

# 1 Non-indigenous seaweeds in the Northeast 2 Atlantic Ocean, the Mediterranean Sea and 3 Macaronesia: a critical synthesis of 4 diversity, spatial and temporal patterns

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## 54 **Abstract**

55 Effective monitoring and combatting the effect of non-indigenous seaweeds relies on a solid  
56 confirmation of the non-indigenous status of the species. We critically analysed the status of  
57 presumed non-indigenous seaweed species reported from the Mediterranean Sea, the Northeast  
58 Atlantic Ocean and Macaronesia, resulting in a list of 140 species whose non-indigenous nature is  
59 undisputed. For an additional 87 species it is unclear if they are native or non-indigenous  
60 (cryptogenic species) or their identity requires confirmation (data deficient species). We discuss the  
61 factors underlying both taxonomic and biogeographic uncertainties and outline recommendations to  
62 reduce uncertainty about the non-indigenous status of seaweeds. Our dataset consisted of over

63 19,000 distribution records, half of which can be attributed to only five species (*Sargassum*  
64 *muticum*, *Bonnemaisonia hamifera*, *Asparagopsis armata*, *Caulerpa cylindracea* and *Colpomenia*  
65 *peregrina*), while 56 species (40%) are recorded no more than once or twice. In addition, our  
66 analyses revealed considerable variation in the diversity of non-indigenous species between the  
67 geographic regions. The Eastern Mediterranean Sea is home to the largest fraction of non-  
68 indigenous seaweed species, the majority of which have a Red Sea or Indo-Pacific origin and have  
69 entered the Mediterranean Sea mostly via the Suez Canal. Non-indigenous seaweeds with native  
70 ranges situated in the Northwest Pacific make up a large fraction of the total in the Western  
71 Mediterranean Sea, Lusitania and Northern Europe, followed by non-indigenous species with a  
72 presumed Australasian origin. Uncertainty remains, however, regarding the native range of a  
73 substantial fraction of non-indigenous seaweeds in the study area. In so far as analyses of first  
74 detections can serve as a proxy for the introduction rate of non-indigenous seaweeds, these do not  
75 reveal a decrease in the introduction rate, indicating that the current measures and policies are  
76 insufficient to battle the introduction and spread of non-indigenous species in the study area.

## 77 **Highlights**

- 78 • Non-indigenous seaweed species in the Northeast Atlantic Ocean, the Mediterranean Sea  
79 and Macaronesia are critically reanalysed.
- 80 • >19,000 distribution records revealed considerable variation in diversity of non-indigenous  
81 seaweed species in the study area.
- 82 • Taxonomic and biogeographic uncertainties hamper a critical evaluation of the non-  
83 indigenous status of many seaweed species.

84 **Keywords:** biodiversity, Chlorophyta, Europe, invasive alien species, non-indigenous species,  
85 Phaeophyceae, Rhodophyta

## 86 **Introduction**

87 Over the course of several centuries, human-mediated transport has led to the introduction and  
88 establishment of more than 14,000 non-indigenous species in Europe (EASIN, 2022). Some of  
89 these non-indigenous species profoundly affect the abundance, diversity, interactions and evolution  
90 of native biota and consequently affect ecosystem structure, functions and services (Simberloff *et*  
91 *al.*, 2013; Dawson *et al.*, 2017; Blakeslee *et al.*, 2020). The introduction of non-indigenous species  
92 can also result in substantial negative economic impacts (Hulme *et al.*, 2009). The reported costs of

93 biological invasions, at a global level, were estimated to be at least 1.288 trillion US Dollars over  
94 1970–2017 (Diagne *et al.*, 2021). Furthermore, biotic homogenisation and consequently also the  
95 impact of non-indigenous species on native ecosystems are expected to increase in the context of  
96 climate change (Bennett *et al.*, 2021).

97         The management of biological invasions depends heavily on lists of reliably identified non-  
98 indigenous species. Such lists form an essential tool underpinning prevention, control, mitigation or  
99 eradication strategies (Kolar & Lodge, 2001), and in particular to facilitate prevention and early  
100 detection, which are the most cost-effective for management (Simberloff *et al.*, 2013). In addition,  
101 government and management agencies use lists of non-indigenous species in their policies to  
102 protect nature and reverse the degradation of ecosystems. For instance, the primary criterion for the  
103 descriptor D2 dedicated to non-indigenous species under the European “Marine Strategy  
104 Framework Directive” is the rate of novel introductions per 6-year period (European Commission *et*  
105 *al.*, 2021). Comprehensive and accurate lists of non-indigenous species, their respective origin, and  
106 geographical and temporal spread are therefore crucial for an effective response and legislation to  
107 battle threats imposed by non-indigenous species. Unfortunately, the compilation of such lists is  
108 marred by the challenges involved (McGeoch *et al.*, 2012; Costello *et al.*, 2021). At local scales,  
109 lists may be confounded by limited occurrence data and hence underestimate the number and spread  
110 of non-indigenous species. At a more fundamental level, taxonomic uncertainty and the associated  
111 lack of expertise in species identification are regarded as severe problems (Zenetos *et al.*, 2017).  
112 The effects of taxonomic uncertainty are likely more pronounced for less studied taxa and poorly  
113 sampled regions. For example, upon re-examination of about 100 potential non-indigenous taxa of  
114 marine molluscs, almost half of the records turned out to be misidentifications or the distributional  
115 data were incorrect (Zenetos *et al.*, 2017). While DNA-assisted identification has the potential to  
116 solve identification problems, misidentifications of entries in genetic databases combined with  
117 geographic and taxonomic sampling bias make it a challenge in itself to correctly interpret gene  
118 sequence data (Viard *et al.*, 2019; Fort *et al.*, 2021; Tran *et al.*, 2022). In addition, taxonomic  
119 knowledge is not static. Evolving taxonomic insights, often derived from genetic and biogeographic  
120 studies, alter our views on the indigenous or non-indigenous nature of taxa, requiring checklists to  
121 be continuously updated (Taylor, 2010; Guareschi & Wood, 2019). This problem is exacerbated in  
122 the marine environment where many cryptic species have been documented (Appeltans *et al.*,  
123 2012).

124         The above-mentioned problems related to lists of non-indigenous species definitely apply to  
125 seaweeds, which represent one of the largest groups of marine non-indigenous organisms,  
126 constituting between 20 and 29% of all marine non-indigenous species in the Northeast Atlantic

127 Ocean, the Mediterranean Sea and Macaronesia (hereafter referred to as “the study area”)  
128 (Schaffelke *et al.*, 2006; Molnar *et al.*, 2008; Katsanevakis *et al.*, 2013) (Fig. 1; Fig. 2). The  
129 consequences of non-indigenous species on native ecosystems have only been studied in a very  
130 limited number of species. Although some non-indigenous species have been observed to have  
131 positive ecosystem effects (e.g. *Gracilaria vermiculophylla* in the Venice Lagoon and Northeast  
132 Atlantic mudflats; Davoult *et al.*, 2017; Sfriso, 2020), impact studies on such seaweeds have mostly  
133 detected negative ecological effects, with reduction in abundance of native biota being most  
134 frequently reported (Williams & Smith, 2007; Weinberger *et al.*, 2008; Hammann *et al.*, 2013;  
135 Katsanevakis *et al.*, 2014; Maggi *et al.*, 2015; Bulleri *et al.*, 2017; Anton *et al.*, 2019). However,  
136 contrary to the evidence of substantial negative impact on coastal ecosystems of many non-  
137 indigenous seaweeds (e.g. *Caulerpa cylindracea*, *Caulerpa taxifolia*, *Codium fragile*), so far  
138 *Rugulopteryx okamurae* is the only seaweed included in the list of invasive alien species of Union  
139 concern (COMMISSION IMPLEMENTING REGULATION (EU) 2022/1203 of 12 July 2022  
140 amending Implementing Regulation (EU) 2016/1141). This EU regulation enforces member states  
141 to adopt measures to prevent, minimise or mitigate the adverse impact of those species.

142 Regional lists of non-indigenous seaweed species have been regularly published until  
143 recently. For the Mediterranean Sea, which has been disproportionately affected by non-indigenous  
144 species as well as other stressors (Lejeusne *et al.*, 2010; Katsanevakis *et al.*, 2014), non-indigenous  
145 seaweeds have been critically revised on a regular basis (Verlaque *et al.*, 2015; Zenetos *et al.*, 2017;  
146 Galil *et al.*, 2021). Non-indigenous seaweeds of Macaronesia were included in Borges *et al.* (2010),  
147 Chainho *et al.* (2015), Gallardo *et al.* (2016) and Castro *et al.* (2022). Bárbara *et al.* (2005) and  
148 Brodie *et al.* (2016) provided a list of non-indigenous seaweeds as part of a revised check-list of  
149 Galician and British seaweeds, respectively. However, there are gaps and uncertainties for some  
150 regions, and more importantly, a critical compilation encompassing the Northeast Atlantic Ocean,  
151 Macaronesian and Mediterranean regions is currently lacking. The absence of a critically revised  
152 list in the study area not only impedes a comprehensive overview of non-indigenous seaweeds, but  
153 may also introduce ambiguity related to the status of specific taxa due to differences in the criteria  
154 used to define non-indigenous species (see Materials and Methods). In addition, in the absence of a  
155 comprehensive list, spatial and temporal patterns of introductions are difficult to deduce.

156 To address this knowledge gap, we compiled a database of non-indigenous seaweeds in the  
157 Northeast Atlantic Ocean, the Mediterranean Sea and Macaronesia with their distribution records,  
158 their likely origin and putative introduction vectors. These data are used to provide a quantitative  
159 assessment of the spatio-temporal dynamics of primary and secondary introductions and to detect

160 shortcomings in the monitoring and legislation required to tackle the introduction of non-indigenous  
161 species more effectively.

162

## 163 **Materials and methods**

### 164 **Data compilation**

165 We compiled a database of non-indigenous marine seaweed species records from three regions,  
166 namely the Northeast Atlantic Ocean (excluding Greenland), the Mediterranean Sea and  
167 Macaronesia (Fig. 2). For some of the analyses we subdivided the Northeast Atlantic Ocean into  
168 Lusitania and Northern Europe and the Mediterranean Sea into a Western and Eastern part. With  
169 respect to Macaronesia, the compilation includes records from the Azores, Canary Islands, Madeira  
170 and the Salvagen Islands, but not Cape Verde. The dataset builds on previous lists by Mineur *et al.*  
171 (2010) and Verlaque *et al.* (2015), and includes published records of species occurring in a natural  
172 environment and flagged as non-indigenous in the study area irrespective of taxonomic confidence  
173 and biogeographic status (see below). In addition, we included unpublished records produced by  
174 various research projects conducted by, amongst others, the Station Biologique de Roscoff (France),  
175 National Biodiversity Data Centre (Ireland), Stichting ANEMOON (the Netherlands), Scottish  
176 Natural Heritage (Scotland), the ICES Working Group on Introductions and Transfers of Marine  
177 Organisms 2004, as well as the European Alien Species Information Network (EASIN, 2022)  
178 records, collection data, GBIF records and personal data. All records were added to the database  
179 under the name they were reported as. Names were updated according to the most recent taxonomic  
180 consensus (AlgaeBase, Guiry & Guiry, 2023).

181 The species listed as non-indigenous include those that are naturalised (i.e. having  
182 established permanent, self-maintaining populations), as well as species for which no information is  
183 available on population status (i.e. species referred to as ‘alien’ by Verlaque *et al.* 2015). Species  
184 that have been demonstrated to be misidentifications or unsupported records are excluded from the  
185 list. To promote consistency in definitions and criteria used to determine whether a species is non-  
186 indigenous, we have adopted the criteria for assessing the biogeographic status proposed by Essl *et*  
187 *al.* (2018) (Fig. 3). This framework stresses 1) the need for crossing a biogeographic barrier, 2) the  
188 involvement of direct or indirect human agencies in the physical movement of individuals, spores or  
189 fragments, and 3) the ability of the species to reproduce without human assistance in the introduced  
190 range. The combination of these criteria excludes records of species which are in the process of

191 expanding their range naturally, for example as a result of global warming. Species entering the  
192 Mediterranean Sea through the Suez Canal (i.e. Lessepsian migrants), on the other hand are  
193 considered non-indigenous because of the anthropogenic nature of the dispersal corridor. In  
194 contrary, species entering the Mediterranean Sea through the strait of Gibraltar , without a human-  
195 vector, are not considered as non-indigenous. The dataset also includes species indigenous to the  
196 study area that have demonstrably become displaced within he study area as a result of human-  
197 mediated exchanges. Examples include exchanges of species between Atlantic and Mediterranean  
198 shores. Species for which the area of origin is unknown are assigned as ‘cryptogenic’ (sensu  
199 Carlton, 1996). In cases where there is not sufficient information to be conclusive on their  
200 biogeographic status, species are labelled as ‘data deficient’. Species with low uncertainty, for  
201 which there is no doubt about their non-indigenous status, have been labelled ‘non-indigenous’.

202         Added to these criteria but highly relevant with respect to seaweeds, where a solid  
203 taxonomic framework is often lacking for many taxa, is taxonomic confidence. We assigned a  
204 ‘high-confidence score’ (score = 1) to accepted nominal species that had not been shown to be a  
205 species complex based on molecular studies in their introduced or native ranges. A high score was  
206 also assigned to species for which, so far, there is sufficient confidence in unambiguous  
207 identification based on morphology. We acknowledge, however, that the latter does not rule out the  
208 potential existence of cryptic species hidden under the accepted nominal species. Conversely,  
209 species that belong to an understudied complex of cryptic species were assigned a low-confidence  
210 score (score = 0). A cryptic species is defined here as a taxon composed of two or more species that  
211 have been classified as a single nominal species, because they were initially not distinguished based  
212 on their morphological characteristics (Bickford *et al.*, 2007; Pante *et al.*, 2015).

213         Recognising we cannot be conclusive about the non-indigenous status of many seaweed  
214 species, we explicitly acknowledge the uncertainty in the assessment of the taxonomic as well as  
215 biogeographic status of putative non-indigenous seaweeds in the study area (Fig. 3). The status of  
216 each species is concisely described in Suppl. Material Table S1.

217         For every species we determined the year when the species was first reported in the  
218 Northeast Atlantic Ocean, Mediterranean Sea and/or Macaronesia. Where possible, this date refers  
219 to the year the species was detected (i.e. collection date) rather than when the record was published  
220 (i.e. publication date). We acknowledge that detection dates may not portray the actual date the  
221 species was introduced. For each species an estimate is provided for its native biogeographic range.  
222 If the native range could not be assessed, we indicated ‘uncertain’. The putative distribution of the

223 species was based on literature reports included in AlgaeBase (Guiry & Guiry, 2023). Species traits  
224 (e.g. thallus size) were obtained from AlgaeTraits (Vranken *et al.*, 2022). For spatial and temporal  
225 analyses, distribution records were filtered on a combination of unique year, coordinates and  
226 species name to eliminate potential duplicate records. The complete dataset has been archived at  
227 Zenodo and is available at DOI: 10.5281/zenodo.7798640. This dataset contains the following  
228 information for each record: currently accepted scientific name, the scientific name under which it  
229 was originally reported, year of record, location, country, coordinates and reference.

230

## 231 **Results and Discussion**

232 A total of 19,724 records of non-indigenous seaweeds were collected dating from 1808 to 2022  
233 (Fig. 2). Of these, 17,104 were retained after removing duplicates and incomplete data. The  
234 geographical distribution of the records highlights considerable sampling of non-indigenous  
235 seaweeds from all coastlines in the study area (Fig. 2). The list contains 227 species (Table 1). Non-  
236 indigenous species make up approximately 10% of the seaweed flora in the Mediterranean Sea, 6%  
237 in the Northeast Atlantic Ocean and 4% of the Macaronesian flora. The total number of 227  
238 includes all species regardless of taxonomic and biogeographic uncertainty. For 84 species neither  
239 their non-indigenous status nor their taxonomy is challenged (Fig. 4). These species make up 83%  
240 of the distribution records in the database. Half of the distribution records can be attributed to only  
241 five species (*Sargassum muticum*, *Bonnemaisonia hamifera*, *Asparagopsis armata*, *Caulerpa*  
242 *cylindracea* and *Colpomenia peregrina*). Fifty-six species are most likely non-indigenous, but  
243 decisions are hampered by taxonomic uncertainties (Fig. 4). On the other hand, 87 of the 227  
244 species have a cryptogenic or data deficient status (30 species with an uncertain biogeographic  
245 status, and 57 species for which both the geographic status and taxonomic confidence are  
246 uncertain), meaning that the evidence for a non-indigenous status is mediocre to weak (Fig. 4).

247 We emphasise that the categorisation of putative non-indigenous species according to  
248 biogeographic uncertainty and taxonomic confidence emerged as a consensus among the authors of  
249 this paper. A literature search will undoubtedly reveal several additional species names that could  
250 potentially be added to the list of cryptogenic or data deficient species. However, there is little  
251 added value in incorporating species names which are wholly unsupported or most likely result  
252 from misidentifications or other mistakes. Evidently, both taxonomic and biogeographic uncertainty  
253 plague the compilation of lists and databases of non-indigenous species. Below we discuss how the

254 level of sophistication of systematic and biogeographic knowledge translates to uncertainty in the  
255 number of non-indigenous seaweeds in the study area.

256

### 257 **Taxonomic confidence**

258 For 140 species the non-indigenous nature of the species itself is not disputed. However, the reliable  
259 identification of 56 of those species is challenging, and therefore their current distribution as well as  
260 their putative region of origin are questionable. In most cases this uncertainty can be attributed to a  
261 poorly established taxonomic framework. Taxonomic uncertainty is rife in seaweeds. In the absence  
262 of DNA sequence data the identification of many seaweed species is particularly difficult (e.g. Van  
263 Oppen *et al.*, 1996; Maggs *et al.*, 2007; Cianciola *et al.*, 2010; De Clerck *et al.*, 2013; Verbruggen,  
264 2014). Taxonomic uncertainty is much higher among small-sized species: 67% of species smaller  
265 than 5 cm are flagged as taxonomically uncertain, compared to 34% of species larger than 5 cm. Of  
266 the taxa larger than 5 cm with high taxonomic uncertainty are many that belong to genera that are  
267 widespread in tropical and warm-temperate regions (e.g. *Avrainvillea*, *Caulerpa*, *Codium*,  
268 *Dichotomaria*, *Ganonema*, *Hypnea*). From a biogeographic perspective, taxonomic uncertainty  
269 plagues “only” 20% of species with a Northwest Pacific origin (11 of 56 species), but 62% of  
270 species with a likely Lessepsian or tropical Indo-Pacific origin (26 of 42 species) (Table 1).

271         Recent advances in the taxonomy of several genera, nearly always assisted by DNA  
272 sequence data, have demonstrated that many so-called wide-ranging (or cosmopolitan) seaweeds  
273 actually consist of species complexes of morphologically almost indistinguishable species  
274 (pseudocryptic species), or even truly cryptic species which are indistinguishable based on  
275 morphological criteria. The individual species are often confined to specific geographic areas (e.g.  
276 Won *et al.*, 2009; Vieira *et al.*, 2017; Diaz-Tapia *et al.*, 2018; Leliaert *et al.*, 2018; Diaz-Tapia *et al.*,  
277 2020). A more refined taxonomic framework therefore alters our understanding of the biogeography  
278 of the species in many cases and consequently our interpretation of their native versus non-  
279 indigenous status. The *Caulerpa racemosa* complex is highly representative of how evolving  
280 insights into species diversity alter our views of the taxa being non-indigenous in the study area.  
281 While initially *Caulerpa* specimens with vesiculate branchlets collected in the Mediterranean Sea  
282 were identified as *C. racemosa*, the latter proved to be a complex of at least eight species, three of  
283 which (*C. chemnitzia*, *C. cylindracea* and *C. requienii*) are currently considered non-indigenous in  
284 the Mediterranean Sea (Verlaque *et al.*, 2000; Verlaque *et al.*, 2003; Draisma *et al.*, 2014; Verlaque  
285 *et al.*, 2015). Similarly, a better understanding of the taxonomy of foliose *Grateloupia* species

286 resulted not only in the recognition that *G. turuturu* was introduced in the study area from the  
287 Northwest Pacific, as opposed to *G. doryphora* whose distribution is likely to be restricted to the  
288 Pacific coast of South America (Gavio & Fredericq, 2002), but also revealed that so-called non-  
289 indigenous foliose *Grateloupia* species in the study area were actually a mixture of two non-  
290 indigenous species, *G. lanceolata* and *G. turuturu*, and a native species, *G. lanceola*, which had  
291 been regarded a synonym of *G. doryphora* (Verlaque *et al.*, 2005; Figueroa *et al.*, 2007).

292 In many other instances, however, conspecificity of populations from the native and non-  
293 native regions remains to be demonstrated. There are also examples where several non-indigenous  
294 species are thought to be conspecific by some authors but regarded as distinct species by others. For  
295 example, some authors consider *Antithamnion hubbsii* distinct from *A. nipponicum* (Athanasiadis,  
296 1996), while others treat the former as a synonym of the latter (e.g. Kim & Lee, 2012). Similarly,  
297 records of *Polysiphonia morrowii* and *P. senticulosa* likely belong to the same species, even though  
298 both species are regarded as distinct (D'Archino *et al.*, 2013; Stegenga & Karremans, 2015;  
299 Piñeiro-Corbeira *et al.*, 2020). Given the widespread nature of cryptic and pseudocryptic diversity  
300 in seaweeds, continuous efforts of DNA-assisted identifications through Sanger sequencing will  
301 probably continue to revise our view on non-indigenous species.

302 Although DNA sequence data are in many cases a great help in verifying species identities,  
303 this does not mean DNA solves every single problem like a magic wand. Apart from reference  
304 sequences in repositories not being available or reliable, patterns of genetic divergence can be  
305 complicated and prone to different interpretations. For example, differences in the interpretation of  
306 genetic patterns and species boundaries in the genus *Melanothamnus* led to the recognition of a  
307 single species, *M. harveyi* s.l. (McIvor *et al.*, 2001) or by contrast to the recognition of at least three  
308 separate species, including *M. akkeshiensis*, *M. japonicus* and *M. harveyi* s.s. (Savoie & Saunders,  
309 2015). The narrower species concept would result in an interpretation whereby *M. harveyi* is native  
310 to the Northeast Atlantic Ocean rather than a non-indigenous species introduced to the study area  
311 from the Northwest Pacific Ocean. Under the alternative scenario which recognises a single  
312 genetically diverse species, *M. harveyi* is widely distributed globally with both cryptogenic and  
313 non-indigenous haplotypes in the study area (Piñeiro-Corbeira *et al.*, 2019). One should note that  
314 despite the availability of a good number of sequences of these species/haplotypes, the potential  
315 native area of the species (Northwest Pacific Ocean) has been scarcely sampled. Therefore, it is still  
316 possible that *M. harveyi* s.s. can be present in this region but remained undetected. Distribution  
317 records of *M. harveyi* and *M. japonicus* are included as *M. harveyi/japonicus* in our dataset.

318

### 319 **Biogeographic uncertainty**

320 A lack of baseline data with respect to the global distribution of seaweeds is the major contributor  
321 to biogeographic uncertainty reported for 87 taxa (Fig. 4). Brown and green seaweeds display  
322 slightly less biogeographic uncertainty, 28% and 34%, respectively, compared to 42% for red  
323 seaweeds. Baseline data of seaweed diversity along coastlines in the study area as well as the  
324 putative native regions in the form of herbarium collections, censuses and historical checklists can  
325 serve as a reference for the presence of species in a given area. Here as well, low confidence in the  
326 taxonomy and identification of seaweeds makes the interpretation of species lists exceedingly  
327 difficult. If a species is not reliably identified, its distribution is not reliable. As a result,  
328 biogeographic and taxonomic uncertainties usually go hand-in-hand. Three different categories of  
329 factors that lead to biogeographic uncertainty are discussed below.

### 330 **Pseudo-indigenous species**

331 Several seaweed species have been described from the study area that were presumed native, but  
332 later turned out to be non-indigenous species. Carlton (2009) named such species pseudo-  
333 indigenous. For example, *Dictyota cyanoloma* was described as a new species from the  
334 Mediterranean Sea and Macaronesia (Tronholm *et al.*, 2010), but subsequent collecting efforts  
335 revealed that the species most likely represents a cryptic introduction (Aragay Soler *et al.*, 2016;  
336 Steen *et al.*, 2017; Tran *et al.*, 2021). Similarly, *Porphyra olivii* described from Greece (Brodie *et*  
337 *al.*, 2007a) turned out to be conspecific with *Neopyropia koreana* (Vergés *et al.*, 2013; Yang *et al.*,  
338 2020), a species native to the Northwest Pacific. Such insights invariably result from DNA-assisted  
339 species identification and subsequent interpretations of biogeographic patterns. Hereby widely  
340 disjunct distribution ranges are interpreted as non-natural and therefore the result of human-  
341 mediated dispersal.

342 Evidently, determining the non-indigenous nature of a species becomes more difficult for  
343 historic introductions. In such cases we fully rely on DNA signatures which can point toward a non-  
344 indigenous nature of the species. DNA-assisted identification of historic voucher specimens of  
345 *Codium fragile* revealed that the invasive (sub)species was already introduced into the study area as  
346 early as 1845 (Provan *et al.*, 2008), which is roughly a century before phycologists realised the  
347 species was actually native to the Northwest Pacific Ocean and non-indigenous to the study area as  
348 well as several other parts of the world. In the case of *Cutleria multifida*, described from Norfolk,

349 England as early as 1801, genetic signatures point toward an introduction of the Mediterranean Sea  
350 populations from the Northwest Pacific. The Northeast Atlantic Ocean populations, however, are  
351 genetically more diverse and well-differentiated from those in Japan and are therefore considered  
352 native (Kawai *et al.*, 2016). It remains to be determined if *Cutleria multifida* is native to the  
353 Northeast Atlantic Ocean as well as the Pacific, or whether an even more complex history of  
354 historic introductions underlies this pattern.

