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The Global Dispersal of the Non-Endemic Invasive Red Alga *Gracilaria vermiculophylla* in the Ecosystems of the Euro-Asia Coastal Waters Including the Wadden Sea Unesco World Heritage Coastal Area: Awful or Awesome?

Vincent van Ginneken* and Evert de Vries

Bluegreentechnologies, Heelsum, Netherlands

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Corresponding author: Vincent van Ginneken, Bluegreentechnologies, Heelsum, Netherlands, Email: vvanginneken@hotmail.com

Abstract

Gracilaria vermiculophylla (Ohmi) Papenfu ß 1967 (Rhodophyta, Gracilariaceae) is a red alga and was originally described in Japan in 1956 as *Gracilariopsis vermiculophylla*. It is thought to be native and widespread throughout the Northwest Pacific Ocean. *G. vermiculophylla* is primarily used as a precursor for agar, which is widely used in the pharmaceutical and food industries. It has been introduced to the East Pacific, the West Atlantic and the East Atlantic, where it rapidly colonizes new environments. It is highly tolerant of stresses (nutrient, salinity, temperature) and can grow in an extremely wide variety of conditions; factors which contribute to its invasiveness. It invades estuarine areas where it out-competes native algae species and modifies environments. The following European coastal and brackish water seas are already invaded: Atlantic, North Sea, Mediterranean and Baltic Sea. The Euro-Asian brackish Black-Sea have not yet been invaded but are very vulnerable to intense invasion with *G. vermiculophylla* because they are isolated from direct marine influences and have a harsh environment with large salinity, nutrient and temperature fluctuations. The risk of this macro-algae becomes clear that scientists placed *G. vermiculophylla* among the most potent invaders out of 114 non-indigenous macro-algae species in Europe. Also, some states in the US are invaded (Rhode Island, California, N.& S. Carolina and Virginia), but also Canada, Mexico, Morocco and the North Pacific Ocean. Molecular work indicated its native range is Asia (China, Japan, Korea, South-eastern Russia and Vietnam). Worldwide dispersal is mainly caused by transmission vectors like aquaculture (oysters transport/import) and shipping ballast water. A further global dispersal on this invasive macro-algae can be achieved by strict rules regarding legislation and certification. A possible invasion of new water bodies can also have in some cases positive effects via an extension of the ecological habitat. An unexpected invasion of this invasive drift algae *G. vermiculophylla* (and other spp.) Furthermore we will calculate on a global scale what contribution *G. vermiculophylla* might have in the 70% more green biomass which has to be produced before the 2050 when we will live with around 10 billion people at our planet. It is estimated that at 2050 around 350 billion kg of dry weight green biomass needs to be produced in order to solve "The global Ten Billion People Issue" so in theory *G. vermiculophylla* could account on a global scale around 8, 23% of this tremendous amount of urgently needed green biomass in the salt water marshes of the south-eastern US, coasts of Asia, South America, and Australia without any production costs. Finally, the Rhine feeding the Wadden Sea through the North Sea has a large sewerage system and therefore the water in the Dutch part of the Wadden Sea is phosphate-limited, which does not cover the German and Danish part of the Wadden Sea fed by smaller phosphate loaded rivers. This is the main reason that this Japanese drift algae *G. vermiculophylla* in the neighboring countries has been doing so well in these parts of the Wadden Sea and is overgrowing our Unesco World Heritage.

Keywords: Non-endemic; Invasive; Non-indigenous; Macroalgae; *Gracilaria vermiculophylla*; Euro-Asian coastal waters; Atlantic; North sea; Baltic sea; Mediterranean; Global dispersal; Mitigation management; Transmission vectors; Green biomass

Politics related to the Netherlands, Denmark, Germany (Wadden Sea)

The Wadden Sea a European Coastal water extending along the North Sea coasts of the Netherlands, Germany and Denmark and is the largest unbroken system of intertidal sand and mud flats in the world, with natural processes undisturbed throughout most of the area. It encompasses a multitude of transitional zones between the land, sea and freshwater environment, and therefore is a highly dynamic ecosystem with an extremely high biological productivity and biodiversity and is rich in species specially adapted to the demanding environmental conditions. It is considered one of the most important areas for migratory birds in the world, and is connected to a network of other key sites for migratory birds around the globe. Because in the Wadden Sea up to 6.1 million birds can be present at the same time, and an average of 10 to12 million birds pass through it each year it is of extremely importance in the context of the East Atlantic Flyway but it also plays a critical role in the conservation of African-Eurasian migratory waterbirds population.

The Wadden Sea has its own exceptional manner of showing how nature, plants and animals continually adapt to the daily changing circumstances on the flats. Another unique feature is its ecological hydrodynamics which can be characterized by twice a day an inflow by tide of ≈15 km3 of seawater originating from the North Sea doubling the volume of this estuary shallow sea to some 30 km3. In this estuary area where fresh river water mixes with salty seawater and processes such as tides, wind and deposition of sand and mud still occur, you can find plants and animals that have ingeniously adapted. Thanks to its many faces, the Wadden Sea offers a tremendous variety of plants and animals a place to grow, live, breed, nurse, grow up, or rest. The wealth of life in the Wadden Sea is phenomenal. Not only do you find lots of permanent residents, there are also lots of visitors. Every year, at least 10 to 12 million migrating birds make use of the Wadden region. Around 10,000 different plants and animals can be found living on land or in water. Such an enormous variety as found in the Wadden Sea exists nowhere else in the world.

The Convention on Wetlands, known as the Ramsar Convention, is an intergovernmental environmental treaty established in 1971 by UNESCO, and coming into force in 1975. It provides for national action and international cooperation regarding the conservation of wetlands, and wise sustainable use of their resources. Ramsar identifies wetlands of international importance, especially those providing waterfowl habitat. The Convention on Wetlands, called the Ramsar Convention, is an intergovernmental treaty that provides the framework for national action and international cooperation for the conservation and wise use of wetlands and their resources. A Ramsar Site is a wetland site designated of international importance under the Ramsar Convention. In 2016 there are 2,231 Ramsar Sites, protecting 214,936,005 hectares (531,118,440 acres). 169 national governments are currently participating.

The governments of the Netherlands, Denmark and Germany have been working together since 1978 on the protection and conservation of the Wadden Sea. Co-operation covers management, monitoring and research, as well as political matters. Furthermore, in 1982, a Joint Declaration on the Protection of the Wadden Sea was agreed upon to co-ordinate activities and measures for the protection of the Wadden Sea. In 1997, a Trilateral Wadden Sea Plan was adopted. Each of the three countries designated Ramsar sites in the region (see Wadden Sea National Parks). Although the Wadden Sea is not yet listed as a transboundary Ramsar site, a great part of the Wadden Sea is protected in cooperation of all three countries.

In 1986, the Wadden Sea Area was declared a biosphere reserve by UNESCO. In June 2009, the Wadden Sea (comprising the Dutch Wadden Sea Conservation Area and the German Wadden Sea National Parks of Lower Saxony and Schleswig-Holstein) was placed on the World Heritage list by UNESCO. The Danish part was added to the site in 2014.

The Wadden Sea has been designated as a UNESCO World Heritage Site for its outstanding geomorphological and ecological values. The awareness of national governments of the Netherlands, Germany and Denmark of the uniqueness of the Wadden sea area resulted in a trilateral joint cooperation declaration in 1982, the so called "Esbjerg-II-Declaration", which delimitated a 13,500km2 coastal area to national conservation area with all its obligations for all three governments. In June 2014 some parts of the Wadden Sea in the Netherlands and Germany –covering an area of ≈ 9.685km2 were added at Doha meeting Wednesday, 25 June 2014 to the list of UNESCO World Heritage.

Figure 1: Dutch-, German- and Danish part of the Wadden sea. Clearly visible in white are its unbroken system of intertidal sand and mud flats.

Recently, the Wadden Sea became invaded by a non-endemic invasive seaweed species *Gracilaria vermiculophylla* (Figure 1), originally described from the Pacific (Japan) [5] which recently established in European waters as an invasive species. The "success ≈ doom scenario" of this species may lay in its biological properties as an eury-thermal seaweed with a large salinity tolerance. In the Netherlands *G. vermiculophylla* was probably already in the late 1990s been sampled in the brackish Oostvoornse, close to Rotterdam, the Netherlands [1,2]. Other reports mention its first finding in the Netherlands close to Yerseke [3]. In the European coastal waters, *G.vermiculophylla* often forms mono-generic stands were few other seaweeds and sea-grasses [4] will survive which will hamper the ecological variation and biodiversity. During the inventory of 4.5. [5,6] *Gracilaria vermiculophylla* was found in a large area from Texel to Lauwersoog. Locally this species dominated the ecosystem, covering a large part of the sandy bottom surfaces of the Netherlands Wadden Sea. Gittenberger et al., (2009) concluded that the exotic species *G.*

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vermiculophylla has already at this moment an enormous impact on the ecosystem of the Dutch- Wadden Sea. For the German-Wadden Sea and the Danish Wadden- Sea the situation is even more alarming, threatening the whole Wadden Sea ecosystem. If no ecological management is performed in the Dutch Wadden Sea we can expect an explosion of this species in the Dutch Wadden Sea.

Introduction

Invasion of the European coastal waters by the non-endemic invasive seaweed species *Gracilaria vermiculophylla*

The European coastal waters became invaded by a non-endemic invasive seaweed species *Gracilaria vermiculophylla* (Ohmi) Papenfu ß 1967 (Rhodophyta, Gracilariaceae), (Figure 2). *G.vermiculophylla* is thought to be a temperate to subtropical alga probably originating from the Eastern hemisphere -the Sea of Japan [7] and can grow in both temperate and tropical regions. The first discovery of *G.vermiculophylla* in Europe, and consequently its chronological spreading over Europe, was reviewed by [2]. This Asiatic red algae was first seen in Europe near Roscoff, NW France, in 1996, although being sterile it was difficult to identify [1]. The identity was later accomplished by genetic analysis [1]. Probably it had already been sampled in the late 1990s in the Netherlands in the brackish 'Oostvoornse'-lake, close to Rotterdam [1,5,6]. In contrast, others report its first finding in the Netherlands close to Yerseke [3]. Next, it was recognized in the archipelago area of Göteborg in 2003, followed by the 'German Wadden Sea' area in 2002, and in 2003 in Horsens Fjord, Denmark, [8], in all places correctly identified some years later after sampling. It has also established in Spain and Portugal [1], in the Kiel Bight in the western Baltic Sea, as well as in the West Atlantic and East Pacific [2,8]. The possible vector for its introduction in European waters as an invasive species is possibly by transport of oysters [1,3,9-11]. Indeed, *G.vermiculophylla* is a highly efficient recruiter around oyster reefs as they attach to shells via small holdfasts, causing them to be moved with translocation of oysters [10-13].

