Chapter 6

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 the algal diversity found in various 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 135 species, of which 7 species are flagged as introduced in Europe with 5 of them reported as invasive. Thermal niche 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 indicates that aquarium trade poses a potential but limited risk of new introductions. However, the large reservoir of macroalgal species in aquaria calls for a cautious approach with the highest risk coming from aquaria on in coastal cities and on board of mega yachts.

Introduction

Macroalgae represent one of the largest groups of marine aliens, which may account for 10 to 30% of all marine introduced species in Europe (Schaffelke et al., 2006; Williams & Smith, 2007; Zenetos et al., 2012; Katsanevakis et al., 2013). In areas such as the Thau Lagoon on 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 & 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 (Neill et al., 2006; Schaffelke & Hewitt, 2007; Irigoyen et al., 2011).

The most important vector for alien seaweeds in Europe appears to be aquaculture and shell fish trade (Zenetos et al., 2012). Indirect evidence, such as the northwestern Pacific origin, time and location of first records, as well as experimental evidence demonstrate the role of oyster transfers as a vector of many seaweed introductions (Mineur et al., 2007a, 2014, 2015). The importance of shellfish transfer as a vector, 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 species (Hay, 1990; Flagella et al., 2007) 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, only cosmopolitan opportunistic species are found in standard maritime vectors (Mineur et al., 2007b). Another putative vector is presented by aquarium trade (Padilla & Williams, 2004).

Even though only one introduction, of *Caulerpa 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* & *Caulerpa taxifolia*) are even assumed to be caused by accidental release from aquaria on board mega yachts that travel the world (Meinesz, 1999; Guidetti et al., 2015; Verlaque et al., 2015). Aquarium trade as a pathway for the introduction of marine alien species is, however, still largely unexplored. Moreover, during the last 15 years, the internet has revolutionised how consumers purchase commodities. Trade in living organisms, terrestrial as well as aquatic, forms no exception to this trend. Aquarium hobbyists can obtain assorted living organisms from a wide 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 (Padilla & Williams, 2004; Walters et al., 2006; Mazza et al., 2015). Most research focuses on freshwater fishes (Rixon et al., 2005; Strecker et al., 2011; Mendoza et al., 2015), the marine seaweed *Caulerpa* (Wiedenmann et al., 2001; Stam et al., 2006; Walters et al., 2006), or on aquarium e-commerce in the USA which is one of the major importers of aquarium species (Padilla & Williams, 2004; Stam et al., 2006; Odom & Walters, 2014). 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. Those porous cobbles/boulders are usually pieces of natural reefs (dead scleractininan corals) that have been naturally colonized by a wide range of organisms as coralline and other macro- and microalgae, invertebrates, and bacteria. Such living assemblages not only give the natural look to aquarium reefs that aquarists aspire, but it also serves 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 1970's (Falls et al., 2008). Unfortunately, live rock also increases the odds of a successful invasion of a wide diversity of species if the aquaria contents are accidentally discharged into the wild. For example, live rock has been reported as a successful vector for jellyfish (Bolton & Graham, 2006).

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 thermal niche modelling analysis. Since rising temperatures due to climate change are also 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 extended to total seaweed diversity.

Material 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 available on the Seas-era EUPF7ERA-NET INVASIVES projects website (INVASIVES, 2016). ‘Introduced’ refers to alien species that are directly or indirectly transferred through human activities beyond their natural range of occurrence (Lucy et al., 2016).

Again, 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. ICE estimates the total species richness by estimating the proportion of the total richness covered by the samples in a set of replicated incidence samples (Gotelli & Colwell, 2010). All calculations were conducted with the program EstimateS 9.1.0 (Colwell & Elsensohn, 2014). Additionally, species accumulation curves were calculated using the R package *vegan* (Oksanen et al., 2017).

Aquarium sampling survey

In order to obtain specimens we contacted associations of aquarists in order to locate owners of ornamental seaweeds and 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. 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 and light controlled saltwater aquaria and surveyed them for several months. As similarly done with a focus on *Caulerpa* by Walter et al. (2006), we sampled the first seaweeds 4 weeks after the setup, the last after 8 weeks. We preliminarily assigned all the samples to the lowest taxonomic rank possible based on morphology. This resulted in most of cases in an 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 & Saunders, 2009; Saunders & Kucera, 2010; Saunders & Moore, 2013). A complete overview of primers and references is given in Table S1 in Supporting Information. We submitted all the newly generated sequences to Genbank. A complete list of samples and corresponding GenBank accession numbers is provided in Table S2 in Supporting information. 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. 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'. Asymptotic species richness was estimated with the incidence-based coverage estimator (ICE) using EstimateS 9.1.0 (Chazdon et al., 1998; Colwell & Elsensohn, 2014) and a species accumulation curve was calculated using the R package *vegan* (Oksanen et al., 2017).

Thermal niche

For every unambiguously identified seaweed species, 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 & Barber, 2013). After excluding species occurring in less than 30 grid cells, we obtained a data set of 39 species. For each species we calculated the thermal range as the 5^{th} percentile of the SST of the three coldest months and the 95^{th} 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 (increase of 1.4°C by 2055) 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 (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. Only 1 vendor gave information about the invasive potential of the traded species. The majority of the vendors (27) was situated in the USA. Only one of the US vendors exported 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. These vendors all shipped to or within Europe. Only one vendor gave information on the origin or the invasive potential of species.

In total we estimated the 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 estimated diversity of 123 species and 100 genera based on 39 vendors (Fig. 1). This large number is confirmed by the non-asymptotic nature of the species accumulation curve created for 39 online vendors (Fig. S1 in Supporting information). For three quarter 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 advertisements it was not possible to ship to Europe, or shipping details were not provided. Only one third of the seaweeds 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 *Caulerpa taxifolia* and *C. cylindracea* (often under the name *C. racemosa*). Other species of *Caulerpa*, *Codium*, and *Sargassum* were considered as potentially invasive (Boudouresque & Verlaque, 2002; Streftaris & Zenetos, 2006; Provan et al., 2008).

Table 1. Genera found on the online trade market with their status of introduction in Europe and the number of record available in and outside the European online market. ‘introduced’ (INT) represents genera that include species introduced in Europe, ‘not introduced’ (NI) genera that do not include species introduced in Europe, when unclear or unknown the status is represented by ’uncertain’ (UNC).

