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A risk assessment of aquarium trade introductions of seaweed in European waters

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Abstract Aquaculture and maritime traffic have been identified as the main vectors for introductions of alien marine species. Except for one notorious case of *Caulerpa taxifolia*, the role of aquarium trade towards the introduction of alien seaweeds has been largely unassessed. Here, we address the risk of accidental release of seaweed species from the aquarium trade market in European waters. We assessed the importance and diversity of seaweed species in the European online aquarium retail circuit. Our web survey revealed more than 30 genera available for online sale into Europe, including known introduced and invasive species. A second aspect of the study consisted in sampling algal diversity found in aquaria. While allowing direct and accurate identification of the specimens, this approach was targeting not only ornamental species, but also seaweeds that may be accidentally present in the aquarium circuit. By DNA-barcoding we identified no less than 134 taxa, 7 of which are flagged as introduced in Europe and 5 reported as invasive. Climate envelope models show that at least 23 aquarium species have the potential to thrive in European waters. As expected by the tropical conditions in most aquaria, southern Atlantic regions of Europe and the Mediterranean are the most vulnerable towards new introductions. Further predictions show that this risk will increase and shift northwards as global warming proceeds. Overall our data indicate that aquarium trade poses a potential risk

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of new seaweed introductions, and calls for a cautious approach.

Keywords Marine macroalgae · Aquarium trade · Marine invasive species · e-commerce · DNA barcoding · Climate enveloping

Introduction

Macroalgae represent one of the largest groups of marine aliens, accounting for 10–30% of all introduced marine species in Europe (Katsanevakis et al. 2013; Schaffelke et al. 2006; Williams and Smith 2007; Zenetos et al. 2012). In areas such as the Thau Lagoon along the French Mediterranean coast, aliens may account for up to one-third of the seaweed diversity and up to 100% of the local biomass on hard substrates (Boudouresque et al. 2010). Invasive marine macroalgae may outcompete native biodiversity and affect the functioning of coastal ecosystems (Hammann et al. 2013). For example, *Codium fragile,* one of the most hazardous invasive marine macroalgae in temperate regions, is known to outcompete native kelp species (Levin et al. 2002; Scheibling and Gagnon 2006). Invasions of alien seaweeds do not only pose biodiversity and ecological threats. From an economic perspective, invasive seaweed species may disturb aquaculture and tourism, and eradication and control effort can easily rise to a few million dollars on a local scale (Irigoyen et al. 2011; Neill et al. 2006; Schaffelke and Hewitt 2007).

The most important vectors for primary introductions of alien seaweeds in Europe appear to be aquaculture and shellfish trade (Zenetos et al. 2012), while hull fouling most likely plays a lesser role (Mineur et al. 2007b). The role of oyster transfers as an important vector of seaweed introductions is indicated by experimental and indirect evidence, such as the northwestern Pacific origin of many seaweed species, and timing and location of first records (Mineur et al. 2007a, 2014, 2015). The importance of shellfish transfer as a vector for seaweed introductions, however, does not imply that other potential pathways are by definition ineffective. Hull fouling or transport by ballast water have been suggested as vectors of invasive seaweed species (Flagella et al. 2007; Hay 1990) but compared to other marine species, these maritime vectors are deemed less important since they exert strong selective pressures. These pressures include the presence of antifouling coatings on ship hulls and the absence of light in non-coated area such as sea chests where heterotrophic fouling organisms can thrive. Moreover, macroalgal propagules do not usually go through a resistant phase that would allow survival or prevent sedimentation in the ballast tanks. As a result, generally only cosmopolitan opportunistic species are found in standard maritime vectors (Mineur et al. 2007b). Hull fouling does become more important, however, on a more local scale as a mechanism of secondary introductions as has been discussed for the *Caulerpa taxifolia* (West et al. 2007), and *Acanthophora spicifera,* which has been found attached to hulls (Russell 1992).

Another putative vector is presented by aquarium trade (Padilla and Williams 2004, Thomsen et al. 2016). Even though only one introduction, of *C. taxifolia*, can be ascribed with certainty to aquarium trade (Jousson et al. 1998; Wiedenmann et al. 2001), several other species, including the lionfish *Pterois volitans*, are suspected to have been introduced by accidental releases from aquaria (Whitfield et al. 2002; Zenetos et al. 2012). Some introductions of marine species (*Zebrasoma xanthurum* and *C. taxifolia*) are even assumed to be caused by accidental release from aquaria on board mega yachts that travel the world (Guidetti et al. 2015; Meinesz and Simberloff 2001; Verlaque et al. 2015). Aquarium trade as a pathway for the introduction of marine alien species is, however, still largely unexplored. During the last 15 years, the internet has revolutionised how consumers purchase commodities. Aquarium hobbyists can obtain assorted living organisms from a variety of online sources, ranging from unofficial amateurs to established international suppliers. Recent studies start to point out the importance of biological invasions in aquatic environments associated with online trade (Mazza et al. 2015; Padilla and Williams 2004; Walters et al. 2006). Most research focuses on freshwater fishes (Mendoza et al. 2015; Rixon et al. 2005; Strecker et al. 2011), the marine seaweed *Caulerpa* (Stam et al. 2006; Walters et al. 2006; Wiedenmann et al. 2001), or on aquarium e-commerce in the USA which is one of the major importers of aquarium species (Odom and Walters 2014; Padilla and Williams 2004; Stam et al. 2006). For many other taxa and geographic regions the risk of introducing alien species by aquarium trade remains hitherto unexplored. The risk of accidental release encompasses not only ornamental species that are directly sold through online or conventional commerce, but also non-target species (i.e. hitchhikers) that can end up in aquarium tanks. One potentially important source for non-target organisms can be found in live rock, which has for example been reported as a successful vector for jellyfish (Bolton and Graham 2006). Those porous cobbles/boulders are usually pieces of natural reefs (dead scleractinian corals) that have been naturally colonized by a wide range of organisms, including coralline algae and other macro- and microalgae, invertebrates, and bacteria (Bolton and Graham 2006). Such living assemblages not only give the natural look to aquarium reefs that aquarists aspire, but they also serve as a shelter for fishes and invertebrates, as a substrate to sessile organisms, and as biological filtration mechanisms. The popularity of live rock by marine aquarists has been constantly growing since the 1970s (Falls et al. 2003). Unfortunately, live rock also increases the odds of a successful invasion of a wide diversity of species if the aquaria contents are discharged into the wild.