Figure 2: Image of *Gracilariavermiculophylla* (Ohmi) Papenfuss, 1967 (Rhodophyta, Gracilariaceae).

It can be observed in Europe that many *G.vermiculophylla* populations are in the vicinity of oyster farms [1]. Also, other bivalves like clams [14], probably from Asia, Japan [9,15,16] and/or the Phillipines [14] and shellfish (bivalves, oysters) [17,18] are suspected species as transmission vector (vide Figure 3). Other vectors of dispersal of *G. vermicullophyla* is possible via transport/import of shellfish (bivalves, oysters), shipping transport in general, ballast water, fouling organism, fisheries were thalli fragments can be connected to fish nets, but also local dispersal via water currents and -flows cannot be excluded [18]. In addition, dispersal via migrating birds and via eutrophication are considered as serious vectors. This topic will be further discussed and is enlisted in Table 1 which gives an overview of possible vectors for dispersal of *G.vermicullophyla.* Regarding global invasion and dispersal a very comprehensive recent molecular study of Kim [7] at this invasive seaweed gave very important information regarding its (sub) species dispersal characteristics. More detailed molecular information about this study [7] will be given in the paragraph "taxonomy" but in this extended study 312 individuals of *G.vermiculophylla* collected in 37 native and 32 introduced locations were investigated. A total of 19 haplotypes were detected: 17 in northeast Asia and three in Europe and eastern and western North America, with only one shared among all regions. This implies that there is only one invasive haplotype which was only found in three individuals at a single location in Korea, in only one of five locations in Japan, and in all three species from a single location in Russia. Based on the results of [7] it is suggested that the East Sea/Sea of Japan may be the donor region of this invasive haplotype of *G.vermiculophylla.*

Table 1: Potential dispersal methods for global spreading of *G.vermiculophyllus* from its native range, probably the Northwest Pacific ocean including Japan and East-Asia (Table 5)[1] towards the introduced area's enlisted in Table 3 (Europe) and Table 4 (outside Europe) after Weinberger et al. (2008) &Bellorin et al. (2004).

Aquaculture (Local)	*G. vermiculophylla* is a highly efficient recruiter around oyster reefs as they attach to shells via small holdfasts, causing them to be moved with translocation of oysters [10,34,45]. Indeed in Europe many *G. vermiculophylla* populations are in the vicinity of oyster farms [1].
Boat	Secondary dispersal between regions and estuaries is probably facilitated by entanglement to boat screws, fishing gear, trawling nets and various 'extensions' of smaller boats [45]
On Animals	Migrating seabirds [32].
Other (Local)	Ship/boat hull fouling [32]
Translocation of Machinery/ Equipment (Local)	Fishing gear[32].
Water Currents	Drifting fragments and spores are dispersed by currents [7]

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Figure 3: *Gracilariavermiculophylla* is always found in the close to clamps (mussels, oysters etc.).

Taxonomy

Gracilaria, belonging to Rhodophyta, Florideae, Gigartinales, Gracilariaceae, is a genus of red algae (Rhodophyta) notable for its economic importance as an agarophyte [19,20]. The occurrence of similar morphologies in separate species and genera, and of apparently sterile specimens collected in the field, makes assessment of systematic classification extremely difficult or impossible. Delimitation of taxa of gracilarioid algae has been notoriously difficult. These economically important agarophytes of worldwide distribution have nearly 300 species assigned to the genus Gracilaria Greville, of which about 110 are currently recognized worldwide [21]. However, its official taxonomic status and name has recently been accepted the "World Register of Marine Species" ("WoRMS"), while in this document the history and possible origin can be tracked. A summary is given in Table 2 (see also the cited references: [15,16,22].

Table 2: Accepted taxonomy for *Gracilariavermiculophylla*(Ohmi) Papenfuss, 1967, by World Register of Marine Species (WoRMS) with in this Table WoRMS taxon details. See also http://www.algaebase.org and cited literature references (in Reference List of this mini-review).

WoRMS taxon details for *Gracilaria vermiculophylla* (Ohmi) Papenfuss, 1967	
Literature	AphiaID: 236157; [16]; [15]; [22]
Classification	Biota>Plantae (Kingdom)>Biliphyta (Subkingdom)> Rhodophyta (Division)>Eurodophytina (Subdivision)>Florideophyceae (Class)>Rhodymeniophycidae (Subclass)>Gracilariales (Order)>Gracilariaceae (Family)>Gracilaria (Genus)
Status	Accepted
Rank	Species
Parent	*Gracilaria Greville*, 1830
Synonymized Taxa	*Gracilaria asciata* [15] *Gracilarlopsis vermiculophylla* Ohmi, 1956
Direct Child Taxa	Variety: *Gracilaria vermiculophylla var* zhengi [15]
Environment	Marine
Distribution	For the most recent update see this mini-review (see Table 3-5).

New species are continuously being identified and taxonomic problems are gradually being resolved by combining studies of reproductive morphology with comparative analyses of selected DNA sequences [23-29]. Over 179 species are included in the genera Gracilaria and Gracilariopsis.

The delineation of species in these genera has been notoriously difficult due to morphological similarities between species [1,23]. Taxonomic problems have been particularly pronounced for *G.vermiculophylla* [29,30]. *G.vermiculophylla* is a red macroalga that is cartilaginous, cylindrical and up to 50cm long. It is coarsely branched, often profusely so. *G.vermiculophylla* can be found as loose-lying thalli or attached to small stones or shells. Red algae are often found in the vegetative state, and characterization of reproductive structures is often necessary for correct identification of Gracilaria species [1,27,31,32].

In a recent review [33] reduced *Gracilaria asiatica* [15] into synonymy with *G.vermiculophylla*. The morphological similarities between *G. vermiculophylla* and other related algal species mean that the invasion of this alga is often cryptic, requiring DNA analysis for reliable identification. Its global dispersal is depicted in Figure 4. To avoid future taxonomic confusion, [34] recommended researchers to create silica-gel, air-dried, and/or herbarium presses as voucher specimens so that the correct identification could be confirmed using morphological and molecular analysis. Some examples for a reliable identification of *G. vermiculophylla* based on DNA techniques was performed in the study of [35] were species identification was based on cytochrome c oxidase I alignments.

Figure 4: Map depicting in red the places where *Gracilariavermiculophyllahas* been recorded as an invasive species. Green depicts where it is native.

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Furthermore, in the study of [36], for *Gracilaria changii*, intraspecific diversity was demonstrated based on mitochondrial cytochrome c oxidase subunit I (coxI). [7] analysed the mitochondrial cytochrome c oxidase subunit I (cox1) gene from 312 individuals of *G. vermiculophylla* collected in 37 native and 32 introduced locations (Figure 5).

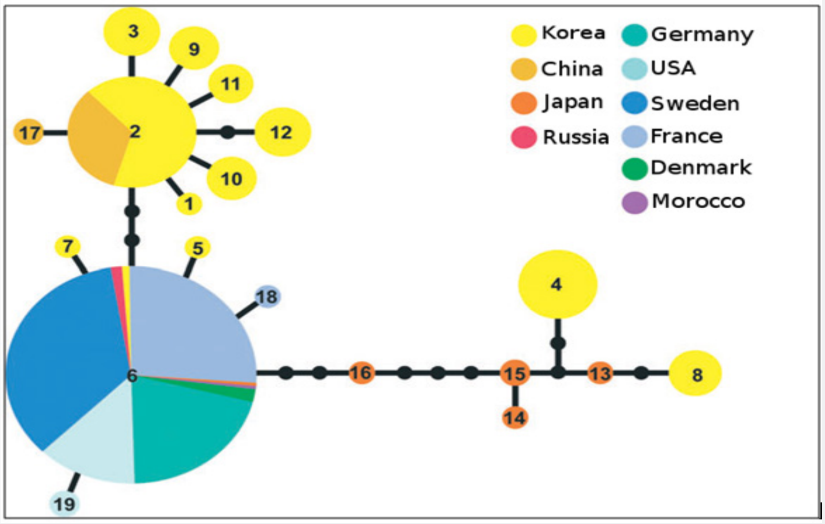

Figure 5: Statistical parsimony network of the cytochrome c oxidase subunit I (cox1) haplotypes per country mentioned in the legends. The black circles correspond to missing haplotypes, and the size of each circle is proportional to the number of individuals with that haplotype (modified Source:[37]).

Their major conclusions were:

I. *G. vermiculophylla* has an extreme homogeneity in its introduced range, which contrasts with high heterogeneity in its native range;

II. A total of 19 haplotypes were detected: 17 in northeast Asia and three in Europe and eastern and western North America, with only one shared among all regions;

III. The shared haplotype was present in all introduced populations and in ~99% of individuals in the introduced areas;

IV. The invasive haplotype was mainly found in the East Sea/Sea of Japan which makes it most probable that this is the donor region of this invasive haplotype of *G. vermiculophylla* [7]. (Figure 4 & 5).

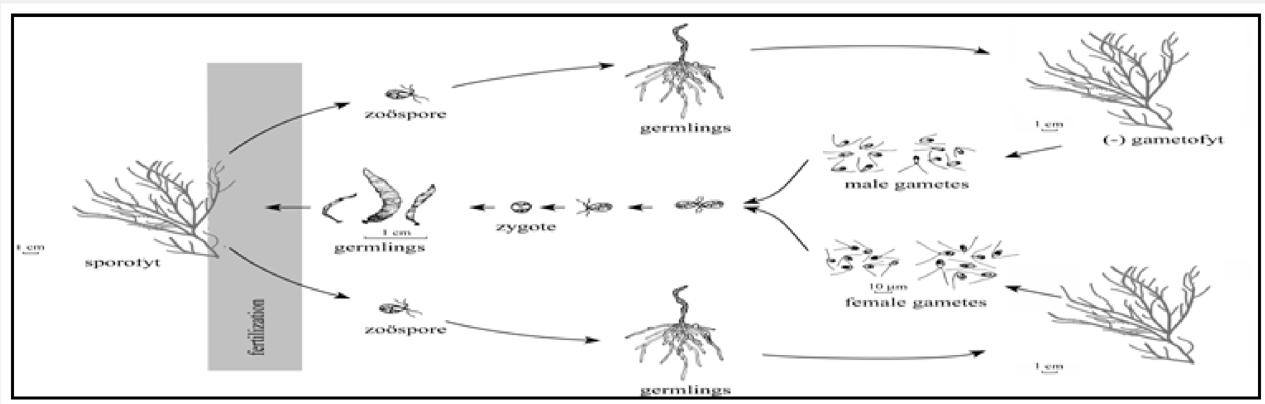

Figure 6: Sporulation of *Gracilariavermiculophylla.*

Gracilaria reproduces both vegetatively and by sporulating (Figure 6). Gametophytes of Gracilaria are herothallic. The male thalli produce spermatonogia. The eggs produced by the female gametophyte are fertilized and develop into carpo-sporophytes, which produce carpospores. The carpospores develop into tetra-sporophytes which convert to tertra-sporophytes. Tetra-spores are produced from the tetrasporophytes and germinate into male and female gametophytes. A single Gracilaria plant produces over 60 000 tetra-spores and more than 40 000 carpospores. Gracilaria spores settle after release, divide upon attaching to the substratum and form a thick-centered disc from which the initial erect shoots grow. The tissues of the erect fronds are pseudo-parenchymatous [39].