### 355 **Discerning natural from human-mediated dispersal**

356 Eventually, the possibility of introductions needs to be evaluated against historic and ongoing  
357 natural dispersal events. The recent observation of *Flabellia petiolata* from the south coast of  
358 England confronts researchers with exactly this question (Díaz-Tapia *et al.*, 2020). Despite a long  
359 tradition of seaweed studies and regular surveys, *F. petiolata* was never recorded from the British  
360 Isles prior to 2013. The closest populations of the species are found in the Mediterranean Sea and  
361 the Canary Islands. A recent introduction would be the most obvious explanation. However, the  
362 English populations of *F. petiolata* could also be interpreted as a relic of a formerly more  
363 widespread Atlantic Ocean distribution. The species' range might have been continuous during  
364 warmer periods in the Holocene, but persisted in the Northeast Atlantic Ocean in a handful of  
365 refugia during colder periods. After all, several native species, e.g. *Cladophora battersii*, *Codium*  
366 *bursa* and *Halopithys incurva* display similar distribution patterns (Maggs & Hommersand, 1993;  
367 Brodie *et al.*, 2007b).

368         Quaternary climatic cycling probably also facilitated dispersal of temperate species across  
369 the tropical Atlantic Ocean connecting southern Africa with Europe. The presence of *Schizymenia*  
370 *apoda* in the Azores, the British Isles and Namibia may have resulted from natural amphi-equatorial  
371 dispersal events in recent geological times, but also a human-mediated introduction in the Atlantic  
372 Ocean cannot be ruled out given the presence of *S. apoda* in Australia and China (Gabriel *et al.*,  
373 2019; Gunnarsson *et al.*, 2020). Natural dispersal events from the Northeast Pacific Ocean to  
374 Northern Europe through the Bering Strait may be difficult to discern from introductions  
375 (Lindstrom, 2001; Bringloe & Saunders, 2019). For instance, *Schizymenia jonssonii*, a species  
376 recently described from Iceland, may have colonised the northern Atlantic Ocean naturally via the  
377 Bering Strait but it is equally possible the species is a relatively recent introduction (Gunnarsson *et*  
378 *al.*, 2020).

379 Population-level sampling and the application of genetic markers with sufficient  
380 intraspecific resolution (e.g. fast evolving spacer regions, microsatellite markers or SNP data) have  
381 the potential to shed light on natural versus human-mediated dispersal events, and more generally to  
382 help in reconstructing introduction history (Viard & Comtet, 2015), but are rarely used in studies of  
383 putative seaweed introductions. Notable exceptions include the invasive history of *Fucus* species,  
384 *Sargassum muticum* and *Gracilaria vermiculophylla*.

385 Coyer *et al.* (2011) demonstrated a North Pacific origin of *Fucus distichus* followed by at  
386 least two separate colonisation events of the North Atlantic Ocean prior to the last glacial  
387 maximum, which makes this species native to Europe. However, the taxon, having a predominantly  
388 northern distribution, was accidentally introduced in the Oslofjord followed by further expansion in  
389 the Kattegat region as a result of an introduction event in the late 19<sup>th</sup> century (Coyer *et al.*, 2002, as  
390 *F. evanescens*, currently regarded as a subspecies of *F. distichus*). *Fucus serratus* was also exported  
391 from mainland Europe to Atlantic North America, Iceland and the Faroes (Coyer *et al.*, 2006;  
392 Brawley *et al.*, 2009). Discharging of ballast stones in destination harbours is considered the prime  
393 source of introductions in Atlantic North America and Iceland in the 19<sup>th</sup> century. The *F. serratus*  
394 population in the Faroes is of more recent origin (late 20<sup>th</sup> century) and was most likely introduced  
395 from Iceland (Coyer *et al.*, 2006). Many marine benthic organisms including seaweeds but also  
396 many invertebrates display amphi-Atlantic distribution (Haydar, 2012). For such disjunct  
397 distributions, distinguishing scenarios of post-glacial relicts or natural long-distance dispersal from  
398 human-assisted dispersal (and introduction) is challenging and most often requires a combination of  
399 life-history traits assessment and high resolution molecular markers. The power of genome-wide  
400 genetic variation was demonstrated for *Sargassum muticum* (Le Cam *et al.*, 2020); whereas  
401 microsatellite markers failed to reveal any genetic variation in the invaded range of the species, a  
402 panel of single-nucleotide polymorphisms (SNPs) obtained from ddRAD sequencing confirmed a  
403 secondary introduction to the Northeast Atlantic Ocean from the Northeast Pacific Ocean, but also  
404 revealed two additional cryptic introductions to Europe. Similarly, Krueger-Hadfield *et al.* (2017)  
405 identified the areas in the native region that most likely contributed to the European invasions of the  
406 red alga *Gracilaria vermiculophylla*. Subsequent work used SNPs to refine the origins and  
407 understand evolution during invasion (Flanagan *et al.*, 2021).

408 In Macaronesia, several confounding factors further complicate the interpretation of the non-  
409 indigenous nature of species. The geographical location of Macaronesia, bordering the tropical  
410 Atlantic Ocean, contributes significantly to this difficulty in interpretation. Several tropical and

411 subtropical taxa are, probably erroneously, attributed a pantropical distribution, which not only  
412 contributes to high taxonomic uncertainty, but the latter also translates into biogeographic  
413 uncertainty. In addition, it is not always evident to preclude natural dispersal to explain the presence  
414 of particular species. *Halimeda incrassata*, a species that naturally occurs in the tropical western  
415 Atlantic Ocean (Verbruggen *et al.*, 2006), was reported from Porto Santo, Madeira, by Wirtz &  
416 Kaufmann (2005) and more recently from the Balearic Islands by Alós *et al.* (2016). Further  
417 surveys indicated the species is also present in the Canary Islands (Sangil *et al.*, 2018) and Azores  
418 (Costa *et al.*, 2017). Even though in the Mediterranean Sea the species displays typical invasive  
419 behaviour, the involvement of human activities in its establishment is not clear. Another species  
420 from tropical western Atlantic Ocean, *Caulerpa ashmeadii*, was recently reported from Porto Santo,  
421 Madeira, and may represent a similar case of natural range expansion across the Atlantic (Ribeiro *et*  
422 *al.*, 2023). Amphi-Atlantic Ocean distributions have been confirmed using molecular markers for  
423 several seaweed taxa (*Cladophoropsis membranacea*, Leliaert *et al.*, 2009; *Laurenciella marilzae*,  
424 Cassano *et al.*, 2012; *Laurencia catarinensis*, Machin-Sanchez *et al.*, 2012; Tronholm *et al.*, 2012;  
425 *Vertebrata foetidissima*, Díaz-Tapia *et al.*, 2013; *Dictyota* spp., Tronholm *et al.*, 2013; *Caulerpa*  
426 *prolifera*, Varela-Álvarez *et al.*, 2015; *Laminaria digitata*, Neiva *et al.*, 2020; *Lobophora* spp.,  
427 Vieira *et al.*, 2020). In these examples presumed natural distribution ranges have not been  
428 challenged.

429         Also of note is that Macaronesia covers a large geographic area, encompassing several  
430 biologically diverse archipelagos. Several taxa that have long been reported from the Canary Islands  
431 and Madeira and are considered native in those areas, have recently been reported from the Azores.  
432 The geographic position of the Azores and the actual oceanographic current circulation in the North  
433 Atlantic Ocean would not seem favourable for natural range expansions from the Canary Islands  
434 and Madeira. In some cases, initial reports from anthropogenic habitats, such as harbour  
435 environments (e.g. *Caulerpa webbiana*), favour the hypothesis of an anthropogenic factor in the  
436 range expansion, although evidence is lacking for several other species which are presumed non-  
437 indigenous (e.g. *Halimeda incrassata*, *Xiphosiphonia pinnulata*, *Hypoglossum heterocystideum*).

438         A final category of uncertainty in natural vs. human-mediated dispersal mechanisms concerns  
439 those non-indigenous species which have been displaced within the study area. The biogeographic  
440 history of the Mediterranean Sea biota is closely intertwined with the Northeast Atlantic Ocean to  
441 which it is connected by the narrow Strait of Gibraltar (Bianchi & Morri, 2003; Patarnello *et al.*,  
442 2007; Le Gall *et al.*, 2021), which results in a subset of species being shared between both regions.

443 However, several Northeast Atlantic Ocean species have been recently introduced into the  
444 Mediterranean Sea, often in lagoons with extensive aquaculture facilities, e.g. *Ascophyllum*  
445 *nodosum*, *Chorda filum*, *Fucus spiralis* and *Grateloupia minima* (Petrocelli *et al.*, 2013). In some  
446 cases however, patterns become more complex, for example, when native and non-indigenous  
447 populations co-occur as is the case for *Chondria coerulescens*, *Vertebrata fucoides* and possibly  
448 also *Ganonema farinosum* (Verlaque *et al.*, 2015). It is worth remembering that many  
449 Mediterranean Sea species naturally dispersed from the Atlantic Ocean after the Zanclean flood  
450 which occurred after the Messinian salinity crisis about 5.33 myr (Blondel *et al.*, 2010).

#### 451 **Species of unresolved origin**

452 In several cases the non-indigenous nature of certain seaweeds remains unresolved. Some recently  
453 described species in the study area, such as *Polysiphonia radiata* and *P. delicata*, are mainly known  
454 from marinas and are probably non-indigenous but their origin remains unknown because it is likely  
455 that they remained undescribed in their native area (Díaz-Tapia *et al.*, 2017). Morphological  
456 similarity of putative non-indigenous species to native species can also complicate interpretation of  
457 non-indigenous patterns as demonstrated by *Anotrichium furcellatum*. The latter was originally  
458 described from Naples, but considered non-indigenous in the Northeast Atlantic Ocean. The  
459 Mediterranean Sea populations, however, may have been largely replaced by a cryptic introduction  
460 of *A. okamurae*, originally from the Northwest Pacific Ocean (Verlaque *et al.*, 2015). The status of  
461 *A. furcellatum* and *A. okamurae* has not yet been tested with molecular data.

462 Similar arguments could be made for species that are considered native in the study area. In  
463 the case of *Lobophora delicata*, which is not considered as non-indigenous, a lack of baseline data  
464 makes it difficult to be conclusive on its status as a native species. As pointed out by Vieira *et al.*  
465 (2019), the first records of *Lobophora* in the Mediterranean Sea date back to 1955 (Edelstein,  
466 1960), which is surprising for a distinctive seaweed genus which can be easily found in many places  
467 growing at a depth of 0.5 m. In contrast, other genera of Dictyotales were invariably reported from  
468 the Mediterranean Sea in the 18th or early 19th century. Has *L. delicata* been overlooked or does  
469 the late discovery of the species correspond to a more recent introduction? Without proper baseline  
470 data, e.g. herbarium records, this is difficult to test, and if the species does not display typical  
471 invasive behaviour its native status may simply never come into question.

472 A puzzling case is presented by several taxa with clear Indo-Pacific affinities which  
473 appeared in the Mediterranean Sea prior to the opening of the Suez Canal in 1869, e.g.

474 *Acanthophora nayadiformis*, *Asparagopsis taxiformis* and *Ganonema farinosum*. For instance,  
475 *Asparagopsis taxiformis* was first described from Alexandria in the Mediterranean Sea as *Fucus*  
476 *taxiformis* Delile (1813), and thus reported as a native species. However, further molecular work  
477 revealed that this accepted species was made of five distinct lineages, possibly corresponding to two  
478 cryptic species (Ní Chualáin *et al.*, 2004; Andreakis *et al.*, 2007; Dijoux *et al.*, 2014), one of them  
479 presumably present in the Mediterranean Sea prior to the opening of the Suez Canal, and one more  
480 recently introduced. Similar complexity was revealed for the closely related species *Asparagopsis*  
481 *armata*, supposedly introduced in the study area, for which novel sampling in the South Pacific  
482 Ocean showed the existence of two highly divergent clades, presumably corresponding to two  
483 cryptic species, one of them distributed in Europe, South Africa and Tasmania, and one restricted  
484 (so far) to Western Australia, New Zealand and Tasmania (Dijoux *et al.*, 2014). Such cases  
485 highlight the difficulty in establishing whether a species is non-indigenous in the absence of large  
486 sampling encompassing the global distribution of the targeted presumably non-indigenous species.

487

## 488 **The spatial patterns and origins of non-indigenous seaweeds**

489 Analysis of the distribution of non-indigenous seaweeds in the study area reveals clear patterns in  
490 richness and the number of species shared among regions. The large-scale spatial patterns are  
491 discussed below in a context of dispersal vectors that determine spread and establishment of non-  
492 indigenous species.

493         The Eastern Mediterranean Sea is home to the highest number of non-indigenous seaweeds  
494 (77 species), followed by the Western Mediterranean Sea (47 species) and Lusitania (45 species).  
495 Macaronesia and Northern Europe harbour somewhat lower numbers (36 and 40 species,  
496 respectively). These numbers refer to high-confidence non-indigenous species only. Adding  
497 cryptogenic and data deficient species further underscores the higher number of non-indigenous  
498 species in the Eastern Mediterranean Sea. In the latter region an extra 47 species are flagged as  
499 cryptogenic or data deficient, which is considerably higher compared to the other regions which  
500 typically host 20 or less cryptogenic and data deficient species. In all regions, most of the non-  
501 indigenous seaweeds belong to Rhodophyta (between 63-76% of the species non-indigenous in each  
502 region), followed by brown seaweeds (18-22%), while green seaweeds contribute to 8-18% of the  
503 species recorded (Fig. 5).

504 We did not detect a significant correlation between the number of non-indigenous species  
505 and the number of records (Pearson correlation = -0.18, p-value = 0.74), which indicates that  
506 differences of non-indigenous species between regions are not a mere artefact of sampling effort.  
507 The number of non-indigenous species also does not scale with the length of the coastline (Pearson  
508 correlation = 0.10, p-value = 0.88). As will be argued below, the number of non-indigenous species  
509 in a given region and the fraction of species shared between regions is a complex function including  
510 the efficiency of primary and secondary dispersal vectors combined with abiotic (and potentially  
511 biotic) ecological factors that determine the establishment of non-indigenous species in the recipient  
512 ecosystems (reviewed in Maitner *et al.*, 2021).

513 The Mediterranean Sea and the Northeast Atlantic Ocean share 45 high-confidence non-  
514 indigenous species, while Macaronesia shares roughly an equal number of non-indigenous species  
515 with the Mediterranean Sea (24 species) and the Northeast Atlantic Ocean (21 species) (Fig. 6A).  
516 Within the Northeast Atlantic Ocean, Macaronesia and Lusitania share 22 high-confidence non-  
517 indigenous species, while Macaronesia and Northern Europe share none other than the 14 non-  
518 indigenous species present in all three Northeast Atlantic regions (Fig. 6B). A relatively low  
519 number, 18 high-confidence non-indigenous species out of 140, are shared between the Northeast  
520 Atlantic Ocean, Macaronesia and the Mediterranean Sea (Fig. 6A). The broad distribution of these  
521 non-indigenous species is noteworthy for it reflects a very wide amplitude in abiotic and biotic  
522 parameters. At least nine of these widely distributed non-indigenous species (*Antithamnion*  
523 *hubbsii/nipponicum*, *Antithamnionella spirographidis*, *Asparagopsis armata*, *Bonnemaisonia*  
524 *hamifera*, *Codium fragile* subsp. *fragile*, *Colpomenia peregrina*, *Dictyota cyanoloma*, *Grateloupia*  
525 *turuturu*, *Scytosiphon dotyi*) are reported from all five regions. The remaining species have a more  
526 restricted distribution range, being only present in the three central regions Macaronesia, Lusitania  
527 and the Western Mediterranean Sea (*Phycocalidia suborbiculata*, *Spongoclonium caribaeum*,  
528 *Symphocladia marchantioides*), or being absent from either of the two peripheral regions, i.e. the  
529 Eastern Mediterranean Sea (*Antithamnionella ternifolia*, *Sargassum muticum*) or Northern Europe  
530 (*Asparagopsis taxiformis*, *Rugulopteryx okamurae*, *Pachymeniopsis gargiuloi*).

531 The number of high-confidence non-indigenous species currently only found in the  
532 Mediterranean Sea (66 species) is striking. Including cryptogenic or data deficient species brings  
533 this number to 115. However, there is considerable differentiation of non-indigenous species  
534 between the Western and Eastern Mediterranean Sea. Only 34 non-indigenous species are shared  
535 between both regions, representing 38% of the total non-indigenous species diversity in the

536 Mediterranean Sea (Fig. 6C). In addition, the fraction of non-indigenous species unique to the  
537 Eastern Mediterranean Sea (27 species) is considerably larger than for the Western Mediterranean  
538 Sea (8 species) (Fig. 6C). The latter pattern is largely the result of dispersal of warm-adapted  
539 species from the Red Sea and by extension the Indo-Pacific Ocean via the Suez Canal. At present,  
540 only a fraction of these have spread to the Western Mediterranean Sea resulting in a higher diversity  
541 of non-indigenous species in the Eastern Mediterranean Sea.

542         The non-indigenous species reported from the Thau Lagoon in France, and the Mar Piccolo  
543 and Venice Lagoon in Italy are quite distinct compared to those of surrounding Mediterranean  
544 waters. A combination of anthropogenic disturbances and intense aquaculture activities (trade and  
545 exchanges), more specifically import of shellfish, has resulted in a very high diversity of non-  
546 indigenous species in these lagoon systems (66 species), comparable to that of the surrounding  
547 Mediterranean Sea locations despite their much smaller area. The non-indigenous species in  
548 Mediterranean lagoons have, moreover, more affinities with the Atlantic Ocean than with the  
549 Mediterranean Sea, likely to be due to exchanges between shellfish production areas (see below).  
550 Nearly half of the non-indigenous species encountered in Mediterranean aquaculture lagoons are  
551 not (yet) reported from surrounding Mediterranean water, while 36 are shared with the Northeast  
552 Atlantic Ocean. Of these 36 non-indigenous species, 13 have only been recorded in aquaculture  
553 lagoons within the Mediterranean Sea. These mainly include species with a Northwest Pacific  
554 Ocean origin, e.g. *Dasysiphonia japonica*, *Neopyropia yezoensis* and *Nitophyllum*  
555 *stellatocorticatum*. Differences in the abiotic physico-chemical environment between  
556 Mediterranean lagoons and surrounding coastlines probably underlie the failure of these species to  
557 spread widely in the Mediterranean Sea. *Rugulopteryx okamurae*, however, presents a striking  
558 counterexample of this trend. The species was collected in the Thau Lagoon for the first time in  
559 2002 (Verlaque *et al.*, 2009). Initially *R. okamurae* appeared to be rather non-invasive, but in 2015  
560 it was reported from the Strait of Gibraltar (Ocaña *et al.*, 2016; El Aamri *et al.*, 2018; García-  
561 Gómez *et al.*, 2020), where the species forms dense stands rapidly overgrowing most native  
562 seaweed species. More recently the same alarming invasive behaviour of *R. okamurae* has been  
563 noted in the Marseille area (Ruitton *et al.*, 2021) as well as southwest Portugal (Liulea *et al.*, 2023)  
564 and Macaronesia (Faria *et al.*, 2022).

565         A Northwest Pacific origin of the largest part of the non-indigenous species present in the  
566 Mediterranean lagoons and Northern Europe is well established (Fig. 7, Table 1) (Boudouresque *et*  
567 *al.*, 2010). Regular monitoring and surveys demonstrated that many of those species had been first

568 accidentally introduced in the Mediterranean lagoons (notably the Thau lagoon) and were then  
569 transported to the Northeast Atlantic Ocean hitchhiking with oyster transfers (Mineur *et al.*, 2007a).  
570 *Undaria pinnatifida* presents a notable exception to this pattern. Following its accidental  
571 introduction in the Thau lagoon, the species was deliberately introduced in Brittany for aquaculture  
572 purposes (Floc'h *et al.*, 1991) from which it rapidly spread and established itself as one of the  
573 dominant non-indigenous species in artificial as well as natural habitats in the Northeast Atlantic  
574 Ocean (Voisin *et al.*, 2005; Guzinski *et al.*, 2018). Note that commercial transfers of oysters  
575 between the Mediterranean Sea and the Atlantic coasts of France is still fully allowed under French  
576 and European regulations, which results in a quasi-continuous series of secondary introduction  
577 events. Aquaculture- and fisheries-associated transport (e.g. nets, packing material) between the  
578 Atlantic Ocean and Mediterranean Sea is also undoubtedly responsible for the introduction of a  
579 range of native Atlantic Ocean species to the Mediterranean lagoons (e.g. *Ascophyllum nodosum*,  
580 *Chorda filum*, *Grateloupia minima*, *Fucus spiralis* and *Vertebrata fucoides*).

581         The Mediterranean Sea, Macaronesia and Lusitania are also home to 35 high-confidence  
582 non-indigenous species with presumed or established Australasian origin (Fig. 7). Species with  
583 Australasian origin are much less represented in Northern Europe, reflecting the warm temperate  
584 nature of these species. The introduction vectors for this category of species remain, however,  
585 largely elusive. For *Acrothamnion preissii* and *Womersleyella setacea* ship traffic has been  
586 suggested as vector based on their first observation close to a major harbour (Livorno, Italy), but  
587 accidental release from scientific laboratories and public or private aquaria is also a possibility. As  
588 with the notorious case of *Caulerpa taxifolia* (Verlaque *et al.*, 2015), aquarium releases have likely  
589 resulted in the introduction of other seaweeds, mainly in the Mediterranean Sea (Vranken *et al.*,  
590 2018).

591         Despite the abovementioned clear categories of non-indigenous species and associated  
592 pathways, for circa one third of the species there is considerable uncertainty regarding the area of  
593 origin and the potential dispersal vectors. Complicating identification of native range and vectors  
594 even further, population-level molecular studies on several non-indigenous species have unveiled  
595 multiple independent introductions possibly involving different vectors (McIvor *et al.*, 2001; Voisin  
596 *et al.*, 2005; Geoffroy *et al.*, 2016; Le Cam *et al.*, 2020).

597

598

## 599 **Introduction hotspots**

600 Of the 140 high-confidence non-indigenous species, 65% have been reported for the first time in the  
601 Mediterranean Sea, 26% in the Northeast Atlantic Ocean and 9% in Macaronesia. The distributions  
602 of the first record of each species in the study area underscore the importance of aquaculture for  
603 introductions of seaweeds. The Thau lagoon, with 30 reports of first introductions in the study area,  
604 is one of the major introduction hotspots. In total 58 species, constituting 32% of the total seaweed  
605 diversity or 48-99% of the biomass, have become established in this coastal lagoon (Boudouresque  
606 *et al.*, 2010). The Thau lagoon is an important centre of oyster cultivation in the Mediterranean Sea.  
607 However, the oyster farmers rely on the import of oyster spat produced in other regions because the  
608 lagoon is not particularly suitable for oyster reproduction. Since 1977, only spat of Pacific oysters  
609 spat produced in the Atlantic Ocean is allowed to be laid in the French Mediterranean lagoons  
610 (Verlaque *et al.*, 2007). However, it is likely that some non-official imports from outside of Europe  
611 occur, as reported by Verlaque (1996). These continuous transfers across different biogeographic  
612 regions result in astonishingly high numbers of non-indigenous species. A low native diversity due  
613 to the low occurrence of natural hard substrata in lagoons and relatively recent construction of hard  
614 substrata for aquaculture purposes, concomitant with transfers of livestock which seed the new  
615 substrata, makes these lagoons hotspots for non-indigenous species establishment (Mineur *et al.*,  
616 2015).

617 The Southeast Mediterranean Sea constitutes another introduction hotspot, which accounts  
618 for 24 first reports and a total of 32 non-indigenous species. The inauguration of the Suez Canal in  
619 1869 resulted in an open connection between the Northern Red Sea and the Eastern Mediterranean  
620 Sea. As a result, more than 500 marine species are believed to have invaded the Mediterranean Sea  
621 through the Suez Canal, so-called Lessepsian migrants (Zenetos *et al.*, 2010; Zenetos *et al.*, 2012;  
622 Galil *et al.*, 2021). With respect to non-indigenous seaweeds, many species were first reported in a  
623 series of papers by the Egyptian phycologist Anwar Aleem (Aleem, 1948; Aleem, 1950; Aleem,  
624 1951; Aleem, 1993). Recent efforts by Greek, Lebanese, Israeli and Turkish phycologists have  
625 expanded the list of Lessepsian seaweeds considerably (e.g. Tsiamis, 2012; Hoffman, 2013; Bitar *et*  
626 *al.*, 2017; Israel & Einav, 2017; Çinar *et al.*, 2021; Galil *et al.*, 2021). Nevertheless, a paucity of  
627 historic baseline data makes it often difficult to establish the Lessepsian origin of many species or to  
628 point to the exact date of introduction. As outlined above, records of species with clear Indo-Pacific  
629 affinities which predate the opening of the Suez Canal (e.g. *Ganonema farinosum* and  
630 *Acanthophora nayadiformis*) still puzzle phycologists. In addition, the identities of many species  
631 reported for the first time by Aleem and others (e.g. *Gracilaria arcuata*, *G. disticha*, *Hypnea*

632 *flagelliformis*, *Solieria dura*, *Spatoglossum variable*) have never been confirmed using molecular  
633 markers and are highly uncertain. In general, a detailed understanding of past and contemporary  
634 temporal dynamics of seaweed introductions in the Eastern Mediterranean Sea remains a challenge.  
635 More than in any other region it remains difficult to link the observation of a new seaweed species  
636 with the introduction date. This uncertainty has bearing on the monitoring of migration through the  
637 Suez Canal which has been regarded as an ongoing process (Boudouresque, 1999; Por, 2012). The  
638 current construction of the new Suez Canal, doubling the capacity of the current corridor, is  
639 expected to further increase the influx of Red Sea species (Galil *et al.*, 2015) and contribute to  
640 further tropicalisation of the Mediterranean Sea (Bianchi & Morri, 2003; Coll *et al.*, 2010).

