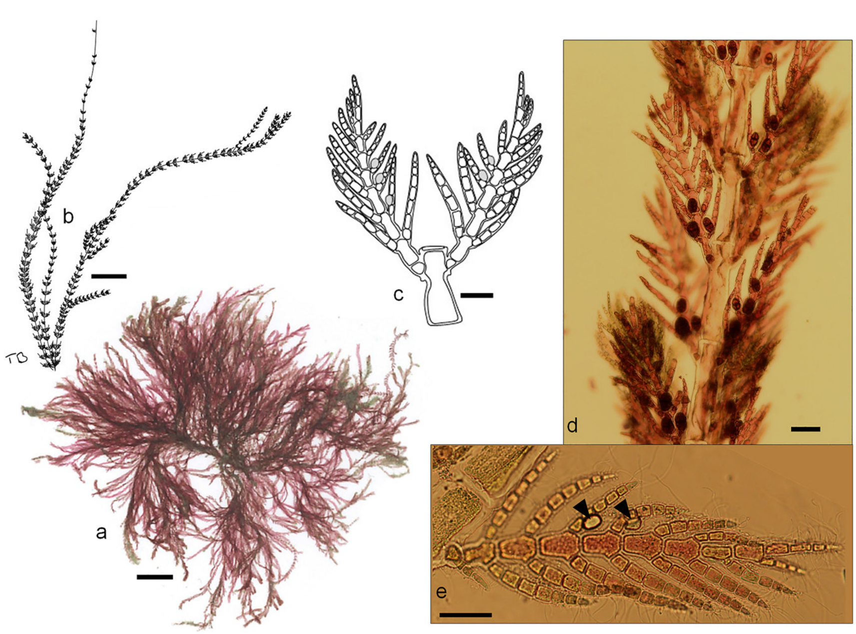

Figure 3: *Antithamnion hubbsii* from Brittany: (a) dried specimen from Brest marina (herbarium of the European Institute for Marine Studies); (b) general habit; (c) characteristic segment showing a cell of the main axis, the opposite distichous branching and the opposite branchlets bearing glandular cells; (d) portion of axis with tetrasporangia; (e) branches and branchlets bearing glandular cells (arrowheads). Scale bars: (a) 5 mm; (b) 2 mm; (c–e) 50 µm.

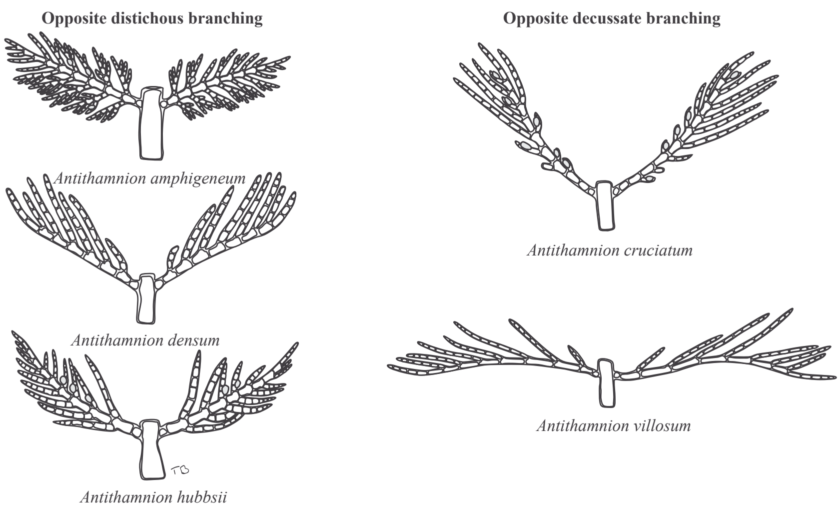

Figure 4: *Antithamnion* spp. in the north-east Atlantic, showing the different morphologies of segments and the branching patterns.