Genus	Status	Number of records (European market)	Number of records (non-European market)	Total
Chlorophyta				
Acetabularia	NI		1	1
Boergesenia	NI	1		1
Bornetella	NI	1		1
Caulerpa	INT	20	32	52
Chaetomorpha	UNC	4	17	21
Chlorodesmis	NI	2	3	5
Cladophora	INT	6	3	9
Codium	INT	1	6	7
Cymopolia	NI		4	4
Enteromorpha	NI		1	1
Halimeda	NI	6	9	15
Neomeris	INT	1	2	3
Penicillus	NI		3	3
Rhipocephalus	NI		2	2
Udotea	NI	1	3	4
Ulva	INT	1	9	10
unknown	UNC		1	1
Valonia	NI	2		2
Rhodophyta				
Acanthophora	INT		3	3
Actinotrichia	NI	1		1
Agardhiella	INT		1	1
Amansia	NI	1		1
Amphiroa	NI	2		2
Amphiroa	INT		3	3
Botryocladia	INT	3	7	10
Bryothamnion	NI		1	1
Carpopeltis	NI		4	4
Ceramium	INT	1		1
Cryptomenia	INT		1	1
Dichotomaria	NI	3		3
Eucheuma	NI		2	2
Fauchea	NI		1	1
Galaxaura	INT	1	4	5
Gracilaria	INT		17	17
Haliptilon	NI	1		1
Halymenia	NI	1	4	5
Heterosiphonia	NI		2	2
Hypnea	INT		1	1
Jania	NI	1		1
Kappaphycus	NI	1		1
Liagora	NI		1	1
Lithothamnion	NI	1		1
Mastophora	NI	1		1

Genus	Status	Number of records (European market)	Number of records (non-European market)	Total
Osmundaria	NI		1	1
Peyssonnelia	NI	1		1
Portieria	NI		4	4
Ptilophora	NI		2	2
Scinaia	NI		1	1
Phaeophyceae				
Canistrocarpus	NI		1	1
Dictyota	INT	1		1
Lobophora	NI		2	2
Padina	NI	1	1	2
Sargassum	INT	1	1	2
Turbinaria	NI	1		1
unknown	UNC		6	6
Total		69	167	236

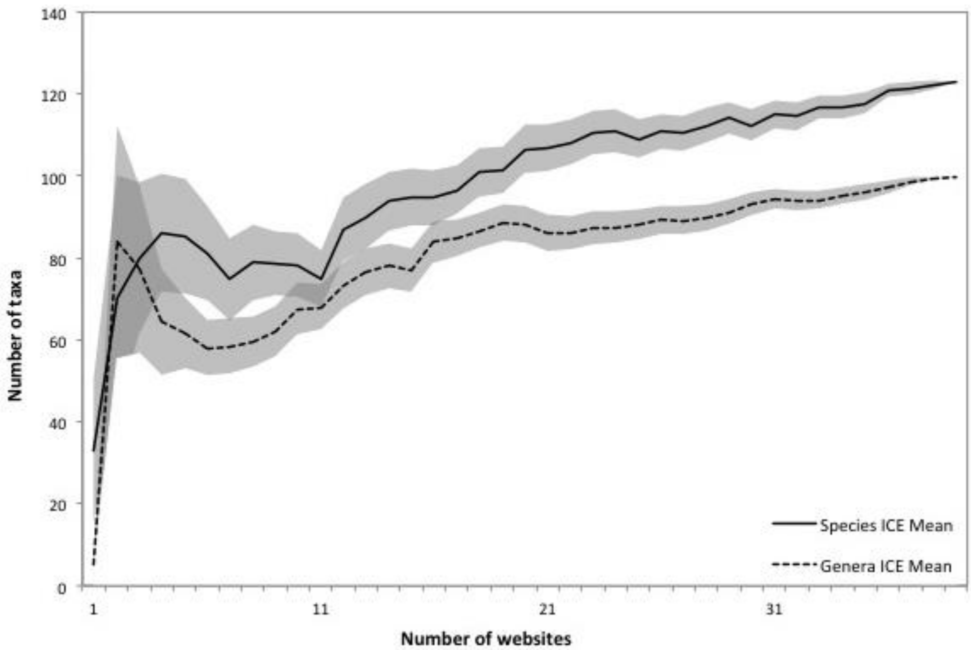

Figure 1. Incidence-based Coverage Estimator (ICE) for species and genera found on the global e-market (mean ± SE).

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). 29 samples were identified to genus level and 189 specimens to species level, of which more than half were assigned to named species. Half of the species not assigned to a named species belonged to the coralline algae (Corallinales). In total, we found 135 unique seaweed taxa (Table 2), of which almost half 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 significantly higher. Especially coralline red algae (subclass Corallinophycidae) were highly divers and abundant; they accounted for 57% of total seaweed diversity found and for 26% of the samples collected. Within the Rhodophyta, the following 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. The ICE diversity coverage estimator estimates the total diversity on 370 species and 128 genera (Fig. 2). Similar to e-commerce websites, this large number is confirmed by the clearly non-asymptotic nature of the species accumulation curve for the aquarium samples (Fig. S2 in Supporting information). We found 6 species that are known to be introduced in Europe of which 5 species are reported as invasive: *Caulerpa taxifolia*, *Asparagopsis taxiformis*, *Hypnea valentiae*, *Womersleyella setaceae* and *Sargassum muticum* (Table 2) (Boudouresque & Verlaque, 2002; Chualáin et al., 2004; Streftaris & Zenetos, 2006; Provan et al., 2008; Nikolić et al., 2010). Another 40 species were closely related to introduced species. These account for 30% of all specimens sampled in the European aquaria.

