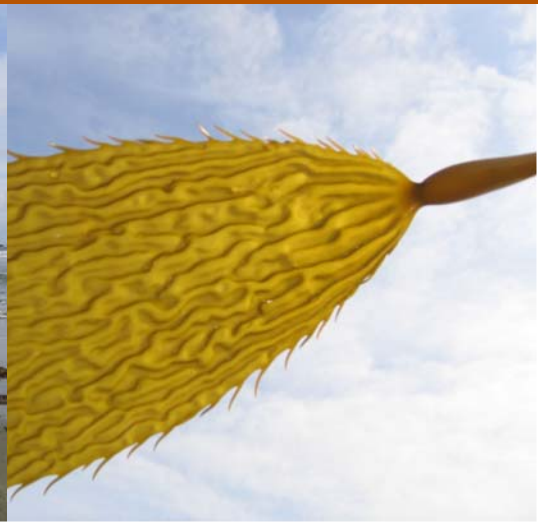
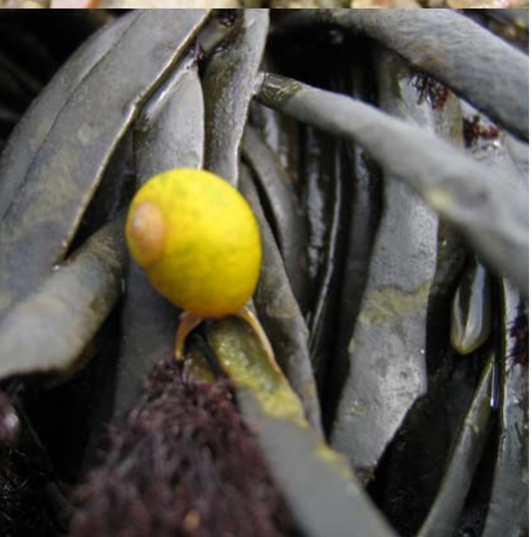





# Introduced marine macroalgae and habitat modifiers

## - their ecological role and significant attributes



Cecilia D Nyberg

Doctoral Thesis
Dept. of Marine Ecology
Göteborg University
2007



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Akademisk avhandling för filosofie doktorsexamen i Marin Botanik vid Göteborgs universitet. Avhandlingen kommer att försvaras offentligt fredagen den 11 maj 2007, kl 10:00 i stora föreläsningssalen, Institutionen för Marin Ekologi, Carl Skottsbergs gata 22B, Göteborg.

***Opponent:*** Førsteamanuensis Kjersti Sjøtun, Institutt for Biologi, Universitetet i Bergen, Bergen, Norge.

***Examinator:*** Professor Inger Wallentinus, Institutionen för Marin Ekologi, Göteborgs universitet, Göteborg, Sverige.

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Cover, from top left horizontally: *Sargassum muticum, Homo sapiens* with *Macrocystis integrifolia, Macrocystis integrifolia, Colpomenia perigrina, Littorina obtusata* on *Ascophyllum nodosum, Mastucarpus stellatus, Carcinus maenas, Gracilaria vermiculophylla.* Photo: Cecilia D Nyberg

# ABSTRACT

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Invasive, non-indigenous species (NIS) have become an increasing problem worldwide, with impacts on the diversity and ecosystem functioning of native communities. Marine invasive NIS also have a negative economical impact through increased abundance of toxic species, fouling of man-made underwater structures, and reduced recreational values of beaches. Only a small proportion of the NIS becomes invasive (i.e., having a negative ecological and/or economical impact), but once a species has been established much effort and resources are needed to remove it.

In the present thesis I discuss possible factors determining the success of macroalgal introductions and their impacts. A species of special concern in this thesis is the non-indigenous marine red alga *Gracilaria vermiculophylla* (Ohmi) Papenfuss, seen for the first time in the archipelago of Göteborg, Sweden, in the summer of 2003. ***Firstly***, I highlight some positive and negative impacts caused by NIS as habitat modifiers. ***Secondly,*** I describe, by quantitative ranking, whether there are any common patterns of species traits increasing the likelihood of macroalgal NIS, introduced into a new area, becoming established and spread. In general, introduced and invasive species were ranked more hazardous than the native and non-invasive species introduced in Europe. Applying the quantitative species traits ranking on *G. vermiculophylla* rendered it among the most invasive red algae in Europe. ***Thirdly***, I show the ability of *G. vermiculophylla* to withstand an emerged situation of more than five months, e.g. simulating transportation in a dredger or among fishing nets. The results indicate that *G. vermiculophylla* can easily survive long transportation in darkness such as in a ballast tank, and without being submerged in water. It also survived salinities down to 2 in a laboratory experiment, indicating that this species can survive in the innermost parts of the Baltic Sea (the Bothnian Bay). With the help of an event tree I illustrate the potential impact an establishment of *G. vermiculophylla* could have in the Baltic Sea. ***Fourthly***, I show the distribution pattern within 150 km of the Swedish west coast in two years time for *G. vermiculophylla*. Furthermore, I describe the community associated with this species collected from Sweden, Denmark and the United States. In total, nearly 100 different taxa in twelve phyla were found associated with *G. vermiculophylla*. ***Finally***, the impact of *G. vermiculophylla* on the native eelgrass, *Zostera marina*, was assessed using a modelling approach. The model output showed a negative effect on *Z. marina* already at low densities of *G. vermiculophylla*.