In this mini-review, we make a future scenario of the potential risk of this species for the European coastal waters based on biological growth data from Denmark [11], Sweden [32] and the Baltic Sea [40]. Recently *G. vermiculophylla* has also been observed in three of the five European coastal zone seas enlisted in Table 3.

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[14] reported recently based on molecular data for the first time the occurrence of *G. vermiculophylla* in the Mediterrenean Sea. Only for the Black-Sea no reports are available of the finding and identification of *G. vermiculophylla* in this Eurasian water bodies but because of the vulnerability of the ecosystem with extremely harsh environmental conditions (salinity, temperature, nutrients) it is only a matter of time of the dispersal of this non-indigenous invasive macroalgae intruder to both seas were it can be expected it will out-compete indigenous local species. The characteristics of the ecosystems of this latter Euro-Asian sea will be described in combination with suggestions to prevent a *G. vermiculophylla* invasion in these fragile ecosystems as long as possible.

Table 3: Some geomorphic-, human- and river basin attributes of/to the European coastal zone split up to the 5 most important seas: the Baltic-, Mediterranean-, Black-sea and the European-Atlantic coast [41].

Variable	Baltic Sea	Mediterre-nean Sea	Black Sea	European- Atlantic	World-coastal zone
% of EU coastal zone	17%	21%	6%	56%	1190.48%
Area (106km^2)	0.37	0.45	0.23	1.23	25.84
Volume (106km^3)	18.17	29.07	7.25	95.59	No data
Mean depth±SD (m)	46±43	67±54	56±49	78±53	No data
Median depth (m)	35	56	40	73	No data
Coastal length (km)	77,802	56,650	10,738	133,357	278,547
Coastal population density (inhabitants/ km^2 land area)	13.1	58.5	30.9	19.4	No data
Total river basin (106km^2 attributed to certain part of European coastal area	1.86	8.68	2.49	2.19	No data

The biological importance of the European coastal waters

The coastal zone is a transition area between land and the open ocean. The coastal ocean is the portion of global ocean where physical, biological and biogeochemical processes are directly affected by land. It is either defined as the part of the global ocean covering the continental shelf (usually defined by the 200m depth isobath) or the continental margin. The coastal zone usually includes the coastal ocean as well as the portion of the land adjacent to the coast that influences coastal waters (reviewed: Gazeau et al. 2004). The European coastal zone covers 8.4% of the world coastal zone with a major sea the Baltic-, the Mediterranean-, the Black-Sea and finally the European Atlantic area. Some characteristics of this European coastal area is, split up to the above mentioned four water bodies, which are given in Table 3 but also in the review of [41]. For the Black Sea information was obtained from the publications of [42] and [43].

In this mini-review we will consider the dispersal and the described effect –as far is investigated- of five European seas: the Baltic-, the Mediterranean-, the Black-Sea and finally the European Atlantic area and the North Sea (see Figure 7, Table 3).

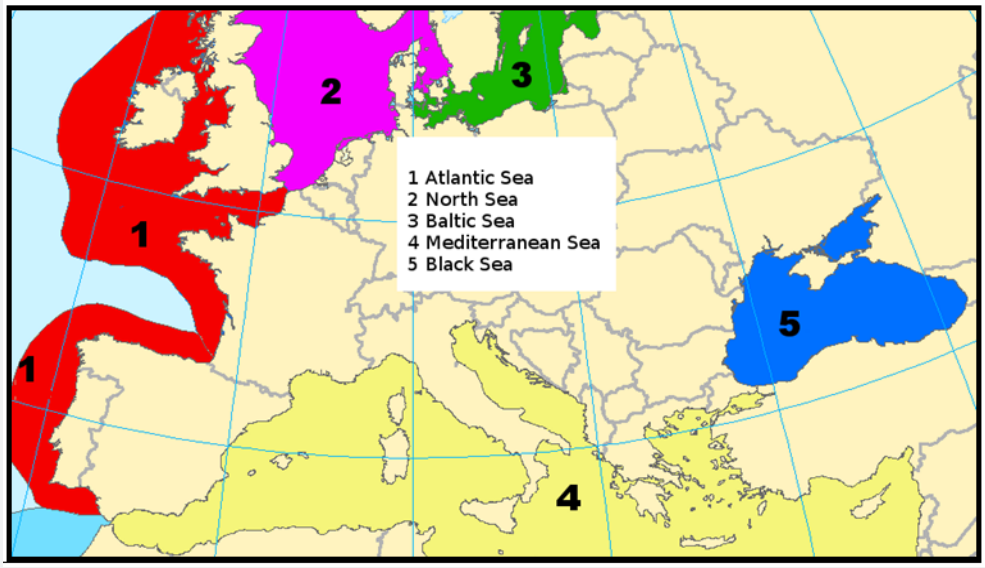

Figure 7: The location of the five investigated European seas: The North- &Wadden-sea, the Baltic-, the Mediterranean-, the Black-Sea and finally the European Atlantic ocean (see Table 2, details).

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The first characteristic for coastal waters in general is that they are shallow. So light can easily penetrate to a rather significant depth in the water-column, which is a precondition for a high primary production. The second prerequisite for a high primary production is abundance of available nutrients. It may be clear that the enormous variation and difference of the four selected coastal Euro-Asian waters without nearly any synergy makes comparable studies elucidating why all these different ecosystems are vulnerable for invasion by *G. vermicullophyla* of an enormous complexity. A complex, and possibly in case of the topic of this mini-review devastating environmental factor is that the European coastal waters ecosystem can be characterized as very dynamic with regular and unexpected changes from one extreme situation to another. Factors such as temperature with the possibility of ice, salinity, storms, waves and currents vary greatly. Only species, which have adapted to these extreme environmental harsh conditions can exist here. That is why in principle, the European coastal waters species, and consequently the ecosystem itself, have a large potential for survival because few organisms are adapted to such harsh and adverse environmental conditions. A totally different situation can be ascribed for the Euro-Asian coastal Black sea. Despite that their ecosystem is totally different from the previous mentioned European coastal waters this doesn't make them less vulnerable for an invasion with the intruder *G. vermicullophyla*. In summary, it is very difficult to stipulate one general factor as main cause why the five mentioned Euro-Asian coastal seas are invaded -or are very vulnerable to an invasion- of *G. vermicullophyla*.

Description European coastal waters

a. European Atlantic coastal zone and North Sea, which is mainly supplied by the nutrients originating by the annual run-off of nearly 35 large European river basins among else the rivers Rhine, Maas, Elbe, the Scheldt, Rhone etcetera.

b. Mediterranean Sea which is mainly supplied by nutrients of mainly one single river, the Nile (reviewed: Gazeau et al. 2004).

c. Baltic Sea replenishment system can be characterized in spring by a very slow surface flow of suppletion water of low salinity mixed with the Norwegian melting water, which runs through the narrow Cattegat to the North Sea. At the same time there is in opposite direction a bottom water flow of high salinity originating from the North Sea and/or Atlantic. This water exchange mechanism along the narrow Cattegat is the cause why a total replenishment of this water body takes several decades.

d. Black Sea were marine water enters via the Bosphorus Strait while major rivers like Danube, Dniepr and Dniestr contribute (nutrient-rich) freshwater [42]

Examples of Invasion with *Gracilaria vermiculophylla* in Euro-Asian Coastal Waters, its Global Dispersion and its Native Area

Europe

At the NE Atlantic coast the known distribution area of the red macroalga *Gracilaria vermiculophylla* (Ohmi) Papenfuss extends in latitude from Morocco to SW Sweden (Table 4) [51]. In 2005 the species was detected for the first time east of the Danish Belt at Kiel (Germany; [40,52]. Also recently, molecular data confirmed for the first time the occurrence of *G.vermiculophylla* in the Mediterrenean Sea [14]. The authors report that this invasive algae species was for the first time recorded in the Po Delta lagoons in May and October 2008, probably introduced by the importation of the Manila clam Tapes philippinarum [14]. This statement about the global spreading of *G. vermiculophylla* by a clam originating from Asia is in line with earlier reports where the spread of *G. vermiculophyllas* was associated with the transport/import of other bivalves namely oysters [1,3,45]. On the West-coast of Sweden invasion of the non-vegetated soft sediment estuaries with *G.vermiculophylla* lead to an increase in abundance of small native invertebrates (e.g. gastropods and crustaceans) and epiphytic algae, with likely cascading effects on higher trophic levels [32]. The risk of this macroalgae becomes clear from the work of [51], who placed *G. vermiculophylla* among the most potent invaders out of 114 non-indigenous macroalgal species in Europe.

Table 4: Spreading of *Gracilaria vermiculophylla* (Ohmi) Papenfuss, 1967 over the different European coastal waters and the countries where it has been recorded and identified. Modified from [2] and [44].