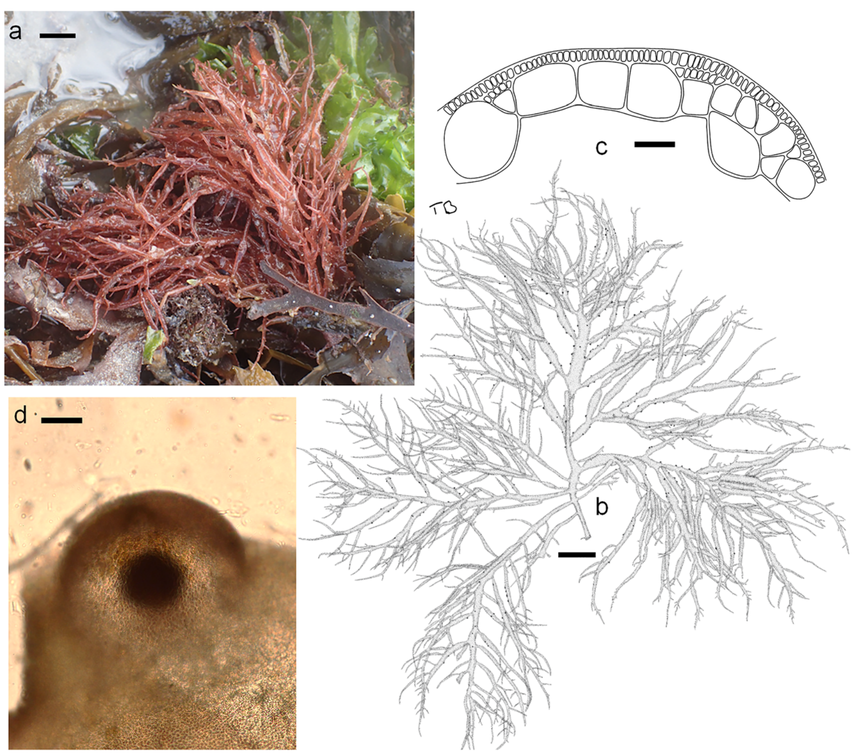

Figure 5: *Botryocladia wrightii* from Brittany: (a) in situ material from Tréveneuc (picture by F. Gully and M. Cochu); (b) general habit; (c) cortex and subcortex in transverse section; (d) immature cystocarp lacking carpostome in surface view. Scale bars: (a and b) 2 cm; (c and d) 100 µm.

together in rocky and sandy pools from the upper and mid-shore.

3.4 *Polyopes lancifolius* (Harvey) Kawaguchi *et* Wang 2002

Polyopes lancifolius is a red seaweed belonging to the order Halymeniales and the family Halymeniaceae (Kawaguchi et al. 2002). This species was first described as *Gigartina lancifolia* Harvey and is native to Japan, China (Liu 2008) and Korea (NW Pacific Ocean). The species was found during summer 2008 on the shore of Toulindac (Baden, Gulf of Morbihan) (Mineur et al. 2010). This finding, the first outside the native distribution range of the species, is the result of a recent introduction because the species does not appear in the list of marine species introduced in Morbihan published in 2008 (Le Roux 2008). For many years the species was circumscribed to this single location. It has since spread in the Gulf of Morbihan and is found now at Locmiquel and in the port of Arradon. The second European record of the species, outside the Gulf of Morbihan, was in May 2011 on the island of Jersey, English Channel (Chambers 2011) but it has not been observed there since 2013. In North Brittany, it was

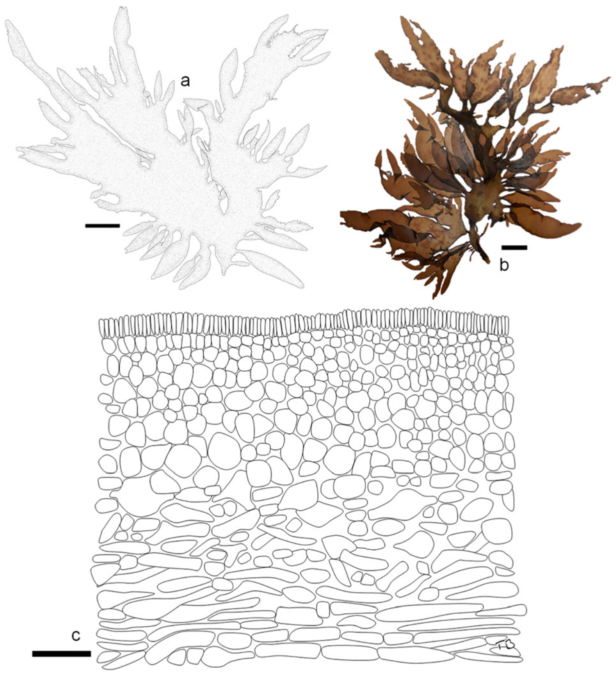

Figure 6: *Pachymeniopsis lanceolata* from Brittany: (a) general habit; (b) tetrasporophyte with numerous marginal proliferations (Herbarium T. Burel); (c) longitudinal section. Scale bars: (a–c) 2 cm; (d) 100 µm.