The present study aims to assess the seaweed diversity currently present in the European aquarium network. To this end, we used two approaches: (1) a surveillance of the online aquarium market for seaweeds that are subject to direct trade, and (2) sampling of aquarium tanks (private, retail shops and wholesalers, and public aquaria) coupled with a DNA barcoding approach, aiming at assessing the total diversity of both traded and accidentally introduced seaweeds. In order to identify the vulnerability of the European regions toward introductions of aquarium-associated seaweeds, we performed a climate-envelope modeling analysis. Since global warming is considered amongst the main threats to biodiversity, these analyses were performed for present and future climate scenarios. To our knowledge, this is the first study that systematically examines the risk of seaweed introductions by aquarium trade and focuses on more than one specific seaweed species or genus.

Materials and methods

E-trade survey

We monitored the diversity of seaweeds available through e-commerce from August 1 to September 30, 2014. Thereto, we screened online retail and auction sites. Private forums were not monitored because of access restrictions. As similarly done for *Caulerpa* in the US by Walters et al. (2006), a database containing every unique item advertised for sale was compiled, recording the search terms used, vernacular and scientific names mentioned in the advertisement, URL of the commercial site, geographic location of the site, origin of the seaweed, price, availability of information regarding invasive potential, and possibility to ship to Europe. Every online advertisement was saved as a pdf file.

Based on the pictures in the advertisements, we identified all records with best accuracy possible. Every taxon was labelled as 'introduced' or 'not introduced' based on the introduced seaweed distribution maps created for the Seas-era EUPF7ERA-NET INVASIVES projects, available through the Federation of European Phycological Societies: http://www.feps-algae.org/resources (FEPS 2017). 'Introduced' refers to alien species that are directly or indirectly transferred through human activities beyond their natural range of occurrence (Lucy et al. 2016). The term 'invasive' is restricted to those species that have been reported to cause economic or ecological harm to coastal ecosystems, while 'potentially invasive' refers to species that belong to the same genus as known invasive species.

We estimated the number of species offered for sale with the incidence-based coverage estimator (ICE), considering every online vendor as a unique sample and the algal species as the diversity. All calculations were conducted with the program EstimateS 9.1.0 (Colwell 2013).

Aquarium sampling survey

In order to obtain specimens we contacted associations of aquarists in order to locate owners of ornamental seaweeds, live rocks (i.e. pieces of rock harbouring a rich variety of microorganisms, invertebrates, and algae collected from tropical reefs), public aquaria, and retail shops. We sampled seaweeds in 5 private aquaria, 4 public aquaria, and 3 retail shops with a distance to the coast ranging between 500 m and more then 120 km. The identity of the above is not disclosed but can be obtained upon request. We also purchased about 15 live rocks assumed to be originating from Indonesia. We distributed the live rocks in three temperature (27 °C) and light controlled (LD 12:12) aquaria filled with artificial seawater, and surveyed them for several months, as has been done for *Caulerpa* by Walters et al. (2006). We sampled the first seaweeds 4 weeks after the setup when a substantial amount and larger algae (i.e. *Caulerpa*, *Chaetomorpha*) were visible in the tanks. We resampled after 8 weeks as we noticed no new seaweed species were developing. We preliminarily assigned all the samples to the lowest taxonomic rank possible based on morphology. This resulted in most of cases in identification to the genus level. We photographed every sample and preserved it in silica gel. Voucher specimens (herbarium and/or formalin preserved) are deposited in the Ghent University Herbarium (GENT). To increase the accuracy of the identifications, we identified the samples by DNA-barcoding. We extracted DNA from silica gel dried specimens with the DNeasy Blood & Tissue kit of Qiagen (Qiagen, Valencia, California, USA) following the manufacturer's instructions. For DNA amplification we followed previously published protocols (McDevit and Saunders 2009; Saunders and Kucera 2010; Saunders and Moore 2013). A complete overview of primers and references is given in Online Resource 1. A complete list of samples and corresponding EMBL accession numbers is provided in Online Resource 2. PCR products were sequenced by Macrogen. The obtained sequences were aligned with reference sequences from our personal library (Phycology Group, Ghent University) and GenBank with MEGA version 6 (Tamura et al. 2013). We aligned sequences and assigned them to the least inclusive taxonomic rank possible using phylogenetic trees or BLAST searches. 44 samples were solely identified by morphological identification due to failed DNA extraction of sequencing. Every taxon was again labelled as 'introduced' or 'not introduced' according to the rules described above. Species phylogenetically related to a known introduced species, i.e. belonging to the same genus, were flagged as a 'related'. Estimated total richness was calculated with the incidence-based coverage estimator ICE using EstimateS 9.1.0 (Colwell 2013).

Climate envelope modelling

For every unambiguously identified seaweed species found in the aquarium sampling survey, we determined the thermal distribution (i.e. the climatic niche). We used geo-referenced occurrences of the Global Biodiversity Information Facility (GBIF 2016), the OBIS database (OBIS 2016), and published literature sources. To limit the redundancy of neighbouring occurrence records, we used the Behrmann cylindrical equal-area projection and maintained 1 record per 25 km^2 grid cell. Secondly, we matched these occurrences to the long-term mean monthly sea surface temperature (SST) values from MARSPEC (Sbrocco and Barber 2013). After excluding species occurring in < 30 grid cells, we obtained a subset of 39 species that we used for climate envelope modelling. For each of these species we calculated the thermal range as the 5th percentile of the SST of the three coldest months and the 95th percentile of the SST of the three warmest months. By using these percentiles as endpoints instead of the minimum and maximum values, we exclude rarities and consider as such the non-static range boundaries of marine species ranges (Bates et al. 2015).