This thesis contributes to a wider understanding of macroalgal introductions in general and of the ecology and ecophysiology of the invasive red alga *G. vermiculophylla* in particular. Such knowledge is important for management and stresses the importance of monitoring the Swedish coastline for early detection of NIS.

***Keywords:*** Assessment, Community structure, Darkness, Distribution, Event tree, *Gracilaria vermiculophylla,* Habitat modification, Impact, Introduced species, Invasive, Macroalgae, NIS (non-indigenous species), Risk, Species traits, Tolerance.

# POPULÄRVETENSKAPLIG SAMMANFATTNING

De flesta människor fascineras av växter och djur från andra länder. Det gamla paret fyller trädgården med färgsprakande exotiska blommor, hobbyfiskaren går till sjön där det finns inplanterad fisk, den unge mannen flyttar signalkräftor från Skåne till sjön vid sommarstugan i Norrland och barnfamiljen köper en sköldpadda. Men vad händer när dessa arter släpps fria eller rymmer, och sprider sig? Vad får det för konsekvenser för våra inhemska arter?

Människan har genom tiderna flyttat arter avsiktligt (men även oavsiktligt) för att de är vackra eller kan ge ekonomisk vinning. Allt detta har skett och sker ideligen utan den minsta tanke på konsekvenserna. En liten andel av alla främmande arter blir invasiva, vilket betyder att de har en negativ effekt på den inhemska ekologin och/eller ekonomin. Invasiva arter har blivit ett ökande problem världen över, med påverkan på bl.a. den biologiska mångfalden, samt kostnader för att ta bort påväxt på undervattenskonstruktioner och minskat rekreationsvärde av stränder. När en art väl har etablerat sig är det dyrt och tidskrävande, om ens möjligt, att ta bort den. Denna avhandling belyser användbarheten av algers egenskaper för att förutsäga vad som kan hända och visar hur de kan påverka miljön och hur man kan göra en riskbedömning av främmande arter. Jag fokuserar på den introducerade marina perukalgen (*Gracilaria vermiculophylla*), som hittades i Göteborgs skärgård sommaren 2003.

I avhandlingens första studie belyser jag positiva och negativa effekter som främmande arter orsakar när de fungerar som habitatmodifierare d.v.s. att de aktivt eller passivt ändrar sin omgivning så att det gynnar dem själva. I den andra studien beskriver jag en metod för att kunna se hur potentiellt invasiva arter är, baserat på deras specifika artkaraktärer (som storlek, växtsätt, tolerans mot t.ex. uttorkning och föroreningar). Generellt visade denna metod att alger som tidigare ansetts vara invasiva verkligen också blev det i jämförelse med övriga introducerade eller inhemska alger. När metoden testades på perukalgen blev den klassad som en av de mest invasiva rödalgerna i Europa, men om den blir invasiv i Sverige återstår att se. Jag visar även i avhandlingen hur perukalgen kan överleva i totalt mörker under fuktiga förhållanden. Denna egenskap är väsentlig vid transport i barlasttankar eller fastsnärjd i fiskenät och liknande förhållanden. Dessa resultat tyder på att perukalgen lätt överlever långa transporter. Den överlever även i salthalter ner till 2 promille, vilket tyder på att den skulle överleva i de innersta delarna av Östersjön (Bottenviken). I den tredje studien beskriver jag hur perukalgen har spridit sig inom ett område av 150 km längs Sveriges väst-kust under bara två års tid. Jag beskriver även vilka arter som man hittar på och intrasslade i en perukalg. Sammantaget från tre olika länder hittades nästan 100 olika organismer. I den sista studien har vi utvecklat en modell för att kunna förutsäga påverkan av en främmande art på en inhemsk art. Vi har använt perukalgen som modellorganism och testat hur den påverkar det inhemska ålgräset (*Zostera marina*). Modellen visade en negativ påverkan redan vid relativt låga tätheter av perukalgen.