found in August 2021 on the island of Bréhat and more recently on October 8, 2021, on the island of Carantec (île Callot). Specimens collected in North Brittany are smaller and narrower than those observed by Mineur et al. (2010) in the Gulf of Morbihan. They reach a total length of 15–20 cm and a width of 1–1.5 cm (Figure 7c). Their shape and texture are similar to that already reported: main axes are elongated and lanceolate, they have little to no branching, the texture is cartilaginous and the thickness of blade is 350–500 µm (Figure 7d). They are covered with lanceolate proliferations found on both blade and margins of the thallus, whose size is around 1 cm. These proliferations are very characteristic of the species and give the thallus a spiky appearance (Figure 7a). Even if young thalli are reddish-brown in color, they discolor by late summer and become yellowish or greenish (Figure 7b).

3.5 *Polysiphonia morrowii* Harvey 1857

Polysiphonia morrowii was originally described from Japan, and its native range is the north-western Pacific (Chihara 1970; Kudo and Masuda 1992). The species was introduced in several locations in the Pacific Ocean (Kim et al. 2004; Raffo et al. 2014) and in the Atlantic Ocean (Geoffroy et al. 2016). This filamentous species, belonging to the Tribe Polysiphonieae in the Rhodomelaceae can be difficult to identify. The occurrence of uncut rhizoids (Figure 8e), arising directly from periaxial cells, distinguishes *P. morrowii* from most other *Polysiphonia s.l.*, but it was previously misidentified with the native *Polysiphonia stricta* (Mertens ex Dillwyn) Greville (see illustrations for *P. stricta* in Loiseaux-de Goër and Noailles 2008, pp. 118–119). It differs from the latter species by the shape of its apical cells, which are always rounded in *P. stricta*, but spiky in *P. morrowii* (Figure 8b, c and f). Plants of *P. morrowii* collected in Brittany can be found as epiliths in tidepools or on pontoons, growing up to 25–30 cm (Figure 8a), and as a floating mass of free-living entangled filaments in marinas. The species was also found in intertidal maerl beds, growing on *Lithothamnion corallioides* (Helias and Burel 2023). In transverse section, plants of *P. morrowii* have a central cell surrounded by four periaxial cells (Figure 8d). Tetrasporangia develop on ultimate and auxiliary branchlets, in series of 3–5 mature tetrasporangia (Figure 8g). Some plants bearing urceolate cystocarps were observed. Intertidal plants living in tidepools are most fully developed during winter and early spring, disappear in summer and are absent in autumn.

3.6 *Solieria* sp. J. Agardh, 1842

Solieria sp. has been present since at least 2005 in the Gulf of Morbihan, and was also detected in 2011 in the Thau Lagoon (Mineur et al. 2012). This species, first identified and sequenced by Mineur et al. (2012), is a NIS for Brittany and closely related, morphologically and molecularly, to unidentified specimens first detected in New Zealand in 1992. Furthermore specimens from both locations are closely related to *Solieria chordalis* (C. Agardh) J. Agardh and *Solieria filiformis* (Kützing) Gabrielson (Fredericq et al. 1999; Mineur et al. 2012). Specimens in both localities were lacking conspicuous reproductive structures. *Solieria* sp. specimens from Morbihan ranged from 5 to 26 cm long, with a pale-red to orange-red color (Figure 9a). Main axes were 500–1570 µm wide. The ramifications were irregular to sub-dichotomous, straight and bearing tapering apices (Figure 9b). Plants that have been dried for herbarium leave behind a characteristic brown mark on the paper. Plants of *Solieria* sp. can be distinguished from *S. chordalis* by a bright orange color (*S. chordalis* plants are red to dark-red), by the larger axes and the irregular branching pattern. Specimens of *Solieria* sp. can also be misidentified as *Gracilaria* spp. (Nelson et al. 2015), but in transverse section, *Solieria* plants have a two-part medulla with big round cells surrounding more elongated rhizoidal cells, while *Gracilaria* spp. have a medulla only composed of rounded cells.