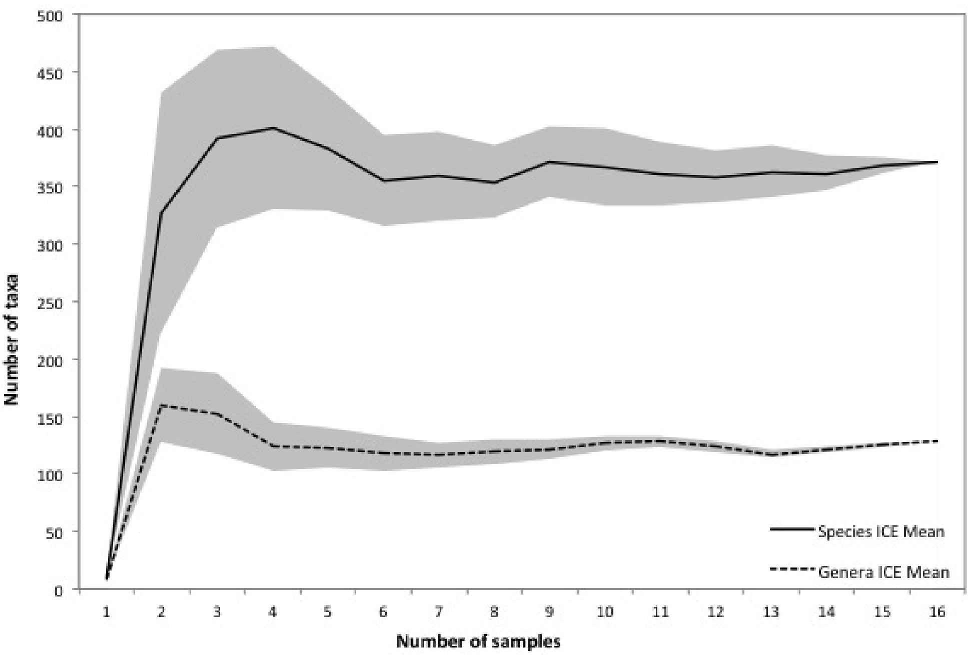

Figure 2. Incidence-based Coverage Estimator (ICE) for species and genera found in the European aquarium trade market (mean ± SE).

Table 2. Seaweed diversity found in the European aquarium network and their status of introduction in Europe. ‘not introduced’ (NI) indicates species not known to be introduces in Europe, ‘introduced’ (INT) indicates species reported as introduced in Europe, ’uncertain’ (UNC) indicates that the status of introduction is unclear or unknown, ‘related’ (REL) indicates that a congeneric species is reported as introduced in Europe.

Chlorophyta			**Rhodophyta**			**Phaeophyceae**		
Species	Status	Nr of Records	Species	Status	Nr of Records	Species	Status	Nr of Records
Caulerpa parvifolia	NI, REL	9	*Mesophyllum sp1*	NI	5	*Dictyota friabilis1*	NI, REL	4
Chaetomorpha vieillardii	NI	7	*Haraldiophyllum sp1*	NI	4	*Dictyota ceylanica4*	NI, REL	1
Caulerpa racemosa	UNC	6	*Sporolithon sp1*	NI	3	*Dictyota implexa*	NI, REL	1
Caulerpa constricta	NI, REL	5	*Titanophora sp1*	NI	3	*Halopteris filicina*	NI, REL	1
Caulerpa taxifolia	INT	5	*Acanthophora spicifera*	NI, REL	2	*Sargassum muticum*	INT	1
Cladophora	REL	4	*Acrosymphyton sp1*	NI	2	*Sargassum sp1*	REL	1
Chaetomorpha	UNC	3	*Antithamnion*	REL	2			
Cladophora albida/sericea	NI, REL	3	*Asparagopsis taxiformis*	INT	2			
Derbesia	REL	3	*Botryocladia sp1*	NI, REL	2			
Halimeda gigas	NI	3	*Cryptonemia sp1*	NI, REL	2			
Valonia macrophysa	NI	3	*Gracilaria vieillardii*	NI, REL	2			
Bryopsis	NI	2	*Harveylithon sp1*	NI	2			
Bryopsis sp1	NI	2	*Lithophyllum sp2*	REL	2			
Bryopsis sp3	NI	2	*Melobesioideae sp2*	NI	2			
Caulerpa cupressoides	NI, REL	2	*Peyssonnelia japonica*	NI	2			
Caulerpa prolifera	NI, REL	2	*Peyssonnelia sp3*	NI	2			
Caulerpa sertularioides	NI, REL	2	*Polysiphonia*	REL	2			
Cladophora herpestica	INT	2	*Polysiphonia sp1*	NI, REL	2			
Cladophora pellucida	NI, REL	2	*Ramicrusta sp1*	NI	2			
Cladophora prolifera	NI, REL	2	*Sporolithon sp3*	NI	2			
Derbesia sp3	NI, REL	2	*Yonagunia zollingeri*	NI	2			
Halimeda minima	NI	2	*Amphiroa*	NI	1			
Valonia utricularis	NI	2	*Asparagopsis*	REL	1			
Boergesenia forbesii	NI	1	*Botryocladia*	REL	1			
Boodlea sp1	NI	1	*Botryocladia sp2*	NI, REL	1			
Boodlea sp13	NI	1	*Ceramium codii*	NI, REL	1			

Chlorophyta			Rhodophyta			Phaeophyceae		
Species	Status	Nr of Records	Species	Status	Nr of Records	Species	Status	Nr of Records
Boodlea sp2	NI	1	*Ceratodictyon repens*	NI	1			
Bryopsis sp2	NI	1	*Chondracanthus saundersii*	NI, REL	1			
Caulerpa chemnitzia	NI, REL	1	*Coelarthrum*	NI	1			
Caulerpa flexilis	NI, REL	1	*Crouania attenuata*	NI	1			
Caulerpa lentillifera	NI, REL	1	*Cryptonemia lomation*	NI, REL	1			
Caulerpa oligophylla	NI, REL	1	*Erythrotrichia carnosa*	NI	1			
Caulerpa serrulata	NI, REL	1	*Griffithsia sp1*	NI, REL	1			
Chaetomorpha sp1	UNC	1	*Halymenia durvillei1*	NI	1			
Chaetomorpha sp2	UNC	1	*Halymenia durvillei2*	NI	1			
Chaetomorpha sp3	UNC	1	*Hydrolithon sp1*	NI	1			
Chlorodesmis	NI	1	*Hydrolithon sp2*	NI	1			
Cladophoropsis	REL	1	*Hydrolithon sp3*	NI	1			
Codium	REL	1	*Hypnea sp1*	NI, REL	1			
Codium arenicola	NI, REL	1	*Hypnea valentiae*	INT	1			
Codium dwarkense	NI, REL	1	*Incendia sp1*	NI	1			
Derbesia sp1	NI, REL	1	*Laurencia sp1*	NI, REL	1			
Derbesia sp4	NI, REL	1	*Lithophyllum sp1*	REL	1			
Halimeda disoidea	NI	1	*Lithophyllum sp3*	REL	1			
Halimeda opuntia	NI	1	*Lithophyllum sp4*	REL	1			
Parvocaulis parvula	NI	1	*Lithophyllum sp5*	REL	1			
Ulva	REL	1	*Mastophoroideae sp1*	NI	1			
Ulva laetevirens	NI, REL	1	*Mastophoroideae sp2*	NI	1			
Ulva sp1	NI, REL	1	*Melobesioideae sp1*	NI	1			
Ulva sp2	NI, REL	1	*Meredithia sp1*	NI	1			
Ulvella	NI	1	*Mesophyllum sp2*	NI	1			
Ulvella leptochaete	NI	1	*Mesophyllum sp3*	NI	1			
			Mesophyllum sp4	NI	1			
			Neosiphonia sp1	NI, REL	1			
			Palisada sp1	NI	1			
			Peyssonnelia sp1	NI	1			