Denna avhandling ger en vidare förståelse av introduktion av alger, ekologin hos den introducerade perukalgen och dess interaktion med omgivningen. Denna kunskap är viktig för hantering av främmande arter och understryker också vikten av att övervaka den svenska kusten för att tidigt kunna upptäcka främmande arter. [1]

[1] Ett tips till den som vill veta mer är att gå till http://www.frammandearter.se

*To Mum and Dad*

## LIST OF PAPERS

The research for this thesis was performed as part of the Aquatic Alien species programme (AquAliens), financed by the Swedish Environmental Protection Agency (Naturvårdsverket). The thesis is based on the following published articles and submitted manuscripts, referred to by their Roman number in the text.

**I** Wallentinus I & Nyberg CD (2007) **Introduced marine organisms as habitat modifiers**. Marine Pollution Bulletin 55: 323-332

**II** Nyberg CD & Wallentinus I (2005) **Can species traits be used to predict marine macroalgal introductions?** Biological Invasions 7: 265-279

**III** Nyberg CD, Thomsen MS & Wallentinus I (submitted) **Are there species using the new habitat provided by *Gracilaria vermiculophylla*?**

**IV** Sahlin U, Larson D & Nyberg CD (submitted) **Dose-response impact assessment of non-indigenous aquatic plants and algae – a modelling approach.**



A doctoral thesis at a Swedish university is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. These have already been published or are manuscripts at different stages (in press, submitted or awaiting submission).

Related paper not included in the thesis:

Thomsen MS, Staehr P, Nyberg CD, Schwærter S, Krause-Jensen D & Silliman BR (in press) ***Gracilaria vermiculophylla* in northern Europe, with emphasis on Danish conditions, and what to expect in the future.** Aquatic Invasions

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# LOOKING INTO THE FIELD OF NON-INDIGENOUS SPECIES

Spread of aquatic species into new areas has occurred constantly since the first organisms were developed on Earth. But due to humans, species are colonizing areas that they never would have reached without our help. An important anthropogenic factor is the escalating use of fast transportations, locally as well as globally. Furthermore, the speed and scale of this process has increased the spread considerably. Another human-induced factor increasing the spread of aquatic non-native species is the construction of corridors to remote places (through breakage of natural boundaries such as construction of canals and artificial waterways). Some examples are the Kiel Canal (connecting the North Sea with the Baltic Sea), the Suez Canal (linking the Red Sea with the Mediterranean Sea) and the Panama Canal (connecting the Caribbean Sea with the Pacific Ocean).

## Introductions of macroalgae

Non-indigenous species (NIS) are species colonizing new areas, across major geographical barriers, where they previously were not present (Boudouresque and Verlaque 2002). The extension of the species range should be linked, directly or indirectly, to human activity (Boudouresque and Verlaque 2002). The fact that introduced species can invade new areas indicates that the introduced species itself creates a new niche or that the introduced species is a superior competitor, utilizing resources and responding to disturbance better than existing species (Myers and Bazely 2003). But it can also be that there are empty niches in the new environment (Myers and Bazely 2003).

### *From native to invasive species*

During the last decades, the study of patterns and processes behind biological invasions and the success of introduced species have grown as research topics. In the beginning, terrestrial and freshwater systems were the most studied, but during the last two decades marine systems have been studied intensely (Grosholz 2002).

The invasion process can be divided into several phases, i.e., introduction, establishment and spread (cf. **Paper II**). The majority of previous studies have focused on establishment (Puth and Post 2005). For the ***introduction*** (or initial dispersal) to occur, the species (whole specimen, fragment, propagule or spore) must be picked up by a vector and transported to a new area (Figure 1). The type and speed of the vector determines the introduction success. Algae can be introduced intentionally for aquaculture (e.g. Floc'h et al. 1991; Munro et al. 1999; Wallentinus 2002). Most macroalgae, however, have been introduced unintentionally with discharge of ballast water and sediment, and as fouling on ships or other waterborne structures (e.g. Gollasch et al. 2002; Wallentinus 2002; Minchin et al. 2005). Other unintentional sources are aquaria trade (Wallentinus 2002; Padilla and Williams 2004; Walters et al. 2006), stowaways with import of other species used in aquaculture, and transportation material around shellfish and live bait (Munro et al. 1999; Verlaque 2001; Wallentinus 2002).