Location	Source	Occurence	Status	Invasiveness
North Atlantic Ocean	[1]	Reported	Alien	Invasive
West Atlantic Ocean	[45]			
North Sea	[46]	Established	Alien	Invasive
Baltic Sea	[40]	Established	Alien	Invasive
Sweden	[32]	Established	Alien	Invasive
Denmark	[17,45,47]	Reported	Alien	Invasive
France	[1,48]	Reported	Alien	Not specified
Germany	[9,49]	Reported	Alien	Unknown Uncertain
Italy	[14]	Reported	Alien	Invasive

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Netherlands	[1,3,31]	Reported	Alien	Not specified
Portugal	[1,35]	Reported	Alien	Not specified
Spain	[1,31,50]	Reported	Alien	Not specified

Denmark, Sweden (Baltic Sea) & Italy

The potential risk of this species for the European coastal waters based on biological growth data of *G. vermiculophylla* from Denmark [11], Sweden [32] and the Baltic Sea [40]. On the West coast of Sweden invasion of the non-vegetated soft sediment estuaries with *G. vermiculophylla* lead to an increase in abundance of small native invertebrates (e.g. gastropods and crustaceans) and epiphytic algae, with likely cascading effects on higher trophic levels [32]. Recently *G. vermiculophylla* has also been observed in three of the four European coastal zone seas enlisted in Table 2. Sfriso [14] reported recently based on molecular data for the first time the occurrence of *G. vermiculophylla* in the Mediterrenean Sea. Only for the Black- and the Caspian Sea no reports are available of the finding and identification of *G. vermiculophylla* in these Eurasian water bodies but because of the vulnerability of the ecosystem with extremely harsh environmental conditions (salinity, temperature, nutrients) it is only a matter of time of the dispersal of this non-indigenous invasive macroalgae intruder to both seas were it can be expected it will out-compete indigineous local species. The characteristics of the ecosystems of these two latter Euro-Asian seas will be described in combination with suggestions to prevent a *G. vermiculophylla* invasion in these fragile ecosystems as long as possible.

Black-sea

The Black Sea salinity fluctuations can be in the range of 17-35%, with during summer time very high temperatures of around 22-35 °C so these environmental factors make it a habitat extremely suitable for invasion by non-indigenous intruders [42].

Furthermore, the vulnerability of this Euro-Asian intercontinental sea can be emphasized with the following arguments. As a consequence of intense shipping and opening of new transport routes like for the Black Sea these traditionally isolated areas have been increasingly affected by nonindigenous species [42]. In principle Rotterdam harbor (the Netherlands) is via all transport routes and channels within Europe –via the southern North Sea at Rotterdam (the Netherlands), via the German Baltic Sea- directly connected with the Black sea and the Caspian sea. Mainly by digging the Kiel Channel [53]. There are some examples of Ponto-Caspian amphipod invader e.g. *P. robustoides* which succeeded via this previous long route via water channels –by creating the Kiel Canal [53]- to invade with origin the Caspian Sea the Curonian Lagoon at the Baltic Sea [54]. So, if this has been proven vice versa “traffic” of nonindigenous species from Northern Europe water bodies towards very qua ecosystem very vulnerable Black Sea cannot be excluded and is a realistic option.

Outside Europe, rest of the world

US (Table 5)

During the last 15 years it has been detected at the North American eastern coast [34,55] and western coast, as well as in Europe [1]. In Hog Island Bay, Virginia (USA), in 2006 an invasion with *G. vermiculophylla* was reported [34], Table 5. These are intertidal salt marshes which are considered by ecologists as harsh habitats where relatively few stress-resistant species survive. But *G. vermiculophylla* outnumbered every expectation of any biologist/ecologist and nowadays it is abundant throughout the whole Virginia’s Atlantic coastline [56].

Table 5: Spreading of *Gracilariavermiculophylla*(Ohmi) Papenfuss, 1967 outside Europe over the different coastal waters in the rest of the World and the US-states and other countries where it has been recorded and identified. Modified from[2] and [44].

Location	Source	Occurence	Status	Invasiveness
Rhode Island (US)	[35]	Reported	Alien	Invasive
United States (US) General	[34,57]	Established	Alien	Invasive
California (US)	[30]	Reported	Alien	Not specified
North Carolina (US)	[57,58]	Established	Alien	Invasive
South Carolina (US)	[77,78]	Reported	Alien	Invasive
Virginia (US)	[12,32,34]	Reported	Alien	Invasive
Canada (US)	[35]	Reported	Alien	Invasive
Baja California (Mexico)	[30]	Reported	Alien	Not specified
Morocco	[59]	Reported	Alien	Not specified
North Pacific Ocean	[30]	Reported	Alien	Not specified
East Pacific Ocean	[45] and references there in	Reported	Alien	Not specified

Native distribution in these regions which are at risk: Asian countries (Table 6)

The native distribution area of the red macroalga *G. vermiculophylla* is the Northwest Pacific (Table 6) [9,33,60]. Gollasch et al. state that *Gracilaria vermiculophylla* was originally described from the Pacific, Japan [15,16] and recently established in European waters (possibly by transport of oysters) as an invasive species in Europe.

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Table 6: Spreading of *Gracilariavermiculophylla*(Ohmi) Papenfuss, 1967 in its native Asian countries where it has been recorded and identified and water bodies in the same region which are at risk for invasion. Modified from: [2] and [44].

Location	Source	Occurence	Status	Invasiveness
China	[7,60]	Established	Native	Not specified
Japan	[1,7]	Established	Native	Not specified
Korea, Democratic People's Republic of	[7,60]	Established	Native	Not invasive
Korea, Republic of	[7,60]	Established	Native	Not specified
South-eastern Russia	[37,61,62]	Reported	Native	Not specified
Black Sea	[35]	Not reported	Alien	Not specified
Viet Nam (Vietnam)	[22,60]	Reported	Native	Not specified

Habitat preferance of *Gracilaria vermiculophylla* in relation to European coastal waters

Gracilaria spp. grow the best in an environment where the location is protected from waves, were there is little water motion with high fertilizer regimes [39], and fluctuating salinity because it has a large salinity tolerance [63]. *Gracilaria vermiculophylla* is subjected to osmotic stress caused by variable periods of emersion in the European coastal waters. The origin of the plague of *G. vermiculophylla* in the European coastal waters can originate by its tolerance to a wide range of salinity variation. This species can grow in a salinity environment in the range of 5- 60% [19]. The maximal growth of *G. vermiculophylla* occurred at 15-30% while the highest growth rates were observed under hyposaline conditions of 20% [19]. Furthermore *G. vermiculophylla* is able to grow in a wide range of temperatures (5-35 °C) which corresponds to other *Gracilaria* spp. [64], light intensities (20-100µmol photons m-2 s-1). Optimum growing conditions are between 15-25 °C [1,65]. Also, the large temperature tolerance range of *G. verminculophylla* as an eurythermal species in the range of 5-30 °C The maximum growth rate is at 15-20 °C [66]. This eurythermal responses of *G. vermiculophylla* in combination with its large salinity tolerance [63], may be the basis for its success as a non-endemic invasive species in some of the European coastal waters. Furthermore, the stress tolerance of *G. vermiculophylla* to harsh environmental conditions can be characterized by resistance to desiccation, burial and in combination with (as already earlier mentioned) not negatively be influenced by either high or low light or nutrient levels [1,8].

Nyberg [32] found in one instance that this seaweed was able to survive in complete darkness for more than five months in the laboratory. All these ecological traits of G*racilaria vermiculophylla* like:

i. Extremely high growth rates often resulting in covering a certain area forming monogeneric stands (see Figure 8).

Figure 8: *Gracilariavermiculophylla* showing its ability to overgrow and outcompete other species.

ii. Habitat stress-resistance characterized by resistance to desiccation, burial and grazing in combination that this macroalgae is not negatively influenced by either high or low light or nutrient levels.

iii. Its rapid spreading by water drift, are all contributing factors which will hamper the ecological variation and biodiversity in traditional (Euro-Asian coastal) ecosystems.

iv. As mentioned earlier *G. vermiculophylla* is a highly efficient recruiter around oyster reefs as they attach to shells via small holdfasts, causing them to be moved with translocation of oysters [10,13,34,45]. It can be observed in Europe that many *G. vermiculophylla* populations are in the vicinity of oyster farms Figure 7; [1].

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Environmental Factors Which Affect Growth and Dispersal of *G. vermiculophylla*

This invasive non-indigenous drift macroalgae, is well-adapted is very stress resistant and can inhabit and cover shallow-bottom bays, lagoons, estuaries, harbors and islets. It forms extensive beds in the intertidal zone and upper sub-littoral zones, where it attaches to rocks or pebbles, often covered with sand and mud [30]. It often occurs as pure stands to the exclusion of other algae species [1]. Furthermore, loose-lying *G. vermiculophylla* populations have the potential to develop into dense mats (Figure 8) which can modify the habitat available for the benthic faunal community and bottom dwelling fish and can also form physical barriers for settling larvae, decrease light intensity, increase the likelihood of anoxia and change water movement patterns, which in turn affects sedimentation rate and thus food availability for deposit feeders. These loose-lying mats and tidal flats can be a contributing factor in its regional dispersal [49]. In addition, the movement, accumulation and decomposition of *G. vermiculophylla* is likely to have important implications for nutrient cycling and trophic dynamics in areas it invades. Also, the mussel-banks in the European coastal waters which are ecologically and economically important, like example gratia the mussel-banks in the Netherlands [67] can be threatened by *G. vermiculophylla* because its impact on the ecosystem can have cascading effects on higher trophic levels [32]. As earlier mentioned transport/import of bivalves (oysters, clams, bivalves) might be an important vector in general in the dispersal of invasive alien intruders. Recently the transport, risk evaluation and recommendations for the management of the shellfish sector in the Netherlands was assigned by the Ministry of Agriculture, Nature Conservation and Food security to the Institute for Marine Resources and Ecosystem Studies (IMARES), Wageningen University (WUR), the Netherlands [18]. Their findings, general conclusions and recommendations are of general concern and can be applied in a broad perspective in neighboring countries also dealing with an economical important shellfish sector.Nevertheless, the following six factors have a large impact on the Euro-Asian coastal ecosystems in the growth (biomass) and dispersal of *G. vermicullophyla:*

i. Light

ii. Nutrients

iii. Shallowness in combination with that portion of land of the coastal zone adjacent to the coast that influences coastal waters (reviewed: Gazeau et al. 2004).

iv. Salinity in combination with environmental temperature fluctuations.

v. Indigenous species richness coupled to availability of habitats (substrates).

vi. Other ecological parameters and anthropogenic influences and vice versa (in this section) its impact on human economic activities.

Light

shallowness in combination with that portion of land of the coastal zone adjacent to the coast that influences coastal waters (see iii, reviewed Gazeau et al. 2004), makes the European coastal zone to a very productive zone in terms of primary production which is preliminary based on the high growth rates of micro-algae. Especially the Atlantic and the North Sea can be considered as European coastal waters with an extremely high bio-productivity and biodiversity with a general function as a habitat for birds, seals, shellfish and fish species. Their high bio-productivity is sometimes compared with that of a tropical forest [68].