641 Compared to the two Mediterranean Sea introduction hotspots, first records appear less  
642 localised in the Northeast Atlantic Ocean. The English Channel (Brittany, southern English coast)  
643 and the Scheldt estuary (the Netherlands) are most prominent as introduction hotspots. To what  
644 extent this spatial pattern reflects the true locations of primary introductions or whether the  
645 locations of first records are biased by the distribution of preferred study areas of phycologists and  
646 research institutes is difficult to assess. There is, indeed, a strong correlation between the  
647 introduction hotspots (i.e. locations from which a high number of first records for the study area  
648 were reported) and the density map of all records of non-indigenous species, which is indicative of  
649 high monitoring activities in areas where many non-indigenous species are found. In addition, it is  
650 noteworthy that the English Channel and Scheldt estuary are important areas for oyster farming, and  
651 many non-indigenous species have been accidentally introduced with oyster transfer from the  
652 Mediterranean Sea.

653

#### 654 **Introduction rates: temporal trends**

655 Disentangling the factors underpinning temporal trends in the accumulation rate of non-indigenous  
656 seaweeds may improve our understanding of introductions and result in better-informed predictions  
657 of future trajectories (Seebens *et al.*, 2018). Deducing temporal trends in the rate of introduction of  
658 non-indigenous species, however, assumes a correlation between the date of introduction and the  
659 moment the species was detected. Although seemingly straightforward, for several species the  
660 timespan between introduction and detection is probably considerable and unpredictable. Detection  
661 obviously depends on collecting effort, but as highlighted in previous sections, the taxonomic and  
662 biogeographic framework will also determine if a species is considered non-indigenous.

663 Furthermore, Costello & Solow (2003) demonstrated that an increasing rate of detection need not  
664 imply an increasing rate of introductions even when collection effort is constant. Given this  
665 complexity, reports that introduction rates have increased or decreased in specific time windows  
666 should be treated with caution.

667 Acknowledging this uncertainty, the detection of non-indigenous species shows two distinct  
668 phases, one prior to 1950-1970 characterised by low accumulation rates, followed by another much  
669 higher accumulation rate from then onward (Fig. 8). Irrespective of taxonomic and biogeographic  
670 uncertainties, there is little to no indication for a decline in the rate at which non-indigenous species  
671 are reported. The observation that the detection, and presumably also the introduction, of non-  
672 indigenous species has not reached saturation (Fig. 8), is in line with the observations by Seebens *et*  
673 *al.* (2017) for other taxonomic groups. For seaweeds, the absence of a decline in the first-record rate  
674 may point to the inefficiency of measures aimed to prevent and mitigate new introductions.  
675 Alternatively, the community of phycologists involved in monitoring of non-indigenous seaweeds  
676 has become larger and more efficient at detecting incoming species, e.g. through the use of DNA-  
677 barcoding methods.

678 According to Mineur *et al.* (2007b) who sampled the hulls of several commercial cargo  
679 vessels, hull fouling seems to play a relatively minor role in the displacement of seaweeds across  
680 the globe. Similarly, ballast water, one of the prime sources of introductions for marine  
681 invertebrates and microalgae (Bolch & de Salas, 2007; Gollasch *et al.*, 2015), is relatively  
682 unimportant with respect to introduction of seaweeds. Yet there is evidence of introduction with  
683 commercial ships not hulls or ballast water but other components such as anchors, for instance in  
684 Australia for *U. pinnatifida* (South *et al.*, 2017). Leisure boats, however, likely contribute to the  
685 local spread of non-indigenous species within the study area. Their role has certainly been  
686 underestimated so far, at least for secondary introductions (Mineur *et al.*, 2008). Contrary to the  
687 Eastern Mediterranean Sea where the opening of the Suez Canal resulted in an ongoing and steady  
688 influx of non-indigenous species (Galil *et al.*, 2015), in the Western Mediterranean Sea a  
689 disproportionate number of non-indigenous seaweed species appears to have been introduced  
690 through import of oyster stocks (Verlaque *et al.*, 2007). In the late 1960s and early 1970s, disease  
691 caused by Asian oysters importation outbreaks in the study area affecting oyster populations caused  
692 a major disruption of production (Mineur *et al.*, 2015). Mitigation procedures involved massive  
693 imports in the 1970s of Pacific oyster from its native range in the Northwest Pacific Ocean, or via  
694 from the Puget Sound in the Northeast Pacific Ocean where the species is also cultivated on a large  
695 scale (Mineur *et al.*, 2014). *Sargassum muticum* introduced into the study area was shown to have

696 several origins including a primary introduction from Asia and a secondary introduction from the  
697 Northeast Pacific Ocean (Le Cam *et al.*, 2020).

698

## 699 **Conclusion and perspectives**

700 In conclusion, our critical synthesis of non-indigenous seaweed diversity in the Northeast Atlantic  
701 Ocean, Mediterranean Sea and Macaronesia revealed widespread taxonomic and biogeographic  
702 uncertainty. This finding negatively impacts efforts to evaluate the effectiveness of measures to  
703 reduce non-indigenous species influx, manage their risks and impacts, and devising potential  
704 control strategies. This uncertainty can be addressed through the progressive use of molecular  
705 markers, particularly standard DNA barcoding approaches, which can in most cases confirm the  
706 identification of presumed non-indigenous seaweeds (Viard & Comtet, 2015). Importantly,  
707 however, a taxonomic and biogeographic reference framework should also be established for  
708 putative indigenous regions. DNA-based identification is relatively well-developed for species with  
709 a Northwest Pacific origin. For tropical taxa such a framework lags behind, resulting in higher  
710 levels of uncertainty regarding the identity of non-indigenous species with presumed tropical origin.  
711 Such a reference framework will also be necessary for early detection of non-indigenous species  
712 and monitoring with the use of bulk sample and eDNA metabarcoding (Darling *et al.*, 2017; Keck  
713 & Altermatt, 2023).

714         However, standard DNA barcoding may not be sufficient to interpret more complex  
715 introduction histories, such as cases where non-indigenous and indigenous populations co-occur, as  
716 suggested for several species in the Mediterranean Sea (Verlaque *et al.*, 2015) or where recent  
717 human-mediated dispersal needs to be evaluated against ongoing and natural dispersal events linked  
718 to Pleistocene or Holocene climatic oscillations (Neiva *et al.*, 2016). In these cases a combination of  
719 population-level sampling strategies and molecular markers that capture intraspecific diversity is  
720 needed to shed light on the number and directions of dispersal events and re-evaluate the status of  
721 taxa currently considered cryptogenic.

722         In parallel with DNA-barcoding efforts, historical and reliable baseline data of seaweed  
723 diversity is needed to reduce the subjective interpretation of non-indigenous species and determine  
724 more precisely their date of introduction. It is likely that the introduction of many non-indigenous  
725 species occurred significantly earlier than the time of their first detection, especially for species that  
726 have morphologically similar congeners in the study area (such as species from the genera *Dictyota*,

727 *Gracilaria*, *Polysiphonia* and *Ulva*). Herbarium collections can serve as a crucial source of primary  
728 data to address this issue, and advances in sequencing technologies make it possible to obtain  
729 genetic data from voucher specimens tens or even hundreds of years old as demonstrated for the  
730 *Codium fragile*-complex (Provan *et al.*, 2008). We anticipate that herbaria will play an increasingly  
731 important role in documenting spatio-temporal patterns of non-indigenous seaweeds, alongside  
732 large-scale digitization efforts for these collections. More precise estimates of the date of  
733 introduction will also reduce uncertainty regarding the accumulation rate of non-indigenous species.  
734 Our analyses suggest that the rate of introduction in the study area has not decreased. However, it is  
735 unclear whether this trend reflects a steady accumulation of non-indigenous species or increased  
736 and more efficient detection through monitoring or advanced identification methods. Based on  
737 reliable baselines, temporal surveys will allow to uncover the trends in non-indigenous species  
738 introduction rates. Diversifying the type of survey, from punctual surveys (e.g. Bio-Blitzes or Rapid  
739 Assessment surveys) to systematic comprehensive surveys (e.g. full inventories), including  
740 morphological-based and DNA-based assessments, such as metabarcoding (see above), is a need for  
741 effective prevention and early detection and also to monitor trends over time in new species  
742 introductions.

743 Our study also reveals significant differences in the geographical distribution of non-  
744 indigenous seaweed species across the study area, with only 18 species shared between the three  
745 main regions. Non-indigenous species distribution reflects both their abiotic niche and the  
746 efficiency of primary and secondary dispersal vectors. It is expected that current patterns will  
747 become increasingly homogenous with time due to various factors. First, recently introduced  
748 species may continue to expand as part of the ongoing invasion process. Secondly, evolutionary  
749 processes such as selection, genetic admixture and hybridisation may occur during the invasion  
750 process, leading to adaptation and expansion of the species in new ecological conditions. Last,  
751 further range expansions are expected for non-indigenous species with affinities for warm temperate  
752 to tropical temperatures as a result of ongoing ocean warming. This could result in an influx of  
753 warm-water adapted species into regions where conditions are currently unfavourable, while  
754 warming may also render regions unfavourable for non-indigenous species that currently thrive  
755 there. It is anticipated that under ocean warming, Eastern Mediterranean Sea non-indigenous  
756 species would likely expand their range in western direction, while species ranges in Lusitania  
757 would shift northward. The accurate estimation of the rate at which non-indigenous species expand  
758 their ranges, either as invasion fronts or more erratically by jump dispersals, rely on detailed

759 monitoring. Such estimates can inform on dispersal vectors at various spatial scales and guide  
760 policy makers to take effective measures to prevent or limit the spread of these species.

761 We advocate that combining the efforts of taxonomists who provide a reliable framework on  
762 the number and likely geographic origin of non-indigenous seaweeds, together with environmental  
763 monitoring, offers the best strategy to identify species of concern, characterise their life history  
764 traits, and develop effective management strategies. Especially for the species entering the  
765 Mediterranean Sea through the Suez Canal, a combination of horizon scanning exercises, intensive  
766 monitoring and rapid-response eradication efforts at the local level may be the only tools to try and  
767 control the establishment of Lessepsian migrants. With respect to non-indigenous species that  
768 hitchhike with shellfish transport, effectively limiting imports into Europe and controlling  
769 translocations between regions in Europe should effectively reduce the rate of primary and  
770 secondary introductions (Mineur *et al.*, 2014). Alternatively, immersion for shorter periods (3  
771 seconds) at temperatures of 80–85°C is effective in killing macroalgal propagules (Mineur *et al.*,  
772 2007a). In addition, hull fouling has an important role for introductions, especially towards  
773 secondary spread of already introduced non-indigenous seaweeds (Clarke Murray *et al.*, 2011). The  
774 related guidance developed in the context of the Marine Environmental Protection Committee  
775 (MEPC, 2011) is a step forward, but we stress the need for more enforceable control of this  
776 pathway. Mitigating the negative effects of non-indigenous species that have already established  
777 will likely prove to be even more difficult. Solid baseline data will allow us to detect introduction  
778 patterns and non-indigenous species range shifts in early stages and act accordingly.

779 Combatting the effects of non-indigenous seaweeds will require coordinated action at the  
780 European and international level to prevent the introduction of species, to quickly detect and rapidly  
781 eradicate species to prevent them from establishing, and to manage established species to minimise  
782 their ecological and economic impact (IAS Regulation (EU) 1143/2014 on invasive alien species).  
783 These measures will require significant efforts and collaboration between science, management,  
784 policy, and society. Our dataset supports these regulatory actions by providing a solid baseline on  
785 non-indigenous seaweeds. This baseline contributes to the assessment of the current situation, helps  
786 authorities to identify new introductions and monitor the status of already established species, and  
787 importantly identifies the current knowledge gaps concerning taxonomic and biogeographic  
788 uncertainties.

789

790

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802

## 803 **Disclosure statement**

804 No potential conflict of interest was reported by the authors.

805

## 806 **Supplementary information**

807 Supplementary Table S1: concise description of the status of species flagged as non-indigenous in  
808 the Northeast Atlantic Ocean, the Mediterranean Sea, and Macaronesia.

809 The complete dataset containing all records is available at Zenodo (DOI:10.5281/zenodo.7798640).

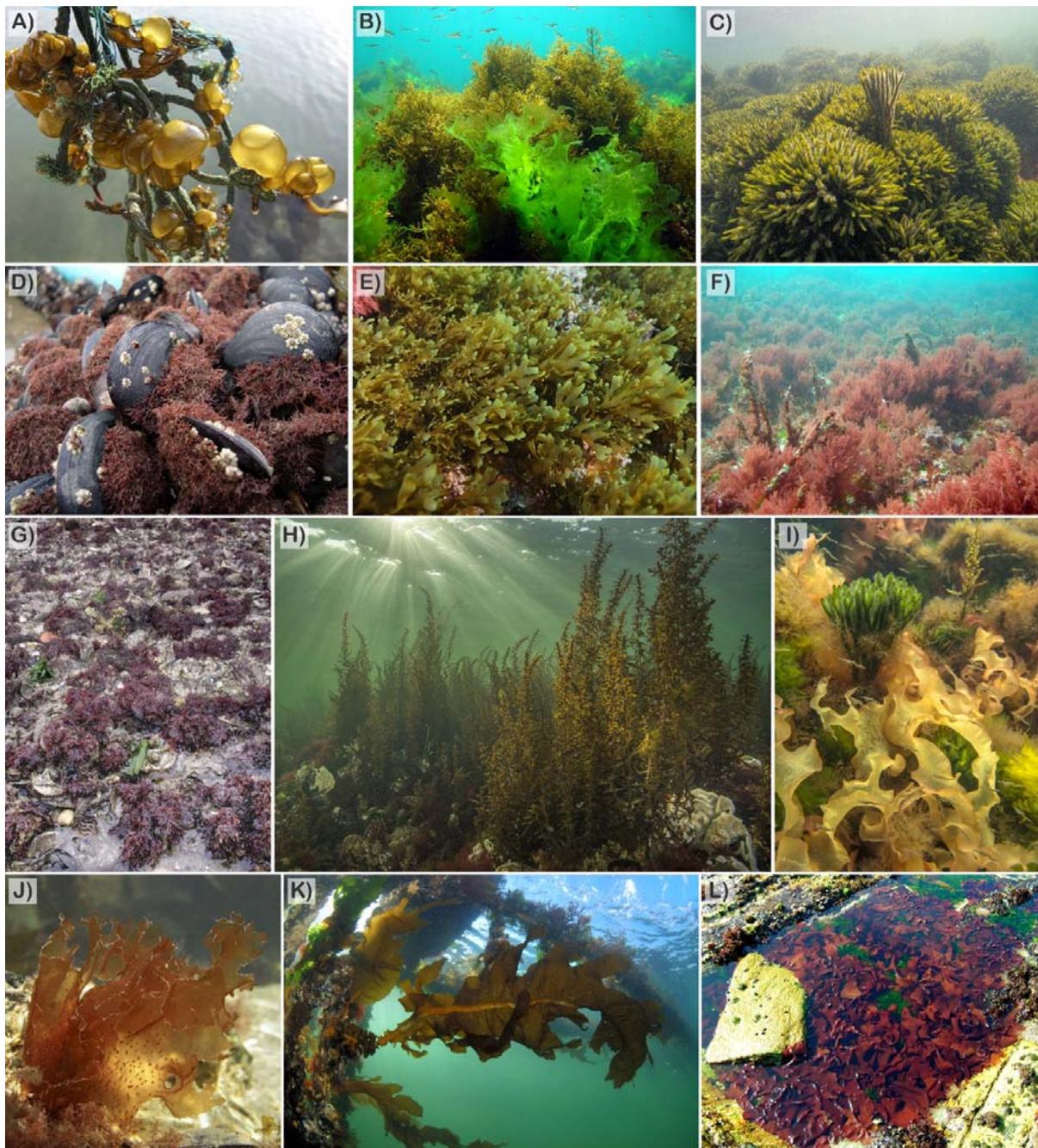
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## 811 **Author contributions**

812 LM. van der Loos + Q. Bafort +S. Bosch: concept, data acquisition, analyses, writing; F. Leliaert +  
813 O. De Clerck: concept, data acquisition, analyses, writing. Other authors: data acquisition, writing.

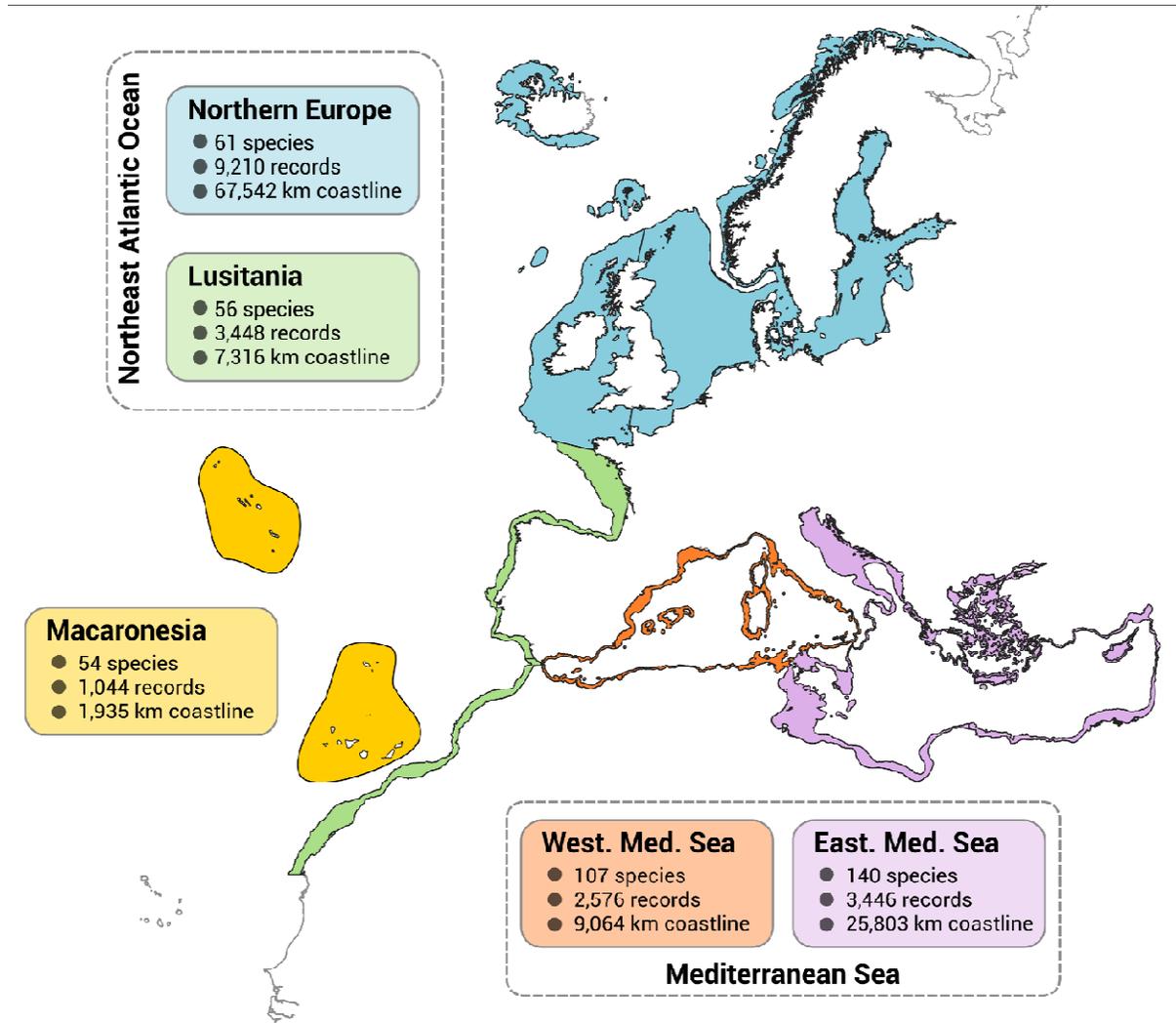
814

815 **Table 1.** Overview of the non-indigenous seaweed species (Charophyta, Chlorophyta,  
816 Phaeophyceae, Xanthophyceae, Rhodophyta) reported from the Northeast Atlantic Ocean, the  
817 Mediterranean Sea, and Macaronesia.



818  
819 **FIGURE 1.** Illustration of selected non-indigenous species in the study area. A) *Colpomenia*  
820 *peregrina* growing attached to nylon fishing net in a harbour (photo: Frank Perk, the Netherlands);  
821 B) The green non-indigenous species *Ulva australis* (photo: Ignacio Bárbara, Atlantic coast Spain);  
822 C) A dense *Codium fragile* subsp. *fragile* reef (photo: Mick Otten, the Netherlands); D)  
823 *Caulacanthus okamurae* often grows high in the intertidal (photo: Ignacio Bárbara, Atlantic coast  
824 Spain); E) *Rugulopteryx okamurae* has been introduced in the Northeast Atlantic Ocean,  
825 Mediterranean Sea and in Macaronesia (photo: Sandrine Ruitton, Mediterranean coast France); F)  
826 *Asparagopsis armata* is often regarded as a high-nuisance invasive species (photo: Ignacio Bárbara,

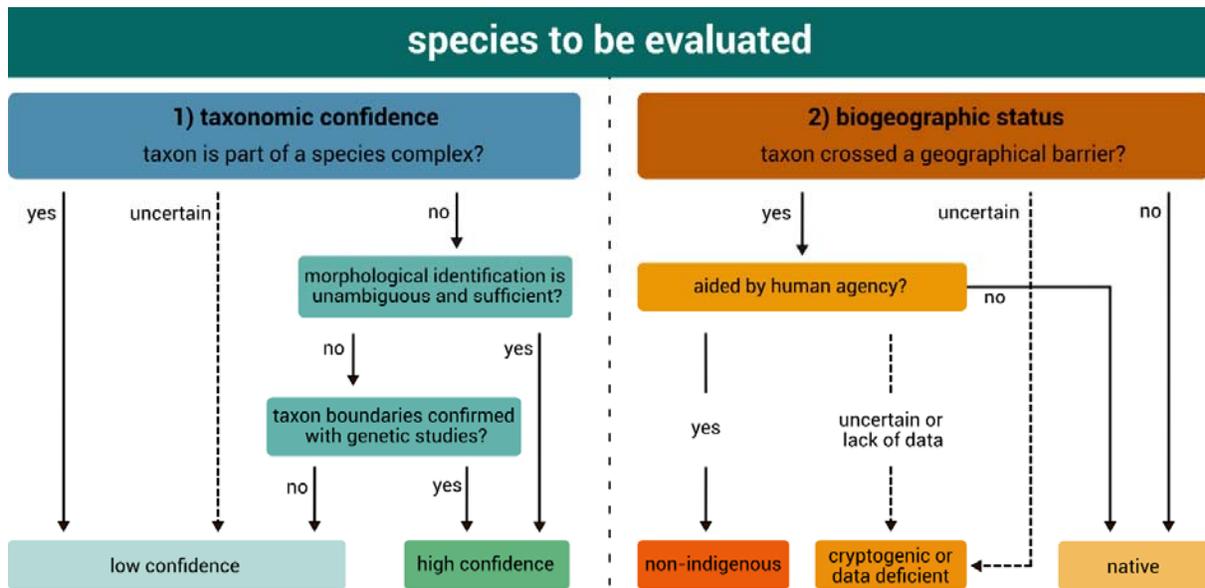
827 Atlantic coast Spain); G) *Gelidium vagum* has only been reported from the Netherlands but is  
828 locally very abundant (photo: Mart Karremans, the Netherlands); H) A *Sargassum muticum* forest  
829 (photo: Rob Aarsen, the Netherlands); I) *Grateloupia turuturu*, *Codium fragile* subsp. *fragile*, and  
830 *Sargassum muticum* covering the seabed (photo: Ad Aleman, the Netherlands); J) A fertile  
831 specimen of *Nitophyllum stellatocorticatum* (photo: Mart Karremans, the Netherlands); K) *Undaria*  
832 *pinnatifida* growing attached to aquaculture facilities (photo: Ron Offermans, the Netherlands); L)  
833 A tidal pool with *Grateloupia turuturu* (photo: Ignacio Bárbara, Atlantic coast of Spain).



834

835 **FIGURE 2.** Flowchart for assessing the taxonomic confidence and biogeographic status of putative

836 non-indigenous species. This figure builds on the concepts from Essl *et al.* (2018).