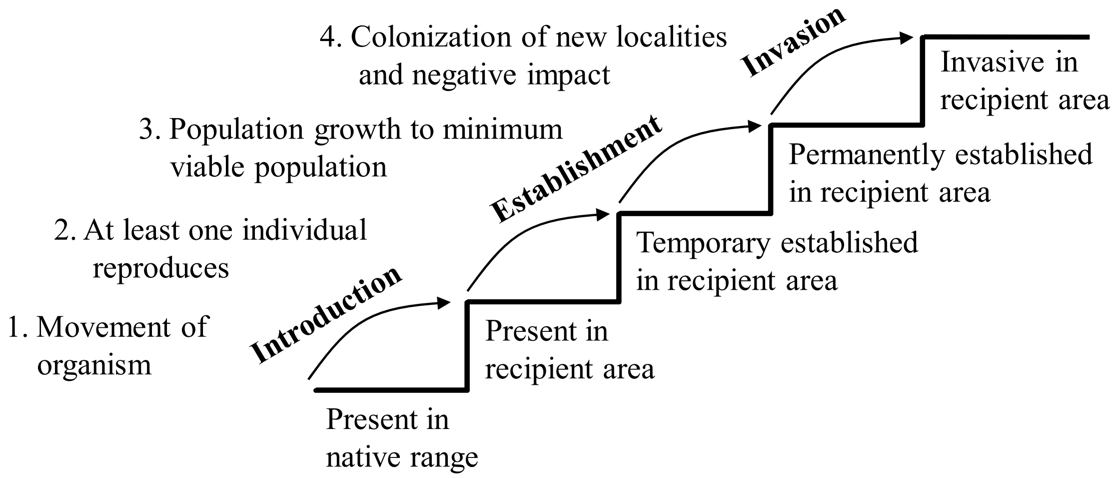



Figure 1. The different stages in an invasion process and the requirement to go from one step to the next. Modified from Heger and Trepl (2003).

At the arrival**,** it is important that the species finds a suitable habitat with temperature, salinity, light and nutrient regimes sufficient for its growth. Regions with similar climate and salinity may have a higher potential of successfully exchanging species. To proceed from the phase of introduction to ***establishment,*** at least one individual must succeed to reproduce in the new area. For species with vegetative propagules, it is enough if one individual is brought to the new area. This may also be the case for species having self-fertilization. The species is regarded as permanently established in the new area when they have developed a self-sustaining population (Boudouresque and Verlaque 2002). Once established, the NIS may ***spread*** naturally (e.g. by currents), or by human activities from continuing long-distance dispersal from ancestral sources, and/or from short-distance dispersal with expansion of the established population (Sakai et al. 2001), a process called secondary introduction.

Species have different life history traits that directly affect their fitness e.g. size, growth pattern and number of propagules. These traits can also promote the success of an invasion (discussed in **Paper II**), but they are not the sole determinants, since the conditions in the recipient area also are crucial for the settlement and establishment of new species. The importance of a specific life history trait varies with the different phases of the invasion process (**Paper II**). The capacity of some seaweeds to survive long periods in darkness and in emerged conditions may be crucial for human-mediated transportations and successful dispersal to recipient areas. In the cases where the recipient area is dissimilar from the native area, the survival chance will increase if the species have a wide environmental tolerance, which means that the species can tolerate the stress of environmental fluctuations and extremes (Boudouresque and Verlaque 2002; **Paper II**). The possibility to reproduce both sexually and asexually, and to show a rapid growth from germling to sexual maturity, increases the success of becoming established and to disperse (Sakai et al. 2001). If the NIS becomes abundant in the recipient region and has negative impact on the environment and/or economy it is referred to as ***invasive*** (Boudouresque and Verlaque 2002). This is the definition used in this thesis. However, the term "invasive" has also been used by several scientists for a species that has established and dispersed from the recipient area, without necessarily having a negative impact.

### Consequences of introductions

Some NIS have neutral or even beneficial impacts on native species and ecosystems, while others become invasive. Understanding the negative impacts, caused by the invasive species, may aid in reversing or preventing them from happening, but much more research is needed (Schaffelke et al. 2006). However, an important question is whether the impacts of introduced species can ever be reversed or, if once a non-indigenous species is established, the community reaches a new 'equilibrium state' (Zavaleta et al. 2001; Myers and Bazely 2003).