Nutrients

As a consequence of an abundance of nutrients supplied to the European coastal waters due to the high population density along the rivers this can have an effect on growth and dispersal of this non-indigenous invasive alga. For the ecosystem itself one should be aware that the movement, accumulation and decomposition of *G. vermiculophylla* is likely to have important implications for nutrient cycling and trophic dynamics of seagrasses like Spartina alterni flora dominating low marshes [69]. Additionally, the movement, accumulation and decomposition of *G. vermiculophylla* is likely to have important implications for nutrient cycling and trophic dynamics in areas it invades [69].

Shallowness and adjacent area

At a higher trophic level in the ecosystem macro-algae and sea-grasses [70] in combination to the interaction between the strong coupling between pelagic and benthic processes [41], results in a very complicated ecosystem with an enormous richness in species.

Salinity in combination to environmental temperature fluctuations

Salinity is a very important parameter for the ecosystems of the two Euro-Asian water which are by their intercontinental location almost excluded from marine influences. To illustrate their specific ecosystems: for the Black Sea salinity fluctuations can be in the range of 17-35%, with during summer time very high temperatures of around 22-35 °C [42]. The Baltic-and the Black Sea have in common for their ecosystem that they have local or in general fluctuating salinities and have a minimum of native species richness and are therefore more vulnerable to intense invasion of non-indigenous species [42]. Besides there is an enormous oil/gas/petrol industry in the Euro-Asian Black-Sea [43]. Therefore, the ecosystem of these three seas will be discussed separately and more in detail than the other European coastal waters -the Atlantic, North- and the Mediterranean Sea in this mini-review regarding the dispersal of *G. vermicullophyla*. Because the Baltic-Sea is locally or in general a brackish water bodies we will use in correspondence with the manuscript of Paavola et al. use the terminology of the Venice system for the several ranges of salinity (see Table 7).

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Table 7: The Venice system [71].

Zone	Salinity Range (in %)
Limnetic	<0.5
β-Oligohaline	0.5-3
α-Oligohaline	3-5
β-Mesohaline	5-10
α-Mesohaline	10-18
Polymixohaline	18-30
Euhaline	30-40
Hyperhaline	> 40

Richness indigineous species coupled to available habitat (substrate)

Unless species appear, which are better adapted and even have a much better tolerance to these harsh fluctuating coastal environmental conditions in comparison to their European counterparts, like example gratia invasions by non-indigenous macro algal species, which have as a species in principle the biological potency to cause severe impacts on native species and local ecosystems [56]. For the Baltic Sea as a consequence there is an increased intensity of eutrophication and this in combination with a warming climate in the Baltic Sea region due to global warming lead to competitive interactions between indigenous and non-indigenous species. An example for gammarid species is the competition between the non-indigenous invader *Gammarus tigrinus* (an invader from littoral ecosystems), which was more hypoxia tolerant, survived higher temperatures and had a better reproduction performance in comparison to the indigenous *Gammarus zaddachi* [72]. Although one study indicated that also among the benthos nonindigenous species may occur [73]. A matter which makes these kinds of studies of an enormous complexity.

Other Factors Affecting the Ecosystem Due to Anthropogenic Activities

Other ecological parameters like contamination with heavy metals and other industrial and/or other compounds as a result of anthropogenic activity; but also growth of microorganisms, anaerobic conditions like hypoxia or anoxia the problems *G. vermiculophylla* is causing problems for human society and activities. This red drift algae is severely hampering the commercial fishing industry and other industries making use of water from the Cape Fear River estuary in southeastern North Carolina [74]. Furthermore for *G. vermiculophylla* is has been reported to be a problem in fishing industries through fouling of nets [55].

Effect of *Gracilaria vermiculophyll*a on the coastal ecosystem

Increases in the heterogeneity of these habitats can lead to changes in species composition of these ecosystems [32]. This can have a positive as well a negative impact on the ecosystem. On the West coast of Sweden invasion of the non-vegetated soft sediment estuaries with *G. vermiculophylla* lead to an increase in abundance of small native invertebrates (e.g. gastropods and crustaceans) and epiphytic algae, with likely cascading effects on higher trophic levels [32]. It is not known if increase of substrate and more biomass in the ecosystem has a positive impact on the ecosystem. An example of a negative impact on the ecosystem is that accumulation of *G. vermiculophylla* may impair environmental conditions for threatened and endangered species like the seagrasses Charophytes and *Zostera noltii* in Sweden [32].

Habitat alteration in a positive way

For Sweden, *G. vermiculophylla* competes with native vegetation in Gothenburg's archipelago in Sweden [75]. Increases in the heterogeneity of ecological habitats can lead to changes in species composition of these ecosystems [32]. These can on one hand be positive e.g. large populations of *G. vermiculophylla* in shallow, soft bottom ecosystems adds structural complexity to these relatively homogenous ecosystems and add new attachment sites for filamentous algae and sessile animals [32,34]. Thus *G. vermiculophylla* can provide shelter, increase attachment sites and increase food availability for other organisms, including microalgae, gastropods, crustaceans, polychaetes and many other small invertebrates. In this way *G. vermiculophylla* may contribute and even increase the complexity of the ecosystem and give structure to previously relatively homogenous systems [8,32,76]. Also, in Virginia (US), on mudflats the native polychaete worm *Diopatra cuprea* creates habitat for *G. vermiculophylla* and influences its persistence [56]. *G. vermiculophylla* also creates attachment sites for epiphytic filamentous species and enhances local diversity by adding structural complexity and habitat for bryozoans, crustaceans, polychaetes, gastropods and various algal epiphytes [12,77]. In addition, recent research of Thomsen, (2010) confirmed the above mentioned positive effects of *G. vermiculophylla* on the ecosystem. In a study with *G. vermiculophylla* in East Jutland (Denmark), positive effects of this non-indigenous macroalgae were found on most invertebrates, with statistically significant results for "all invertebrates", "gastropods", and "bivalves", and a near significant result for "crustaceans". The author explains these unexpected results with the statement, casu quo new hypotheses, that following a "quantitative" model for explanation "more habitats" will be generated by the new intruder *G. vermiculophylla*, while following the "qualitative" model for explanation of these unexpected results, the increased diversity probably can be caused by the "habitat differs" explanation which is based on the assumption that two totally different species (a seaweed vegetation of *G. vermiculophylla* together with a the seagrass bed vegetation of (Zostera marina) will result in habitat diversification due to species differences and/or common habitat interaction [70].

Habitat alteration in a negative way

In high abundance *G. vermiculophylla* may have dramatic effects on ecosystems. In these habitats Gracilaria often forms monogeneric stands were few other seaweeds and sea-grasses like *Zostera marina* will survive [4]. In high densities *G. vermiculophylla* inhibits the growth and reduces germling survival of native *Fucus*

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vesiculosus algae. This is the most common perennial alga in the Baltic Sea and forms important habitats [78]. *G. vermiculophylla* may also have negative effects on native Zostera marina sea-grass beds by decreasing net leaf photosynthesis [79], studying the interaction between the small ephemeral seagrass *Halophilia ovalis* with abundance of *G. vermiculophylla*, found (among else) the following two major conclusions:

a. A stress-resistant drift algae like this non-indigenous Gracilaria spp. can have a strong negative effect on a small ephemeral sea-grass like this Halophilia spp;

b. This negative effect can increase both additively and synergistically with increasing temperature depending on performance measure [80]. Negative effects on sea-grass are greater at higher densities and high temperatures, suggesting that impacts could increase with future global Earth warming [79,81].

Management to Eliminate *Gracilaria vermiculophylla* from the European Coastal Waters and Further Global Dispersal

In this mini-review we try to find proper management solutions to eliminate this non-endemic intruder. First of all, management of the standing stock of *G. vermiculophylla* is in great extent based on physical control. Mechanical removal (harvesting) of *G. vermiculophylla* for use in the production of agar and other applications is a potential control method [20,82]. Different tools for harvesting Gracilaria in subtidal systems have been tested, either from boats or by divers [83]. Commonly, to harvest Gracilaria boats are used. Raking in 1 to 12m depths from boats has been used to harvest the standing crop and in the case of the European coastal waters, raking may alter the bottom and reduce productivity because the underground thallus system of Gracilaria is damaged [39]. Also *Gracilaria* spp. can be stressed by covering them by sand because they have a low ability to grow through a layer of sediment [84]. When harvesting Gracilaria spores and fragments are released. These fragments are able to survive even buried in sediment for up to 6 months [85]. When the thallus fragments become uncovered they can start growing [39]. It is of vital importance that no biomass is left and can be reused for stocking [85]. On Gracilaria farms it is observed that biomass production can drop abrupt after 2-3 years of high yields. It is believed that this situation is the result of thallus aging, and seems to be influenced by the harvesting method [19]. Also repeated harvesting can lower the productivity and ultimately the loss of the standing stock of algae [86]. For G. vermiculophylla specific traits have been considered as indicative of its considerable invasive potential: a remarkable ability to recruit from spores and grow from fragments [1,51,87] and a high tolerance to environmental stress like its eurythermal responses [66] and large salinity tolerance [63], especially to low salinities [1,45,51,65,88].

Another recommendation is to stimulate endemic seaweed species and sea-grasses [4], so that competition occurs which can be a controlling factor in the interaction of a *Gracilaria* dominated community. These patterns of seaweed interaction were observed in *Ulva*-dominated seaweed communities [89]. The mechanism is unknown, but epiphyte-host algae interaction and *Ulva-Gracilaria* interaction may cause light reduction which in this way partially explain the reduction in *Gracillaria* production [90].