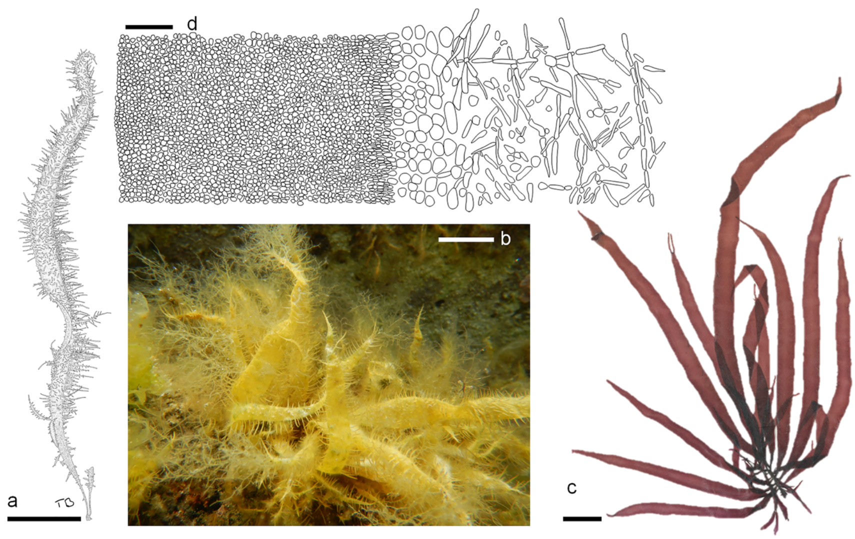

Figure 7: *Polyopes lancifolius* from Brittany: (a) general habit showing characteristic proliferations; (b) *in situ* material from Bréhat (picture by T. Burel); (c) dried specimen from the Gulf of Morbihan (Herbarium A. Le Roux), winter form lacking proliferations; (d) vertical section through old axis showing a thick cortex. Scale bars: (a–c) 2 cm; (d) 50 µm.