The most evident impact a NIS has on a native species is through competition for limiting resources (e.g. light, substrate and nutrients), causing reduced growth or reduced reproduction of the native species. Non-indigenous animal species may also be important as predators or grazers, or causing trophic cascades, which may affect both native and non-indigenous species. Some macroalgae compete with allelopathy and actively suppress other species through release of chemical compounds (e.g. Friedlander et al. 1996; Råberg et al. 2005; **Paper I**). The impacts can also have consequences for the population dynamics of native species, causing changes in abundance, distribution, structure, population growth rate, and in a worst case scenario, extinction of native species (Parker et al. 1999). On a community level, changes can appear in species richness, evenness and diversity (Parker et al. 1999). Other impacts are hybridization and genetic alterations (Parker et al. 1999). Some NIS alter the character of the ecosystem to an environment more favourable for themselves (Vitousek et al. 1997); these are called ***habitat modifiers*** or ***ecosystem engineers***. Examples of alterations are reduced water movements and changes in resource pools and supply rates (modifications are exemplified in **Paper I**). However, NIS may also have positive effects on the ecosystem. For example, more fish have been attracted to an area previously lacking macrovegetation, in which *Sargassum muticum* (Yendo) Fensholt now have colonized (Wallentinus 1999). Also the recently introduced red alga *Gracilaria vermiculophylla* has been seen to have the same effect in Sweden (pers. obs., see also results in **Paper III**).

Negative impact on economy can occur with the presence of NIS (Sakai et al. 2001). Examples of problems are the introduction of toxic algae affecting aquaculture, competition with species exploited by humans, fouling on water intakes and underwater constructions, drifting algal mats making the navigation routes hazardous (Critchley 1983), clogging of fishing equipment, reduced recreational value of beaches and costs for controlling methods. But the new species can also be of economical value, through harvesting, usage in aquaculture, aquarium trade, as food and in the industry (e.g. for producing gelling agents or medicines).

## Predicting invasions

Only a small number of NIS that manage to arrive to a new area will survive and become established, and even fewer will cause disturbance. It is said that roughly 1% of species will go from being introduced to becoming invasive (Williamson and Fitter 1996b). However, an intentional introduction to a suitable area may result in a higher percentage. Since the eradication of introduced species is difficult and often expensive, it would be valuable to be able to predict which species may become invasive, so resources can be directed towards measures against those species (Hewitt et al. 2005). Several approaches have been presented on how to predict future invaders. The most basic approach is to focus on the invasion history of species and create lists of species that are invasive in some parts of the world, and hence would be likely to cause negative impacts in other areas as well (Lowe et al. 2000; Hayes and Sliwa 2003). The lists are often divided into three categories; black (lists of species that cause damage and their spread must be prevented), grey (species which have the potential to cause damage and their spread needs to be monitored and risk analyses undertaken for intentional introductions) and white lists ("safe species"). A disadvantage with this approach is the exclusion of species not yet introduced anywhere, thereby giving such lists a low predictive value.

Another approach is to search for common patterns among species and environmental traits that can increase the likelihood of a successful invasion. Several attempts to find such patterns have been made for terrestrial plants (Williamson and Fitter 1996a; Kolar and Lodge 2001; Prinzing et al. 2002) and marine algae (Maggs and Stegenga 1999; Boudouresque and Verlaque 2002; **Paper II**). Some studies have focused on finding characters separating native species in a community from established non-indigenous species (e.g. Williamson and Fitter 1996a). Others have studied patterns separating established species from species within the same species pool that have not been introduced, (e.g. Prinzing et al. 2002) as well as invasive and non-invasive species (Radford and Cousens 2000; **Paper II**). An additional approach is to develop questionnaire schemes for screening of invasive species. Pheloung and coworkers (1999) developed a screening system that successfully predicts serious weeds in Australia. The screening system is based on 49 questions based on the main attributes and impacts of weeds. It classifies the species into one of three categories (accept, further evaluation or reject) which decides whether a NIS plant can be imported without posing a large environmental risk. With this questionnaire, all weeds with serious or less serious impact on native communities, treated in the study, were rejected or demanded further evaluation, and only 7% of the non-weeds were rejected. Another method giving rough estimate of invasion success is the climate-matching model, which predicts the potential new range of introduced species (Mack and Barrett 2002a). The climate-matching model is, however, a rather limited model (Williamson 2006), since species sometimes adapt to new environments and evolve. The green alga *Caulerpa taxifolia* (M. Vahl) C. Agardh, introduced into the Mediterranean Sea, is an example of a strain tolerating other climates compared to the original tropical strain (Rodríguez-Prieto et al. 1996). Features that make ecosystems more susceptible to invasion have also been studied; for example, some studies have shown that disturbed or stressed environments are more susceptible to invasions (Gollasch and Leppäkoski 1999). Approaches that consider only one aspect of the relationship between the invaded ecosystem and the invader are termed non-relational (Heger and Trepl 2003). Approaches relating the traits of the invader to those of the ecosystem are called key-lock models (Heger and Trepl 2003). Further development of these approaches leads to a differentiation of invasion processes in time, based on the premise that the traits of an invader have to fit the specific environmental condition during each phase in time (Heger and Trepl 2003).