837

838

**FIGURE 3.** Map of the study area (Northern Europe, Lusitania, Macaronesia, Western

839

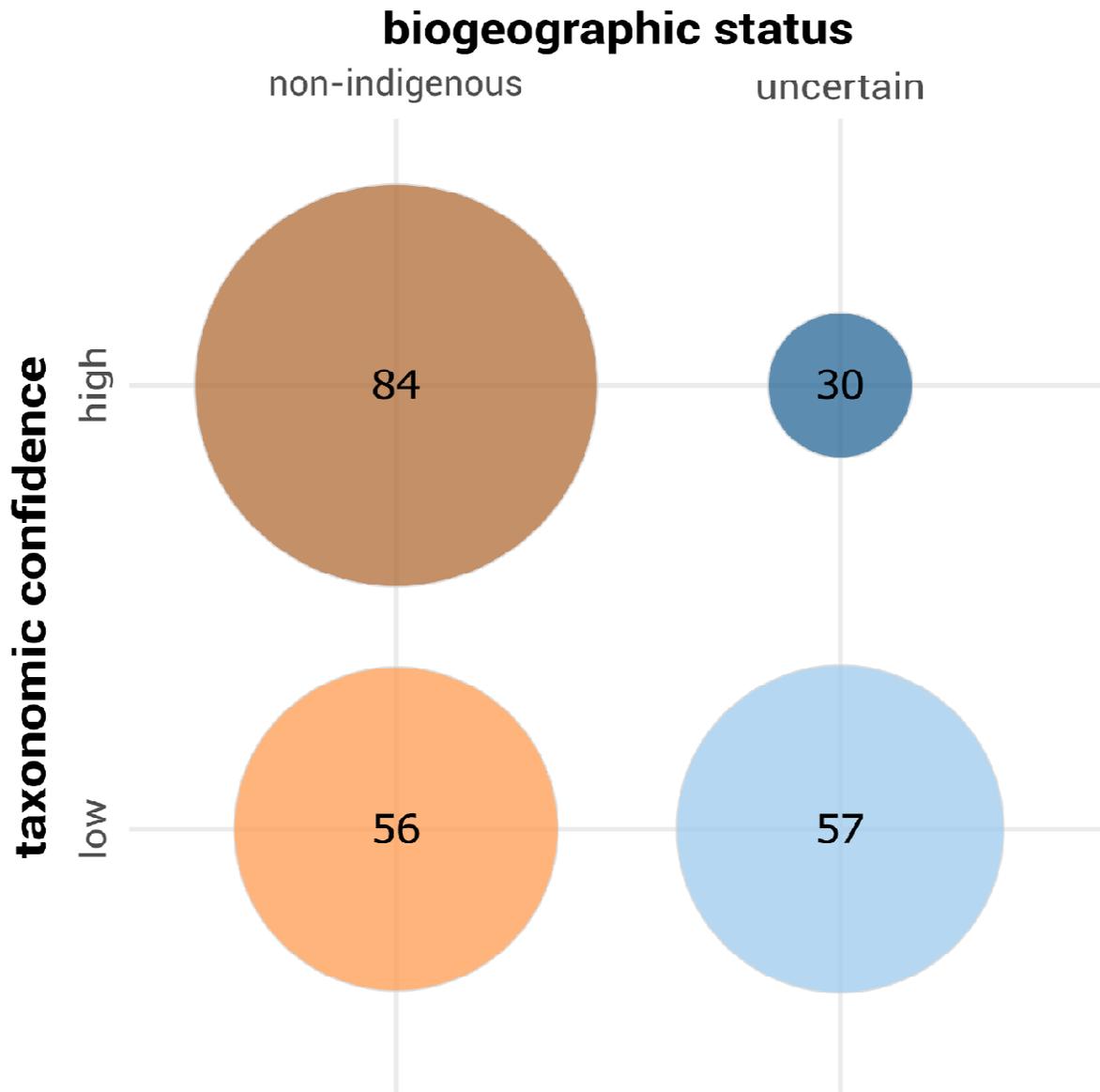
Mediterranean Sea, and Eastern Mediterranean Sea), with indication of the number of recorded non-

840

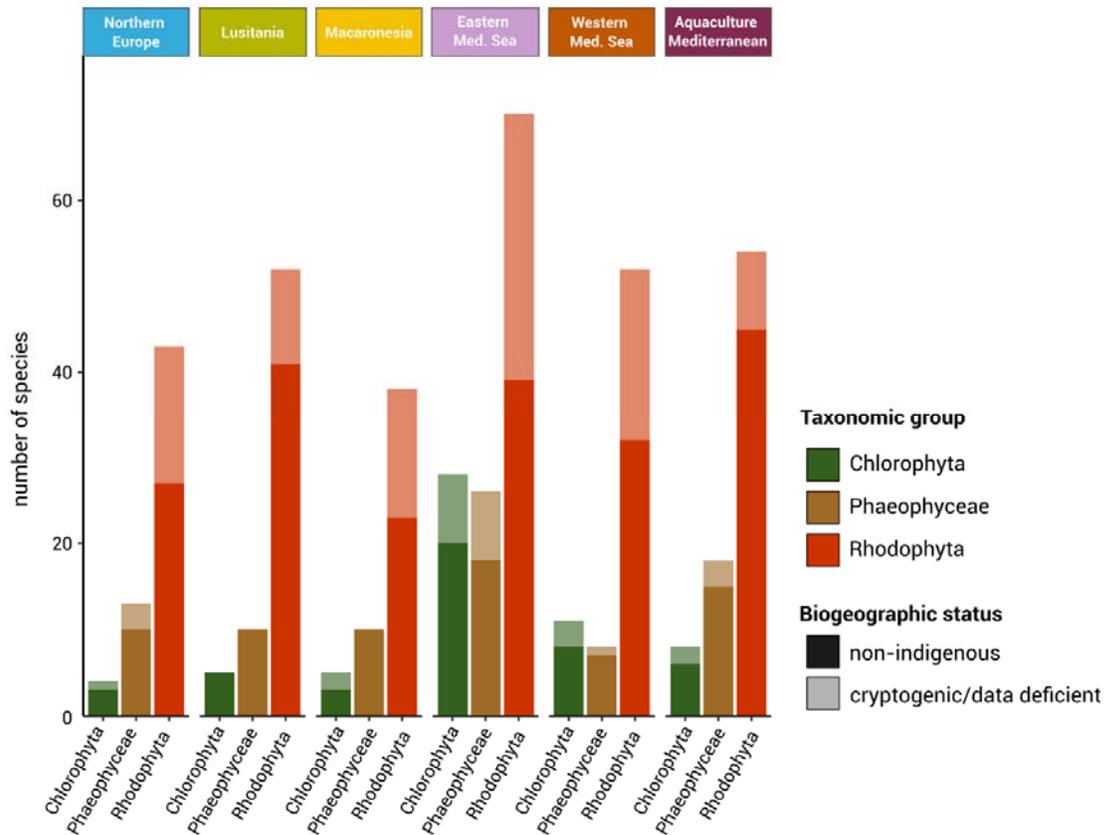
indigenous species, number of records and the length of the coastline. The number of species

841

includes cryptogenic and data deficient species.



842  
843 **FIGURE 4.** Biogeographic status (either non-indigenous or uncertain, the latter category including  
844 the 'cryptogenic' and 'data deficient' species) and taxonomic confidence of seaweed species  
845 flagged as non-indigenous in the study area. Circle surface area corresponds to the number of  
846 species.



847

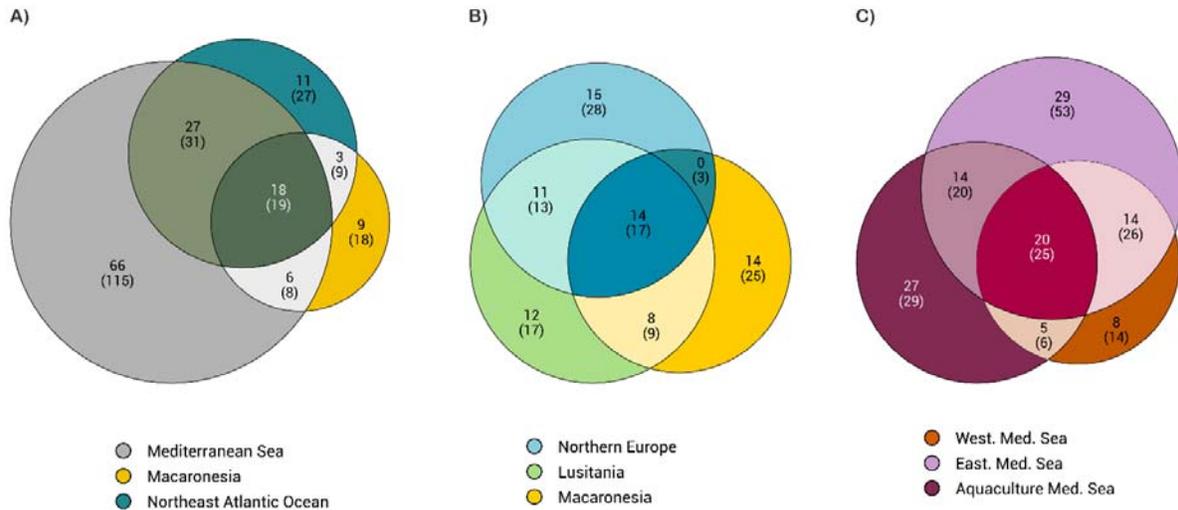
848 **FIGURE 5.** Number of non-indigenous green (Chlorophyta), brown (Phaeophyceae) and red

849 (Rhodophyta) non-indigenous species in Northern Europe, Lusitania, Macaronesia, the Eastern and

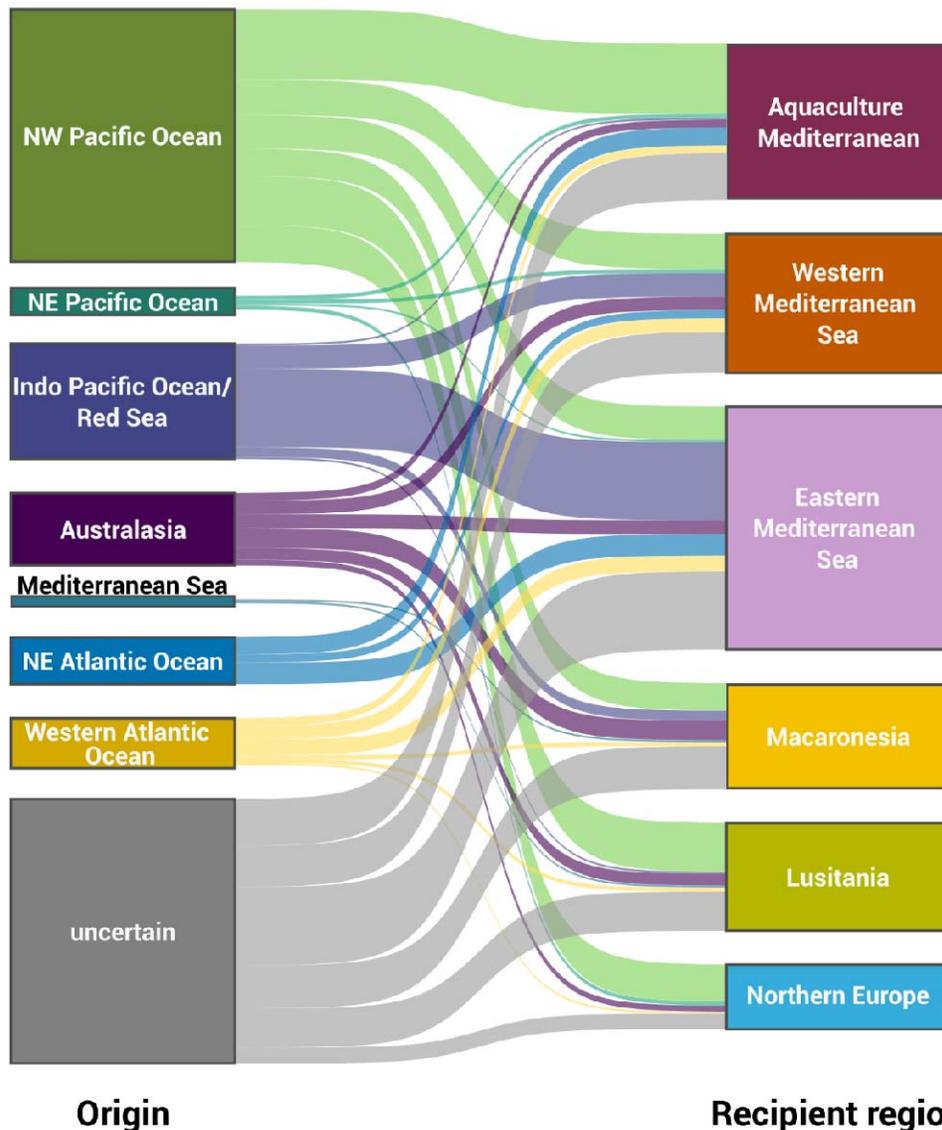
850 Western Mediterranean Sea, and aquaculture sites in the Mediterranean Sea. Dark shaded colours

851 represent numbers of high-confidence non-indigenous species; light shaded colours represent

852 cryptogenic and data deficient species.



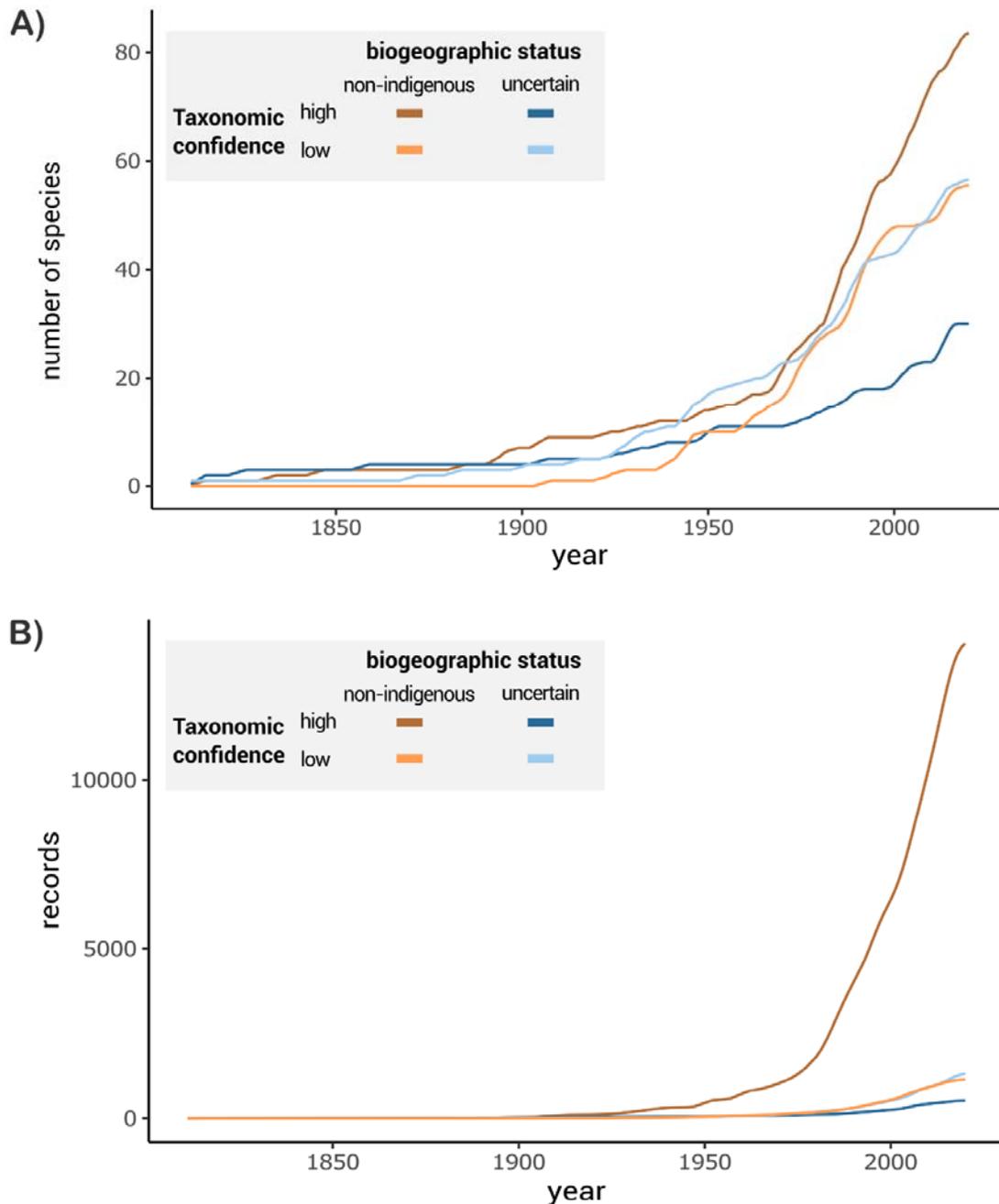
853  
854 **FIGURE 6.** Number of non-indigenous species shared among regions. A) Mediterranean Sea,  
855 Macaronesia, and Northeast Atlantic Ocean; B) Northern Europe, Lusitania, and Macaronesia; C)  
856 Western Mediterranean Sea, Eastern Mediterranean Sea, and aquaculture sites in the Mediterranean  
857 Sea. Numbers display the high-confidence non-indigenous species (excluding cryptogenic and data  
858 deficient species), with total number of non-indigenous species including cryptogenic and data  
859 deficient species in brackets.



**FIGURE 7.**

860

861 The origin of non-indigenous species. For each of the recipient study regions, the Sankey diagram  
862 displays what proportion of non-indigenous species have likely originated from a specific area  
863 (Northwest Pacific Ocean, Northeast Pacific Ocean, Indo Pacific Ocean/Red Sea, Australasia,  
864 Mediterranean Sea, Northeast Atlantic Ocean, Western Atlantic Ocean, or uncertain). The width of  
865 the flow arrows is proportional to the number of non-indigenous species (including non-indigenous,  
866 cryptogenic and data deficient species).



867  
868 **FIGURE 8.** The accumulation of A) the number of records, and B) the number of non-indigenous  
869 species through time (1808-2022). Colours indicate taxonomic confidence and biogeographic  
870 status: dark brown (taxonomic confidence = high, biogeographic status = non-indigenous), light  
871 brown (taxonomic confidence = low, biogeographic status = non-indigenous), dark blue (taxonomic  
872 confidence = high, biogeographic status = uncertain), light blue (taxonomic confidence = low,  
873 biogeographic status = uncertain). All trends are displayed as moving averages over 5 years.

874

## 875 **References**

- 876 Aleem, A.A. (1948). The recent migration of certain Indopacific algae from the Red Sea into the  
877 Mediterranean. *New Phytologist* **47**: 88-94.
- 878 Aleem, A.A. (1950). Some new records of marine algae from the Mediterranean Sea. With  
879 reference to their geographical distribution. *Acta Horti Gothoburgensis* **18**: 275-288.
- 880 Aleem, A.A. (1951). Algues marines de profondeur des environs d'Alexandrie (Egypte). *Bulletin de*  
881 *la Société Botanique de France* **98**: 249-252.
- 882 Aleem, A.A. (1993). *Marine algae of Alexandria*. Privately published, Alexandria.
- 883 Alós, J., Tomas, F., Terrados, J., Verbruggen, H., & Ballesteros, E. (2016). Fast-spreading green  
884 beds of recently introduced *Halimeda incrustata* invade Mallorca island (NW Mediterranean  
885 Sea). *Marine Ecology Progress Series* **558**: 153-158.
- 886 Andreakis, N., Kooistra, W.H.C.F., & Procaccini, G. (2007). Microsatellite markers in an invasive  
887 strain of *Asparagopsis taxiformis* (Bonnemaisoniales, Rhodophyta): Insights in ploidy level and  
888 sexual reproduction. *Gene* **406**: 144-151.
- 889 Anton, A., Geraldi, N.R., Lovelock, C.E., Apostolaki, E.T., Bennett, S., Cebrian, J., Krause-Jensen,  
890 D., Marbà, N., Martinetto, P., Pandolfi, J.M., Santana-Garcon, J., & Duarte, C.M. (2019). Global  
891 ecological impacts of marine exotic species. *Nature Ecology & Evolution* **3**: 787-800.
- 892 Appeltans, W., Ah Yong, S.T., Anderson, G., Angel, M.V., Artois, T., Bailly, N., Bamber, R., Barber,  
893 A., Bartsch, I., Berta, A., Błażewicz-Paszkowycz, M., Bock, P., Boxshall, G., Boyko, C., B. Nunes  
894 Brandão, S., N. Bray, R.A., Bruce, N.L., Cairns, S.D., Chan, T.Y., Chan, L., Collins, A.G., Cribb,  
895 T., Curini-Galletti, M., Dahdouh-Guebas, F., Davie, P.J.F., Dawson, M.N., De Clerck, O., Decock,  
896 W., De Grave, S., de Voogd, N.J., Domning, D.P., Emig, C.C., Erséus, C., Eschmeyer, W., Fauchald,  
897 K., Fautin, D.G., Feist, S.W., Fransen, C.H.J.M., Furuya, H., Garcia-Alvarez, O., Gerken, S., Gibson,  
898 D., Gittenberger, A., Gofas, S., Gómez-Daglio, L., Gordon, D.P., Guiry, M.D., Hernandez, F., Hoeksema,  
899 B.W., Hopcroft, R., Jaume, D., Kirk, P., Koedam, N., Koenemann, S., Kolb, J.B., Kristensen, R.M., Kroh,  
900 A., Lambert, G., Lazarus, D.B., Lemaitre, R., Longshaw, M., Lowry, J., Macpherson, E., Madin,  
901 L.P., Mah, C., Mapstone, G., McLaughlin, P., Mees, J., Meland, K., Messing, C., Mills, C.E., Molodtsova,  
902 T.N., Mooi, R., Neuhaus, B., Ng, P.K.L., Nielsen, C., Norenburg, J., Opresko, D.M., Osawa, M., Paulay,  
903 G., Perrin, W., Pilger, J.F., Poore, G.C.B., Pugh, P., Read, G.B., Reimer, J.D., Rius, M., Rocha, R.M., Saiz-  
904 Salinas, J.I., Scarabino, V., Schierwater, B., Schmidt-Rhaesa, A., Schnabel, K.E., Schotte,  
905 M., Schuchert, P., Schwabe, E., Segers, H., Self-Sullivan, C., Shenkar, N., Siegel, V., Sterrer, W., Stöhr,  
906 S., Swalla, B., Tasker, M.L., Thuesen, E.V., Timm, T., Todaro, A., Turon, X., Tyler, S., Uetz, P., van der  
907 Land, J., Vanhoorne, B., van Ofwegen, L.P., van Soest, R.W.M., Vanaverbeke, J., Walker-Smith,

- 908 G.Walter, T.C.Warren, A.Williams, G.Wilson, S.P. & Costello, M.J. (2012). The magnitude of  
909 global marine species diversity. *Current Biology* **23**: 2189-2202.
- 910 Aragay Soler, J., vitales, D., Gómez Garreta, A., Ribera Siguan, M.A., Steen, F., De Clerck, O.,  
911 Garnatje, T., & Rull Lluçh, J. (2016). Phenological and molecular studies on the introduced  
912 seaweed *Dictyota cyanoloma* (Dictyotales, Phaeophyceae) along the Mediterranean coast of the  
913 Iberian Peninsula. *Mediterranean Marine Science* **17**: 766-776.
- 914 Athanasiadis, A. (1996). Morphology and classification of the Ceramioideae (Rhodophyta) based  
915 on phylogenetic principles. *Opera Botanica* **128**: 1-216.
- 916 Bárbara, I., Cremades, J., Calvo, S., López-Rodríguez, M.C., & Dosil, J. (2005). Checklist of the  
917 benthic marine and brackish Galician algae (NW Spain). *Anales del Jardín Botánico de Madrid*  
918 **62**: 69-100.
- 919 Bennett, S., Santana-Garçon, J., Marbà, N., Jorda, G., Anton, A., Apostolaki, E.T., Cebrian, J.,  
920 Geraldi, N.R., Krause-Jensen, D., Lovelock, C.E., Martinetto, P., Pandolfi, J.M., Duarte, C.M.,  
921 & Tittensor, D. (2021). Climate-driven impacts of exotic species on marine ecosystems. *Global*  
922 *Ecology and Biogeography* **30**: 1043-1055.
- 923 Bianchi, C.N. & Morri, C. (2003). Global sea warming and “tropicalization” of the Mediterranean  
924 Sea: biogeographic and ecological aspects. *Biogeographia* **24**.
- 925 Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K., & Das,  
926 I. (2007). Cryptic species as a window on diversity and conservation. *Trends in Ecology &*  
927 *Evolution* **22**: 148-155.
- 928 Bitar, G., Ramos-Esplá, A.A., Ocaña, O., Sghaier, Y.R., Forcada, A., Valle, C., El Shaer, H., &  
929 Verlaque, M. (2017). Introduced marine macroflora of Lebanon and its distribution on the  
930 Levantine coast. *Mediterranean Marine Science* **18**: 138-155.
- 931 Blakeslee, A.M.H., Manousaki, T., Vasileiadou, K., & Tepolt, C.K. (2020). An evolutionary  
932 perspective on marine invasions. *Evolutionary Applications* **13**: 479-485.
- 933 Blondel, J., Aronson, J., Bodiou, J.-Y., & Boeuf, G. (2010). *The Mediterranean region: biological*  
934 *diversity in space and time*. Oxford University Press.
- 935 Bolch, C.J. & de Salas, M.F. (2007). A review of the molecular evidence for ballast water  
936 introduction of the toxic dinoflagellates *Gymnodinium catenatum* and the *Alexandrium*  
937 “*tamarensis* complex” to Australasia. *Harmful Algae* **6**: 465-485.
- 938 Borges, P.A., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A.F., Melo, I., Parente, M.,  
939 Raposeiro, P., & Rodrigues, P. (2010). Listagem dos organismos terrestres e marinhos dos  
940 Açores. A list of the terrestrial and marine biota from the Azores. *Cascais: Princípia*.