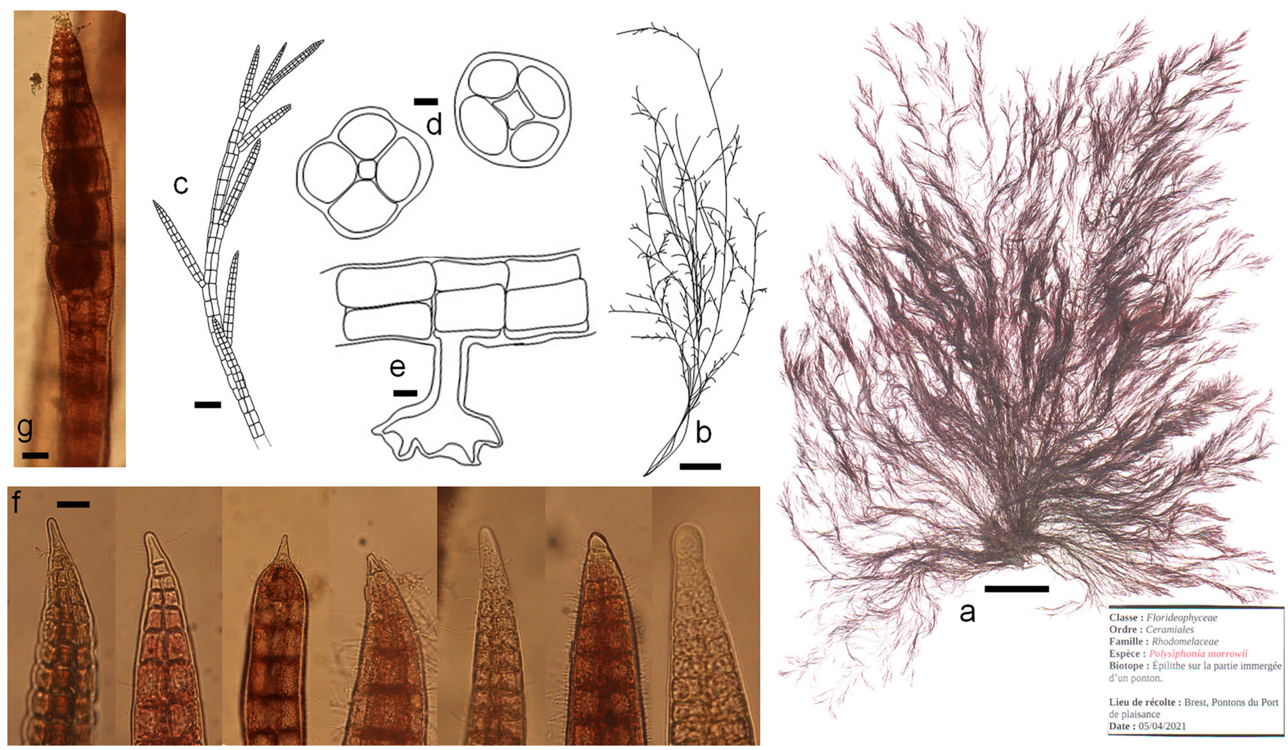

Figure 8: *Polysiphonia morrowii* from Brittany: (a) dried specimen from Brest marina (Herbarium M. Helias); (b) general habit showing characteristic spike branches; (c) apex with secondary branches giving a spike aspect; (d) transverse section with four pericentral cells; (e) rhizoid with open section; (f) variation in branch tips; (g) tetrasporangia. Scale bars: (a) 5 cm; (b) 500 µm; (c) 100 µm; (d–g) 20 µm.

3.7 *Symphyocladiella dendroidea* (Montagne) Bustamante, B.Y. Won, S.C. Lindstrom *et* T.O. Cho 2019

Symphyocladiella dendroidea is a species belonging to the family Rhodomelaceae. It is native to the Pacific (Bustamante et al. 2016, 2019). The first European record was from the Thau Lagoon in 1995 as *Pterosiphonia* sp. (Verlaque et al. 2015). It was then found in 2005 in the Bay of Arcachon (Verlaque et al. 2008) and in the Gulf of Morbihan (Le Roux 2018) as *Pterosiphonia tanakae* Uwai *et* Masuda, probably introduced by oyster spat. The species has continued to spread northward and is now present in the marinas of the bay of Concarneau, the marinas of Brest and of Perros-

Figure 9: *Solieria* sp. from Brittany: (a) *in situ* material from Locmiquel (picture by M. Helias); (b) dried specimen from the Gulf of Morbihan. Scale bar: 2 cm.

Guirec. In this study, all specimens were found attached on pontoons, suggesting an extension through maritime traffic. *Symphyocladiella dendroidea* is a small dark red to blackish purple Pterosiphonieae growing up to 7 cm (Figure 10a and b). Fertile tetrasporophytes were found in Brest, growing tetraspores in series of 8–12 within lateral branchlets (Figure 10e). Female specimens were also observed with mature cystocarps (Figure 10d). Cystocarps were ovoid, with dimensions equal to 126–136 × 95 µm and were oriented toward apices. Morphologically, *S. dendroidea* may be easily distinguished from most other native Pterosiphonieae by the pyramidal outline of the thallus (Figure 10c). *Symphyocladiella dendroidea* can still be confused with the local *Deltalsia parasitica* (Hudson) Díaz-Tapia *et* Rodríguez-Buján which differs by the number of pericentral cells in the axes (8–12 *vs.* 7–9, respectively) and the cortication (light cortication *vs.* absence of cortication). Identification can be difficult as cryptic diversity occurs in the latter species as described by Díaz-Tapia et al. (2022). Further studies are needed to clarify the taxonomic status of the complex *Symphyocladiella dendroidea* (Díaz-Tapia et al. 2018).