Chlorophyta Species	Status	Nr of Records	**Rhodophyta** Species	Status	Nr of Records	**Phaeophyceae** Species	Status	Nr of Records
			Peyssonnelia sp2	NI	1			
			Peyssonnelia sp4	NI	1			
			Peyssonnelia sp5	NI	1			
			Peyssonnelia sp6	NI	1			
			Peyssonnelia sp7	NI	1			
			Phymatolithon sp1	NI	1			
			Plocamium sp1	NI, REL	1			
			Pneophyllum	NI	1			
			Polystrata sp1	NI	1			
			Porolithon sp	NI	1			
			Pterocladiella caerulescens	NI	1			
			Pterocladiella sp1	NI	1			
			Ptilophora scalaramosa	NI	1			
			Rhodymenia ardissonei	NI, REL	1			
			Rhodymeniaceae	NI	1			
			Sarconema filiforme	INT	1			
			Sarconema sp1	NI, REL	1			
			Sporolithon sp2	NI	1			
			Titanoderma sp1	NI	1			
			Womersleyella setacea	INT	1			
			Yonagunia sp1	NI	1			
Total		104	Total		105	Total		9

Thermal niche

Comparison of the thermal distribution of the aquarium species with the current temperature conditions demonstrated that at least 23 of these species could possibly thrive in European seas under current climate conditions. This number increases to minimum 26 species in 2055 under future climate change scenario CMIIP5, RCP4.5. The majority of these species is already present in Europe and not known to be invasive (Table 3). 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 (Table S3 in Supporting Information). 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).

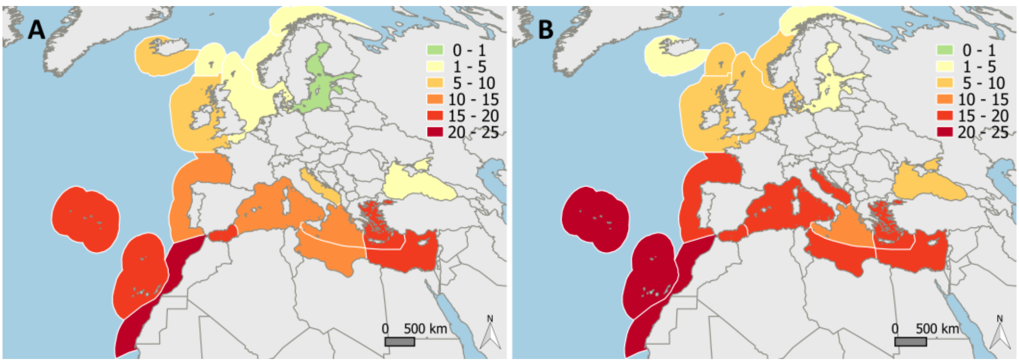

Figure 3. The risk of new introductions by aquarium seaweed species in Europe estimated by the number of species with a thermal distribution falling within the mean maximum and minimum SST for each ecoregion under current (A, 2010) and future (B, 2055) climate conditions (model CMIIP5 scenario RCP4.5).

Table 3. Number of aquarium species found (actual records) and estimated under current and future (2055) climatic conditions for all European ecoregions. Between brackets are the number of species that are known to be introduced in Europe or (/) in another part of the world.

Ecoregion	Actual records	Current climate	Future (2055)
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)

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 (Padilla & Williams, 2004; Rixon et al., 2005; Walters et al., 2006; Mazza et al., 2015; Howeth et al., 2016). The vast majority of these studies focus on freshwater species and the USA which is considered as one of the major importers of aquarium species of the world (Padilla & Williams, 2004). Our survey confirms that online aquarium trade in marine macroalgae is best established in the USA. Only a minority of the online vendors ship to or in 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 in or to Europe. Only one third of the species is advertised on both the European and the non-European e-market.

Aquarists often purchase or exchange organisms informally, in aquarist clubs, or through internet forums (personal communication aquarists). 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 proven 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 *Caulerpa 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 minimum 135 taxa in the private and public aquaria, and retail shops. The number of 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) (Saunders, 2005; Leliaert et al., 2014). 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 identifying species, we identified 85% of the 217 samples to species level based on molecular data. This shows that aquaria host substantial unknown diversity.

Like the available online seaweed diversity, the diversity sampled in aquaria was highest for Rhodophyta. This high diversity in Rhodophyta is mainly due to the high abundance of coralline red algae (44 species). These calcified 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 & Walters, 2014). Popular macroalgae, such as *Bortryocladia, Chaetomorpha, Caulerpa*, are easily maintained in aquarium conditions because they have broad environmental tolerances, exhibit rapid growth, vegetative reproduction and high reproductions rates. These are also characteristics linked to invasive seaweeds (Thomsen & McGlathery, 2007; Andreakis & Schaffelke, 2012). A worrying concern emerging from our survey is the presence of introduced and known invasives or species related to invasives, including *Caulerpa taxifolia*, *Asparagopsis taxiformis* and *Womersleyella setacea*. Aquarium associated species may therefore 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 the aquaria through other organisms or live rocks. Especially live rocks prove to be a successful vector for a variety of species (Bolton and Graham 2006; Walters et al. 2006; this study). Walters et al., (2006) mentioned the development of 25 seaweed species, next to 4 *Caulerpa* species from live rock. Several genera we observed (e. g. *Caulerpa*, *Hydrolithon, Peyssonnelia, Dictyota, Cladophoropsis,* and *Valonia*) were already recorded to develop from live rock by Fosså & Nilsen (1996). Furthermore, we observed polychaetes, hydroids and cyanobacteria developing from the live rocks. These specimens have not been further surveyed but this highlights that live rock is a successful vector for an unknown variety of organisms, including inconspicuous microorganisms. Next to tropical seaweed species we found in warm water aquaria, we also found European species in cold water aquaria (e.g. *Dictyota implexa, Halopteris filicina, Cladophora albida*). These examples were the result of private samplings by the responsible of the aquarium (personal communication). This indicates that aquarists also acquire seaweeds through informal ways and in this case even facilitates intra-European introductions.