- 941 Boudouresque, C.F. (1999). The Red Sea-Mediterranean link: unwanted effects of canals. In  
942 *Invasive species and biodiversity management*, 213-228. Kluwer Academic Publishers  
943 Dordrecht.
- 944 Boudouresque, C.F., Klein, J., Ruitton, S., & Verlaque, M. (2010). Biological invasion: the Thau  
945 Lagoon, a Japanese biological island in the Mediterranean Sea. In *Global change: mankind-  
946 marine environment interactions*, 151-156. Springer.
- 947 Brawley, S.H., Coyer, J.A., Blakeslee, A.M.H., Hoarau, G., Johnson, L.E., Byers, J.E., Stam, W.T.,  
948 & Olsen, J.L. (2009). Historical invasions of the intertidal zone of Atlantic North America  
949 associated with distinctive patterns of trade and emigration. *Proceedings of the National  
950 Academy of Sciences of the United States of America* **106**: 8239-8244.
- 951 Bringloe, T.T. & Saunders, G.W. (2019). DNA barcoding of the marine macroalgae from Nome,  
952 Alaska (Northern Bering Sea) reveals many trans-Arctic species. *Polar Biology* **42**: 851-864.
- 953 Brodie, J., Bartsch, I., Neefus, C., Orfanidis, S., Bray, T., & Mathieson, A.C. (2007a). New insights  
954 into the cryptic diversity of the North Atlantic-Mediterranean *Porphyra leucosticta* complex: *P.  
955 olivii* sp. nov. and *P. rosenfurtii* (Bangiales, Rhodophyta). *European Journal of Phycology* **42**:  
956 3-28.
- 957 Brodie, J., Maggs, C.A., & John, D.M. (2007b). *The green seaweeds of Britain and Ireland*.
- 958 Brodie, J., Wilbraham, J., Pottas, J., & Guiry, M.D. (2016). A revised check-list of the seaweeds of  
959 Britain. *Journal of the Marine Biological Association of the United Kingdom* **96**: 1005-1029.
- 960 Bulleri, F., Benedetti-Cecchi, L., Ceccherelli, G., & Tamburello, L. (2017). A few is enough: a low  
961 cover of a non-native seaweed reduces the resilience of Mediterranean macroalgal stands to  
962 disturbances of varying extent. *Biological Invasions* **19**: 2291-2305.
- 963 Carlton, J.T. (1996). Biological invasions and cryptogenic species. *Ecology* **77**: 1653-1655.
- 964 Carlton, J.T. (2009). Deep Invasion Ecology and the Assembly of Communities in Historical Time.  
965 In *Biological Invasions in Marine Ecosystems* (Rilov, G. & Crooks, J.A., editors), 13-56.
- 966 Cassano, V., Diaz-Larrea, J., Senties, A., Oliveira, M.C., Gil-Rodriguez, M.C., & Fujii, M.T.  
967 (2009). Evidence for the conspecificity of *Palisada papillosa* with *P. perforata* (Ceramiales,  
968 Rhodophyta) from the western and eastern Atlantic Ocean on the basis of morphological and  
969 molecular analyses. *Phycologia* **48**: 86-100.
- 970 Castro, N., Carlton, J.T., Costa, A.C., Marques, C.S., Hewitt, C.L., Cacabelos, E., Lopes, E., Gizzi,  
971 F., Gestoso, I., Monteiro, J.G., Costa, J.L., Parente, M., Ramalhosa, P., Fofonoff, P., Chainho, P.,  
972 Haroun, R., Santos, R.S., Herrera, R., Marques, T., Ruiz, G.M., Canning-Clode, J., & Briski, E.  
973 (2022). Diversity and patterns of marine non-native species in the archipelagos of Macaronesia.  
974 *Diversity and Distributions* **28**: 667-684.

- 975 Chainho, P., Fernandes, A., Amorim, A., Ávila, S.P., Canning-Clode, J., Castro, J.J., Costa, A.C.,  
976 Costa, J.L., Cruz, T., Gollasch, S., Grazziotin-Soares, C., Melo, R., Micael, J., Parente, M.I.,  
977 Semedo, J., Silva, T., Sobral, D., Sousa, M., Torres, P., Veloso, V., & Costa, M.J. (2015). Non-  
978 indigenous species in Portuguese coastal areas, coastal lagoons, estuaries and islands. *Estuarine,  
979 Coastal and Shelf Science* **167**: 199-211.
- 980 Cianciola, E.N., Popolizio, T., Schneider, C.W., & Lane, C.E. (2010). Using molecular-assisted  
981 alpha taxonomy to better understand red algal biodiversity in Bermuda. *Diversity* **2**: 946-958.
- 982 Çınar, M.E., Bilecenoğlu, M., Yokeş, M.B., Öztürk, B., Taşkin, E., Bakir, K., Doğan, A., & Açıık,  
983 Ş. (2021). Current status (as of end of 2020) of marine alien species in Turkey. *Plos One* **16**:  
984 e0251086.
- 985 Clarke Murray, C., Pakhomov, E.A., & Therriault, T.W. (2011). Recreational boating: a large  
986 unregulated vector transporting marine invasive species. *Diversity and Distributions* **17**: 1161-  
987 1172.
- 988 Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E.,  
989 Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil, B.S.,  
990 Gasol, J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.-S.,  
991 Koukouras, A., Lampadariou, N., Laxamana, E., López-Fé de la Cuadra, C.M., Lotze, H.K.,  
992 Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., San Vicente,  
993 C., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., & Voultsiadou, E. (2010).  
994 The Biodiversity of the Mediterranean Sea: Estimates, Patterns, and Threats. *Plos One* **5**:  
995 e11842.
- 996 Costa, A.C., Parente, M., Botelho, A.Z., Micael, J., Fuste, R., Torres, R., Figueras, D., Gabriel, D.,  
997 Ávila, S., Cordeiro, R., Monteiro, J., Fontes, J., Graça, G., Schmiing, M., Jardim, N., & A., G.  
998 (2017). Relatório Final do Programa de implementação da Diretiva-Quadro Estratégia Marinha.  
999 69.
- 1000 Costello, C.J. & Solow, A.R. (2003). On the pattern of discovery of introduced species.  
1001 *Proceedings of the National Academy of Sciences* **100**: 3321-3323.
- 1002 Costello, M.J., Dekeyzer, S., Galil, B., Hutchings, P., Katsanevakis, S., Pagad, S., Robinson, T.,  
1003 Turon, X., Vandepitte, L., & Vanhoorne, B. (2021). Introducing the World Register of  
1004 Introduced Marine Species (WRiMS). *Management of Biological Invasions* **12**: 792–811.
- 1005 Coyer, J.A., Hoarau, G., Skage, M., Stam, W.T., & Olsen, J.L. (2006). Origin of *Fucus serratus*  
1006 (Heterokontophyta; Fucaeeae) populations in Iceland and the Faroes: a microsatellite-based  
1007 assessment. *European Journal of Phycology* **41**: 235-246.

- 1008 Coyer, J.A., Hoarau, G., Van Schaik, J., Luijckx, P., & Olsen, J.L. (2011). Trans-Pacific and trans-  
1009 Arctic pathways of the intertidal macroalga *Fucus distichus* L. reveal multiple glacial refugia and  
1010 colonizations from the North Pacific to the North Atlantic. *Journal of Biogeography* **38**: 756-  
1011 771.
- 1012 Coyer, J.A., Peters, A.F., Hoarau, G., Stam, W.T., & Olsen, J.L. (2002). Hybridization of the  
1013 marine seaweeds, *Fucus serratus* and *Fucus evanescens* (Heterokontophyta : Phaeophyceae) in a  
1014 100-year-old zone of secondary contact. *Proceedings of the Royal Society of London Series B-  
1015 Biological Sciences* **269**: 1829-1834.
- 1016 D'Archino, R., Neill, K.F., & Nelson, W.A. (2013). Recognition and distribution of *Polysiphonia*  
1017 *morrowii* (Rhodomelaceae, Rhodophyta) in New Zealand. *Botanica Marina* **56**: 41-47.
- 1018 Darling, J.A., Galil, B.S., Carvalho, G.R., Rius, M., Viard, F., & Piraino, S. (2017).  
1019 Recommendations for developing and applying genetic tools to assess and manage biological  
1020 invasions in marine ecosystems. *Marine policy* **85**: 56-64.
- 1021 Davoult, D., Surget, G., Stiger-Pouvreau, V., Noisette, F., Riera, P., Stagnol, D., Androuin, T., &  
1022 Poupart, N. (2017). Multiple effects of a *Gracilaria vermiculophylla* invasion on estuarine  
1023 mudflat functioning and diversity. *Marine Environmental Research* **131**: 227-235.
- 1024 Dawson, W., Moser, D., van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M.,  
1025 Lenzner, B., Blackburn, T.M., Dyer, E.E., Cassey, P., Scrivens, S.L., Economo, E.P., Guénard,  
1026 B., Capinha, C., Seebens, H., García-Díaz, P., Nentwig, W., García-Berthou, E., Casal, C.,  
1027 Mandrak, N.E., Fuller, P., Meyer, C., & Essl, F. (2017). Global hotspots and correlates of alien  
1028 species richness across taxonomic groups. **1**: 0186.
- 1029 De Clerck, O., Guiry, M.D., Leliaert, F., Samyn, Y., & Verbruggen, H. (2013). Algal Taxonomy: A  
1030 Road to Nowhere? *Journal of Phycology* **49**: 215-225.
- 1031 Delile, A.R. (1813). *Description de l'Égypte ou recueil des observations et des recherches qui ont*  
1032 *été faites en Égypte pendant l'expédition de l'armée française, publié par les ordres de Sa*  
1033 *Majesté l'Empereur Napoléon le Grand. Histoire naturelle. Tom. Second. Histoire naturelle. Vol.*  
1034 *2 (fasc. 2 'troisième livraison')*. Imprimerie Impériale., Paris.
- 1035 Diagne, C., Leroy, B., Vaissiere, A.C., Gozlan, R.E., Roiz, D., Jaric, I., Salles, J.M., Bradshaw,  
1036 C.J.A., & Courchamp, F. (2021). High and rising economic costs of biological invasions  
1037 worldwide. *Nature* **592**: 571-576.
- 1038 Díaz-Tapia, P., Baldock, L., & Maggs, C.A. (2020). Discovery of *Flabellia petiolata*  
1039 (Halimedaceae, Chlorophyta) in the southern British Isles: A relict population or a new  
1040 introduction? *Aquatic Botany* **160**: e103160.

- 1041 Díaz-Tapia, P., Bárbara, I., Cremades, J., Verbruggen, H., & Maggs, C.A. (2017). Three new  
1042 cryptogenic species in the tribes Polysiphonieae and Streblocladieae (Rhodomelaceae,  
1043 Rhodophyta). *Phycologia* **56**: 605-623.
- 1044 Diaz-Tapia, P., Ly, M., & Verbruggen, H. (2020). Extensive cryptic diversity in the widely  
1045 distributed *Polysiphonia scopulorum* (Rhodomelaceae, Rhodophyta): Molecular species  
1046 delimitation and morphometric analyses. *Molecular Phylogenetics and Evolution* **152**: e106909.
- 1047 Diaz-Tapia, P., Maggs, C.A., Macaya, E.C., & Verbruggen, H. (2018). Widely distributed red algae  
1048 often represent hidden introductions, complexes of cryptic species or species with strong  
1049 phylogeographic structure. *Journal of Phycology* **54**: 829-839.
- 1050 Díaz-Tapia, P., Sook Kim, M., Secilla, A., Barbara, I., & Cremades, J. (2013). Taxonomic  
1051 reassessment of *Polysiphonia foetidissima* (Rhodomelaceae, Rhodophyta) and similar species,  
1052 including *P. schneideri*, a newly introduced species in Europe. *European Journal of Phycology*  
1053 **48**: 345-362.
- 1054 Dijoux, L., Viard, F., & Payri, C. (2014). The more we search, the more we find: Discovery of a  
1055 new lineage and a new species complex in the genus *Asparagopsis*. *Plos One* **9**: e103826.
- 1056 Draisma, S.G., Prud'homme van Reine, W.F., Sauvage, T., Belton, G.S., Gurgel, C.F.D., Lim, P.-E.,  
1057 & Phang, S.M. (2014). A re-assessment of the infra-generic classification of the genus *Caulerpa*  
1058 (*Caulerpaceae*, Chlorophyta) inferred from a time-calibrated molecular phylogeny. *Journal of*  
1059 *Phycology* **50**: 1020-1034.
- 1060 EASIN (2022). European Alien Species Information Network. <http://easin.jrc.ec.europa.eu>.
- 1061 Edelstein, T. (1960). The biology and ecology of deep sea algae of the Haifa Bay. (PhD) Hebrew  
1062 University, Jerusalem.
- 1063 El Aamri, F., Idhalla, M., & Tamsouri, M.N.J.M.F. (2018). Occurrence of the invasive brown  
1064 seaweed *Rugulopteryx okamurae* (EY Dawson) IK Hwang, WJ Lee & HS Kim (Dictyotales,  
1065 Phaeophyta) in Morocco (Mediterranean Sea). *Journal of Mediterranean Fisheries Aquaculture*  
1066 *Research* **1**: 92-96.
- 1067 Essl, F., Bacher, S., Genovesi, P., Hulme, P.E., Jeschke, J.M., Katsanevakis, S., Kowarik, I., Kühn,  
1068 I., Pyšek, P., Rabitsch, W., Schindler, S., van Kleunen, M., Vilà, M., Wilson, J.R.U., &  
1069 Richardson, D.M. (2018). Which Taxa Are Alien? Criteria, Applications, and Uncertainties.  
1070 *Bioscience* **68**: 496-509.
- 1071 European Commission, Centre, J.R., Tsiamis, K., Palialexis, A., & Connor, D. (2021). Marine  
1072 strategy framework directive, descriptor 2, non-indigenous species: delivering solid  
1073 recommendations for setting threshold values for non-indigenous species pressure on European  
1074 seas, Publications Office. <https://data.europa.eu/doi/10.2760/035071>.

- 1075 Faria, J., Prestes, A.C.L., Moreu, I., Martins, G.M., Neto, A.I., & Cacabelos, E. (2022). Arrival and  
1076 proliferation of the invasive seaweed *Rugulopteryx okamurae* in NE Atlantic islands. *Botanica*  
1077 *Marina* **65**: 45-50.
- 1078 Figueroa, F.L., Korbee, N., De Clerck, O., Barbara, I., & Gall, E.A.R. (2007). Characterization of  
1079 *Grateloupia lanceola* (Halymeniales, Rhodophyta), an obscure foliose *Grateloupia* from the  
1080 Iberian Peninsula, based on morphology, comparative sequence analysis and mycosporine-like  
1081 amino acid composition. *European Journal of Phycology* **42**: 231-242.
- 1082 Flanagan, B.A., Krueger-Hadfield, S.A., Murren, C.J., Nice, C.C., Strand, A.E., & Sotka, E.E.  
1083 (2021). Founder effects shape linkage disequilibrium and genomic diversity of a partially clonal  
1084 invader. *Molecular Ecology* **30**: 1962-1978.
- 1085 Floc'h, J.Y., Pajot, R., & Wallentinus, I. (1991). The Japanese brown alga *Undaria pinnatifida* on  
1086 the coast of France and its possible establishment in European waters. *ICES Journal of Marine*  
1087 *Science* **47**: 379-390.
- 1088 Fort, A., McHale, M., Cascella, K., Potin, P., Perrineau, M.M., Kerrison, P.D., da Costa, E., Calado,  
1089 R., Domingues, M.D.R., Costa Azevedo, I., Sousa-Pinto, I., Gachon, C., van der Werf, A., de  
1090 Visser, W., Beniers, J.E., Jansen, H., Guiry, M.D., & Sulpice, R. (2021). Exhaustive reanalysis  
1091 of barcode sequences from public repositories highlights ongoing misidentifications and impacts  
1092 taxa diversity and distribution. *Molecular Ecology Resources* **22**: 86-101.
- 1093 Gabriel, D., Schils, T., Parente, M.I., Draisma, S.G.A., Neto, A.I., & Fredericq, S. (2019).  
1094 Taxonomic studies in the Schizymeniaceae (Nemastomatales, Rhodophyta): on the identity of  
1095 *Schizymenia* sp. in the Azores and the generic placement of *Nemastoma confusum*. *Phycologia*  
1096 **50**: 109-121.
- 1097 Galil, B., Boero, F., Campbell, M., Carlton, J., Cook, E., Fraschetti, S., Gollasch, S., Hewitt, C.,  
1098 Jelmert, A., Macpherson, E., Marchini, A., McKenzie, C., Minchin, D., Occhipinti-Ambrogi, A.,  
1099 Ojaveer, H., Olenin, S., Piraino, S., & Ruiz, G. (2015). 'Double trouble': the expansion of the  
1100 Suez Canal and marine bioinvasions in the Mediterranean Sea. *Biological Invasions* **17**: 973-976.
- 1101 Galil, B.S., Mienis, H.K., Hoffman, R., & Goren, M. (2021). Non-indigenous species along the  
1102 Israeli Mediterranean coast: tally, policy, outlook. *Hydrobiologia* **848**: 2011-2029.
- 1103 Gallardo, T., Bárbara, I., Alfonso-Carrillo, J., Bermejo, R., Altamirano, M., Gómez-Garreta, A.,  
1104 Barceló, C., Rull, J., Ballesteros, E., & De la Rosa, J. (2016). Nueva lista crítica de las algas  
1105 bentónicas marinas de España. *Algas. Boletín Informativo de la Sociedad Española de Ficología*  
1106 **51**: 7-52.
- 1107 García-Gómez, J.C., Sempere-Valverde, J., González, A.R., Martínez-Chacón, M., Olaya-Ponzzone,  
1108 L., Sánchez-Moyano, E., Ostalé-Valriberas, E., & Megina, C. (2020). From exotic to invasive in

- 1109 record time: The extreme impact of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in the  
1110 strait of Gibraltar. *Science of the Total Environment* **704**: e135408.
- 1111 Gavio, B. & Fredericq, S. (2002). *Grateloupia turuturu* (Halymeniaceae, Rhodophyta) is the correct  
1112 name of the non-native species in the Atlantic known as *Grateloupia doryphora*. *European*  
1113 *Journal of Phycology* **37**: 349-359.
- 1114 Geoffroy, A., Destombe, C., Kim, B., Mauger, S., Raffo, M.P., Kim, M.S., & Le Gall, L. (2016).  
1115 Patterns of genetic diversity of the cryptogenic red alga *Polysiphonia morrowii* (Ceramiales,  
1116 Rhodophyta) suggest multiple origins of the Atlantic populations. *Ecology and Evolution* **6**:  
1117 5635-5647.
- 1118 Gollasch, S., Minchin, D., & David, M. (2015). The transfer of harmful aquatic organisms and  
1119 pathogens with ballast water and their impacts. *Global Maritime Transport and Ballast Water*  
1120 *Management: Issues and Solutions*: 35-58.
- 1121 Guareschi, S. & Wood, P.J. (2019). Taxonomic changes and non-native species: An overview of  
1122 constraints and new challenges for macroinvertebrate-based indices calculation in river  
1123 ecosystems. *The Science of the total environment* **660**: 40-46.
- 1124 Guiry, M.D. & Guiry, G.M. (2023). AlgaeBase. World-wide electronic publication.
- 1125 Gunnarsson, K., Russell, S., & Brodie, J. (2020). *Schizymenia jonssonii* sp. nov. (Nemastomatales,  
1126 Rhodophyta): a relict or an introduction into the North Atlantic after the last glacial maximum?  
1127 *Journal of Phycology* **56**: 324-333.
- 1128 Guzinski, J., Ballenghien, M., Daguin-Thiébaud, C., Lévêque, L., & Viard, F. (2018). Population  
1129 genomics of the introduced and cultivated Pacific kelp *Undaria pinnatifida*: Marinas—not  
1130 farms—drive regional connectivity and establishment in natural rocky reefs. *Evolutionary*  
1131 *Applications* **11**: 1582-1597.
- 1132 Hamman, M., Buchholz, B., Karez, R., & Weinberger, F. (2013). Direct and indirect effects of  
1133 *Gracilaria vermiculophylla* on native *Fucus vesiculosus*. *Aquatic invasions* **8**: 121-132.
- 1134 Haydar, D. (2012). What is natural? The scale of cryptogenesis in the North Atlantic Ocean.  
1135 *Diversity and Distributions* **18**: 101-110.
- 1136 Hoffman, R. (2013). Alien benthic algae and seagrasses in the Mediterranean Sea and their  
1137 connection to global warming. In *The Mediterranean Sea: Its History and Present Challenges*.  
1138 (Goffredo, S., Baader, H., & Dubinsky, Z., editors)Springer.
- 1139 Hulme, P.E., Pyšek, P., Nentwig, W., & Vilà, M. (2009). Will Threat of Biological Invasions Unite  
1140 the European Union? *Science* **324**: 40-41.
- 1141 Israel, A. & Einav, R. (2017). Alien seaweeds from the Levant basin (Eastern Mediterranean Sea),  
1142 with emphasis to the Israeli shores. *Israel Journal of Plant Sciences* **64**: 99-110.

- 1143 Katsanevakis, S., Coll, M., Piroddi, C., Steenbeek, J., Ben Rais Lasram, F., Zenetos, A., & Cardoso,  
1144 A.C. (2014). Invading the Mediterranean Sea: biodiversity patterns shaped by human activities.  
1145 *Frontiers in Marine Science* **1**.
- 1146 Katsanevakis, S., Gatto, F., Zenetos, A., & Cardoso, A.C. (2013). How many marine aliens in  
1147 Europe. *Management of Biological Invasions* **4**: 37-42.
- 1148 Kawai, H., Kogishi, K., Hanyuda, T., Arai, S., Gurgel, C.F., Nelson, W., Meinesz, A., Tsiamis, K.,  
1149 & Peters, A.F. (2016). Phylogeographic analysis of the brown alga *Cutleria multifida*  
1150 (Tilopteridales, Phaeophyceae) suggests a complicated introduction history. *Phycological*  
1151 *Research* **64**: 3-10.
- 1152 Keck, F. & Altermatt, F. (2023). Management of DNA reference libraries for barcoding and  
1153 metabarcoding studies with the R package refdb. *Molecular Ecology Resources* **23**: 511-518.
- 1154 Kim, H.-S. & Lee, I.K. (2012). *Algal flora of Korea. Volume 4, Number 5. Rhodophyta:*  
1155 *Florideophyceae: Ceramiales: Ceramiaceae I (Non-corticate species)*. Incheon, National  
1156 Institute of Biological Resources.
- 1157 Kolar, C.S. & Lodge, D.M. (2001). Progress in invasion biology: predicting invaders. *Trends in*  
1158 *Ecology & Evolution* **16**: 199-204.
- 1159 Krueger-Hadfield, S.A., Kollars, N.M., Strand, A.E., Byers, J.E., Shinker, S.J., Terada, R., Greig,  
1160 T.W., Hammann, M., Murray, D.C., Weinberger, F., & Sotka, E.E. (2017). Genetic identification  
1161 of source and likely vector of a widespread marine invader. *Ecology and Evolution* **7**: 4432-  
1162 4447.
- 1163 Le Cam, S., Daguin-Thiebaut, C., Bouchemousse, S., Engelen, A.H., Mieszkowska, N., & Viard, F.  
1164 (2020). A genome-wide investigation of the worldwide invader *Sargassum muticum* shows high  
1165 success albeit (almost) no genetic diversity. *Evolutionary Applications* **13**: 500-514.
- 1166 Le Gall, L., Gey, D., & Rousseau, F. (2021). Mediterranean and Atlantic Algae, a Fraternal  
1167 Relationship? In *Systematics and the Exploration of Life*, 147-169.
- 1168 Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C.F., & Pérez, T. (2010).  
1169 Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean  
1170 Sea. *Trends in Ecology & Evolution* **25**: 250-260.
- 1171 Leliaert, F., Payo, D.A., Gurgel, C.F.D., Schils, T., Draisma, S.G., Saunders, G.W., Kamiya, M.,  
1172 Sherwood, A.R., Lin, S.M., Huisman, J.M., Le Gall, F., Anderson, R.J., Bolton, J.J., Mattio, L.,  
1173 Zubia, M., Spokes, T., Vieira, C., Payri Claude, E., Coppejans, E., D'Hondt, S., Verbruggen, H.,  
1174 & De Clerck, O. (2018). Patterns and drivers of species diversity in the Indo-Pacific red  
1175 seaweed *Portieria*. *Journal of Biogeography* **45**: 2299-2313.

- 1176 Leliaert, F., Verbruggen, H., Wylor, B., & De Clerck, O. (2009). DNA taxonomy in  
1177 morphologically plastic taxa: Algorithmic species delimitation in the *Boodlea* complex  
1178 (Chlorophyta: Cladophorales). *Molecular Phylogenetics and Evolution* **53**: 122-133.
- 1179 Lindstrom, S.C. (2001). The Bering Strait connection: dispersal and speciation in boreal  
1180 macroalgae. *Journal of Biogeography* **28**: 243-251.
- 1181 Liulea, S., Serrão, E.A., & Santos, R. (2023). Spread and impact of the invasive brown algae  
1182 *Rugulopteryx okamurae* on the algarve coast, southern portugal (NE Atlantic). Available at  
1183 SSRN: <https://ssrn.com/abstract=4446622> or <http://dx.doi.org/10.2139/ssrn.4446622>.
- 1184 Machin-Sanchez, M., Cassano, V., Diaz-Larrea, J., Senties, A., Fujii, M.T., & Gil-Rodriguez, M.C.  
1185 (2012). Morphological and molecular evidence demonstrates the amphi-Atlantic distribution of  
1186 *Laurencia catarinensis* (Ceramiales, Rhodophyta). *Botanica Marina* **55**: 241-252.
- 1187 Maggi, E., Benedetti-Cecchi, L., Castelli, A., Chatzinikolaou, E., Crowe, T., Ghedini, G., Kotta, J.,  
1188 Lyons, D., Ravaglioli, C., & Rilov, G. (2015). Ecological impacts of invading seaweeds: a  
1189 meta-analysis of their effects at different trophic levels. *Diversity and Distributions* **21**: 1-12.
- 1190 Maggs, C. & Hommersand, M.H. (1993). Seaweeds of the British Isles. Volume 1 Rhodophyta, Part  
1191 3A Ceramiales.
- 1192 Maggs, C.A., Verbruggen, H., & De Clerck, O. (2007). Molecular systematics of red algae: building  
1193 future structures on firm foundations. In *Unravelling the algae: the past, present, and future of*  
1194 *algal systematics* (Brodie, J. & Lewis, J., editors), 103-121. Taylor and Francis.
- 1195 Maitner, B.S., Park, D.S., Enquist, B.J., & Dlugosch, K.M. (2021). Where we've been and where  
1196 we're going: the importance of source communities in predicting establishment success from  
1197 phylogenetic relationships. *Ecography* **2022**: e05406.
- 1198 McGeoch, M.A., Spear, D., Kleynhans, E.J., & Marais, E. (2012). Uncertainty in invasive alien  
1199 species listing. *Ecological Applications* **22**: 959-971.
- 1200 McIvor, L., Maggs, C.A., Provan, J., & Stanhope, M.J. (2001). rbcL sequences reveal multiple  
1201 cryptic introductions of the Japanese red alga *Polysiphonia harveyi*. *Molecular Ecology* **10**: 911-  
1202 919.
- 1203 Mineur, F., Arenas, F., Assis, J., Davies, A.J., Engelen, A.H., Fernandes, F., Malta, E.-J., Thibaut,  
1204 T., Van Nguyen, T., Vaz-Pinto, F., Vranken, S., Serrão, E.A., & De Clerck, O. (2015). European  
1205 seaweeds under pressure: Consequences for communities and ecosystem functioning. *Journal of*  
1206 *Sea Research*: 91-108.
- 1207 Mineur, F., Belsher, T., Johnson, M.P., Maggs, C.A., & Verlaque, M. (2007a). Experimental  
1208 assessment of oyster transfers as a vector for macroalgal introductions. *Biological Conservation*  
1209 **137**: 237-247.