3.8 Dispersion pathways

Non-indigenous species can be intentionally or non-intentionally introduced to new environments and then can disperse through a variety of human activities, such as shipping, aquaculture, and recreational boating. Figure 11 displays a map that accounts for possible interconnections along the coast of Brittany. The map highlights the significant oyster basins and primary ports that feature floating pontoons within the region (Figure 11a) and outlines the vectors that are believed to have primarily facilitated the dispersion of the seven Rhodophyta species discussed earlier (Figure 11b). Nevertheless, it is important to acknowledge that various factors might have contributed to their dispersal. This is called polyvectism. Asexual reproduction is a common way for plants and particularly NIS to propagate and can be an efficient and rapid way for them to colonize new areas. In the case of *Solieria* sp., plants were found directly outside the Gulf of Morbihan (25 km away). They seem to have spread naturally, through currents for example, and are able to continue to do so through natural processes, as already reported for *Solieria chordalis* (Floc'h et al. 1987), *Solieria* sp. is able to reproduce through fragmentation. The brittle lateral branches are easily detachable and may facilitate the spread. Furthermore, reproductive plants (tetrasporophytes) have already been detected in Breton waters (Le Roux 2018). These two types of spreading combined together are considered as a very high risk of propagation (Nyberg and Wallentinus 2005) and this species must therefore be closely monitored, particularly in the surroundings of areas it has already reached. Another example of marginal dispersion by NIS is *Pachymeniopsis lanceolata* (which was found about 20 km away from the Gulf of the Morbihan), as reproductive plants (tetrasporophytes) were spotted (Figure 6).

The finding of *Bortyocladia wrightii* in Locmariaquer and of *Polyopes lancifolius* in Saint-Pierre Quiberon, *i.e.* directly at the exit of the Gulf of Morbihan, is also consistent with a marginal spread of the species as already mentioned for other species. The other locations where they were found, from Préfailles to Tréveneuc, show large discrepancies in the distribution of the species, rather suggesting a transfer *via* oysters. As was already suggested for another introduced species, the Ceramiales *Centroceras clavulatum* (C. Agardh) Montagne (Le Duff and Ar Gall 2018), the new locations of *B. wrightii* and *P. lancifolius* correspond to the large French oyster basins (Figure 11). Shellfish production and particularly oyster farming is often considered as a prime factor for both primary and secondary introductions (Mineur et al. 2014). Oyster production companies regularly transfer spats from farm to farm, locally, or between different countries (*e.g.* France, Ireland or Spain) and different marine regions (English Channel, Bay of Biscay and Mediterranean Sea) as described by Auby (1993). In Brittany, the Gulf of Morbihan appears to be one of the most successful locations for NIS primary introduction due to both the large presence of Oyster farms and the favorable hydrodynamics, temperature conditions and the variety of habitat (Le Roux 2008, 2018). With these characteristics, the Gulf of Morbihan is comparable to the lagoon of Venice (Sfriso and Curiel 2007), the Oosterschelde estuary (Mineur et al. 2012) and the Thau Lagoon (Verlaque 2001).