The estimated asymptotic species richness was both for the e-trade as well as the aquaria far larger than the number of species identified indicating that there is relatively large remaining diversity to be uncovered (Figs. 1 & 2). This was confirmed by the species accumulation curves

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 (*Asparagopsis taxiformis, Caulerpa taxifolia, Sargassum muticum, Womersleyella setacea*) are all able to thrive in more ecoregions after climate change then under current conditions (Table S3). 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 suitable for a species. Consequently, the estimated number of species that can thrive in an ecoregion may be higher than we calculated. Conversely, given that only temperature was used to estimate the introduction risk, other factors restricting the distribution of macroalgae such as salinity and substrate may render specific ecoregions less suitable. We expect this to be especially the case for the Baltics and the Black Sea as they have a very specific salinity profile. These findings 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 & Olden, 2008). Research like this study, that focuses on identification of possible vectors of invasive species geographic regions and ecosystems most susceptible to them, is therefore essential in the development of effective management strategies (Stam et al., 2006; Vander Zanden & Olden, 2008; Corriero et al., 2016). Although global awareness regarding invasive species is growing, the development of legal restrictions is slow. 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 Parliament, 2014; European Commission, 2016). 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 (Johnston & Purkis, 2014; Guidetti et al., 2015). Personal communication with aquarists revealed that many aquarists dispose their waste in ways that should prevent future introductions; i.e. putting waste in solid waste for landfill or solid waste for compost, which is encouraging. There were unfortunately also aquarists that dump their aquarium waste in the indoor plumbing or garden (personal communication), which may be dangerous in regions in close vicinity of the coast. Adding bleach to or boiling waste before dumping are possible solutions to avoid new introductions. Next to trade related legislations, proper education of aquarists has proven to help to prevent new introductions (Padilla & Williams, 2004; Walters et al., 2006) and is welcome here. But to fully eliminate the introduction risk by aquarium trade, policy-making bodies should further legal restrictions.

Acknowledgements

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Supporting information

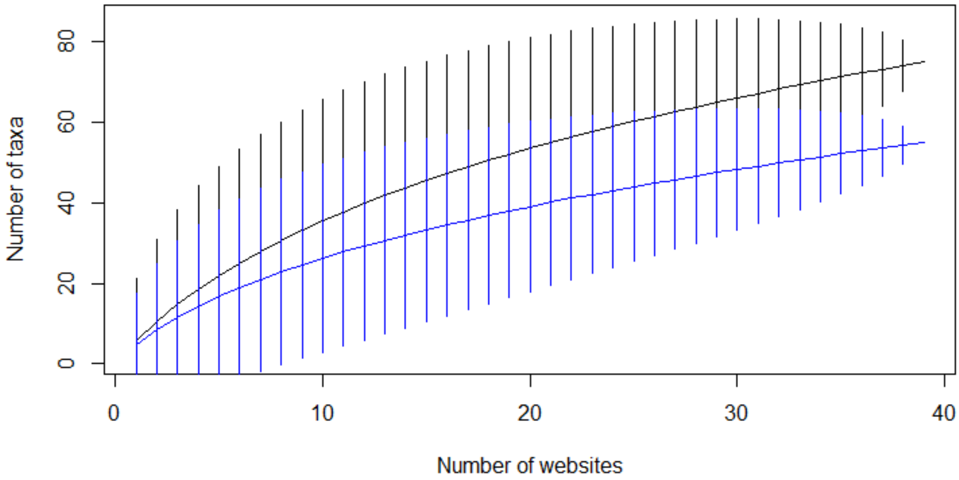

Figure S1. Species accumulation curves for the number of species (black) and genera (blue) found in the e-commerce websites, each website represents one sample event and the vertical bars represent the standard deviation.

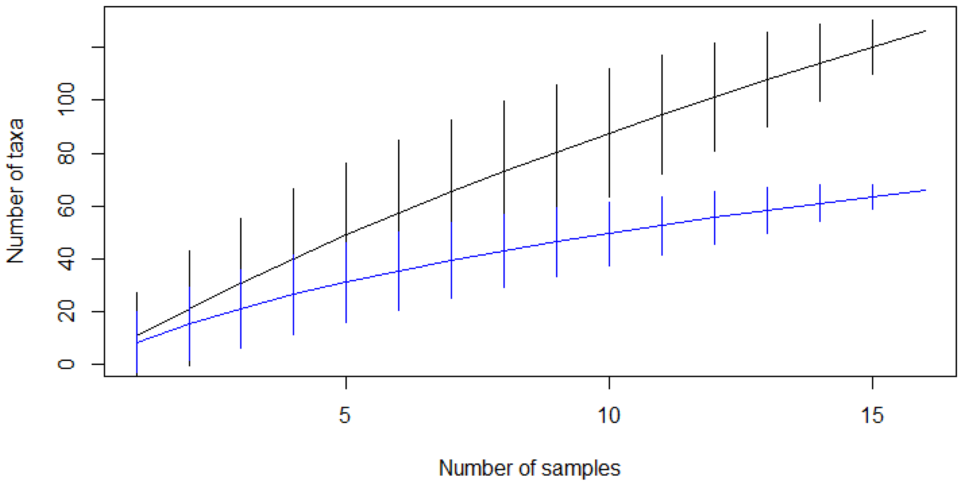

Figure S2. Species accumulation curves for the number of species (black) and genera (blue) found in the 16 public and private aquaria and retail shops, each aquarium representing one sample event and the vertical bars representing the standard deviation.