***The key to success?***

Several hypotheses have been proposed to explain the success of introduced species. According to the Diversity Resistance Hypothesis, less diverse communities of plants and animals are more likely to be invaded by NIS. Sakai and colleagues (2001) suggested that the larger amount of linkages in a species-rich ecosystem, compared to a species-poor ecosystem, would make the former less vulnerable to disturbances. However, some researchers have suggested that species-rich communities may be more susceptible to invasions (see review by Davis 2005). The escape from natural enemies, such as pathogens, parasites (Mitchell and Power 2003; Torchin et al. 2003, respectively) and herbivores in the recipient area, is referred to as the Enemy Release Hypothesis (ERH). The ERH predicts that a decrease in grazing (or parasite) pressure allows allocation of resources to reproduction and growth, previously used for producing defence chemicals or structures (Keane and Crawley 2002). It has also been proposed that the success of the invader can be explained by the Evolution of Increased Competitive Ability Hypothesis (EICA) (Blossey and Nötzold 1995). This hypothesis suggests that in the absence of herbivores (in the recipient area), there will be a selection against allocation of resources for herbivore defence and instead genotypes with improved competitive abilities (e.g. increased vegetative growth or reproduction) will be favoured. In contrast to the ERH and EICA, Wikström and coworkers (2006) found that the non-indigenous brown alga, *Fucus evanesces* C. Agardh had a higher concentration of defence compounds in the new range than in its native range. This indicated an increased allocation to defence rather than as stated by the ERH a release from specialist herbivores. This last hypothesis is called the Intrinsic Resistance Hypothesis (IRH) (Hill 2006) and states that individuals with high levels of defence compounds are the ones capable of invading. Hill (2006) tested the different hypotheses (ERH, EICA and IRH) on three non-indigenous macroalgae to see if any of the hypotheses were applicable. Overall, the results did not support a general release from enemies. However, the red alga *Bonnemaisonia hamifera* Hariot (which has halogenated secondary compounds that may function as grazer deterents) was significantly released from grazers in comparison to the native species in the study, while the two other studied introduced macroalgae (*Sargassum muticum* and *Codium fragile* ssp. *tomentosoides* (van Goor) P.C. Silva) were preferred food items.

## Risk assessment

When discussing subjects involving NIS, the term risk is often used. Risk is the probability of an undesirable event and its specific consequences within a defined time frame (Burgman 2005). Due to the increasing spread of non-indigenous species the importance of using an ecological risk assessment as a tool for assessing, reducing and managing risks has increased. However, risk assessment of NIS is more complex than of other environmental threats, e.g. chemical pollution, since chemicals will be more diluted with time and distance, while organisms can reproduce and disperse actively. Risk management is the process of measuring or assessing risk and developing strategies to manage these. A step in the risk management process is risk assessment, which helps us to make decisions when we are uncertain about future events (Burgman 2005). The ambition with an ecological risk assessment is to evaluate the potential risk to ecosystems due to human activities. The Environmental Protection Agency of the United States (EPA 1992) defines it as "a process that evaluates the likelihood that adverse ecological effects may occur or are occurring as a result of exposure to one or more stressors". The risk assessment assigns magnitudes and probabilities of undesirable effects (Suter 1993). It can predict the probability of future effects due to a specific stressor (prospective) or predict the probability that past effect were caused by a specific stressor (retrospective) (Suter 1993). A risk assessment can be divided into three stages: problem formulation, analysis and risk characterization (Figure 2).

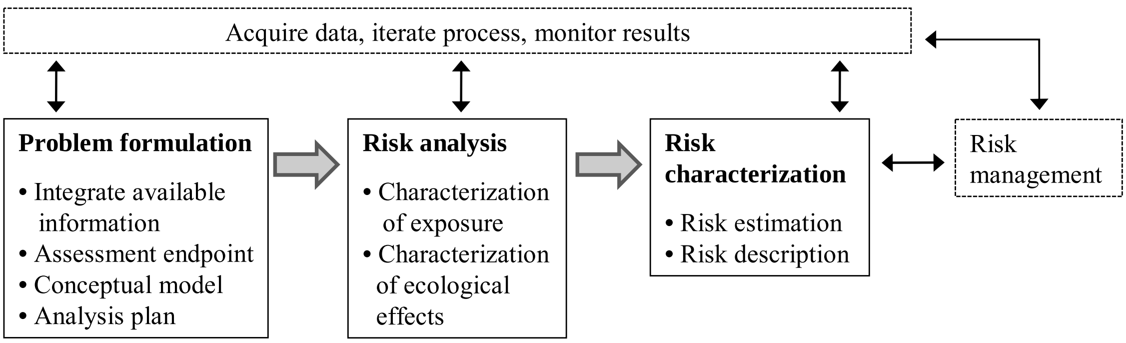



Figure 2. Simplified picture of the framework for ecological risk assessment from US EPA (1992).