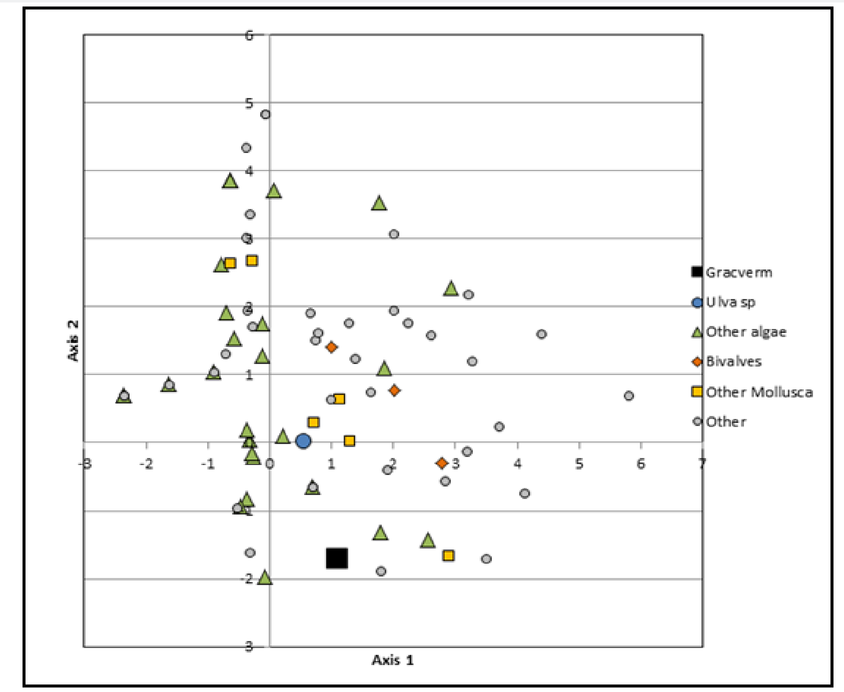

Figure 9: Image of De-trended Correspondence Analysis (DCA) for pooled Ulva sp. (Blue solid circle) in relation to *G.vermicullopylla* (Black quadratic) in the Dutch Wadden Sea (Source: van Ginneken et al 2017, [91]).

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Figure 10: *G. vermiculophylla*in the vicinity of *Ulva* sp. results in "seaweed competition" as described in van Ginneken et al (2017)[91].

In an earlier study our ecological datasets gave via final DCA (Detrended Correspondence Analysis) awareness of the very compelling interaction between Ulva sp. and *G. vermiculophylla* [91]. From Figure 9 we can see that Ulva sp (blue circle) are always close in the vicinity of *G. vermiculophylla* (black quadratic) which we also clearly can see at the image below (Figure 10).

Figure 11: *Gracilariavermiculophylla* and its native grazer enemy *Littorina brevicula.*

Based on LCMS-techniques we discovered that Ulva sp. have the advantage to use the biochemical pathway –solely rarely observed in some euckaryotes- to have the potential to produce the betaine lipid diacylglyceryl-O-4'-(N,N,N,-trimethyl) homoserine (DGTS) which replaces the plant/seaweed cell wall structure phosphatidylcholine (PC) "lecithine" under phosphate-limiting growth conditions. Another solution would be to breed its natural enemies such as the snail *Littorina brevicula* (Figure 11) in special aquaculture units on land in large numbers and then release them in the Wadden Sea on a regular basis. The effect of such an ecological intervention must first be studied on small experimental areas. Principle of proof experiment are in preparation.

Management to eliminate *Gracilaria vermiculophylla* from the European coastal waters and further global dispersal

In this mini-review we try to find proper management solutions to eliminate this non-endemic intruder. First of all, management of the standing stock of *G. vermiculophylla* is in great extent based on physical control. Mechanical removal (harvesting) of *G. vermiculophylla* for use in the production of agar and other applications is a potential control method [20,82]. Different tools for harvesting Gracilaria in subtidal systems have been tested, either from boats or by divers [83]. Commonly, to harvest Gracilaria boats are used. Raking in 1 to 12m depths from boats has been used to harvest the standing crop and in the case of the European coastal waters, raking may alter the bottom and reduce productivity because the underground thallus system of *Gracilaria* is damaged [39]. Also, *Gracilaria* spp. can be stressed by covering them by sand because they have a low ability to grow through a layer of sediment [84]. When harvesting Gracilaria spores and fragments are released. These fragments are able to survive even buried in sediment for up to 6 months [85]. When the thallus fragments become uncovered they can start growing [39]. It is of vital importance that no biomass is left and can be reused for stocking [85]. On Gracilaria farms it is observed that biomass production can drop abrupt after 2-3 years of high yields. It is believed that this situation is the result of thallus aging, and seems to be influenced by the harvesting method [19]. Also repeated harvesting can lower the productivity and ultimately the loss of the standing stock of algae [86]. For *G. vermiculophylla* specific traits have been considered as indicative of its considerable invasive potential: a remarkable ability to recruit from spores and grow from fragments [1,51,87] and a high tolerance to environmental stress like its eurythermal responses [66] and large salinity tolerance [63], especially to low salinities [1,45,51,65,88]. Another recommendation is to stimulate endemic seaweed species and sea-grasses [4], so that competition occurs which can be a controlling factor in the interaction of a Gracilaria dominated community. These patterns of seaweed interaction were observed in Ulva-dominated seaweed communities [89]. The mechanism is unknown, but epiphyte-host algae interaction and *Ulva-Gracilaria* interaction may cause light reduction which in this way partially explain the reduction in Gracillaria production [90].

Biological characteristics of *Gracilaria vermiculophylla* and its concomitantly dispersal

In Table 1 some forms of potential dispersal methods for global spreading of seaweed intruders in an existing ecosystem are summarized [92] wrote an extensive review of introduction events of seaweeds in existing communities and the evolving impacts. They reviewed over 407 global seaweed introduction events and increased the total number of introduced seaweed species to 277. They concluded that hull-fouling and aquaculture are the most significant sources of seaweed invaders and should be carefully regulated. For undisturbed marine communities, (mostly antropogenic) disturbances and eutrophication can facilitate

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invasion. Major research gaps include according to the authors community-level ecological studies and economic assessments [92]. Invasions by nonindigenous seaweed species potentially cause severe impacts on native species and the until that moment existing ecosystem [69]. As mentioned earlier we will describe the positive as well negative effects of invasion of certain coastal areas with the invasive non-indigenous macroalgae *G. vermiculophylla*. With respect its invasion in certain shallow seas, not only it's occurrence in the European coastal waters (Table 4), but all over the world (Table 5 & 6), including its native range area in Asia (Table 6).

Major vectors in the global dispersal of *Gracilaria vermiculophylla*

With respect to this stress-resistant invasive-seaweed based on drift of spores and thallus fragments, it is important to notice that the spores thus cannot transport actively and are totally dependent on drift by water currents for invasion of new (adjacent) areas. Therefore other methods of dispersal might have been important in the past to explain its now global occurrence. According to Williams & Smith hull-fouling and aquaculture are the most significant sources of seaweed invaders (see further). But also uncontrolled drain away of ship ballast water is considered as one of the major causes [2].

In order to prevent a global dispersal on this invasive non-indigenous macroalgae intruder *G. vermiculophylla* management applications should focus on the following topics:

a. Aquaculture: prevention of transport and relocation of oysters and clams

b. Ship ballast water

c. Prevention of floating vegetation and debris

d. Prevention of natural dispersal by controlling water-drift during the fertile period of spore release

e. Other (difficult to accomplish in practice because of not anthropogenic origin) limit the migrating seabirds

f. Sea-freight (container/bulk) in combination with ship hull fouling

g. Vectors such as fishing and leisure boats

h. Translocation of machinery/equipment like fishing gear

Especially in general

I. Aquaculture practices and

II. Ship ballast water are considered as most important vectors in the transmission of invasive nonindigenous macroalgae intruders [2].

III. Aquaculture is expanding rapidly as a direct response to over-exploitation of wild capture fisheries in many regions of the world including Europe.

A major concern related to this "Blue revolution" is the increasing use of non-native (≈non-indigenous or exotic) species in aquaculture and for stocking purposes, with subsequent escapes of these species and associated pathogens, parasites, other seaweeds, posing a serious threat to native communities, habitats, biodiversity, ecosystem function and economic value [93]. Fisheries and aquaculture e.g. oysters import and transfers [2] have to be acknowledged as major vector for harm and risk for invasion of Nature conservation areas with G. vermiculophylla because this invasive non-indigenous macro-algae is indeed often observed in the vicinity of oyster reefs as they attach to shells via small holdfasts, causing them to be moved with translocation of oysters [10,12,13,45]. Also shellfish & oysters (bivalves) are "under suspicion as potential vector [17]. Wijsman & De Mesel [18] describe that on a regular base shellfish are imported from various European countries in the Dutch coastal waters and sometimes even to the Dutch part of the Waddensea. Some (Dutch, German) parts of this unique coastal water were because of its biological importance placed since June 2009 on the list of UNESCO World Heritage Sites. Unintentional introduction of new exotic species (including *G. vermicullophyla*), but also pests and diseases can be the consequence of these shellfish transports [18]. Their report is only an inventory of exotic species, which has or might be introduced, with shellfish transports. Their description is a typical example how economical profits often don't coincide with the interests of the ecological and nature conservation stakeholders, but Wijsman & De Mesel [18] don't come with concrete solutions or recommendations how to come to a general consensus.

Gracilaria vermiculophylla cultured in aquaculture

The worldwide fast growing aquaculture industry has caused a growing attention and concern on the environmental effects of aquaculture by direct discharge of significant nutrient loads on coastal ecosystems. Excess nutrients released by fish are particularly Phosphorus (P) and N-compounds (mainly) ammonia and it is assumed that 2/3 of N and P of the fish feed is released as wastes. Integrated farming using nutrient-assimilating photoautotrophic plants (mainly seaweeds like *G. vermicullophyla)* can use solar energy to turn nutrient-rich effluents into profitable resources. In this way seaweed biofiltration can reduce pollution of the aquatic environment. Another advantage is that addition of macroalgae to the fish food has proven to improve growth rate, nutrient composition and survival rates of several fish species.

Individual fish release nutrients as dissolved inorganic nutrients through excretion (NH4 and PO4), particulate organic nutrients (PON and POP) through defecation, and dissolved organic nutrients (DON and DOP) through resuspension from particulate fractions. On the scale of a fish farm, there will additionally be a direct los off Feed-N and Feed-P (uneaten feed). These different waste components will affect different parts of the marine ecosystem. Feed losses and the larger faeces particles will sink and affect sediments and benthic communities whereas dissolved inorganic nutrients, dissolved organic nutrients, and small faeces particles affect the pelagic communities and state and

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quality of euphotic waters (≈sunlight or (Sunlit) zone is the depth of the water in a lake or ocean that is exposed to such intensity of sunlight which designates compensation point) [94]. Aquaculture and mainly the production of fish in so called fish-farms may have a tremendous impact on aquatic environment and rising feed costs therefore hamper growth of such farms. In a polyculture system plants can drastically reduce feed use and environmental impact of industrialized mariculture and at the same time add to the income of the farmer [95]. These nutrient-assimilating photoautotrophic plants use solar energy to turn nutrient-rich effluents into profitable resources. Plants counteract the environmental effects of the heterotrophic fed fish and shrimp [96] and restore water quality [97]. Today's integrated intensive aquaculture approaches, developed from traditional extensive polyculture, integrate the culture of fish or shrimp with vegetables, microalgae, shellfish and/or seaweeds. Integrated mariculture can take place in coastal waters or in ponds and can be highly intensified [97]. A 1ha land-based integrated seabream-shellfish-seaweed farm can produce 25 tons of fish, 50 tons of bivalves and 30 tons of fresh weight of seaweeds annually [97]. Another farm model can produce in 1ha 55 tons of seabream or 92 tons of salmon, with 385 or 500 fresh weight of seaweed, respectively, without pollution.