Table S1. Primers used for PCR amplification and sequencing.

	Forward primer	Reverse primer	Reference
Chlorophyta			
ITS1	TW3	H1R	(Leliaert et al. 2009)
ITS2	TW5	ITS4	(Leliaert et al. 2009)
RBCL1	7F	712F	(Verbruggen et al. 2009)
TUFA1	Tuf AF	Tuf AR	(Verbruggen et al. 2009)
LSU	C'1FL		(Leliaert et al. 2007)
SSU	SR1 SSU897	SS11H 18Sc2	(Bakker et al. 1994; Hanyuda et al. 2002; Leliaert et al. 2007)
Phaeophyceae			
COX1	COX1F_Dic		(Tronholm et al. 2010)
PsbA	psbAF1		(Yoon et al. 2002)
Rhodophyta			
RBCL2	F8 F481		(Draisma et al. 2001)
PSBA	psbAF1		(Yoon et al. 2002)

Bakker FT, Olsen JL, Stam WT, Van Den Hoek C. 1994. The cladophora complex (Chlorophyta): new views based on 185 rRNA gene sequences. Molecular Phylogenetics and Evolution **3**:365-382.

Draisma SG, Prud'Homme van Reine WF, Stam WT, Olsen JL. 2001. A reassessment of phylogenetic relationships within the Phaeophyceae based on RUBISCO large subunit and ribosomal DNA sequences. Journal of Phycology **37**:586-603.

Hanyuda T, Wakana I, Arai S, Miyaji K, Watano Y, Ueda K. 2002. Phylogenetic relationships within Cladophorales (Ulvophyceae, Chlorophyta) infered from 18S rRNA gene sequences, with special reference to Aegagropila linnaei1. Journal of phycology **38**:564-571.

Leliaert F, De Clerck O, Verbruggen H, Boedeker C, Coppejans E. 2007. Molecular phylogeny of the Siphonocladales (Chlorophyta: Cladophorophyceae). Molecular phylogenetics and evolution **44**:1237-1256.

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Tronholm A, Steen F, Tyberghein L, Leliaert F, Verbruggen H, Antonia Ribera Siguan M, De Clerck O. 2010. Species Delimitation, Taxonomy, and Biogeography of Dictyota in Europe (Dictyotales, Phaeophyceae) 1. Journal of phycology **46**:1301-1321.

Verbruggen H, et al. 2009. A multi-locus time-calibrated phylogeny of the siphonous green algae. Molecular Phylogenetics and Evolution **50**:642-653.

Yoon HS, Hackett JD, Pinto G, Bhattacharya D. 2002. The single, ancient origin of chromist plastids. Journal of Phycology **38**:40-40.

Table S2. List of specimens sampled in aquaria.

Taxon	Sample ID	Location
Caulerpa racemosa	SV0001	Live rock 1
Boodlea sp13	SV0002	Live rock 1
Boergesenia forbesii	SV0003	Live rock 1
*Chaetomorpha vieillar*dii	SV0004	Live rock 1
Chaetomorpha	SV0005	Live rock 1
Chaetopmorpha sp1	SV0006	Live rock 1
Chaetopmorpha sp2	SV0007	Live rock 1
Cladophora	SV0008	Live rock 1
Cladophora	SV0009	Live rock 1
Caulerpa racemosa	SV0010	Live rock 1
Parvocaulis parvula	SV0011	Live rock 1
Caulerpa oligophylla	SV0012	Live rock 1
Palisada sp1	SV0013	Live rock 1
Chlorodesmis	SV0014	Live rock 1
Caulerpa racemosa	SV0015	Live rock 1
Boodlea sp1	SV0016	Live rock 1
Boodlea sp2	SV0017	Live rock 1
Sarconema filiforme	SV0019	Live rock 1
Caulerpa racemosa	SV0020	Live rock 1
Ulva sp1	SV0021	Live rock 1
Ulvella leptochaete	SV0022	Live rock 1
Caulerpa taxifolia	SV0023	Live rock 1
Gracilaria vieillardii	SV0024	Live rock 1
*Chaetomorpha vieillar*dii	SV0025	Live rock 1
*Chaetomorpha vieillar*dii	SV0026	Live rock 1
Chaetopmorpha sp3	SV0027	Live rock 1
Gracilaria vieillardii	SV0035	Live rock 1
*Pterocladiella caerules*cens	SV0036	Live rock 2
Pterocladiella sp1	SV0037	Live rock 2
Caulerpa cupressoides	SV0038	Live rock 2
Peyssonnelia sp5	SV0039	Live rock 2
Peyssonnelia sp3	SV0040	Live rock 2
Hydrolithon sp2	SV0041	Live rock 2
Hydrolithon sp3	SV0042	Live rock 2
Hydrolithon sp1	SV0043	Live rock 2
Peyssonnelia sp6	SV0044	Live rock 2
Peyssonnelia sp3	SV0046	Live rock 2
Peyssonnelia sp2	SV0047	Live rock 2
Valonia macrophysa	SV0048	Live rock 3
Plocamium sp1	SV0049	Public Aquarium 1
Crouania attenuata	SV0050	Public Aquarium 1
Womersleyella setacea	SV0051	Public Aquarium 1
Dictyota implexa	SV0052	Public Aquarium 1
*Rhodymenia ardissone*i	SV0053	Public Aquarium 1
Asparagopsis	SV0054	Public Aquarium 1
Ceramium codii	SV0055	Public Aquarium 1
Antithamnion	SV0056	Public Aquarium 1
Caulerpa prolifera	SV0057	Public Aquarium 1
Caulerpa taxifolia	SV0058	Public Aquarium 1
Caulerpa constricta	SV0059	Public Aquarium 1
Sargassum muticum	SV0060	Public Aquarium 2
Caulerpa prolifera	SV0061	Public Aquarium 2
Caulerpa sertularioides	SV0062	Public Aquarium 2
Caulerpa racemosa	SV0063	Public Aquarium 2
Halimeda disoidea	SV0064	Public Aquarium 2
Polysiphonia sp1	SV0065	Public Aquarium 2
Cladophora	SV0066	Public Aquarium 2
Cladophoropsis	SV0067	Public Aquarium 2
Peyssonnelia sp1	SV0068	Public Aquarium 2
Sporolithon sp1	SV0069	Public Aquarium 2
Mesophyllum sp1	SV0070	Public Aquarium 2
Halopteris filicina	SV0071	Public Aquarium 1