- 1210 Mineur, F., Davies, A.J., Maggs, C.A., Verlaque, M., & Johnson, M.P. (2010). Fronts, jumps and  
1211 secondary introductions suggested as different invasion patterns in marine species, with an  
1212 increase in spread rates over time. *Proceedings of the Royal Society B-Biological Sciences* **277**:  
1213 2693-2701.
- 1214 Mineur, F., Johnson, M.P., & Maggs, C.A. (2008). Macroalgal introductions by hull fouling on  
1215 recreational vessels: Seaweeds and sailors. *Environmental Management* **42**: 667-676.
- 1216 Mineur, F., Johnson, M.P., Maggs, C.A., & Stegenga, H. (2007b). Hull fouling on commercial ships  
1217 as a vector of macroalgal introduction. *Marine Biology* **151**: 1299-1307.
- 1218 Mineur, F., Le Roux, A., Verlaque, M., & Maggs, C.A. (2014). Positive feedback loop between  
1219 intensive aquaculture and marine introductions. *Conservation Biology* **28**: 1667-1667.
- 1220 Molnar, J.L., Gamboa, R.L., Revenga, C., & Spalding, M.D. (2008). Assessing the global threat of  
1221 invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* **6**: 485-492.
- 1222 Neiva, J., Serrão, E.A., Assis, J., Pearson, G.A., Coyer, J.A., Olsen, J.L., Hoarau, G., & Valero, M.  
1223 (2016). Climate Oscillations, Range Shifts and Phylogeographic Patterns of North Atlantic  
1224 Fucaceae. In *Seaweed Phylogeography*, 279-308.
- 1225 Neiva, J., Serrão, E.A., Paulino, C., Gouveia, L., Want, A., Tamigneaux, É., Ballenghien, M.,  
1226 Mauger, S., Fouqueau, L., Engel-Gautier, C., Destombe, C., & Valero, M. (2020). Genetic  
1227 structure of ampho-Atlantic *Laminaria digitata* (Laminariales, Phaeophyceae) reveals a unique  
1228 range-edge gene pool and suggests post-glacial colonization of the NW Atlantic. *European*  
1229 *Journal of Phycology* **55**: 517-528.
- 1230 Ní Chualáin, F., Maggs, C.A., Saunders, G.W., & Guiry, M.D. (2004). The invasive genus  
1231 *Asparagopsis* (Bonnemaisoniaceae, Rhodophyta): Molecular systematics, morphology, and  
1232 ecophysiology of *Falkenbergia* isolates. *Journal of Phycology* **40**: 1112-1126.
- 1233 Ocaña, Ó., Afonso Carrillo, J., & Ballesteros, E. (2016). Massive proliferation of a dictyotalean  
1234 species (Phaeophyceae, Ochrophyta) through the strait of Gibraltar. *Revista de la Academia*  
1235 *Canaria de Ciencias* **28**: 165-170.
- 1236 Pante, E., Puillandre, N., Viricel, A., Arnaud-Haond, S., Aurelle, D., Castelin, M., Chenuil, A.,  
1237 Destombe, C., Forcioli, D., Valero, M., Viard, F., & Samadi, S. (2015). Species are hypotheses:  
1238 avoid connectivity assessments based on pillars of sand. *Molecular Ecology* **24**: 525-544.
- 1239 Patarnello, T., Volckaert, F., & Castilho, R. (2007). Pillars of Hercules: is the Atlantic-  
1240 Mediterranean transition a phylogeographical break? *Molecular Ecology* **16**: 4426-4444.
- 1241 Petrocelli, A., Cecere, E., & Verlaque, M. (2013). Alien marine macrophytes in transitional water  
1242 systems: new entries and reappearances in a Mediterranean coastal basin. *J BioInvasions Record*  
1243 **2**: 177-184.

- 1244 Piñeiro-Corbeira, C., Maggs, C.A., Rindi, F., Bunker, F., Baldock, L., & Díaz-Tapia, P. (2020).  
1245 Molecular Assessment of the Tribes Streblocladiaeae and Polysiphonieae (Rhodomelaceae,  
1246 Rhodophyta) in the British Isles Reveals New Records and Species that Require Taxonomic  
1247 Revision. *Cryptogamie, Algologie* **41**: 55-72.
- 1248 Piñeiro-Corbeira, C., Verbruggen, H., & Díaz-Tapia, P. (2019). Molecular survey of the red algal  
1249 family Rhodomelaceae (Ceramiales, Rhodophyta) in Australia reveals new introduced species.  
1250 *Journal of Applied Phycology* **32**: 2535-2547.
- 1251 Por, F.D. (2012). *Lessepsian migration: the influx of Red Sea biota into the Mediterranean by way*  
1252 *of the Suez Canal*. Springer Science & Business Media.
- 1253 Provan, J., Booth, D., Todd, N.P., Beatty, G.E., & Maggs, C.A. (2008). Tracking biological  
1254 invasions in space and time: elucidating the invasive history of the green alga *Codium fragile*  
1255 using old DNA. *Diversity and Distributions* **14**: 343-354.
- 1256 Ribeiro, C., Sauvage, T., Ferreira, S., Haroun, R., Silva, J., & Neves, P. (2023). Crossing the  
1257 Atlantic: The tropical macroalga *Caulerpa ashmeadii* Harvey 1858 as a recent settler in Porto  
1258 Santo Island (Madeira archipelago, North-eastern Atlantic). *Aquatic Botany* **184**.
- 1259 Ruitton, S., Blanfuné, A., Boudouresque, C.-F., Guillemain, D., Michotey, V., Roblet, S., Thibault,  
1260 D., Thibaut, T., & Verlaque, M. (2021). Rapid spread of the invasive brown alga *Rugulopteryx*  
1261 *okamurae* in a national park in Provence (France, Mediterranean Sea). *Water* **13**: e2306.
- 1262 Sangil, C., Martín-García, L., Afonso-Carrillo, J., Barquín, J., & Sansón, M. (2018). *Halimeda*  
1263 *incrassata* (Bryopsidales, Chlorophyta) reaches the Canary Islands: mid- and deep-water  
1264 meadows in the eastern subtropical Atlantic Ocean. *Botanica Marina* **61**: 103-110.
- 1265 Savoie, A.M. & Saunders, G.W. (2015). Evidence for the introduction of the Asian red alga  
1266 *Neosiphonia japonica* and its introgression with *Neosiphonia harveyi* (Ceramiales, Rhodophyta)  
1267 in the Northwest Atlantic. *Molecular Ecology* **24**: 5927-5937.
- 1268 Schaffelke, B., Smith, J.E., & Hewitt, C.L. (2006). Introduced macroalgae - a growing concern.  
1269 *Journal of Applied Phycology* **18**: 529-541.
- 1270 Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S.,  
1271 Pysek, P., van Kleunen, M., Winter, M., Ansong, M., Arianoutsou, M., Bacher, S., Blasius, B.,  
1272 Brockhoff, E.G., Brundu, G., Capinha, C., Causton, C.E., Celesti-Grapow, L., Dawson, W.,  
1273 Dullinger, S., Economo, E.P., Fuentes, N., Guenard, B., Jager, H., Kartesz, J., Kenis, M., Kuhn,  
1274 I., Lenzner, B., Liebhold, A.M., Mosena, A., Moser, D., Nentwig, W., Nishino, M., Pearman, D.,  
1275 Pergl, J., Rabitsch, W., Rojas-Sandoval, J., Roques, A., Rorke, S., Rossinelli, S., Roy, H.E.,  
1276 Scalera, R., Schindler, S., Stajerova, K., Tokarska-Guzik, B., Walker, K., Ward, D.F.,  
1277 Yamanaka, T., & Essl, F. (2018). Global rise in emerging alien species results from increased

- 1278 accessibility of new source pools. *Proceedings of the National Academy of Sciences of the*  
1279 *United States of America* **115**: E2264-E2273.
- 1280 Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S.,  
1281 Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C.,  
1282 Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., Kartesz, J., Kenis, M.,  
1283 Kreft, H., Kühn, I., Lenzner, B., Liebhold, A., Mosena, A., Moser, D., Nishino, M., Pearman, D.,  
1284 Pergl, J., Rabitsch, W., Rojas-Sandoval, J., Roques, A., Rorke, S., Rossinelli, S., Roy, H.E.,  
1285 Scalera, R., Schindler, S., Štajerová, K., Tokarska-Guzik, B., van Kleunen, M., Walker, K.,  
1286 Weigelt, P., Yamanaka, T., & Essl, F. (2017). No saturation in the accumulation of alien species  
1287 worldwide. *Nature Communications* **8**: 14435.
- 1288 Sfriso, A. (2020). Invasion of alien macroalgae in the Venice Lagoon, a pest or a resource? *Aquatic*  
1289 *invasions* **15**: 245-270.
- 1290 Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F.,  
1291 Galil, B., Garcia-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vila, M. (2013).  
1292 Impacts of biological invasions: what's what and the way forward. *Trends in Ecology &*  
1293 *Evolution* **28**: 58-66.
- 1294 South, P.M., Floerl, O., Forrest, B.M., & Thomsen, M.S. (2017). A review of three decades of  
1295 research on the invasive kelp *Undaria pinnatifida* in Australasia: An assessment of its success,  
1296 impacts and status as one of the world's worst invaders. *Marine Environmental Research* **131**:  
1297 243-257.
- 1298 Steen, F., Aragay, J., Zuljevic, A., Verbruggen, H., Mancuso, F.P., Bunker, F., Vitales, D., Gómez  
1299 Garreta, A., & De Clerck, O. (2017). Tracing the introduction history of the brown seaweed  
1300 *Dictyota cyanoloma* (Phaeophyceae, Dictyotales) in Europe. *European Journal of Phycology* **52**:  
1301 31-42.
- 1302 Stegenga, H. & Karremans, M. (2015). Overzicht van de roodwier-exoten in de mariene wateren  
1303 van Zuidwest-Nederland. *Gorteria: tijdschrift voor de floristiek, de plantenoecologie en het*  
1304 *vegetatie-onderzoek van Nederland* **37**: 141-157.
- 1305 Taylor, E.B. (2010). Changes in taxonomy and species distributions and their influence on estimates  
1306 of faunal homogenization and differentiation in freshwater fishes. *Diversity and Distributions*  
1307 **16**: 676-689.
- 1308 Tran, L.-A.T., Bafort, Q., Steen, F., Gómez Garreta, A., D'Hondt, S., Miller, K.A., Vranken, S.,  
1309 Žuljević, A., Smith, J.E., & De Clerck, O. (2021). *Dictyota cyanoloma* (Dictyotales,  
1310 Phaeophyceae), a Newly Introduced Brown Algal Species in California. *Journal of Phycology*  
1311 **57**: 370-378.

- 1312 Tran, L.-A.T., Vieira, C., Steinhagen, S., Maggs, C.A., Hiraoka, M., Shimada, S., Van Nguyen, T.,  
1313 De Clerck, O., & Leliaert, F. (2022). An appraisal of *Ulva* (Ulvophyceae, Chlorophyta)  
1314 taxonomy. *Journal of Applied Phycology*.
- 1315 Tronholm, A., Afonso-Carrillo, J., Sanson, M., Leliaert, F., Fernandez-Garcia, C., & De Clerck, O.  
1316 (2013). Taxonomy of the *Dictyota ciliolata* - *crenulata* complex (Dictyotales, Phaeophyceae).  
1317 *Phycologia* **52**: 171-181.
- 1318 Tronholm, A., Leliaert, F., Sansón, M., Afonso-Carrillo, J., Tyberghein, L., Verbruggen, H., & De  
1319 Clerck, O. (2012). Contrasting geographical distributions as a result of thermal tolerance and  
1320 long-distance dispersal in two allegedly widespread tropical brown algae. *Plos One* **7**: e30813.
- 1321 Tronholm, A., Steen, F., Tyberghein, L., Leliaert, F., Verbruggen, H., Ribera Siguan, A., & De  
1322 Clerck, O. (2010). Species delimitation, taxonomy and biogeography of *Dictyota* in Europe  
1323 (Dictyotales, Phaeophyceae). *Journal of Phycology* **46**: 1301–1321.
- 1324 Tsiamis, K. (2012). Alien macroalgae of the sublittoral zone of the Greek coasts. (PhD)University  
1325 of Athens, Athens.
- 1326 Van Oppen, M.J., Klerk, H., Olsen, J.L., & Stam, W.T. (1996). Hidden diversity in marine algae:  
1327 some examples of genetic variation below the species level. *Journal of the Marine Biological*  
1328 *Association of the United Kingdom* **76**: 239-242.
- 1329 Varela-Álvarez, E., Balau, A.C., Marbà, N., Afonso-Carrillo, J., Duarte, C.M., & Serrão, E.A.  
1330 (2015). Genetic diversity and biogeographical patterns of *Caulerpa prolifera* across the  
1331 Mediterranean and Mediterranean/Atlantic transition zone. *Marine Biology* **162**: 557-569.
- 1332 Verbruggen, H. (2014). Morphological complexity, plasticity, and species diagnosability in the  
1333 application of old species names in DNA-based taxonomies. *Journal of Phycology* **50**: 26-31.
- 1334 Verbruggen, H., De Clerck, O., N'Yeurt, A.D.R., Spalding, H., & Vroom, P.S. (2006). Phylogeny  
1335 and taxonomy of *Halimeda incrassata*, including descriptions of *H. kanaloana* and *H.*  
1336 *heteromorpha* spp. nov (Bryopsidales, Chlorophyta). *European Journal of Phycology* **41**: 337-  
1337 362.
- 1338 Vergés, A., Sánchez, N., Peteiro, C., Polo, L., & Brodie, J. (2013). *Pyropia suborbiculata*  
1339 (Bangiales, Rhodophyta): first records from the northeastern Atlantic and Mediterranean of this  
1340 North Pacific species. *Phycologia* **52**: 121-129.
- 1341 Verlaque, M. (1996). L'Etang de Thau (France), un site majeur d'introduction d'espèces en  
1342 Méditerranée—Relations avec l'ostreiculture. In *Second international workshop on Caulerpa*  
1343 *taxifolia*, 423-430. Publicacions Universitat Barcelona Brest.
- 1344 Verlaque, M., Boudouresque, C.F., Meinesz, A., & Gravez, V. (2000). The *Caulerpa racemosa*  
1345 complex (Caulerpales, Ulvophyceae) in the Mediterranean Sea. *Botanica Marina* **43**: 49-68.

- 1346 Verlaque, M., Boudouresque, C.F., & Mineur, F. (2007). Oyster transfers as a vector for marine  
1347 species introductions: a realistic approach based on the macrophytes. *CIESM Workshop*  
1348 *Monographs, Monaco* **32**: 39-48.
- 1349 Verlaque, M., Brannock, P.M., Komatsu, T., Villalard-Bohnsack, M., & Marston, M. (2005). The  
1350 genus *Grateloupia* C. Agardh (Halymeniaceae, Rhodophyta) in the Thau Lagoon (France,  
1351 Mediterranean): a case study of marine plurispecific introductions. *Phycologia* **44**: 477-496.
- 1352 Verlaque, M., Durand, C., Huisman, J.M., Boudouresque, C.F., & Le Parco, Y. (2003). On the  
1353 identity and origin of the Mediterranean invasive *Caulerpa racemosa* (Caulerpales,  
1354 Chlorophyta). *European Journal of Phycology* **38**: 325-339.
- 1355 Verlaque, M., Ruitton, S., Mineur, F., & Boudouresque, C.F. (2015). *Macrophytes*. CIESM  
1356 Publishers, Monaco.
- 1357 Verlaque, M., Steen, F., & De Clerck, O. (2009). *Rugulopteryx* (Dictyotales, Phaeophyceae), a  
1358 genus recently introduced to the Mediterranean. *Phycologia* **48**: 536-542.
- 1359 Viard, F. & Comtet, T. (2015). Applications of DNA-based methods for the study of biological  
1360 invasions. *Biological Invasions in Changing Ecosystems—Vectors, Ecological Impacts,*  
1361 *Management and Predictions. Berlin: De Gruyter Open*: 411-435.
- 1362 Viard, F., Roby, C., Turon, X., Bouchemousse, S., & Bishop, J. (2019). Cryptic Diversity and  
1363 Database Errors Challenge Non-indigenous Species Surveys: An Illustration With *Botrylloides*  
1364 spp. in the English Channel and Mediterranean Sea. *Frontiers in Marine Science* **6**: 615.
- 1365 Vieira, C., Aharonov, A., Paz, G., Engelen, A.H., Tsiamis, K., Einav, R., & De Clerck, O. (2019).  
1366 Diversity and origin of the genus *Lobophora* in the Mediterranean Sea including the description  
1367 of two new species. *Phycologia* **58**: 163-168.
- 1368 Vieira, C., Camacho, O., Sun, Z., Fredericq, S., Leliaert, F., Payri, C., & De Clerck, O. (2017).  
1369 Historical biogeography of the highly diverse brown seaweed *Lobophora* (Dictyotales,  
1370 Phaeophyceae). *Molecular Phylogenetics and Evolution* **110**: 81-92.
- 1371 Vieira, C., Henriques, F., D'Hondt, S., Neto, A., Almada, C.H., Kaufmann, M., Sanson, M., Sangil,  
1372 C., & De Clerck, O. (2020). *Lobophora* (Dictyotales) species richness, ecology and  
1373 biogeography across the North-Eastern Atlantic archipelagos and description of two new species.  
1374 *Journal of Phycology* **56**: 346-357.
- 1375 Voisin, M., Engel, C.R., & Viard, F. (2005). Differential shuffling of native genetic diversity across  
1376 introduced regions in a brown alga: Aquaculture vs. maritime traffic effects. *Proceedings of the*  
1377 *National Academy of Sciences of the United States of America* **102**: 5432-5437.

- 1378 Vranken, S., Bosch, S., Peña, V., Leliaert, F., Mineur, F., & De Clerck, O. (2018). A risk  
1379 assessment of aquarium trade introductions of seaweed in European waters. *Biological Invasions*  
1380 **20**: 1171-1187.
- 1381 Vranken, S., Robuchon, M., Dekeyzer, S., Bárbara, I., Bartsch, I., Blanfuné, A., Boudouresque,  
1382 C.F., Decock, W., Destombe, C., de Reviere, B., Díaz-Tapia, P., Herbst, A., Julliard, R., Karez,  
1383 R., Kersen, P., Krueger-Hadfield, S.A., Kuhlenkamp, R., Peters, A.F., Peña, V., Piñeiro-  
1384 Corbeira, C., Rindi, F., Rousseau, F., Rueness, J., Schubert, H., Sjøtun, K., Sansón, M., Smale,  
1385 D., Thibaut, T., Valero, M., Vandepitte, L., Vanhoorne, B., Vergés, A., Verlaque, M., Vieira, C.,  
1386 Le Gall, L., Leliaert, F., & De Clerck, O. (2022). AlgaeTraits: a trait database for (European)  
1387 seaweeds. *Earth Syst. Sci. Data Discuss.* **2022**: 1-57.
- 1388 Weinberger, F., Buchholz, B., Karez, R., & Wahl, M. (2008). The invasive red alga *Gracilaria*  
1389 *vermiculophylla* in the Baltic Sea: adaptation to brackish water may compensate for light  
1390 limitation. *Aquatic Biology* **3**: 251-264.
- 1391 Williams, S.L. & Smith, J.E. (2007). A global review of the distribution, taxonomy, and impacts of  
1392 introduced seaweeds. *Annual Review of Ecology Evolution and Systematics* **38**: 327-359.
- 1393 Wirtz, P. & Kaufmann, M. (2005). Pfennigalgen. *Neu fur Madeira und den Ostatlantik: Halimeda*  
1394 *incrassata*. *Das Aquarium* **431**: 48-50.
- 1395 Won, B.Y., Cho, T.O., & Fredericq, S. (2009). Morphological and Molecular Characterization of  
1396 Species of the Genus *Centroceras* (Ceramiaceae, Ceramiales), Including Two New Species.  
1397 *Journal of Phycology* **45**: 227-250.
- 1398 Yang, L.E., Deng, Y.Y., Xu, G.P., Russell, S., Lu, Q.Q., & Brodie, J. (2020). Redefining *Pyropia*  
1399 (Bangiales, Rhodophyta): Four New Genera, Resurrection of *Porphyrella* and Description of  
1400 *Calidia pseudolobata* sp. nov. From China. *Journal of Phycology* **56**: 862-879.
- 1401 Zenetos, A., Çinar, M.E., Crocetta, F., Golani, D., Rosso, A., Servello, G., Shenkar, N., Turon, X.,  
1402 & Verlaque, M. (2017). Uncertainties and validation of alien species catalogues: The  
1403 Mediterranean as an example. *Estuarine, Coastal and Shelf Science* **191**: 171-187.
- 1404 Zenetos, A., Gofas, S., Morri, C., Rosso, A., Violanti, D., Raso, J.E.G., Cinar, M.E., Almogi-Labin,  
1405 A., Ates, A.S., Azzurro, E., Ballesteros, E., Bianchi, C.N., Bilecenoglu, M., Gambi, M.C.,  
1406 Giangrande, A., Gravili, C., Hyams-Kaphzan, O., Karachle, P.K., Katsanevakis, S., Lipej, L.,  
1407 Mastrototaro, F., Mineur, F., Pancucci-Papadopoulou, M.A., Espla, A.R., Salas, C., San Martin,  
1408 G., Sfriso, A., Streftaris, N., & Verlaque, M. (2012). Alien species in the Mediterranean Sea by  
1409 2012. A contribution to the application of European Union's Marine Strategy Framework  
1410 Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science* **13**:  
1411 328-352.

1412 Zenetos, A., Gofas, S., Verlaque, M., Cinar, M.E., Raso, J.E.G., Bianchi, C.N., Morri, C., Azzurro,  
1413 E., Bilecenoglu, M., Froglija, C., Siokou, I., Violanti, D., Sfriso, A., San Martin, G., Giangrande,  
1414 A., Katagan, T., Ballesteros, E., Ramos-Espla, A., Mastrototaro, F., Ocana, O., Zingone, A.,  
1415 Gambi, M.C., & Streftaris, N. (2010). Alien species in the Mediterranean Sea by 2010. A  
1416 contribution to the application of European Union's Marine Strategy Framework Directive  
1417 (MSFD). Part I. Spatial distribution. *Mediterranean Marine Science* **11**: 381-493.