In literature solely one pilot experiment is described where G. vermicullophylla has been used in an IMTA system. In Portugal in the Ria de Aveira lagoon a pilot experiment was performed using 1200L tanks with sole and turbot in a land based aquaculture facility to evaluate the potential of the *G. vermiculophylla* as the biofilter component of an IMTA system. In general *G. vermiculophylla* was able to maintain a good overall performance; however, results indicate that the culture conditions require adaptations throughout the year in order to attain successful productivities. In the tanks seeded with 3kg fw m2, the production of *G. vermiculophylla* was 0.7±0.05kg dw m2 month−1; this biomass removed 221±12.82gm2 month−1 of carbon and 40.54±2.02gm2 month−1 of nitrogen (±0.03% of the monthly fish N inputs). Temperature and light were the main environmental factors conditioning the growth and nutrient removal performance of the seaweed. The authors concluded that upscaling of this pilot IMTA system is ready for implementation because *G. vermiculophylla* has proved to be an efficient component of land-based IMTA systems with environmental and potentially economic benefits for the fish farm [98]. Recent publications indicate that *G. vermiculophylla* is also grown in aquaculture - probably for its agar production [20,82], but also in Integrated Multi-Trophic Aquaculture Systems (IMTA), in the effluent of fish farms [98]. This poses a huge threat to the environment and can further spread the chance of spreading on a global scale from this aggressive "red algae invader" to ecologically vulnerable areas. It is striking that there are no data on the spread of this red drift algae of the continents of South America, Australia and Africa. Luckily not many other studies were performed using *G. vermiculophylla* in larger IMTA systems because it can contribute towards a further global dispersal.

Is 70% more green biomass production via Gracilaria vermiculophylla culture achievable?

We strongly believe in a "Seaweed based Economy", and increased primary production in order to create the amount of the 70% increase of green biomass as the FAO calculated when "the global ten billion people issue" at the midst of the 21st century has to be dissolved with ample three decades to go!! Starting with the basis of green biomass production=> solar irradiance at planet Earth in an oceanic seaweed community. Luckily, the large magnitude of solar energy available makes it a highly appealing source of electricity. The United Nations Development Program stated in its A.D. 2000 "World Energy Assessment" report that the annual potential of solar energy was in the range of 1,575–49,387 exajoules (EJ) (1018 Joules). So with a total world energy consumption -which was ≈560 EJ in 2012- the annual solar irradiated energy is between ≈2.8 towards ≈88.2 the amounts of the Earthly human civilization needs. In 2011, the "International Energy Agency" said that "The development of affordable, inexhaustible and clean solar energy technologies will have huge longer-term benefits. It will increase countries' energy security through reliance on an indigenous, inexhaustible and mostly import-independent resource, enhance sustainability, reduce pollution, lower the costs of mitigating global warming, and keep fossil fuel prices lower than otherwise. These advantages prices lower than otherwise. These advantages are on a global scale. Hence the additional costs of the incentives for early deployment should be considered learning investments; they must be wisely spent and need to be widely shared". A "Seaweed Based Economy", meets this statement in full extent. Here we will calculate on a global scale the green biomass amount of *G. vermiculophylla* mainly in useless saltwater marshes around our globe. We make a clear distinction between those shallow coastal waters, such as mangrove forests, which are functionally of enormous importance as breeding rooms for many marine fish and other animals and the ecologically insignificant saltwater marshes found on the east coast of the US. Many salt marshes are located in the southern United States, particularly in South Carolina with more than 344,500 acres ≈1395 hectare, which is more marshland than any other state on the Atlantic coast (see Figure 8). Some countries and regions have inventoried salt marsh area – the total from these inventories comprises 22,000km^2. As there is no data on the extent of saltmarshes on the coasts of Asia, South America, and Australia the global area of salt marshes is probably considerably greater [99].

A definition of a salt marsh is an area of coastal grassland that is regularly flooded by seawater. A salt marsh or saltmarsh, also known as a coastal salt marsh or a tidal marsh, is a coastal ecosystem in the upper coastal intertidal zone between land and open salt water or brackish water that is regularly flooded by the tides. It is dominated by dense stands of salt-tolerant plants such as herbs, grasses, or low shrubs [100,101]. These plants are terrestrial in origin and are essential to the stability of the salt marsh in trapping and binding sediments. In recent years,

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ecologists have become more cautious in the appointment that saltwater marshes would be useless. Salt marshes play a large role in the aquatic food web and the delivery of nutrients to coastal waters. They also support terrestrial animals and provide coastal protection [101]. The perception of bay salt marshes as a coastal 'wasteland' has since changed, acknowledging that they are one of the most biologically productive habitats on earth, rivalling tropical rainforests [68,102]. In general terms spoken, salt marshes are ecologically important providing habitats for native migratory fish and acting as sheltered feeding and nursery grounds [102,103]. Also they play an important role for migrating birds in the Asia-Africa transmigration route were the birds were wintering and feeding on the salt marshes in the Waddensea area [104]. This is possibly the main reason why a part of the Wadden Sea to world heritage UNESCO area is declared. Economic interests of governments must be weighed in terms of economic benefits ecological interests and biodiversity. A well-known example is the large-scale destruction of mangrove forests in mainly Asia since several decades to establish ponds for commercial shrimps. It was overlooked that these so-called useless mangrove forests are the breeding chamber of countless fish species and other oceans. The same danger is now threatening the saltwater marshes, which are declared useless by governments. With the global increase in population resulting in migration to coastal areas, mainly China is threatening these "useless" saltwater marshes. In manyAsian countries such as China the ecological value of these saltwater marshlands is still not recognized. With their ever-growing populations and intense development along the coast, the value of salt marshes tends to be ignored and the land continues to be reclaimed [105]. A similar situation like in China might be expected at the African continent with its tremendously growing population (Figure 13-16).

Saltmarshes across 99 countries (essentially worldwide) were mapped [106]. A total of 5,495,089 hectares of mapped saltmarsh across 43 countries and territories are represented in a Geographic Information Systems polygon shapefile. This estimate is at the relatively low end of previous estimates (2.2–40Mha). Considering the foregoing, we make a careful calculation assuming that 22,000km2 of these saltwater marshes are really useless and of low ecological value [106]. (Figure 17-20)

Table 8: Estimated annual green biomass production of several seaweed species in the littoral zone (surface area) of the ocean expressed in biomass (wet weight) production per year in (tonnes ha^{-1}/ $year^{1}$).

Seaweed Species	Estimated Biomass (Wet Weight) Production Per Year in (Tonnes Ha^{-1}/ $Year^{-1}$)	Source
Gracilaria sp.	91-149 t. ha^{-1}/$year^{-1}$	[107]
Gracilaria sp.	72 t. ha^{-1}/$year^{-1}$	[86]
Gracilaria sp.	16 t. ha^{-1}/$year^{-1}$	[108]

Based on the in Table 8 given estimated biomass (wet weight) production data per year in (tonnes ha-1/year-1) an intermediate suggested annual production of 75t. ha-1/year-1 is a feasible option. So if in theory the total amount of 22,000km2 (one square kilometre is 100 hectares) would be covered by *G. vermicullophylla* with the annual production of 70t. ha-1/year-1 a total amount of 2,200,000 hectares would yield 144,000,000t./ year-1 of *Gracilaria vermiculophylla* green biomass. With a moisture content of ≈ 80% for seaweeds in general [109] is 28,800,000t. dry weight biomass on a global scale per year which corresponds to 28,8 billion kg of *G. vermiculophylla* theoretically produced in all global saltwater marshes (Figure 9 red areas along the coastlines). We calculated earlier that 70% more green biomass corresponds to fixation of ≈70 x 1012kg of carbon per annum. Assuming a moisture content of 80% and a fixed "Seaweed Redfield Constant" C:N:P ratio of 550:30:1 an annual dry weight seaweed production of 350 billion kg of dry weight green biomass needs to be produced in order to solve "The global Ten Billion People Issue" so in theory G. vermiculophylla could account on a global scale around 8,23% of this tremendous amount of urgently needed green biomass. Following this vision presently, *G. vermiculophylla* is not considered as a plague anymore but as a seaweed crop with economic value and it is already commercially cultured –mainly in the effluent of IMTA systems- at several places in the world [98]. The experience performed in these studies might lay the fundamental basis for a seaweed based economy facing the "global ten billion people issue" at the midst of the 21st century. In this way an ecological plague of a seaweed species can be transformed towards a tool for humanity for economic benefits and profits. Advantage is that it as aggressive non-indigenous invader nearly needs no management tools.

Some countries and regions have inventoried salt marsh area – the total from these inventories comprises 22,000km2. As there is no data on the extent of saltmarshes on the coasts of Asia, South America, and Australia the global area of salt marshes is probably considerably greater [99].

Conclusion

In conclusion, in an attempt to reduce the risk for a further dispersal of *G. vermicullophyla* in the Euro-Asian Black Sea and more in general to prevent ecological disasters by this red drift algae in other coastal areas around the world we give two recommendations:

I. Transport and/or import of oysters needs to be avoided because It can be observed in Europe that many *G. vermiculophylla* populations are in the vicinity of oyster farms [1,3,9]. Possibly also transportation of other bivalves like shellfish needs to be prevented to vulnerable and even UNESCO protected ecosystems! (see further) needs to be avoided or be placed under strict government control and legislation (≈certification) [17,18].

II. Inspection, procedures and issuance of certificates, ship documents and reporting aspects, sampling, analyzing, baseline studies, monitoring of harbor areas are in this

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respect important topics [2]. But especially ballast water treatment technologies. Scientific studies have shown that after 4 months living zooplankton can be found in ballast tanks and under certain circumstances zooplankton species even reproduce in ballast tanks. Therefore, it is recommended to exchange ballast water in open ocean in order to prevent a dispersal of alien exotic invasive intruders (e.g. zooplankton, micro- and macro-algae) to the vulnerable coastal area or adjacent harbors [9].