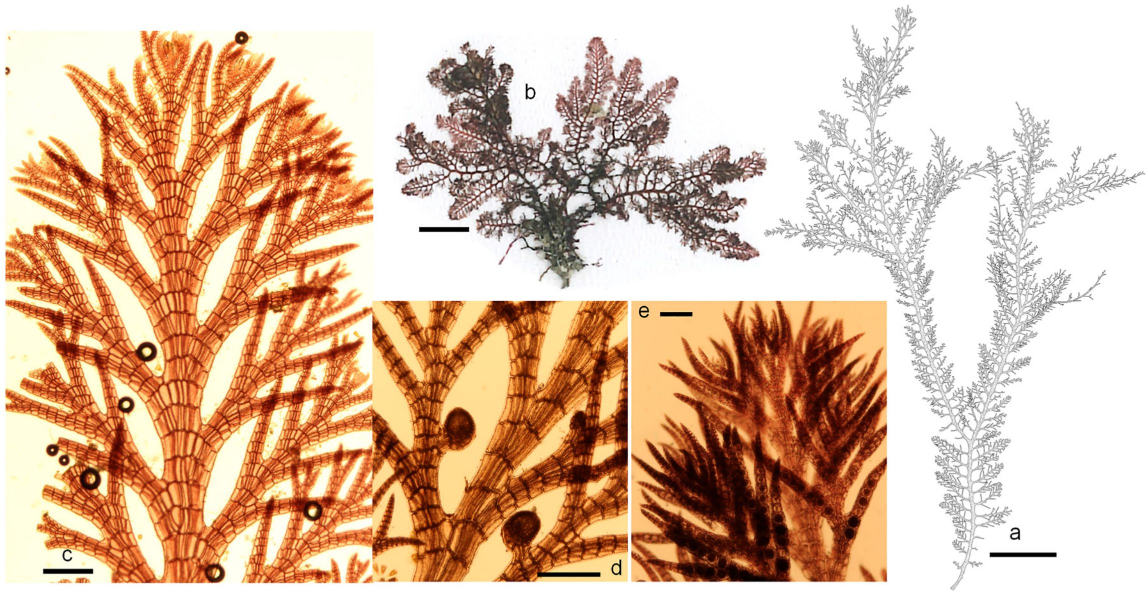

Figure 10: *Symphyocladiella dendroidea* from Brittany: (a) general habit showing alternate branches and ultimate proliferations; (b) dried specimen from Brest marina (Herbarium of the European Institute for Marine Studies); (c) apex with characteristic pyramidal outline aspect; (d) branches bearing cystocarps; (e) series of tetrasporangia in branchlets. Scale bars: (a and b) 500 µm; (c–e) 200 µm.

Concerning the spread of *Antithamnion hubbsii*, *Polysiphonia morrowii* and *Symphyocladiella dendroidea*, the most likely mode of spread is maritime traffic as most of the new records were made in ports or in the direct periphery of these. Pontoons are known for their concentration of NIS in both species richness and biomass (Arenas et al. 2006; Guzinski et al. 2018), and it is highly probable that these three NIS will be found in most of the ports of the North East Atlantic in the upcoming years.

4 Perspectives

Non-indigenous Rhodophyta species have recently extended their range in Brittany, due to different propagation vectors. The present study also legitimizes the use of citizen science in the monitoring of NIS (Lehtiniemi et al. 2020). It is therefore gratifying to see that participatory sciences are increasingly focused on producing scientific publications in collaboration with researchers, thereby enhancing the value of knowledge. Although training people and validating data may require a significant amount of time, the strike force is an invaluable tool as it allows for more accurate coastal monitoring through increased sampling points. To enhance the detection of macroscopically identifiable species, a document for monitoring Atlantic seaweeds, including 150 seaweed species, based on the protocol of Brodie et al. (2022) is being developed as part of the "Observatoire Breton des Changements sur l'Estran" citizen science program (Hily 2018). The introduction of non-native species has been occurring for a long time, with some species being able to find their place in local communities without a noticeable negative impact of their introduction (Mineur et al. 2008). Some can even be considered as successfully integrated into local ecosystems *e.g. Caulacanthus okamurae*, *Colpomenia peregrina* or *Bonnemaisonia hamifera*. These species can be regarded as functionally and structurally equivalent to the native species within the macroalgal community, thus implying their introduction has had a neutral impact (Ar Gall and Le Duff 2014). As the global concern around these issues grows, more and more evidence is being gathered and discussed (see Reise et al. 2023 and references therein).

It is important to note that the spread of more invasive NIS has rather had a damaging effect, with negative ecological and economic impacts spotted, such as competition with native species for resources, habitat degradation, and the alteration of ecosystem functions (Chapman et al. 2006). Of the species found during the present study, at least one is considered invasive (*Pachymeniopsis lanceolata*, Kim et al. 2014). According to the present observations, *P. lancifolius* is the first species whose invasive potential seems very strongly suspected, as large biomasses are currently found on the shores of the Gulf of the Morbihan (Hardouin et al. 2022) and the spread along the Breton coasts appears to be rapid, suggesting an extension comparable to that of *Grateloupia turuturu* (Simon et al. 2001). The second species which appears problematic in terms of its invasive potential is *Solieria* sp. mainly due to its capacity for asexual reproduction through