**Northeast Atlantic Ocean**

**Northern Europe**

- 61 species
- 9,210 records
- 67,542 km coastline

**Lusitania**

- 56 species
- 3,448 records
- 7,316 km coastline

**Macaronesia**

- 54 species
- 1,044 records
- 1,935 km coastline

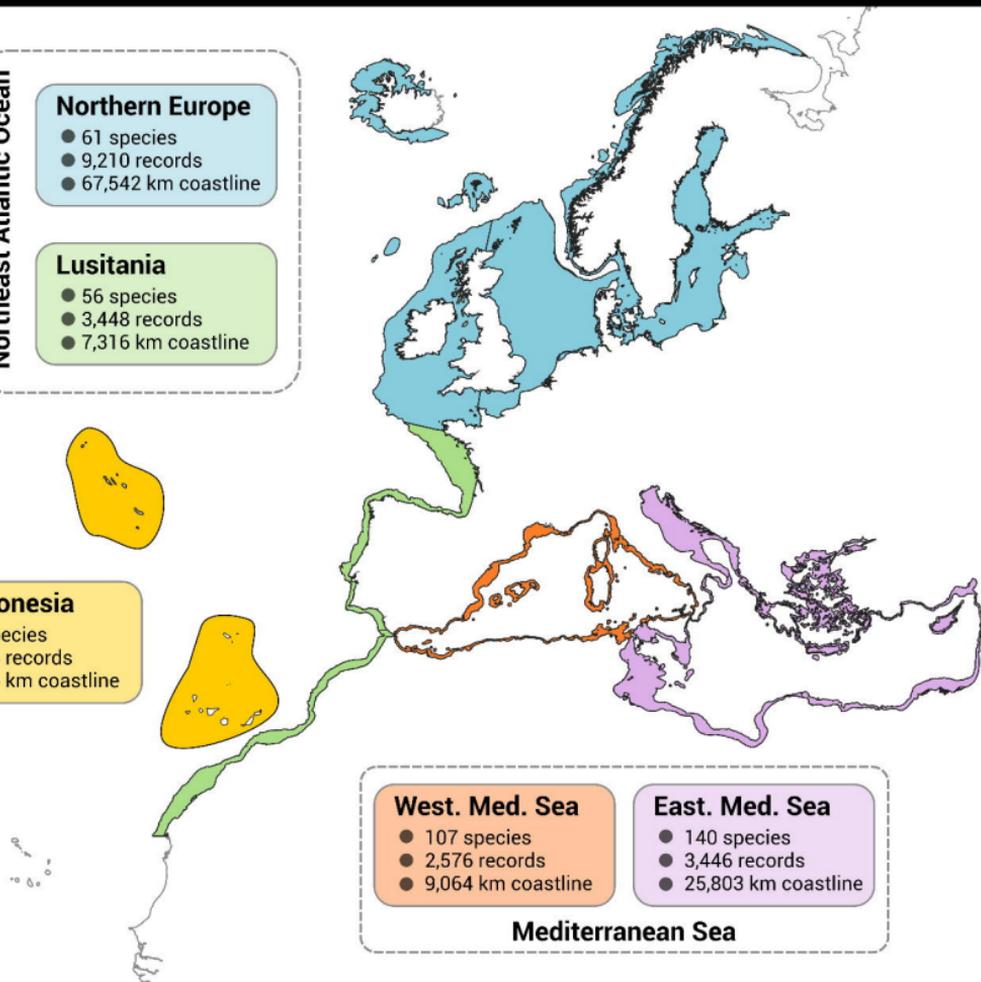
**West. Med. Sea**

- 107 species
- 2,576 records
- 9,064 km coastline

**East. Med. Sea**

- 140 species
- 3,446 records
- 25,803 km coastline

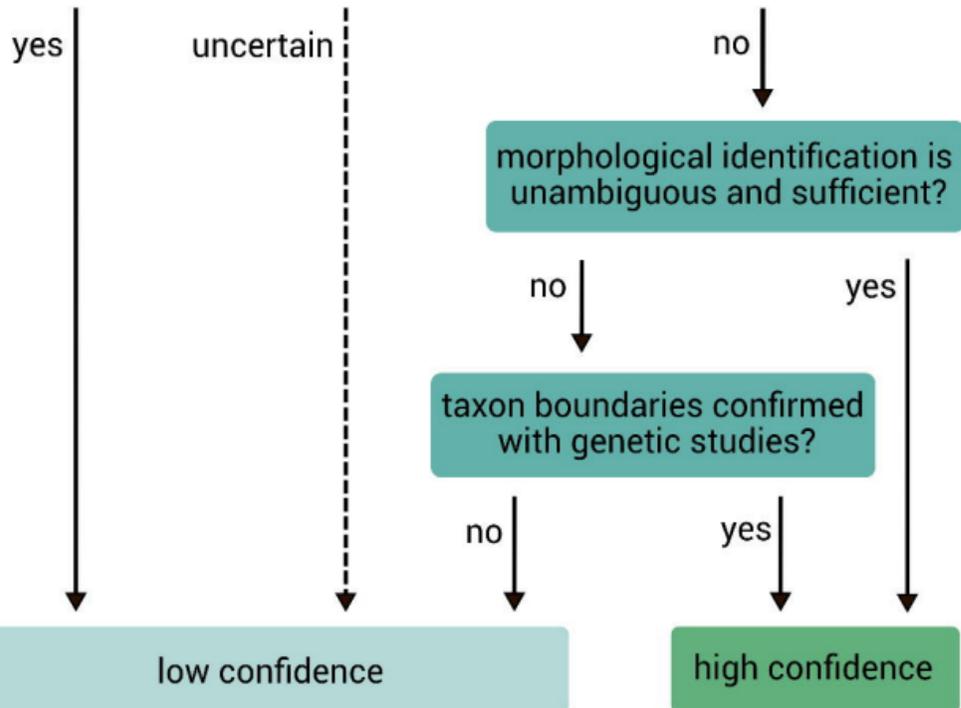
**Mediterranean Sea**



# species to be evaluated

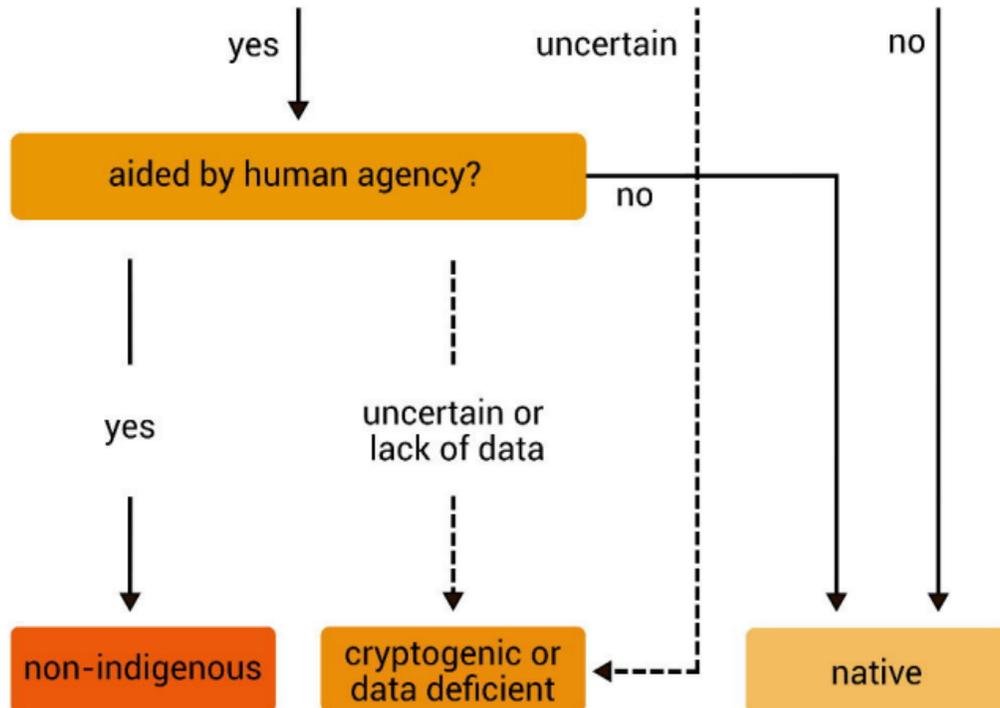
## 1) taxonomic confidence

taxon is part of a species complex?



## 2) biogeographic status

taxon crossed a geographical barrier?



# biogeographic status

non-indigenous

uncertain

taxonomic confidence

high

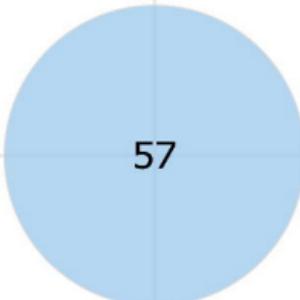
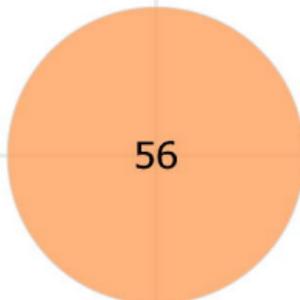
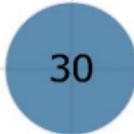
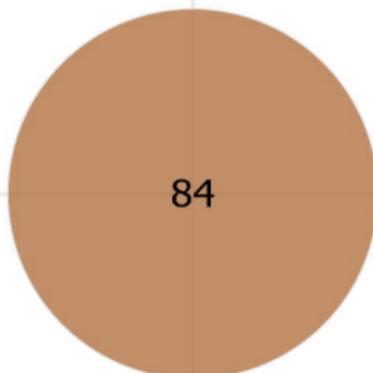
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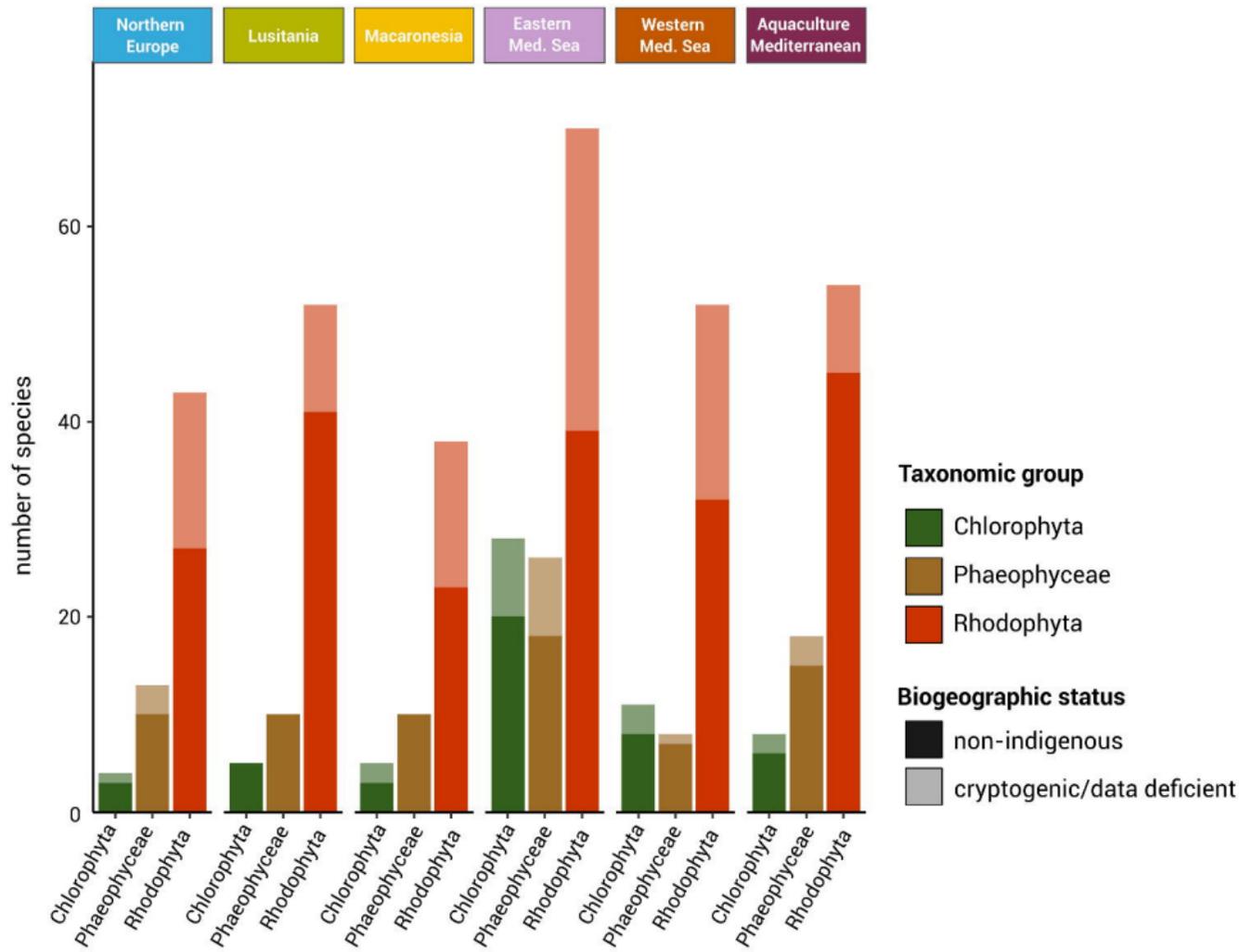
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low

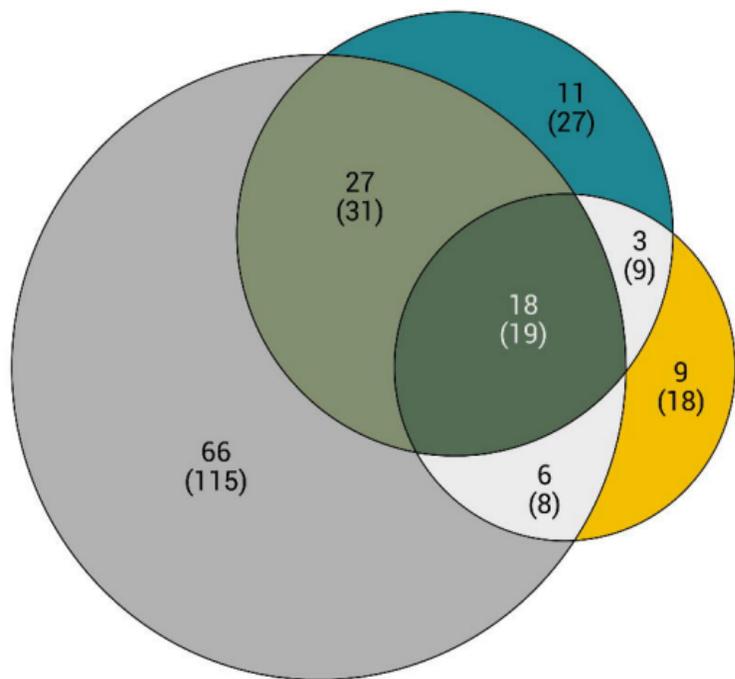
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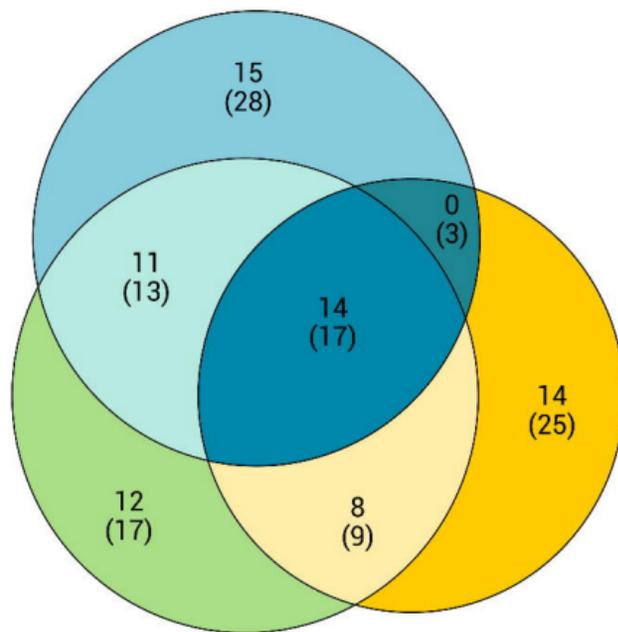


A)



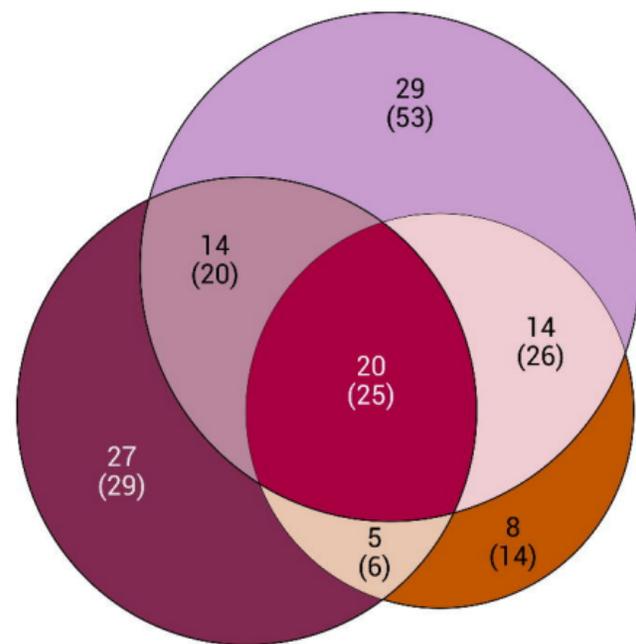
- Mediterranean Sea
- Macaronesia
- Northeast Atlantic Ocean

B)

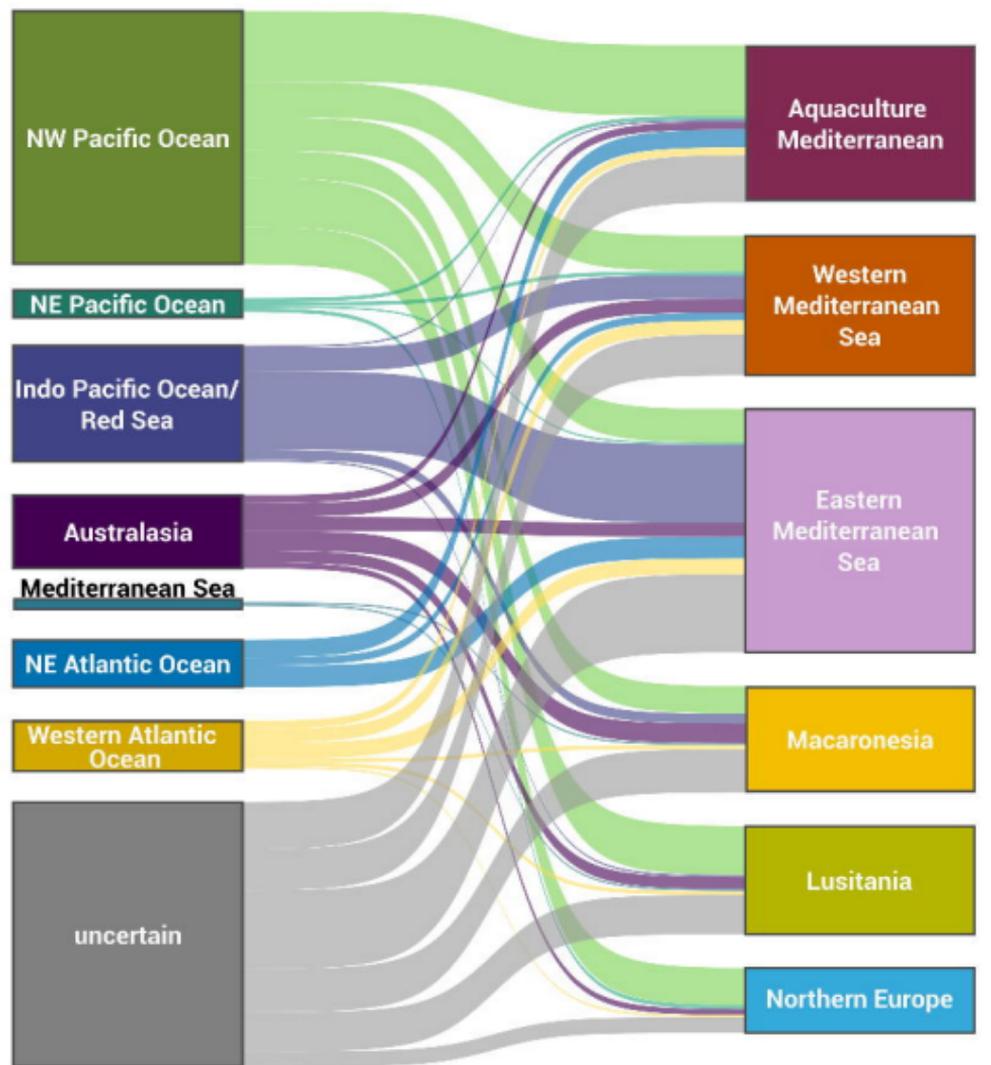


- Northern Europe
- Lusitania
- Macaronesia

C)

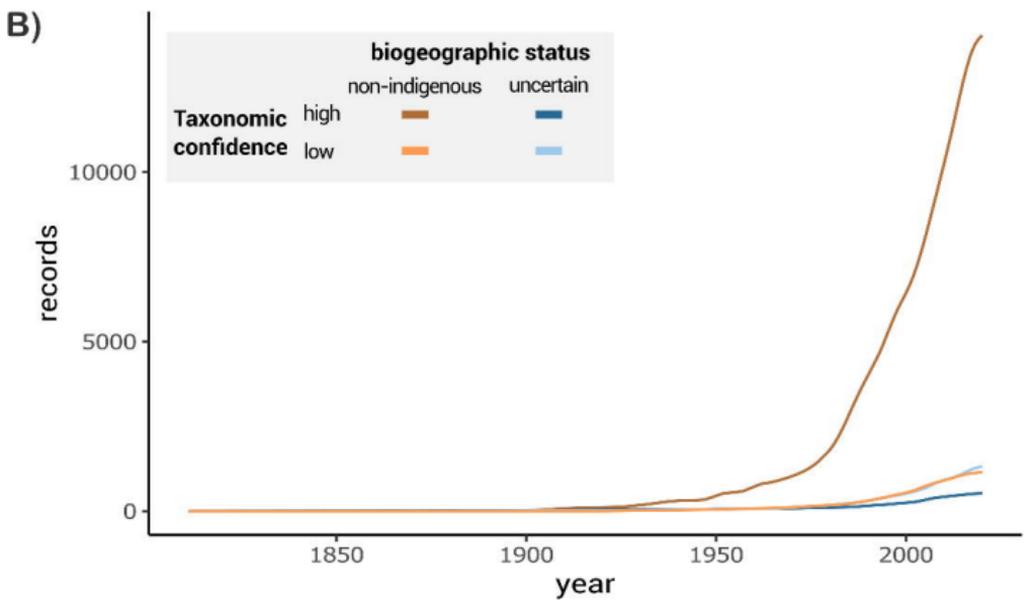
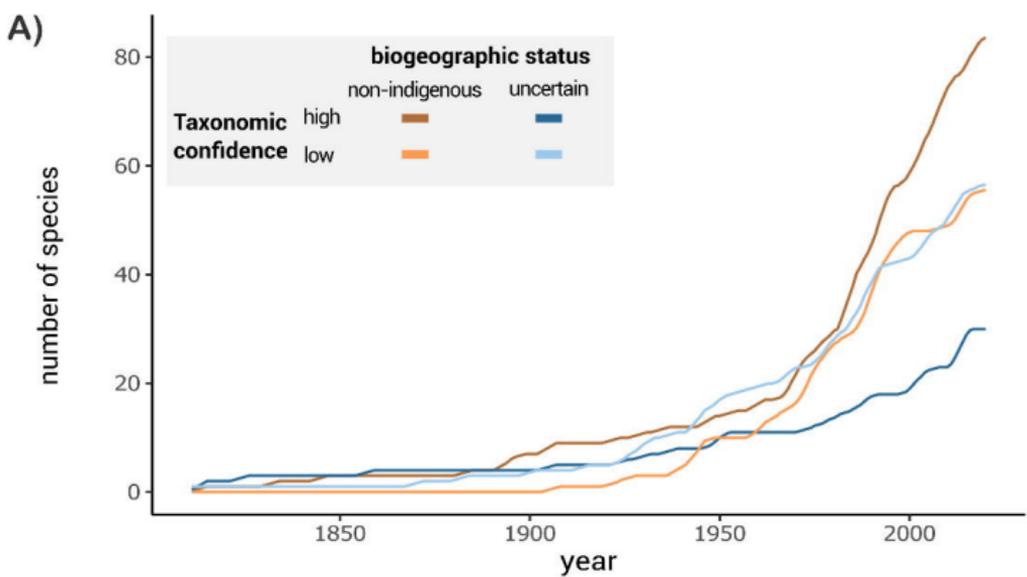


- West. Med. Sea
- East. Med. Sea
- Aquaculture Med. Sea



**Origin**

**Recipient region**



**Table 1.** Overview of the non-indigenous seaweed species (Charophyta, Chlorophyta, Phaeophyceae, Xanthophyceae, Rhodophyta) reported from the study area.