During the ***problem formulation*** it is important to define measurable management goals for the undesired event, i.e., endpoint(s) (Suter 1993; **Paper IV**). These should be of ecological relevance and be susceptible to the selected stressor (e.g. NIS). The problem formulation also includes the preparation of a conceptual model (EPA 1998). This is based on working hypotheses regarding how the stressor might affect the endpoint. The conceptual model links the stressor to the endpoint through direct and indirect exposure pathways (Figure 8). The second stage in the process is ***risk analysis*** – here the distribution of the stressor and its contact with the endpoint is measured, the response elicited by the stressor is identified and quantified and the strength of the potential effect is evaluated. There are several different methods to perform the risk analysis. These are divided into groups (qualitative, semi-quantitative and quantitative) depending on to which degree they can be quantified. A very important part of the risk analysis is the evaluation of uncertainty. If there is no uncertainty of whether or not an undesired event will occur, there is no risk (Suter 1993). Risk assessments involve uncertainties of two types: epistemic and linguistic. Epistemic uncertainty includes measurement errors, systematic errors, insufficient data and natural variations (Burgman 2005). Linguistic uncertainty, arises due to insufficiency of languages (words are used differently or inexactly, they are often ambiguous, vague or dependent of the context)

(Burgman 2005). The purpose of the third stage, the ***risk characterization***, is to provide a complete picture of the risk for further discussions between risk assessors and risk managers. In this stage information on exposure and effect is integrated to evaluate the probability of adverse effects associated with the exposure to the stressor.

**Predicting impact**

Predictions of the impact of living organisms on other biota are difficult to perform, since species disperse, reproduce, mutate and evolve. In contrast to the well developed predictions for chemical emissions, prediction methods for the impact of invasive species are underway of being developed. Several attempts have been made to predict the impact. The most straightforward method is the construction of a logic tree (Bedford and Cooke 2003) which is a diagram that links all the processes and events that could lead to, or develop from, a hazard. There are two approaches: 1) a fault tree works from the top down, linking chains of events to the outcome while 2) an event tree (Figure 16) takes a triggering event and follows all possible outcomes to their final consequences. Another method is to extrapolate the observed impact of a particular NIS in one geographical region to a different situation. A difficulty with this method is that the establishment and spread of introduced species may be site or time specific, resulting in that the impacts observed in one area might not suit its purpose to predict the effect in another area. However, as a precaution they can be used as worst scenarios. Other methods involve demographical studies, removal experiments and for animals also dietary studies, food web analysis and behavioural studies (Park 2004), as well as modulations of the relationships between the NIS and the impact variables.

**Introduced macroalgae**

The number of introduced species in a region varies because of taxonomic uncertainties and due to the number of cryptogenic species (i.e., species that one cannot with certainty say are native) (Carlton 1996). In Europe 113 marine macroalgae have been recognized as introduced (Wallentinus 2002). On the French Atlantic coast 21 introduced algae have been found (Goulletquer et al. 2002) and on the coast of the North Sea 20 introduced algae (Reise et al. 2002). In the Mediterranean Sea Ribera Siguan (2002) has reported 94 introduced algae while Zenetos and coworkers (2005) have found 83 species. The different numbers of species for a geographical area also depend on that there are varying opinions on if some species are introduced or are relicts from ancient seas. The increasing use of molecular techniques may solve these questions in the future.

On the Swedish coasts we currently know of 12 introduced macroalgae; 6 red algae, 3 brown and 3 green algae (Figure 3, Table 1). All these macroalgae have been introduced during the last 150 years. The oldest of the introductions is *Chara connivens*, which today, in some circumstances, is regarded as a native species and is red-listed as 'vulnerable' (Gärdenfors 2005). The low number of macroalgal introductions in Sweden makes new introductions very interesting to study. It is therefore of great interest to be able to predict possible consequences of an introduction and to be able to prevent invasive species from being introduced. Considering that several of the earlier introduced macroalgae have spread southwards from the northern part of the Swedish west coast towards the outer part of the sensitive Baltic Sea, this is also an interesting aspect to study.