To assess the possible risk of aquarium species to European ecoregions, we tested if the mean SST values of the three coldest and warmest months for a certain European ecoregion were within the thermal range of every aquarium species. If positive, we considered this species as a potential threat for this particular ecoregion. This approximation of habitat suitability was carried out for the current and future (2055) climate. We used the climate model CMIIP5, scenario RCP4.5 of Combal (2014) for vulnerability predictions. The vulnerability of each ecoregion towards new introductions of alien species is estimated as the amount of species that meet the latter rules in that region. The assessed European ecoregions are all ecoregions within the provinces: Northern European Seas, Mediterranean Sea, Black Sea and Lusitanian (Fig. 3 in Spalding et al. 2007).

Results

E-trade survey

Using 14 different search terms in Google, we identified 39 unique online vendors. The three most successful search terms were 'Caulerpa for sale UK', 'Marine life aquaria', and 'Macroalgae aquarium store'. Together, they accounted for more than 50% of the positive hits.

Approximately half of the vendors were professional online retail shops, while the remaining half were online auction pages of hobbyists. The majority of the vendors (27) was situated in the USA. Only one of the US vendors explicitly stated to export to Europe, 16 did not ship to Europe, and 10 did not specify the countries shipped to. Other vendors were located in France, Germany, Malaysia, Poland, Thailand, and the United Kingdom.

In total we estimated the global seaweed diversity distributed by the 39 online vendors at 75 species belonging to minimum 53 genera, based on a total of 236 unique sale items (Table 1). The number of species should be considered an underestimation of the true diversity since identification to species level was often not possible based on the limited information provided in the advertisements. Genus-level diversity is therefore more accurate and will be used primarily in the subsequent analyses. The ICE diversity coverage estimator resulted in a total global online diversity 123 species and 100 genera based on 39 vendors (Fig. 1). For three quarters of all online records, species (30%) or genus names (46%) were provided by the vendors, while the remainder did not bear a scientific name. Obvious misidentifications by the vendors at species and genus level occurred, respectively, in 3 and 5% of the cases. Vernacular names ranged from commonly used names like 'sea lettuce' (*Ulva* sp.) to less obvious names like 'dragon's breath' (*Halymenia* sp.) and 'tang heaven' (*Gracilaria* sp.). 60% of the seaweeds available through global e-commerce belonged to the green algae (Chlorophyta), 36% to the red algae (Rhodophyta), and 4% to the brown algae (Phaeophyceae). *Caulerpa*, *Chaetomorpha*, and *Halimeda,* accounted for half the records of Chlorophyta. Within the Rhodophyta most of the records belonged to *Gracilaria* and *Botryocladia.* Phaeophyceae were hardly offered for sale, and only occasionally *Lobophora*, *Padina* or *Sargassum* was encountered. For 71% of the global online advertisements it was not possible to ship to Europe, or shipping details were not provided. Only one-third of the seaweeds found on the global online network could be purchased in Europe.

Biodiversity trends were similar for the European as for the global aquarium trade network with the majority of seaweeds belonging to the Chlorophyta. We found 30 available genera on the European online trade market (Table 1). More than half of the records found on the European e-market belong to genera that include species introduced in Europe. Moreover, several species flagged as invasive, or species closely related to invasive species are offered for sale. On a genus-level 26% of the specimens offered for sale can be classified as invasive or potentially invasive. Invasive species found were *C. taxifolia* and *C. cylindracea* (often under the name *C. racemosa*). Other species of *Caulerpa*, *Codium*, and *Sargassum* were considered as potentially invasive (Boudouresque and Verlaque 2002; Provan et al. 2008; Streftaris and Zenetos 2006).

Aquarium sampling survey

We identified 217 specimens from almost 50 aquarium tanks from private aquaria, public aquaria, and retail shops. Identifications were based on a combination of morphology and DNA barcoding (Table 2). 28 specimens were identified to genus level and 101 specimens to named species. 88 specimens were assigned to the species level but not to a named species. 57% of the species not assigned to a named species belonged to the Rhodophyta. In total, we found 134 unique seaweed taxa (Table 2), of which 96% belonged to either the Chlorophyta or the Rhodophyta. Only a minority of the samples (4%) belonged to the Phaeophyceae. The Chlorophyta and Rhodophyta were equally sampled in aquarium tanks but the diversity of the Rhodophyta was remarkably higher. Especially the coralline and crustose red algae (Corallinophycidae and Peysonneliales) were highly diverse and abundant; together they accounted for 23% of total seaweed diversity found and for 20% of the samples collected. Within the Rhodophyta, the most abundant genera were *Botryocladia*, *Haraldiophyllum* and *Polysiphonia*. *Caulerpa, Chaetomorpha* and *Cladophora* were the most abundant green algae, and *Dictyota* the most abundant brown alga (Table 2).

Table 1 Seaweed genera found on the online trade market with their status of introduction in Europe and the number of records available in and outside the European online market

Genus	Status	Number of records (European market)	Number of records (non-European market)	Total
Chlorophyta				
Acetabularia	Not introduced		1	1
Boergesenia	Not introduced	1		1
Bornetella	Not introduced	1		1
Caulerpa	Introduced	20	32	52
Chaetomorpha	Uncertain	4	17	21
Chlorodesmis	Not introduced	2	3	5
Cladophora	Introduced	6	3	9
Codium	Introduced	1	6	7
Cymopolia	Not introduced		4	4
Enteromorpha	Not introduced		1	1
Halimeda	Not introduced	6	9	15
Neomeris	Introduced	1	2	3
Penicillus	Not introduced		3	3
Rhipocephalus	Not introduced		2	2
Udotea	Not introduced	1	3	4
Ulva	Introduced	1	9	10
Valonia	Not introduced	2		2
Unknown	Uncertain		1	1
Rhodophyta				
Acanthophora	Introduced		3	3
Actinotrichia	Not introduced	1		1
Agardhiella	Introduced		1	1
Amansia	Not introduced	1		1
Amphiroa	Not introduced	2	3	5
Botryocladia	Introduced	3	7	10
Bryothamnion	Not introduced		1	1
Carpopeltis	Not introduced		4	4
Ceramium	Introduced	1		1
Cryptomenia	Introduced		1	1
Dichotomaria	Introduced	3		3
Eucheuma	Not introduced		2	2
Fauchea	Not introduced		1	1
Galaxaura	Introduced	1	4	5
Gracilaria	Introduced		17	17
Haliptilon	Not introduced	1		1
Halymenia	Not introduced	1	4	5
Heterosiphonia	Not introduced		2	2
Hypnea	Introduced		1	1
Jania	Not introduced	1		1
Kappaphycus	Not introduced	1		1
Liagora	Not introduced		1	1
Lithothamnion	Not introduced	1		1