Taxon	Sample ID	Location
Cladophora	SV0072	Public Aquarium 1
Caulerpa constricta	SV0073	Public Aquarium 3
Codium	SV0074	Public Aquarium 3
Caulerpa taxifolia	SV0075	Public Aquarium 3
Yonagunia zollingeri	SV0077	Public Aquarium 3
Caulerpa serrulata	SV0078	Public Aquarium 3
Bryopsis sp3	SV0079	Public Aquarium 3
Bryopsis sp1	SV0080	Public Aquarium 3
Valonia utricularis	SV0081	Public Aquarium 3
Chaetomorpha	SV0082	Public Aquarium 3
Mesophyllum sp1	SV0083	Public Aquarium 3
Chaetomorpha vieillardii	SV0084	Public Aquarium 3
Cladophora	SV0085	Public Aquarium 3
Derbesia sp3	SV0086	Public Aquarium 3
Ceratodictyon repens	SV0087	Public Aquarium 3
Antithamnion	SV0088	Public Aquarium 3
Chaetomorpha	SV0089	Public Aquarium 3
Erythrotrichia carnosa	SV0090	Public Aquarium 3
Polysiphonia	SV0091	Public Aquarium 3
Cladophora albida/sericea	SV0092	Public Aquarium 3
Cladophora pellucida	SV0093	Public Aquarium 3
Derbesia sp4	SV0094	Public Aquarium 3
Cladophora pellucida	SV0095	Public Aquarium 3
Cryptonemia lomation	SV0096	Public Aquarium 3
Coelarthrum	SV0097	Public Aquarium 3
Derbesia	SV0098	Public Aquarium 3
Chondracanthus saundersii	SV0099	Public Aquarium 3
Sarconema sp1	SV0100	Public Aquarium 3
Botryocladia sp1	SV0101	Public Aquarium 3
Rhodymeniaceae	SV0102	Public Aquarium 3
Polystrata sp1	SV0103	Public Aquarium 3
Mesophyllum sp1	SV0104	Public Aquarium 3

Taxon	Sample ID	Location
Caulerpa parvifolia	SV0107	Private aquarium 1
Caulerpa sertularioides	SV0108	Private aquarium 1
Caulerpa chemnitzia	SV0109	Private aquarium 1
Halimeda minima	SV0110	Private aquarium 1
Caulerpa parvifolia	SV0112	Private aquarium 2
Botryocladia sp1	SV0113	Private aquarium 2
Acanthophora spicifera	SV0114	Private Aquarium 3
Acanthophora spicifera	SV0115	Private Aquarium 3
Hypnea valentiae	SV0116	Private Aquarium 3
Caulerpa parvifolia	SV0117	Private Aquarium 3
Caulerpa parvifolia	SV0118	Retail shop 1
Asparagopsis taxiformis	SV0120	Retail shop 1
Mesophyllum sp4	SV0122	Retail shop 1
Incendia sp1	SV0123	Retail shop 1
Botryocladia	SV0124	Retail shop 1
Bryopsis	SV0125	Retail shop 1
Halimeda minima	SV0126	Retail shop 1
Derbesia	SV0127	Retail shop 1
Halimeda gigas	SV0128	Retail shop 1
Ramicrusta sp1	SV0129	Retail shop 1
Polysiphonia sp1	SV0130	Retail shop 1
Meredithia sp1	SV0132	Retail shop 1
Caulerpa constricta	SV0133	Public Aquarium 3
Codium arenicola	SV0134	Public Aquarium 3
Caulerpa constricta	SV0136	Public Aquarium 4
Cladophora herpestica	SV0137	Public Aquarium 4
Yonagunia zollingeri	SV0138	Public Aquarium 4
Mesophyllum sp2	SV0139	Public Aquarium 4
Valonia utricularis	SV0140	Public Aquarium 4
Chaetomorpha vieillardii	SV0141	Public Aquarium 4
Yonagunia sp1	SV0143	Public Aquarium 4
Cladophora herpestica	SV0144	Public Aquarium 4

Taxon	Sample ID	Location
Derbesia sp1	SV0145	Public Aquarium 4
Ulva	SV0146	Public Aquarium 4
Polysiphonia	SV0147	Public Aquarium 4
Cladophora albida/sericea	SV0148	Public Aquarium 4
Bryopsis	SV0149	Public Aquarium 4
Cladophora albida/sericea	SV0150	Public Aquarium 4
Cladophora prolifera	SV0151	Public Aquarium 4
Cladophora prolifera	SV0152	Public Aquarium 4
Phymatolithon sp1	SV0153	Public Aquarium 4
Peyssonnelia sp4	SV0154	Public Aquarium 4
Ulva laetevirens	SV0155	Private Aquarium 4
Caulerpa constricta	SV0156	Private Aquarium 4
Laurencia sp1	SV0157	Private Aquarium 4
Chaetomorpha vieillardii	SV0158	Private Aquarium 4
Griffithsia sp1	SV0159	Private Aquarium 4
Hypnea sp1	SV0166	Private Aquarium 4
Haraldiophyllum sp1	SV0167	Private Aquarium 4
Halimeda opuntia	SV0169	Private Aquarium 4
Caulerpa cupressoides	SV0170	Private Aquarium 4
Halymenia durvillei2	SV0172	Private Aquarium 4
Halimeda gigas	SV0173	Retail shop 2
Halimeda gigas	SV0174	Retail shop 2
Dictyota ceylanica4	SV0175	Retail shop 2
Dictyota friabilis1	SV0176	Retail shop 2
Caulerpa racemosa	SV_0.1	Private Aquarium 5
Titanophora sp1	SV_0.10	Private Aquarium 5
Mesophyllum sp1	SV_0.11	Private Aquarium 5
Melobesioideae sp2	SV_0.12	Private Aquarium 5
Sporolithon sp1	SV_0.13	Private Aquarium 5
Melobesioideae sp2	SV_0.14	Private Aquarium 5
Titanophora sp1	SV_0.15	Private Aquarium 5
Sporolithon sp1	SV_0.16	Private Aquarium 5