Species	date of first record			Taxonomic confidence	Biogeographical status	Origin
	Northeast Atlantic	Mediterranean Sea	Macaronesia			
<b>Charophyta</b>						
<i>Chara connivens</i> Salzmann ex A.Braun	native (Baltic Sea: 1870)	native	1975	0	data deficient	uncertain
<b>Chlorophyta</b>						
<i>Acetabularia calyculus</i> J.V.Lamouroux	absent	1968	absent	0	cryptogenic	uncertain
<i>Avrainvillea amadelpha</i> (Montagne) A.Gepp & E.S.Gepp	absent	2015	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Batophora occidentalis</i> var. <i>largoensis</i> (J.S.Prince & S.Baker) S.Berger & Kaever ex M.J.Wynne	absent	2020	absent	0	non-indigenous	Western Atlantic Ocean
<i>Bryopsis pennata</i> J.V.Lamouroux	absent	1961	native	0	data deficient	uncertain
<i>Caulerpa chemnitzia</i> (Esper) J.V.Lamouroux	absent	1926	native	0	cryptogenic	Indo Pacific Ocean/Red Sea
<i>Caulerpa cylindracea</i> Sonder	absent	1985	1970	1	non-indigenous	Australasia
<i>Caulerpa denticulata</i> Decaisne	absent	1929	native	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Caulerpa integerrima</i> (Zanardini) M.J.Wynne, Verbruggen & D.L.Angel	absent	2020	absent	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Caulerpa lamourouxii</i> (Turner) C.Agardh	absent	1951	absent	1	cryptogenic	Indo Pacific Ocean/Red Sea
<i>Caulerpa mexicana</i> Sonder ex Kützing	absent	1939	native	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Caulerpa prolifera</i> (Forsskål) J.V.Lamouroux	absent	native	native (Azores: 2013)	1	cryptogenic	uncertain
<i>Caulerpa taxifolia</i> (M.Vahl) C.Agardh	absent	1984	native	1	non-indigenous	Australasia
<i>Caulerpa taxifolia</i> var. <i>distichophylla</i> (Sonder) Verlaque, Huisman & Procaccini	absent	2003	absent	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Caulerpa webbiana</i> Montagne	absent	absent	native (Azores: 2002)	1	cryptogenic	uncertain
<i>Cladophora patentiramea</i> (Montagne) Kützing	absent	1991	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Cladophoropsis fasciculata</i> (Kjellman) Wille	absent	1928	absent	0	data deficient	uncertain

<i>Codium arabicum</i> Kützting	2003	2007	absent	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Codium fragile</i> subsp. <i>fragile</i>	1845	1946	1990	1	non-indigenous	Northwest Pacific Ocean
<i>Codium parvulum</i> (Bory ex Audouin) P.C.Silva	absent	2004	absent	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Codium pulvinatum</i> M.J.Wynne & R.Hoffman	absent	2014	absent	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Codium taylorii</i> P.C.Silva	2004	1939	native	0	non-indigenous	uncertain
<i>Derbesia boergesenii</i> (M.O.P.Iyengar & Ramanathan) Mayhoub	absent	1972	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Derbesia rhizophora</i> Yamada	absent	1984	absent	0	non-indigenous	Northwest Pacific Ocean
<i>Flabellia petiolata</i> (Turra) Nizamuddin	2013	native	native	1	cryptogenic	uncertain
<i>Halimeda incrassata</i> (J.Ellis) J.V.Lamouroux	absent	2011	2005	1	non-indigenous	Western Atlantic Ocean
<i>Lychaete herpestica</i> (Montagne) M.J.Wynne	absent	1944	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Neomeris annulata</i> Dickie	absent	2003	absent	1	cryptogenic	Indo Pacific Ocean/Red Sea
<i>Parvocaulis parvulus</i> (Solms-Laubach) S.Berger, Fettweiss, Gleissberg, Liddle, U.Richter, Sawitzky & Zuccarello	absent	1930	native	1	cryptogenic	uncertain
<i>Pseudocodium</i> <i>okinawense</i> E.J.Faye, M.Uchimura & S.Smimada	absent	2017	absent	1	non-indigenous	uncertain
<i>Siphonocladus tropicus</i> (P.Crouan & H.Crouan) J.Agardh	absent	2014	native	1	non-indigenous	Western Atlantic Ocean
<i>Ulva australis</i> Areschoug	1990	1984	absent	1	non-indigenous	uncertain
<i>Ulva californica</i> Wille	1999	2011	absent	0	non-indigenous	Northeast Pacific Ocean
<i>Ulva chaugulii</i> M.G.Kavale & M.A.Kazi	absent	2015	absent	1	cryptogenic	Indo Pacific Ocean/Red Sea
<i>Ulva lactuca</i> Linnaeus	absent	1813	absent	1	cryptogenic	uncertain
<i>Ulva ohnoi</i> M.Hiraoka & S.Shimada	absent	2002	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Ulva tepida</i> Y.Masakiyo & S.Shimada	absent	2002	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Ulvaria obscura</i> (Kützting) Gayral ex Bliding	native	1985	absent	0	non-indigenous	uncertain
<i>Uronema marinum</i> Womersley	absent	2008	absent	0	cryptogenic	uncertain

**Phaeophyceae**

<i>Acrothrix gracilis</i> Kyllin	native	1998	absent	0	non-indigenous	uncertain	
<i>Ascophyllum nodosum</i> (Linnaeus) Le Jolis	native	2009	native	1	non-indigenous	Northeast Atlantic Ocean	
<i>Botrytella parva</i> (Takamatsu) H.S.Kim		1993	1996	absent	0	non-indigenous	uncertain
<i>Chorda filum</i> (Linnaeus) Stackhouse	native		1981	native	1	non-indigenous	Northeast Atlantic Ocean
<i>Cladosiphon zosteræ</i> (J.Agardh) Kyllin	native		1985	native	1	non-indigenous	Northeast Atlantic Ocean
<i>Colpomenia peregrina</i> Sauvageau		1905	1918	1965	1	non-indigenous	Northwest Pacific Ocean
<i>Corynophlaea crispa</i> (Harvey) Kuckuck	native		2003	native	0	data deficient	Northeast Atlantic Ocean
<i>Corynophlaea cystophoræ</i> J.Agardh	absent		absent	1993	0	non-indigenous	Australasia
<i>Corynophlaea umbellata</i> (C.Agardh) Kützing		1986	native	uncertain	0	cryptogenic	Northwest Pacific Ocean
<i>Corynophlaea verruculiformis</i> (Y.-P.Lee & I.K.Lee) Y.-P.Lee		1994	absent	absent	0	non-indigenous	Northwest Pacific Ocean
<i>Cutleria multifida</i> (Turner) Greville	native		1950	native	1	cryptogenic	Northwest Pacific Ocean
<i>Desmarestia viridis</i> (O.F.Müller) J.V.Lamouroux	native		1947	absent	1	non-indigenous	uncertain
<i>Desmotrichum tenuissimum</i> (C.Agardh) Athanasiadis	native		1947	absent	0	non-indigenous	Northwest Pacific Ocean
<i>Dictyota acutiloba</i> J.Agardh	absent		2010	absent	1	non-indigenous	uncertain
<i>Dictyota cyanoloma</i> Tronholm, De Clerck, A.Gómez-Garreta & Rull Lluch		1995	1935	2006	1	non-indigenous	Australasia
<i>Ectocarpus siliculosus</i> var. <i>hiemalis</i> (P.Crouan & H.Crouan ex Kjellman) Gallardo	native		1985	absent	0	cryptogenic	Northeast Atlantic Ocean
<i>Fucus distichus</i> subsp. <i>evanescens</i> (C.Agardh) H.T.Powell	native (Oslofjord: 1883)		absent	absent	1	non-indigenous	Western Atlantic Ocean
<i>Fucus serratus</i> Linnaeus	native (Iceland: 1897)		absent	native	1	non-indigenous	uncertain
<i>Fucus spiralis</i> Linnaeus	native		1987	native	1	non-indigenous	Northeast Atlantic Ocean
<i>Halothrix lumbricalis</i> (Kützing) Reinke	native		1978	absent	0	non-indigenous	uncertain

<i>Hydroclathrus tilesii</i> (Endlicher) Santiañez & M.J.Wynne	absent	absent	2016	1	non-indigenous	Northwest Pacific Ocean
<i>Leathesia marina</i> (Lyngbye) Decaisne	native	1905	native	1	cryptogenic	Northwest Pacific Ocean
<i>Lobophora lessepsiana</i> C.W.Vieira	absent	2017	absent	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Lobophora schneideri</i> C.W.Vieira	absent	2016	native	1	non-indigenous	Western Atlantic Ocean
<i>Microspongium globosum</i> Reinke	native	2003	absent	0	data deficient	Northeast Atlantic Ocean
<i>Myrionema grateloupiae</i> Noda	2006	absent	absent	0	data deficient	Northwest Pacific Ocean
<i>Padina boergesenii</i> Allender & Kraft	absent	1962	native	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Padina boryana</i> Thivy	absent	1974	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Padina tetrastromatica</i> Hauck	absent	2004	absent	0	data deficient	Indo Pacific Ocean/Red Sea
<i>Papenfussiella kuromo</i> (Yendo) Inagaki	absent	absent	1990	0	non-indigenous	Northwest Pacific Ocean
<i>Petalonia binghamiae</i> (J.Agardh) K.L.Vinogradova	absent	absent	1980	0	non-indigenous	uncertain
<i>Pylaiella littoralis</i> (Linnaeus) Kjellman	native	1924	absent	1	cryptogenic	Northwest Pacific Ocean
<i>Rugulopteryx okamurae</i> (E.Y.Dawson) I.K.Hwang, W.J.Lee & H.S.Kim	2017	2002	2019	1	non-indigenous	Northwest Pacific Ocean
<i>Saccharina japonica</i> (Areschoug) C.E.Lane, C.Mayes, Druehl & G.W.Saunders	1979	1976	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Sargassum latifolium</i> (Turner) C.Agardh	absent	1986	absent	0	data deficient	Indo Pacific Ocean/Red Sea
<i>Sargassum muticum</i> (Yendo) Fensholt	1960	1980	2020	1	non-indigenous	Northwest Pacific Ocean
<i>Scytosiphon dotyi</i> M.J.Wynne	1987	1960	1990	0	non-indigenous	Northwest Pacific Ocean
<i>Spatoglossum variabile</i> Figari & De Notaris	absent	1944	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Sphaerotrichia firma</i> (E.S.Gepp) A.D.Zinova	absent	1970	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Stypopodium schimperi</i> (Kützing) Verlaque & Boudouresque	absent	1973	1997	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Ulonema rhizophorum</i> Foslie	native	2012	absent	0	data deficient	Northeast Atlantic Ocean

<i>Undaria pinnatifida</i> (Harvey) Suringar	1982	1971	absent	1	non-indigenous	Northwest Pacific Ocean
<b>Xanthophyceae</b>						
<i>Vaucheria longicaulis</i> Hoppaugh	1993	absent	absent	0	cryptogenic	uncertain
<b>Rhodophyta</b>						
<i>Acanthophora muscoides</i> (Linnaeus) Bory	absent	1977	absent	0	data deficient	uncertain
<i>Acanthophora nayadiformis</i> (Delile) Papenfuss	absent	1813	absent	1	cryptogenic	Indo Pacific Ocean/Red Sea
<i>Acanthosiphonia echinata</i> (Harvey) Savoie & G.W.Saunders	absent	2018	absent	1	non-indigenous	Western Atlantic Ocean
<i>Acrochaetium balticum</i> (Rosenvinge) Aleem & Schulz	1998	absent	absent	0	cryptogenic	Northeast Atlantic Ocean
<i>Acrochaetium catenulatum</i> M.Howe	1967	absent	absent	0	cryptogenic	uncertain
<i>Acrochaetium spathoglossi</i> Børgesen	absent	1944	absent	0	cryptogenic	uncertain
<i>Acrochaetium subseriatum</i> Børgesen	absent	1944	absent	0	cryptogenic	uncertain
<i>Acrothamnion preissii</i> (Sonder) E.M.Wollaston	absent	1969	2009	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Agardhiella subulata</i> (C.Agardh) Kraft & M.J.Wynne	1973	1984	absent	0	non-indigenous	uncertain
<i>Aglaothamnion cordatum</i> (Børgesen) Feldmann-Mazoyer	absent	native	2006	1	cryptogenic	uncertain
<i>Aglaothamnion feldmanniae</i> Halos	native	1975	native	0	non-indigenous	uncertain
<i>Aglaothamnion halliae</i> (Collins) Aponte, D.L.Ballantine & J.N.Norris	1960	2017	absent	0	non-indigenous	Western Atlantic Ocean
<i>Ahnfeltiopsis flabelliformis</i> (Harvey) Masuda	absent	1994	absent	0	non-indigenous	Northwest Pacific Ocean
<i>Anotrichium furcellatum</i> (J.Agardh) Baldock	1914	1926	1930	0	cryptogenic	uncertain
<i>Antithamnion amphigeneum</i> A.Millar	1995	1989	absent	1	non-indigenous	Australasia
<i>Antithamnion densum</i> (Suhr) M.Howe	1968	absent	1990	0	non-indigenous	uncertain
<i>Antithamnion diminuatum</i> Wollaston	absent	absent	1988	1	non-indigenous	Australasia
<i>Antithamnion hubbsii/nipponicum</i>	2003	1988	1989	1	non-indigenous	uncertain
<i>Antithamnionella boergesenii</i> (Cormaci & G.Furnari) Athanasiadis	2004	1937	native	0	cryptogenic	Western Atlantic Ocean

<i>Antithamnionella elegans</i> (Berthold) J.H.Price & D.M.John	1961	1882	uncertain	0	cryptogenic	uncertain
<i>Antithamnionella spirographidis</i> (Schiffner) E.M.Wollaston	1931	1905	1974	1	non-indigenous	uncertain
<i>Antithamnionella sublittoralis</i> (Setchell & N.L.Gardner) Athanasiadis	absent	1980	absent	0	cryptogenic	Northeast Pacific Ocean
<i>Antithamnionella ternifolia</i> (Hooker f. & Harvey) Lyle	1906	1926	2005	0	non-indigenous	Australasia
<i>Asparagopsis armata</i> Harvey	1922	1923	1928	1	non-indigenous	Australasia
<i>Asparagopsis taxiformis</i> (Delile) Trevisan	2000	1813	1840	1	non-indigenous	Australasia
<i>Bonnemaisonia hamifera</i> Hariot	1893	1909	1921	1	non-indigenous	Northwest Pacific Ocean
<i>Botryocladia madagascariensis</i> G.Feldmann	absent	1991	1988	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Botryocladia wrightii</i> (Harvey) W.E.Schmidt, D.L.Ballantine & Fredericq	2002	1978	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Calliblepharis rammediorum</i> R.Hoffman, M.J.Wynne & G.W.Saunders	absent	2013	absent	1	cryptogenic	uncertain
<i>Caulacanthus okamurae</i> Yamada	1986	2004	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Ceramium atrorubescens</i> Kylin	absent	absent	1988	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Ceramium bisporum</i> D.L.Ballantine	absent	1980	absent	0	cryptogenic	Western Atlantic Ocean
<i>Ceramium camouii</i> E.Y.Dawson	absent	2020	absent	0	data deficient	uncertain
<i>Ceramium cingulatum</i> Weber Bosse	absent	absent	1991	0	cryptogenic	uncertain
<i>Ceramium graecum</i> Lazaridou & Boudouresque	absent	1990	absent	0	cryptogenic	uncertain
<i>Ceramium strobiliforme</i> G.W.Lawson & D.M.John	absent	1990	absent	0	non-indigenous	uncertain
<i>Ceramium sungminbooi</i> J.R.Hughey & G.H.Boo	1990	absent	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Champia compressa</i> Harvey	absent	2012	absent	0	data deficient	uncertain
<i>Chondracanthus</i> sp.	2009	absent	absent	1	non-indigenous	uncertain
<i>Chondria coerulescens</i> (J.Agardh) Sauvageau	native	1973	native	1	cryptogenic	Northeast Atlantic Ocean

<i>Chondria curvilineata</i> Collins & Hervey	absent	1980	absent	0	non-indigenous	Western Atlantic Ocean
<i>Chondria polyrhiza</i> Collins & Hervey	absent	1987	absent	0	data deficient	Western Atlantic Ocean
<i>Chondria pygmaea</i> Garbary & Vandermeulen	absent	1974	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Chondrus giganteus</i> Yendo	absent	1994	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Colaconema codicola</i> (Børgesen) Stegenga, J.J.Bolton & R.J.Anderson	1931	1952	native	0	cryptogenic	uncertain
<i>Colaconema dasyae</i> (Collins) Stegenga, I.Mol, Prud'homme & Lokhorst	1951	absent	absent	0	cryptogenic	uncertain
<i>Colaconema robustum</i> (Børgesen) Huisman & Woelkerling	absent	1944	absent	0	cryptogenic	uncertain
<i>Corynomorpha prismatica</i> (J.Agardh) J.Agardh	absent	absent	1990	1	cryptogenic	Indo Pacific Ocean/Red Sea
<i>Cryptonemia hibernica</i> Guiry & L.M.Irvine	1960	absent	absent	1	non-indigenous	uncertain
<i>Dasya baillouviana</i> (S.G.Gmelin) Montagne	1950	native	native	0	cryptogenic	uncertain
<i>Dasya sessilis</i> Yamada	1989	1984	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Dasyisiphonia japonica</i> (Yendo) H.-S.Kim	1984	1998	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Dichotomaria obtusata</i> (J.Ellis & Solander) Lamarck	absent	2014	native	0	non-indigenous	uncertain
<i>Diplothamnion jolyi</i> C.Hoek	uncertain	2012	uncertain	0	data deficient	Western Atlantic Ocean
<i>Dipterosiphonia dendritica</i> (C.Agardh) F.Schmitz	absent	1979	native	0	data deficient	uncertain
<i>Eutrichosiphonia paniculata</i> (Montagne) D.E.Bustamante & T.O.Cho	absent	1967	absent	0	non-indigenous	uncertain
<i>Ezo epiyessoense</i> Adey, Masaki & Akioka	1983	absent	absent	1	data deficient	Northwest Pacific Ocean
<i>Fredericqia deveauniensis</i> Maggs, L.Le Gall, Mineur, Provan & G.W.Saunders	1980	absent	absent	1	cryptogenic	Western Atlantic Ocean
<i>Galaxaura rugosa</i> (J.Ellis & Solander) J.V.Lamouroux	absent	1990	native	1	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Ganonema farinosum</i> (J.V.Lamouroux) K.- C.Fan & Y.-C.Wang	absent	1808	native	0	cryptogenic	Indo Pacific Ocean/Red Sea

<i>Gayliella fimbriata</i> (Setchell & N.L.Gardner) T.O.Cho & S.M.Boo	absent	2013	absent	0	non-indigenous	uncertain
<i>Gelidium vagum</i> Okamura	2010	absent	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Goniotrichopsis sublittoralis</i> G.M.Smith	1975	1989	absent	0	cryptogenic	Northeast Pacific Ocean
<i>Gracilaria arcuata</i> Zanardini	absent	1931	absent	0	cryptogenic	Indo Pacific Ocean/Red Sea
<i>Gracilaria disticha</i> (J.Agardh) J.Agardh	absent	1924	absent	0	data deficient	Indo Pacific Ocean/Red Sea
<i>Gracilaria vermiculophylla</i> (Ohmi) Papenfuss	1994	2008	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Gracilaropsis chorda</i> (Holmes) Ohmi	2010	absent	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Grallatoria reptans</i> M.Howe	absent	absent	1988	0	cryptogenic	uncertain
<i>Grateloupia asiatica</i> S.Kawaguchi & H.W.Wang	2010	1984	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Grateloupia gibbesii</i> Harvey	absent	1992	absent	1	non-indigenous	Western Atlantic Ocean
<i>Grateloupia imbricata</i> Holmes	2014	absent	2006	1	non-indigenous	Northwest Pacific Ocean
<i>Grateloupia minima</i> P.Crouan & H.Crouan	native	1998	absent	1	non-indigenous	Northeast Atlantic Ocean
<i>Grateloupia patens</i> (Okamura) Kawaguchi & H.W.Wang	absent	1994	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Grateloupia subpectinata</i> Holmes	1947	1990	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Grateloupia turuturu</i> Y.Yamada	1969	1982	1983	1	non-indigenous	Northwest Pacific Ocean
<i>Grateloupia yinggehaiensis</i> H.W.Wang & R.X.Luan	absent	2008	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Griffithsia corallinoides</i> (Linnaeus) Trevisan	native	1964	absent	0	non-indigenous	Northwest Pacific Ocean
<i>Gymnophycus hapsiphorus</i> Huisman & Kraft	absent	absent	1989	0	non-indigenous	uncertain
<i>Herposiphonia parca</i> Setchell	2005	1997	absent	0	non-indigenous	uncertain
<i>Hypnea anastomosans</i> Papenfuss, Lipkin & P.C.Silva	absent	1972	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Hypnea cervicornis</i> J.Agardh	absent	1926	uncertain	0	non-indigenous	uncertain
<i>Hypnea cornuta</i> (Kützing) J.Agardh	absent	1894	absent	1	non-indigenous	Indo Pacific Ocean/Red Sea

<i>Hypnea corona</i> Huisman & Petrocelli	absent	2000	absent	1	non-indigenous	uncertain
<i>Hypnea flagelliformis</i> Greville ex J.Agardh	absent	1956	2007	0	cryptogenic	uncertain
<i>Hypnea valentiae</i> (Turner) Montagne	absent	1996	native	0	non-indigenous	uncertain
<i>Hypoglossum caloglossoides</i> M.J.Wynne & Kraft	absent	2013	absent	0	non-indigenous	Australasia
<i>Hypoglossum heterocystideum</i> (J.Agardh) J.Agardh	absent	absent	2014	0	cryptogenic	Australasia
<i>Kapraunia schneideri</i> (Stuercke & Freshwater) Savoie & G.W.Saunders	2010	1992	absent	1	non-indigenous	Western Atlantic Ocean
<i>Laurencia brongniartii</i> J.Agardh	1989	absent	1994	0	cryptogenic	uncertain
<i>Laurencia caduciramulosa</i> Masuda & S.Kawaguchi	absent	1991	2006	0	non-indigenous	uncertain
<i>Laurencia okamurae</i> Yamada	absent	1984	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Lithophyllum yessoense</i> Foslie	absent	1994	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Lomentaria flaccida</i> Tak.Tanaka	absent	2002	absent	1	data deficient	Northwest Pacific Ocean
<i>Lomentaria hakodatensis</i> Yendo	1984	1978	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Lophocladia lallemandii</i> (Montagne) F.Schmitz	absent	1900	absent	0	cryptogenic	Indo Pacific Ocean/Red Sea
<i>Lophocladia trichocladus</i> (C.Agardh) F.Schmitz	absent	uncertain	1896	0	cryptogenic	Western Atlantic Ocean
<i>Melanothamnus collabens</i> (C.Agardh) Díaz-Tapia & Maggs	1824	absent	absent	1	cryptogenic	Northwest Pacific Ocean
<i>Melanothamnus harveyi/japonicus</i>	1832	1958	1990	1	non-indigenous	Northwest Pacific Ocean
<i>Melanothamnus pseudoforcipatus</i> Díaz-Tapia	2014	absent	2018	1	cryptogenic	uncertain
<i>Monosporus indicus</i> Børgesen	absent	2015	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Nemalion vermiculare</i> Suringar	absent	2005	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Neoizziella divaricata</i> (C.K.Tseng) S.-M.Lin, S.-Y.Yang & Huisman	absent	absent	1990	0	cryptogenic	Northwest Pacific Ocean
<i>Neopyropia drachii</i> (Feldmann) J.Brodie	1948	absent	absent	1	cryptogenic	uncertain
<i>Neopyropia koreana</i> (M.S.Hwang & I.K.Lee) L.-E.Yang & J.Brodie	absent	2000	absent	1	cryptogenic	Northwest Pacific Ocean

<i>Neopyropia leucosticta</i> (Thuret) L.-E. Yang & J.Brodie	1857	absent	1897	1	cryptogenic	uncertain
<i>Neopyropia yezoensis</i> (Ueda) L.-E. Yang & J.Brodie	1984	1975	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Nitophyllum stellatocorticatum</i> Okamura	2006	1984	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Osmundea oederi</i> (Gunnerus) G.Furnari	native	1987	native	1	cryptogenic	uncertain
<i>Pachymeniopsis gargiuloi</i> S.Y.Kim, Manghisi, Morabito & S.M.Boo	2010	2000	2007	1	non-indigenous	Northwest Pacific Ocean
<i>Pachymeniopsis lanceolata</i> (Okamura) Yamada ex Kawabata	2019	1982	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Palisada maris-rubri</i> (K.W.Nam & Saito) K.W.Nam	absent	1990	absent	0	cryptogenic	Indo Pacific Ocean/Red Sea
<i>Phrix spatulata</i> (E.Y.Dawson) M.J.Wynne, M.Kamiya & J.A.West	absent	1992	absent	1	non-indigenous	uncertain
<i>Phycocalidia suborbiculata</i> (Kjellman) Santiañez & M.J.Wynne	2010	2010	1993	1	non-indigenous	Northwest Pacific Ocean
<i>Pikea californica</i> Harvey	1967	absent	absent	1	non-indigenous	uncertain
<i>Plocamium ovicorne</i> Okamura	2014	absent	absent	0	non-indigenous	Northwest Pacific Ocean
<i>Plocamium secundatum</i> (Kützing) Kützing	absent	1976	absent	0	non-indigenous	uncertain
<i>Polyopes lancifolius</i> (Harvey) Kawaguchi & Wang	2008	absent	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Polysiphonia atlantica</i> Kapraun & J.N.Norris	native	1969	native	0	cryptogenic	Northeast Atlantic Ocean
<i>Polysiphonia delicata</i> Díaz-Tapia	2014	absent	absent	1	cryptogenic	uncertain
<i>Polysiphonia havanensis</i> Montagne	absent	2012	native	0	cryptogenic	Western Atlantic Ocean
<i>Polysiphonia kampsaxii</i> Børgesen	absent	1986	absent	0	data deficient	Indo Pacific Ocean/Red Sea
<i>Polysiphonia morrowii/senticulosa</i>	1993	1996	absent	1	non-indigenous	uncertain
<i>Polysiphonia radiata</i> Díaz-Tapia	2014	absent	absent	1	cryptogenic	uncertain
<i>Predaea huismanii</i> Kraft	absent	absent	1991	0	non-indigenous	uncertain
<i>Rhodophysemma georgei</i> Batters	native	1978	absent	0	non-indigenous	Northeast Atlantic Ocean
<i>Rhodymenia erythraea</i> Zanardini	absent	1948	absent	0	data deficient	Indo Pacific Ocean/Red Sea

<i>Sarconema filiforme</i> (Sonder) Kylin	absent	1944	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Sarconema scinaoides</i> Børgesen	absent	1945	absent	0	data deficient	Indo Pacific Ocean/Red Sea
<i>Scageliopsis patens</i> E.M.Wollaston	2004	absent	1989	0	non-indigenous	Australasia
<i>Schizyenia apoda</i> (J.Agardh) J.Agardh	2013	absent	2004	0	cryptogenic	uncertain
<i>Schizyenia dubyi</i> (Chauvin ex Duby) J.Agardh	native	2008	native	0	non-indigenous	Northeast Atlantic Ocean
<i>Schizyenia jonssonii</i> K.Gunnarsson & J.Brodie	1897	absent	absent	1	cryptogenic	uncertain
<i>Scinaia acuta</i> M.J.Wynne	absent	absent	1989	0	non-indigenous	Australasia
<i>Solieria chordalis</i> (C.Agardh) J.Agardh	native (British Isles: 1977)	native	absent	0	cryptogenic	uncertain
<i>Solieria dura</i> (Zanardini) F.Schmitz	absent	1944	absent	0	non-indigenous	Indo Pacific Ocean/Red Sea
<i>Solieria filiformis</i> (Kützing) Gabrielson	2005	1922	native	0	non-indigenous	uncertain
<i>Solieria</i> sp.	2005	2011	absent	1	non-indigenous	Northwest Pacific Ocean
<i>Spermothamnion cymosum</i> (Harvey) De Toni	absent	2008	absent	1	non-indigenous	Australasia
<i>Spongoclonium caribaeum</i> (Børgesen) M.J.Wynne	1973	1974	1980	0	non-indigenous	uncertain
<i>Spyridia aculeata</i> (C.Agardh ex Decaisne) Kützing	native	1937	native	1	cryptogenic	uncertain
<i>Symphyocladia marchantioides</i> (Harvey) Falkenberg	2004	1984	1971	1	non-indigenous	uncertain
<i>Symphyocладиella dendroidea</i> (Montagne) D.Bustamante, B.Y.Won, S.C.Lindstrom & T.O.Cho	2005	1993	absent	1	non-indigenous	uncertain
<i>Vertebrata fucoides</i> (Hudson) Kuntze	native	1988	native	1	cryptogenic	Northeast Atlantic Ocean
<i>Womersleyella setacea</i> (Hollenberg) R.E.Norris	absent	1986	1983	0	cryptogenic	uncertain
<i>Xiphosiphonia pinnulata</i> (Kützing) Savoie & G.W.Saunders	native (British Isles: 1990)	native	2006	0	data deficient	Mediterranean