Table 1 continued

Genus	Status	Number of records (European market)	Number of records (non-European market)	Total
Mastophora	Not introduced	1		1
Osmundaria	Not introduced		1	1
Peyssonnelia	Not introduced	1		1
Portieria	Not introduced		4	4
Ptilophora	Not introduced		2	2
Scinaia	Not introduced		1	1
Phaeophyceae				
Canistrocarpus	Not introduced		1	1
Dictyota	Introduced	1		1
Lobophora	Not introduced		2	2
Padina	Not introduced	1	1	2
Sargassum	Introduced	1	1	2
Turbinaria	Not introduced	1		1
Unknown	Uncertain		6	6
Total		69	167	236

Introduced Represents genera that include species introduced in Europe, *Not introduced* genera that do not include species introduced in Europe, when unclear or unknown the status is represented by 'Uncertain'

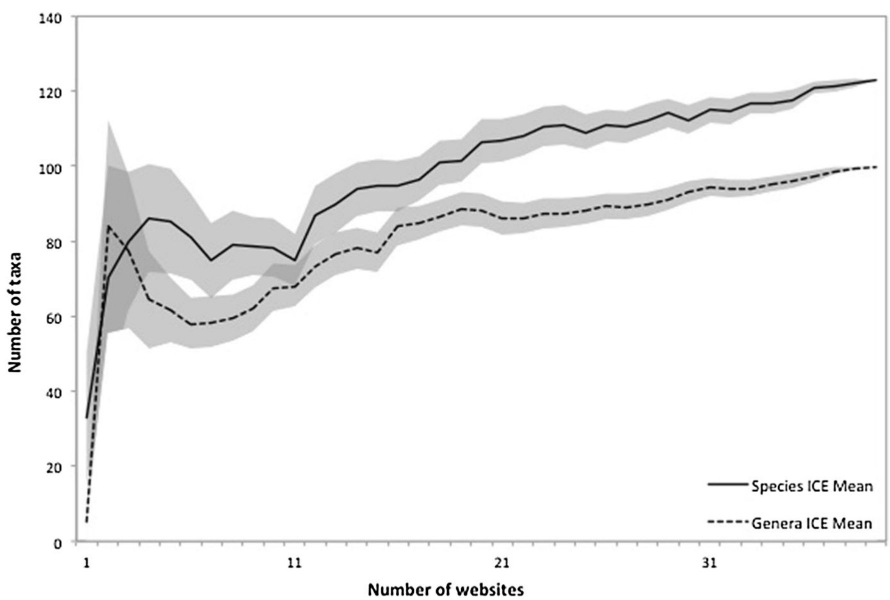

Fig. 1 Incidence-based coverage estimator (ICE) for species and genera found on the global e-market (mean ± SE)

The ICE diversity coverage estimator estimates the total diversity on 370 species and 128 genera (Fig. 2). We found six species that are known to be introduced in Europe of which five species are reported as invasive: *C. taxifolia*, *Asparagopsis taxiformis*, *Hypnea valentiae*, *Womersleyella setacea* and *Sargassum muticum* (Table 2; Boudouresque and Verlaque 2002; Ni Chualain et al. 2004; Nikolić et al. 2010; Provan et al. 2008; Streftaris and Zenetos 2006). Another 40 species were closely related to introduced species. These account for 30% of all specimens sampled in the European aquaria.

Table 2 Seaweed diversity and the number of records found in the European aquarium network with their status of introduction in Europe

Chlorophyta taxon	Status	No. of records	Rhodophyta taxon	Status	No. of records	Phaeophyceae taxon	Status	No. of records
Caulerpa parvifolia	Not introduced, related	9	*Mesophyllum* sp. 1	NOT introduced	5	*Dictyota friabilis1*	Not introduced, related	4
Chaetomorpha vieillardii	Not introduced	7	*Haraldiophyllum* sp. 1	Not introduced	4	*Dictyota ceylanica4*	Not introduced, related	1
Caulerpa racemosa	Uncertain	6	*Sporolithon* sp. 1	Not introduced	3	*Dictyota implexa*	Not introduced, related	1
Caulerpa constricta	Not introduced, related	5	*Titanophora* sp. 1	Not introduced	3	*Halopteris filicina*	Not introduced, related	1
Caulerpa taxifolia	Introduced	5	*Acanthophora spicifera*	Not introduced, related	2	*Sargassum muticum*	Introduced	1
Cladophora	Related	4	*Acrosymphyton* sp. 1	Not introduced	2	*Sargassum* sp. 1	Related	1
Chaetomorpha	Uncertain	3	*Antithamnion*	Related	2			
Cladophora albida/ sericea	Not introduced, related	3	*Asparagopsis taxiformis*	Introduced	2			
Derbesia	Related	3	*Botryocladia* sp. 1	Not introduced, related	2			
Halimeda gigas	Not introduced	3	*Cryptonemia* sp. 1	Not introduced, related	2			
Valonia macrophysa	not introduced	3	*Gracilaria vieillardii*	Not introduced, related	2			
Bryopsis	Not introduced	2	*Harveylithon* sp. 1	Not introduced	2			
Bryopsis sp. 1	Not introduced	2	*Lithophyllum* sp. 3	Related	2			
Bryopsis sp. 2	Not introduced	2	*Melobesioideae* sp. 1	Not introduced	2			
Caulerpa cupressoides	Not introduced, related	2	*Peyssonnelia japonica*	Not introduced	2			
Caulerpa prolifera	Not introduced, related	2	*Peyssonnelia* sp. 3	Not introduced	2			
Caulerpa sertularioides	Not introduced, related	2	*Polysiphonia*	Related	2			
Cladophora herpestica	Introduced	2	*Polysiphonia* sp. 1	Not introduced, related	2			
Cladophora pellucida	Not introduced, related	2	*Ramicrusta* sp. 1	Not introduced	2			
Cladophora prolifera	Not introduced, related	2	*Sporolithon* sp. 3	Not introduced	2			