III. However, if despite these management rules to prevent further dispersal of G. vermicullophyla in the Euro-Asian coastal waters will happen we have "to make the best of it" and in a future manuscript we intend to calculate it even could be economically profitable.

Perspectives

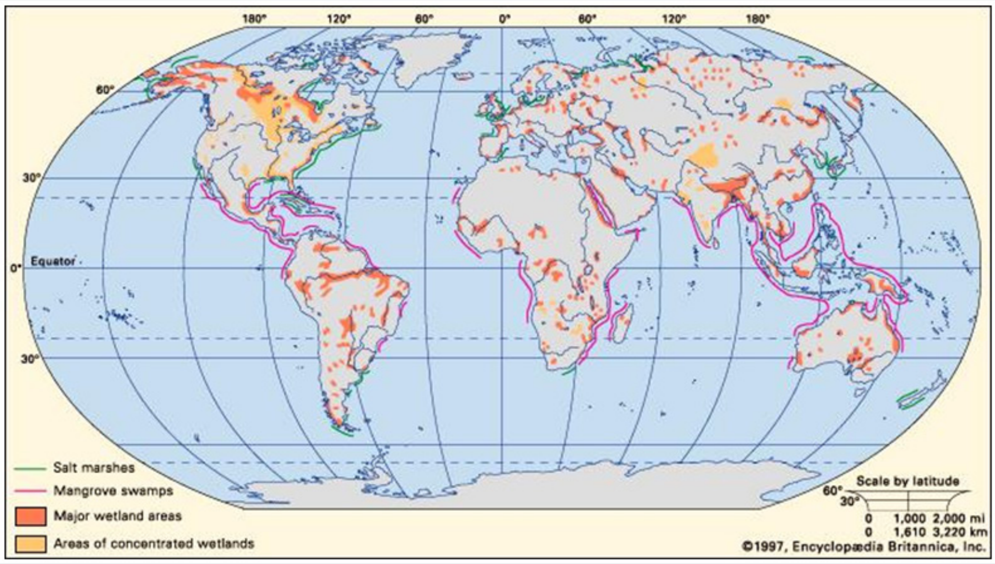

Figure 12: Dispersal of 22,000 km^2 Salt marshes around our globe.

The Wadden Sea is of extreme ecological importance, which can be seen from the large population of harbor and grey seals. But it is especially of importance for millions of migrating birds at the annually Asia-Africa global migration route as an essential stopover to grow and feed. Our recent research shows that, in particular, the Wadden Sea phosphate load: in the Netherlands via the Rhine and the German coast via rivers like the Ems, Weser, Elbe, and Denmark the Elbe and the Elder (Figure 12). As outlined in a previous manuscript by van Ginneken et al 2017 [91] the phosphate load of these rivers on the local Wadden Sea area plays a crucial role in the seaweed competition between native seaweed Ulva species and the non-indigenous Japanese drift algae *G. vermiculophylla*. With exception of the river Rhine in the Netherlands these other small N.W. European rivers (Figure 12) have no sophisticated sewage installation resulting in a load of N and P in the Waddensea area resulting in eutrophic conditions which are beneficial to grow *G. vermiculophylla*. Our ecological datasets gave via final DCA (Detrended Correspondence Analysis) awareness of the very compelling interaction between Ulva sp. and *G. vermiculophylla*. Based on LCMS-techniques we discovered that Ulva sp. have the advantage to use the biochemical pathway –solely rarely observed in some euckaryotes- to have the potential to produce the betaine lipid diacylglyceryl-O-4'-(N,N,N,-trimethyl) homoserine (DGTS) which replaces the plant/seaweed cell wall structure phosphatidylcholine (PC) "lecithine" under phosphate-limiting growth conditions which are solely present in the Dutch part of the Waddensea. Also we hope this lipidomics based compound DGTS can serve as an ecological biomarker in order to protect vulnerable ecosystems like the Wadden Sea (UNESCO World Heritage) [91].

Figure 13: Logo of the United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Committee.

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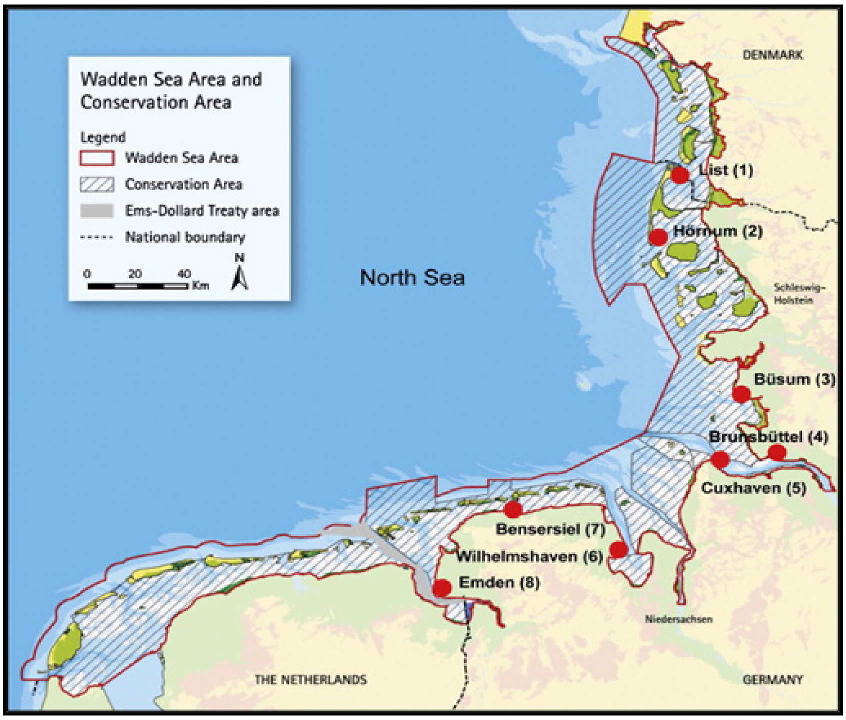

Figure 14: More detailed overview of the Dutch, German and Danish part of the Wadden Sea.

Figure 15: More detailed overview of the Dutch, German and Danish part of the Wadden Sea.

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Figure 16: Images of *Gracilariavermiculophylla* (Ohmi) Papenfuss, 1967 (Rhodophyta, Gracilariaceae). A). In situ, at the sandy bottom near the island 'Ameland' in the Dutch Waddensea. The empty oyster shells (left-top) are indicative for its preference habitat in the vicinity of oyster bancs & farms.B).*In vitro,* (with cystocarps) (Source:[5]).

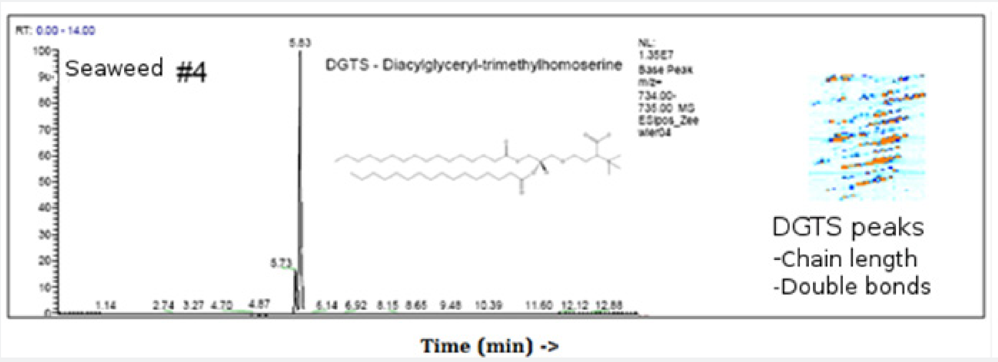

Figure 17: Recently. we found a biomarker for growth of Ulva sp.- a rare betaine lipid solely found in eukaryotes under phosphate limited conditions also named diacylglyceryl-O-4'-(N,N,N,-trimethyl)homoserine (DGTS)- where possible Gracilariavermiculophyllais not capable of.

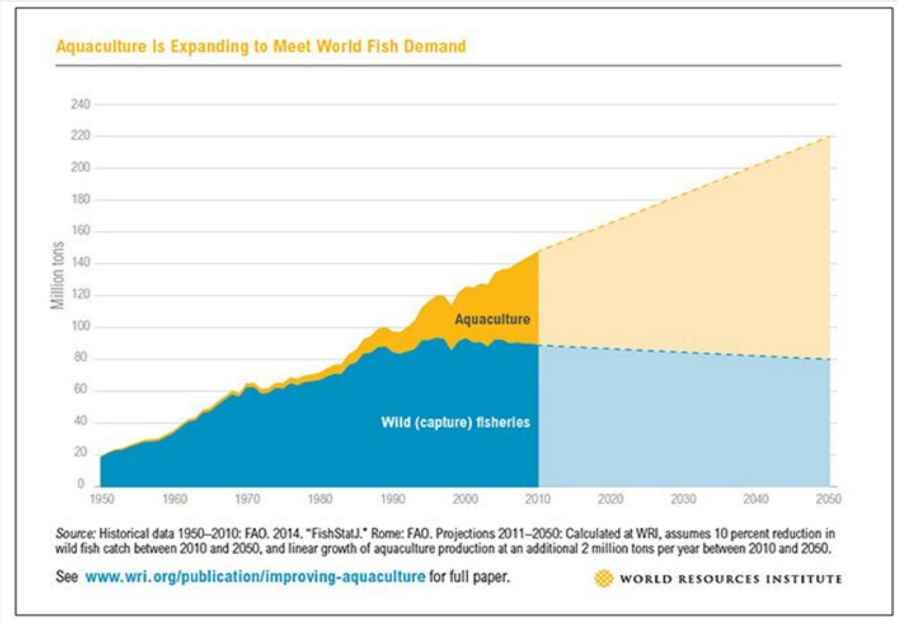

Figure 18: Expected growth of Aquaculture in comparison to Fisheries according to FAO predictions.

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Figure 19: Unattached Gracilaria growing in effluent drains from shrimp pounds in Southern Thailand (Source: FAO).

Figure 20: Important river systems which feed the Wadden Sea: Netherlands (Rhine), Germany (Ems, Weser, Elbe) and Denmark (Elbe & Elder).

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