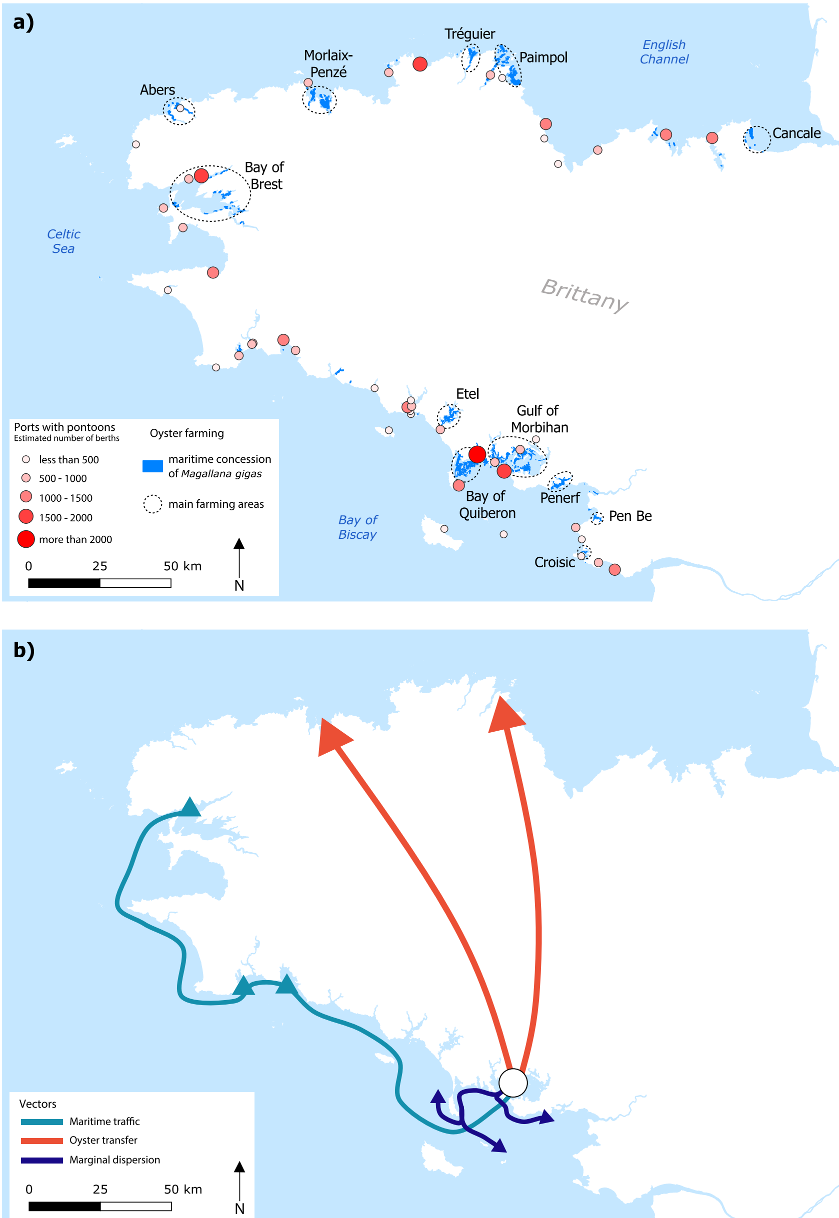

Figure 11: (a) Main regions of interest for non-indigenous species dispersion along the coast of Brittany. Main ports with pontoons (circles in shades of red). Dataset from www.portsdebretagne.fr. Main oyster farming areas in blue (*Magallana gigas*). Dataset "Cadastre conchylicole" obtained on the site geo.data.gouv.fr. Data were updated in 2020 for Finistère and Morbihan, in 2017 for Côtes d'Armor, in 2016 for Ille-et-Vilaine, in 2011 for Loire-Atlantique. (b) Main vectors for non-indigenous species along the coast of Brittany. Some presumed examples of dispersion for maritime traffic in light blue (e.g. *Symphyocladiella dendroidea*), oyster transfer in orange (e.g. *Polyopes lancifolius*), marginal dispersion in dark blue (e.g. *Pachymeniopsis lanceolata* or *Solieria* sp.).

lateral regrowth. It appears anyway that (1) crucial steps must be taken to prevent the introduction and spread of new NIS (Verlaque et al. 2007), and (2) the NIS must be carefully monitored and managed to ensure that any potential negative impacts are minimized.

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