Table 2 continued

Chlorophyta taxon	Status	No. of records	Rhodophyta taxon	Status	No. of records	Phaeophyceae taxon	Status	No. of records
Derbesia sp. 1	Not introduced, related	2	*Yonagunia zollingeri*	Not introduced	2			
Halimeda minima	Not introduced	2	*Amphiroa*	Not introduced	1			
Valonia utricularis	Not introduced	2	*Asparagopsis*	Related	1			
Boergesenia forbesii	Not introduced	1	*Botryocladia*	Related	1			
Boodlea sp. 1	Not introduced	1	*Botryocladia* sp. 3	Not introduced, related	1			
Boodlea sp. 2	Not introduced	1	*Ceramium codii*	Not introduced, related	1			
Boodlea sp. 3	Not introduced	1	*Ceratodictyon repens*	Not introduced	1			
Bryopsis sp. 5	Not introduced	1	*Chondracanthus saundersii*	Not introduced, related	1			
Caulerpa chemnitzia	Not introduced, related	1	*Coelarthrum*	Not introduced	1			
Caulerpa flexilis	Not introduced, related	1	*Crouania attenuata*	Not introduced	1			
Caulerpa lentillifera	Not introduced, related	1	*Cryptonemia lomation*	Not introduced, related	1			
Caulerpa oligophylla	Not introduced, related	1	*Erythrotrichia carnosa*	Not introduced	1			
Caulerpa serrulata	Not introduced, related	1	*Griffithsia* sp. 1	Not introduced, related	1			
Chaetomorpha sp. 1	Uncertain	1	*Halymenia durvillei1*	Not introduced	1			
Chaetomorpha sp. 2	Uncertain	1	*Halymenia durvillei2*	Not introduced	1			
Chaetomorpha sp. 3	Uncertain	1	*Hydrolithon* sp. 1	Not introduced	1			
Chlorodesmis	Not introduced	1	*Hydrolithon* sp. 2	Not introduced	1			
Cladophoropsis	Related	1	*Hydrolithon* sp. 3	Not introduced	1			
Codium	Related	1	*Hypnea* sp. 1	Not introduced, related	1			
Codium arenicola	Not introduced, related	1	*Hypnea valentiae*	Introduced	1			
Codium dwarkense	Not introduced, related	1	*Incendia* sp. 1	Not introduced	1			
Derbesia sp. 2	Not introduced, related	1	*Laurencia* sp. 1	Not introduced, related	1			

Table 2 continued

Chlorophyta taxon	Status	No. of records	Rhodophyta taxon	Status	No. of records	Phaeophyceae taxon	Status	No. of records
Derbesia sp. 3	Not introduced, related	1	*Lithophyllum* sp. 1	Related	1			
Halimeda disoidea	Not introduced	1	*Lithophyllum* sp. 2	Related	1			
Halimeda opuntia	Not introduced	1	*Lithophyllum* sp. 4	Related	1			
Parvocaulis parvula	Not introduced	1	*Lithophyllum* sp. 6	Related	1			
Ulva	Related	1	*Mastophoroideae* sp. 1	Not introduced	1			
Ulva laetevirens	Not introduced, related	1	*Mastophoroideae* sp. 2	Not introduced	1			
Ulva sp. 1	Not introduced, related	1	*Melobesioideae* sp. 3	Not introduced	1			
Ulva sp. 2	Not introduced, related	1	*Meredithia* sp. 1	Not introduced	1			
Ulvella leptochaete	Not introduced	1	*Mesophyllum* sp. 4	Not introduced	1			
			Mesophyllum sp. 5	Not introduced	1			
			Mesophyllum sp. 7	Not introduced	1			
			Neosiphonia sp. 1	Not introduced, related	1			
			Palisada sp. 1	Not introduced	1			
			Peyssonnelia sp. 1	Not introduced	1			
			Peyssonnelia sp. 2	Not introduced	1			
			Peyssonnelia sp. 4	Not introduced	1			
			Peyssonnelia sp. 5	Not introduced	1			
			Peyssonnelia sp. 6	Not introduced	1			
			Peyssonnelia sp. 7	Not introduced	1			
			Phymatolithon sp. 1	Not introduced	1			
			Plocamium sp. 1	Not introduced, related	1			
			Pneophyllum	Not introduced	1			
			Polystrata sp. 1	Not introduced	1			
			Porolithon sp. 1	Not introduced	1			
			Pterocladiella caerulescens	Not introduced	1			
			Pterocladiella sp. 1	Not introduced	1			
			Ptilophora scalaramosa	Not introduced	1			

Table 2 continued

Chlorophyta taxon	Status	No. of records	Rhodophyta taxon	Status	No. of records	Phaeophyceae taxon	Status	No. of records
			Rhodymenia ardissonei	Not introduced, related	1			
			Rhodymeniaceae	Not introduced	1			
			Sarconema filiforme	Introduced	1			
			Sarconema sp. 1	Not introduced, related	1			
			Sporolithon sp. 4	Not introduced	1			
			Titanoderma sp. 1	Not introduced	1			
			Womersleyella setacea	Introduced	1			
			Yonagunia sp. 1	Not introduced	1			
Total		103	Total		105	Total		9

Not introduced Indicates species not known to be introduced in Europe, *Introduced* indicates species reported as introduced in Europe, *Uncertain* indicates that the status of introduction is unclear or unknown, *Related* indicates that a congeneric species is reported as introduced in Europe