Taxon	Sample ID	Location
Acrosymphyton sp1	SV_0.19	Private Aquarium 5
Botryocladia sp2	SV_0.2	Private Aquarium 5
Mesophyllum sp3	SV_0.20	Private Aquarium 5
Melobesioideae sp1	SV_0.3	Private Aquarium 5
Sporolithon sp3	SV_0.4	Private Aquarium 5
Mesophyllum sp1	SV_0.6	Private Aquarium 5
Sporolithon sp2	SV_0.7	Private Aquarium 5
Titanophora sp1	SV_0.8	Private Aquarium 5
Acrosymphyton sp1	SV_0.9	Private Aquarium 5
Asparagopsis taxiformis	SV_1.1	Live rock 4
Titanoderma sp1	SV_1.11	Live rock 4
Peyssonnelia japonica	SV_1.11A	Live rock 4
Lithophyllum sp4	SV_1.11B	Live rock 4
Lithophyllum sp1	SV_1.11C	Live rock 4
Pneophyllum	SV_1.12	Live rock 4
Porolithon	SV_1.13	Live rock 4
Neosiphonia sp1	SV_1.14	Live rock 4
Dictyota friabilis1	SV_1.16	Live rock 4
Bryopsis sp1	SV_1.17	Live rock 4
Ulva sp2	SV_1.19	Live rock 4
Caulerpa parvifolia	SV_1.2	Live rock 4
Lithophyllum sp2	SV_1.21	Live rock 4
Lithophyllum sp3	SV_1.21A	Live rock 4
Lithophyllum sp2	SV_1.21B	Live rock 4
Sporolithon sp3	SV_1.24	Live rock 4
Dictyota friabilis1	SV_1.26	Live rock 4
Ramicrusta sp1	SV_1.27	Live rock 4
Chaetomorpha vieillardii	SV_1.3	Live rock 4
Derbesia	SV_1.6	Live rock 4
Caulerpa flexilis	SV_1.7	Live rock 4
Dictyota friabilis1	SV_1.8	Live rock 4
Valonia macrophysa	SV_1.9	Live rock 4

Taxon	Sample ID	Location
Codium dwarkense	SV_2.1	Retail shop 3
Caulerpa parvifolia	SV_2.10A	Retail shop 3
Mastophoroideae sp1	SV_2.10BV	Retail shop 3
Valonia macrophysa	SV_2.10C	Retail shop 3
Derbesia sp3	SV_2.10D	Retail shop 3
Amphiroa	SV_2.11	Retail shop 3
Bryopsis sp3	SV_2.12	Retail shop 3
Ulvella	SV_2.13A	Retail shop 3
Peyssonnelia japonica	SV_2.13B	Retail shop 3
Haraldiophyllum sp1	SV_2.14A	Retail shop 3
Bryopsis sp2	SV_2.15	Retail shop 3
Caulerpa lentillifera	SV_2.16	Retail shop 3
Caulerpa parvifolia	SV_2.18	Retail shop 3
Harveylithon sp1	SV_2.19A	Retail shop 3
Harveylithon sp1	SV_2.19B	Retail shop 3
Cryptonemia sp1	SV_2.2	Retail shop 3
Sargassum sp1	SV_2.20	Retail shop 3
Haraldiophyllum sp1	SV_2.21	Retail shop 3
Haraldiophyllum sp1	SV_2.22	Retail shop 3
Caulerpa parvifolia	SV_2.23	Retail shop 3
Lithophyllum sp5	SV_2.28A	Retail shop 3
Mastophoroideae sp2	SV_2.28B	Retail shop 3
Ptilophora scalaramosa	SV_2.3	Retail shop 3
Halymenia durvillei1	SV_2.5	Retail shop 3
Caulerpa parvifolia	SV_2.6A	Retail shop 3
Cryptonemia sp1	SV_2.6B	Retail shop 3
Caulerpa taxifolia	SV_2.7	Retail shop 3
Peyssonnelia sp7	SV_2.9	Retail shop 3

Table S3. Species used for the thermal niche modelling analysis with their record count, midpoint of the thermal range, and the number of ecoregions they currently occur in and estimated under current (2010) and future (2055) climate conditions.

Species	Count	Midpoint (°C)	Current	2010	2055
Acanthophora spicifera	319	24.4	0	0	1
Asparagopsis taxiformis	545	21.5	7	8	10
Boergesenia forbesii	111	25.7	0	0	0
Caulerpa brachypus	127	22.3	0	4	6
Caulerpa chemnitzia	76	25.2	0	0	0
Caulerpa cupressoides	474	24.3	0	0	1
Caulerpa flexilis	245	17.1	0	2	2
Caulerpa lentillifera	181	24.5	0	0	1
Caulerpa prolifera	205	21.4	4	8	10
Caulerpa racemosa	954	23.1	1	3	5
Caulerpa serrulata	418	25.1	0	0	0
Caulerpa sertularioides	495	25	0	0	0
Caulerpa taxifolia	467	21.3	2	8	10
Ceramium codii	77	21.7	1	7	9
Cladophora albida	371	14.8	11	17	18
Cladophora herpestica	82	23.1	1	3	4
Cladophora pellucida	408	15.4	6	13	13
Cladophora prolifera	193	18.6	8	11	12
Cladophora sericea	920	12.1	6	8	8
Codium dwarkense	33	26.2	0	0	0
Crouania attenuata	111	18.6	6	11	12
Dictyota ceylanica	159	24.6	0	0	0
Dictyota friabilis	157	24.6	0	0	0
Dictyota implexa	52	19.1	5	11	12
Erythrotrichia carnea	537	15.6	9	16	18
Halimeda discoidea	639	24.7	0	0	0
Halimeda minima	161	25.2	0	0	0
Halimeda opuntia	739	25.4	0	0	0
Halopteris filicina	418	16.1	7	10	12
Halymenia durvillei	72	24.7	0	0	0
Hypnea valentiae	163	21.4	2	9	10
Parvocaulis parvulus	34	25.3	0	0	0
Pterocladiella caerulescens	71	24.3	0	0	0
Rhodymenia ardissonei	204	16	5	8	10
Sarconema filiforme	67	22.5	1	6	8
Sargassum muticum	1094	11.9	6	6	8
Valonia macrophysa	141	21.7	3	8	10
Valonia utricularis	105	19.9	6	10	10
Womersleyella setacea	94	19.7	7	7	10