Climate enveloping

Comparison of the thermal distribution of the aquarium species and the current temperature conditions demonstrated that at least 23 of the 39 species used for climate enveloping could possibly thrive in European seas under current climate conditions (Online resource 3). These 23 species include the six species known to be introduced in Europe. In 2055 under future climate change scenario CMIIP5, RCP4.5 there are minimum 26 species that could possibly thrive in Europe (Online resource 3). The majority of these species is already present in Europe and not known to be invasive. Following our predictions, the number of aquarium seaweed species that is able to survive in the European waters is higher for the warmer southern European regions than for the northern, cooler ecoregions. The Aegean Sea, the Levantine Sea and the Saharan Upwelling were suitable for at least 12 more species than presently reported (Fig. 3a). When only species known to be introduced are considered, 4 more introduced species could thrive in the ecoregions Azores Canaries Madeira, Ionian Sea and Saharan Upwelling under the current climate (Table 3). Extrapolating predictions to the climate predicted in 2055 under CMIIP5, RCP4.5 reflects a northward trend in invasion risk (Fig. 3b). All species considered are estimated to be able to thrive in more ecoregions under future climate conditions (2055) then under actual and estimated current (2010) conditions (Online resource 3). The Adriatic Sea (+ 7 species), the Baltic Sea (+ 4 species), the Black Sea (+ 4 species) and the South-European Atlantic Shelf (+ 4 species) had the biggest increase in invasion risk (Fig. 3b).

Discussion

The risk posed by aquarium trade as a vector for introductions of alien aquatic taxa has relatively recently been raised and demonstrated by several studies (Howeth et al. 2016; Mazza et al. 2015; Padilla and Williams 2004; Rixon et al. 2005; Walters et al. 2006). The vast majority of these studies focus on freshwater species and the USA, which is one of the major importers of aquarium species of the world (Padilla and Williams 2004). Our survey confirms that online aquarium trade in marine macroalgae is best established in the USA. Only a minority of the online

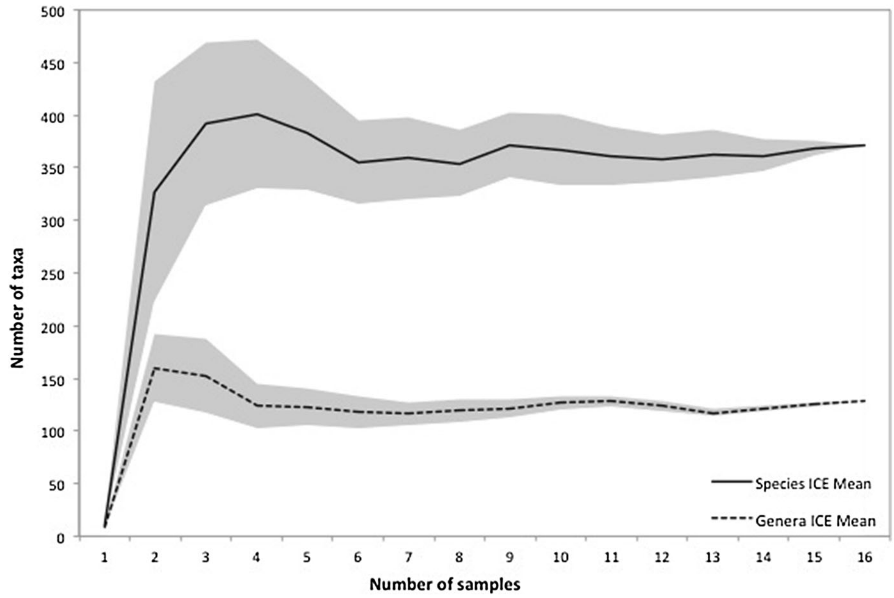

Fig. 2 Incidence-based coverage estimator (ICE) for species and genera found in the European aquarium trade market (mean ± SE)

vendors ship to or within Europe, which limits the possible risk of introductions of aquarium associated introductions in Europe substantially. Despite the smaller market share, the seaweed diversity offered on the European e-market is, nevertheless, almost as high as the diversity on the non-European market. We found 75 species available online of which 30 could be shipped to or within Europe. Only one-third of the species is advertised on both the European and the non-European e-market.

A brief questionnaire of the aquarists where we went sampling (hereafter referred to as personal communication aquarists) revealed that purchase or exchange of organisms often happens informally, in aquarist clubs, or through internet forums. Since these purchasing alternatives are very hard to monitor and not considered in this study, the marine aquarium related diversity remains partly unexplored. Furthermore, these informal pathways will be very hard to regulate with respect to management strategies. Important is that 26% of the macroalgae offered for sale online are flagged as potentially invasive which creates a realistic risk for possible new hazardous introductions. Previous research has shown that *Caulerpa* is an important player of the aquarium trade in the United States (Stam et al. 2006; Walters et al. 2006). But invasive *Caulerpa* strains are rarely encountered on the American e-market, most likely due to awareness campaigns and legal regulation on trade of *C. taxifolia* (Stam et al. 2006; Walters et al. 2006). These authors recommend, however, a full ban of the *Caulerpa* genus due to the poor identification of traded algae (which is confirmed by our results), the need of molecular tools to identify invasive strains, and the lack of understanding of the potential invasive capacity of other *Caulerpa* species (Stam et al. 2006; Walters et al. 2006). Our survey indicates that also in Europe *Caulerpa* is by far the most common genus offered for sale online (Table 1). Corresponding to Mazza et al. (2015) we also found *C. taxifolia* online, confirming the potential dispersal of this invasive species through aquarium e-commerce and illustrating the need of legal restrictions regarding online aquarium trade of macroalgae in Europe. A few cases were identified where tropical seaweeds collected in their natural environment (Malaysia and Thailand) are offered for sale online, thereby increasing the risk of introducing new potentially invasive species. We found no information about the treatment of the shipped seaweed material. Therefore, also inconspicuous organisms attached to the shipped seaweed material or present in the shipping water may be transported. Furthermore, this trade of newly collected specimens would also increase the genetic diversity within aquarium traded and potentially introduced seaweed species and other organisms.

We identified at least 134 taxa in the private and public aquaria, and retail shops. The number of

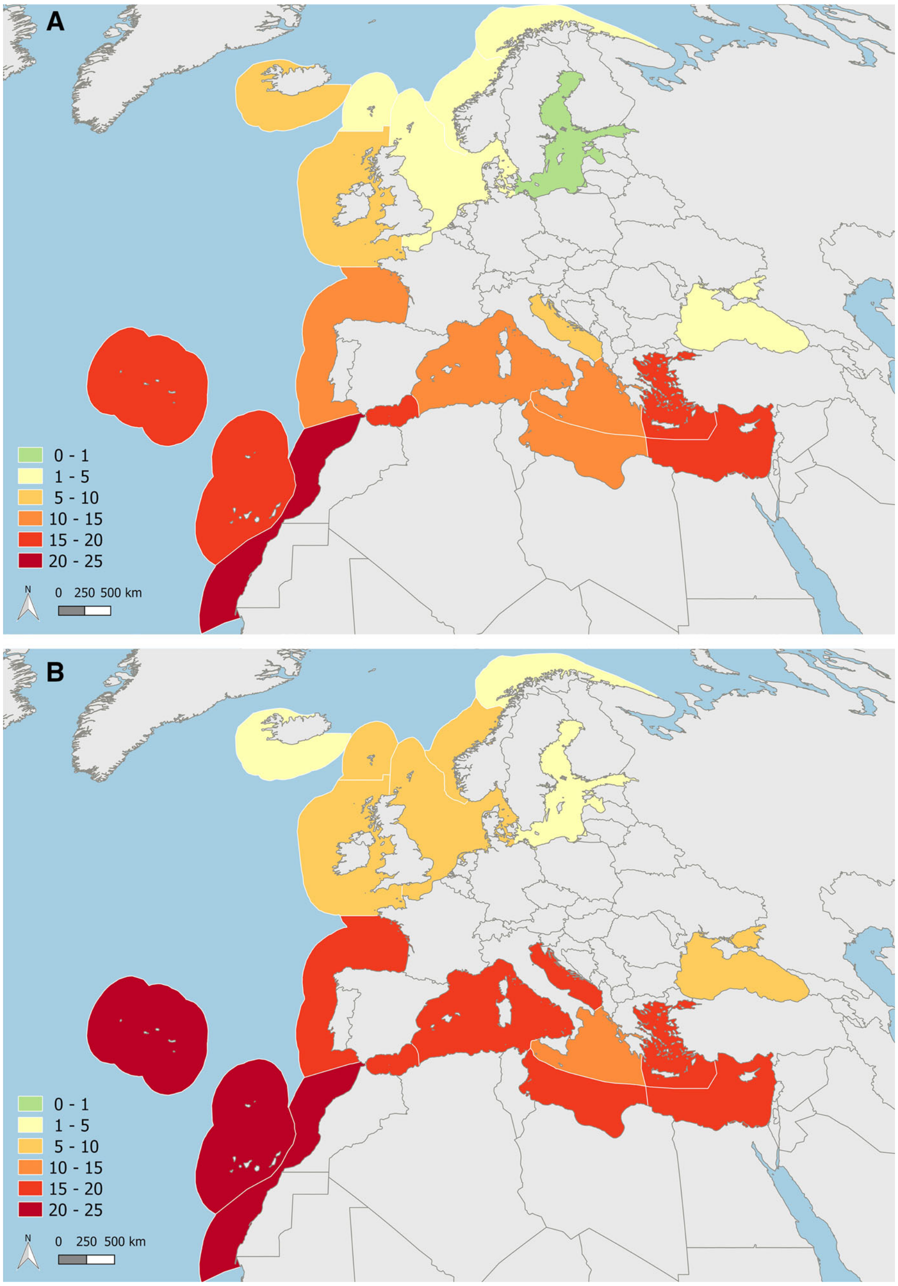

Fig. 3 The risk of new introductions by aquarium seaweed species in Europe estimated by the number of species with a thermal distribution falling within the mean maximum and minimum SST for each ecoregion under current (**a**, 2010) and future (**b**, 2055) climate conditions (model CMIIP5 scenario RCP4.5)

estimated taxa reached a plateau (Fig. 2), which is indicative for a representative sampling. Identification of seaweed species based on morphological features is not straightforward, and therefore DNA sequence data are used to guide species identification (DNA barcoding) (Leliaert et al. 2014; Saunders 2005). Although DNA barcoding has proven effective for rapid species identification in algae, an important limitation is the lack of a comprehensive DNA-based reference framework. This is especially the case for the coralline red algae, a group comprising a large part of unresolved biodiversity. Despite this difficulty of identifying species, we identified 85% of the 216 samples to species level based on molecular data. This shows that aquaria host substantial unknown diversity.

Similar to the available online seaweed diversity, the diversity sampled in the aquaria was highest for the Rhodophyta. This high diversity of Rhodophyta is mainly due to the high diversity of crustose and coralline algae (31 species). Calcified red algae are popular among aquarists because of their appealing colour and good covering of the tank. Therefore, aquarists often add supplements to enhance growth of coralline algae (personal communication aquarists). Chlorophyta are popular among aquarists as biological filtration mechanism (e.g. *Caulerpa*, *Chaetomorpha*) (Odom and Walters 2014). Macroalgae with characteristics linked to invasive seaweeds, such as broad environmental tolerances, rapid growth, vegetative reproduction and high reproductions rates (Andreakis and Schaffelke 2012; Thomsen and McGlathery 2007) are also macroalgae that are easy to maintain in aquaria. *Bortryocladia, Chaetomorpha, Caulerpa*, *Gracilaria* are therefore popular and widespread in the aquarium circuit, which enhances their chances to be released. A worrying concern emerging from our survey is the presence of introduced and known invasives or species related to invasives, including *C. taxifolia*, *A. taxiformis* and *W. setacea*. In combination with a large unknown diversity of seaweed species, for which the potential invasive risk is impossible to assess, aquarium associated species may pose a realistic threat to European coasts.

The diversity found in the sampled aquaria is remarkably larger than the diversity found online. Species found online are mostly large species used for ornamental purposes, fish food, or to a lesser extent, filtration purposes, while the diversity samples in the aquaria also includes small, epibiotic species that are often accidentally introduced in aquaria through other organisms or live rock. Live rock, in particular, proves to be a successful vector for a variety of species (Bolton and Graham 2006; Walters et al. 2006; this study). Walters et al. (2006) observed the development of 29 seaweed species (including 4 *Caulerpa* species) from live rock. Several genera that we observed (i.e. *Caulerpa*, *Hydrolithon*, *Peyssonnelia*, *Dictyota*, *Cladophoropsis*, and *Valonia*) were also recorded to develop from live rock by Fosså and Nilsen (1996). Furthermore, we observed polychaetes, hydroids and cyanobacteria developing from live rock. These specimens have not been further surveyed but this highlights that live rock is an effective vector for a wide variety of organisms, including inconspicuous microorganisms. We mainly found tropical seaweed species in warm water aquaria, but we also found European seaweed species in temperate aquaria (e.g. *Dictyota implexa*, *Halopteris filicina*, *Cladophora albida*). These examples were the result of private sampling by the responsible of the aquarium during his holidays abroad (personal communication). This indicates that aquarists also acquire seaweeds through informal ways and in this case even facilitate intra-European introductions.

Comparison of the mean SST and temperature range of the aquarium species demonstrates that European aquarium trade may not pose an imminent risk towards introductions of new macroalgae in European ecoregions. Most of the species are either already established in Europe or are not able to thrive in European ecoregions. But additional introductions may however result in an expansion of the genetic diversity of these invasive species. The higher risk of introduction in the southern parts of Europe is to be expected, as most species found in the aquaria are tropical species. As climate change proceeds, most ecoregions will become suitable to a higher number of aquarium species (Fig. 3; Table 3). The invasive species included in the risk assessment (*A. taxiformis*, *C. taxifolia*, *S. muticum*, *W. setacea*) are all able to thrive in more ecoregions after climate change then under current conditions (Online resource 3). Note that while a thermal range of a species may not fully overlap the thermal range of an ecoregion, there might be smaller parts of that ecoregion that are yet suitable for a species. Consequently, the estimated number of species that can thrive in an ecoregion may be higher than we calculated. These finding support the hypotheses of Rixon et al. (2005) that the probability of aquarium species establishment along European coasts will increase with climate warming because most aquarium species are of tropical or subtropical origin.

Eradication of invasive species once they are established is very challenging. Hence prevention of new introductions is most effective in avoiding and limiting new biological invasions (Doelle et al. 2007; Vander Zanden and Olden 2008). Research like this study that focuses on identification of possible vectors of invasive species, and geographic regions and ecosystems most susceptible to them is therefore essential in the development of effective management strategies (Corriero et al. 2015; Stam et al. 2006;

Table 3 Number of aquarium species currently found (actual records), and estimated under current and future (2055) climatic conditions in the European ecoregions

Ecoregion	Actual records	Current climate	Future climate
Adriatic Sea	4 (1/1)	9 (0/1)	16 (4/1)
Aegean Sea	4 (2/0)	16 (4/1)	16 (5/1)
Alboran Sea	11 (2/1)	17 (5/1)	19 (5/2)
Azores Canaries Madeira	13 (2/1)	20 (6/2)	21 (6/2)
Baltic Sea	2 (0/1)	0 (0/0)	4 (1/1)
Black Sea	2 (0/0)	4 (0/0)	8 (0/1)
Celtic Seas	9 (1/2)	10 (1/2)	10 (1/2)
Faroe Plateau	2 (0/1)	5 (1/1)	7 (1/1)
Ionian Sea	3 (1/0)	14 (5/1)	15 (5/2)
Levantine Sea	4 (4/0)	16 (5/2)	17 (6/2)
North Sea	7 (1/1)	5 (1/1)	7 (1/1)
Northern Norway and Finnmark	0 (0/0)	2 (0/1)	4 (1/1)
Saharan Upwelling	6 (2/1)	22 (6/3)	23 (6/3)
South and West Iceland	2 (0/1)	6 (1/1)	5 (1/1)
South European Atlantic Shelf	10 (2/1)	14 (3/2)	18 (5/2)
Southern Norway	4 (1/1)	5 (1/1)	6 (1/1)
Tunisian Plateau/Gulf of Sidra	5 (3/1)	14 (4/2)	17 (6/2)
Western Mediterranean	16 (4/1)	15 (4/1)	17 (5/1)
Europe	21 (7/2)	23 (7/3)	26 (7/4)

The number between brackets refers to species known to be introduced in Europe or (/) in other parts of the world

Vander Zanden and Olden 2008). Global awareness regarding invasive species is growing; the European Union has recently developed a blacklist of species for which keeping, importing, selling, breeding, and growing are restricted. This list contains only 37 species (mostly marine and terrestrial animals, and land plants), and no macroalgae (European Commission 2016; European Parliament 2014). The trade of macroalgal species is not restricted by CITES regulations, but the trade of live rocks is (CITES 2006).

It has been previously stated that the probability of introduction of aquarium species is higher in regions close to large coastal cities and in regions where mega yachts with on-board marine aquaria are common due to a higher chance of transfer of seaweed material to the sea (Guidetti et al. 2015; Johnston and Purkis 2014). Personal communication with aquarists revealed that many aquarists dispose aquarium waste in ways that should prevent future introductions; i.e. putting waste in solid waste for landfill or solid waste for compost, indoor plumbing, which is encouraging. Other safe ways to dispose excess of algal material are microwaving, freezing and treatment with acetic acid (Odom et al. 2014, Deslauriers and Walters 2017). Next to trade-related legislations, proper education of aquarists is important to prevent new introductions (Padilla and Williams 2004; Walters et al. 2006). The combination of inappropriate aquarium waste disposal, especially in the vicinity to coastlines, and a large diversity of seaweeds in the aquarium constitutes an inherent risk toward introductions of non-native species.

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