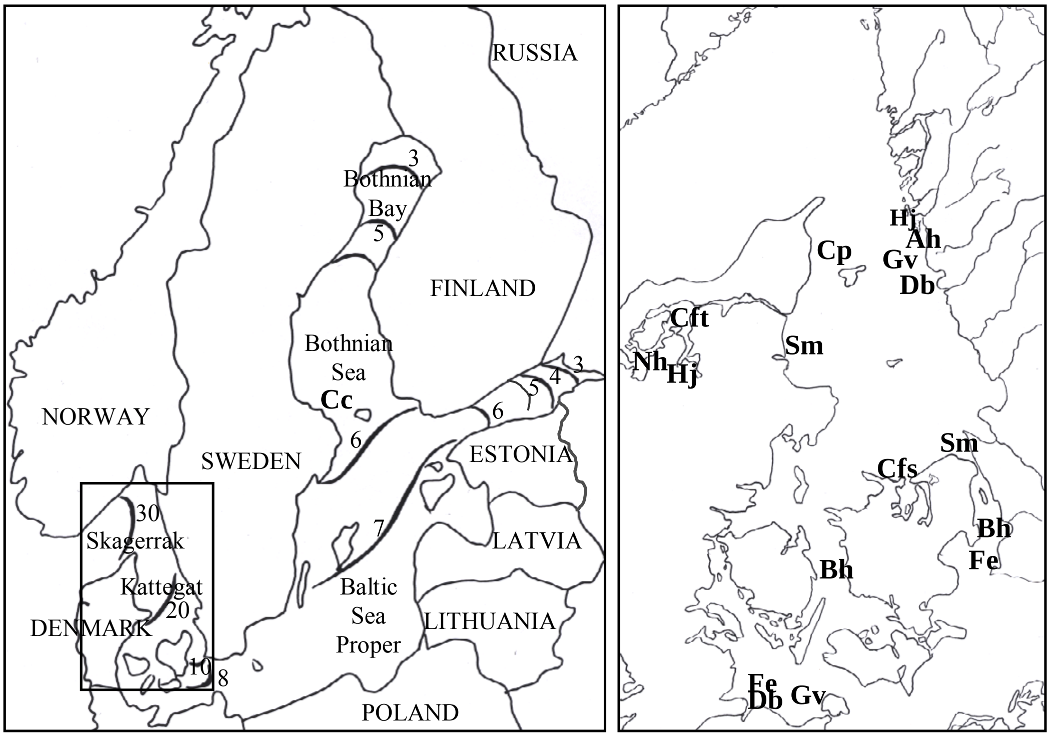



Figure 3. The Baltic Sea area *sensu lato*, with surface salinity isohalines. The innermost distribution of the 12 introduced macroalgal taxa are indicated (all but *Chara connivens* on the magnified map): Ah = *Aglaothamnion halliae*, Bh = *Bonnemaisonia hamifera* (tetrasporophytes), Cc = *Chara connivens*, Cfs = *Codium fragile* ssp. *scandinavicum*, Cft = *Codium fragile* ssp. *tomentosoides*, Cp = *Colpomenia peregrina*, Db = *Dasya baillouviana*, Fe = *Fucus evanescens*, Gv = *Gracilaria vermiculophylla*, Hj = *Heterosiphonia japonica*, Nh = *Neosiphonia harveyi*, Sm = *Sargassum muticum*.

Table 1. Introduced macroalgae in Sweden and their distribution.

| **Species** | **Year of first record** | **Place of first record** | **Furthest distribution into the Baltic Sea** |
|---|---|---|---|
| *Chara connivens* Salzmann ex A. Braun | mid 19th century | Öregrund, Uppland | The Bothnian Sea (Nielsen et al. 1995), outwards to the coast of northern Germany (Luther 1979) |
| *Bonnemaisonia hamifera* Hariot | 1905 | Bohuslän | Öresund (Nielsen et al. 1995); Great Belt (Nielsen 2005) |
| *Fucus evanescens* C. Agardh | 1924 | Fjällbacka, Bohuslän | Öresund (Wikström et al. 2002); the Kiel Bight and adjacent areas (Nielsen et al. 1995) |
| *Codium fragile* ssp. *scandinavium* P.C.Silva | 1932 | Kristineberg, Bohuslän | Isefjorden, the southern Kattegat (Silva 1957) |
| *Codium fragile* ssp. *tomentosoides* (van Goor) P.C.Silva | 1938 | Långö, Bohuslän | Limfjorden and the northern Kattegat (Silva 1957) |
| *Colpomenia peregrina* Sauvageau | 1950 | Kristineberg, Bohuslän | Limfjorden and the northern Kattegat (Nielsen 2005) |
| *Dasya baillouviana* (S.G. Gmelin) Montagne | 1953 | Kristineberg, Bohuslän | The Kiel Bight (Schories and Selig 2006) and adjacent Danish areas, Öresund (Nielsen 2005); Bua, the eastern middle Kattegat (Wallentinus 2006) |
| *Sargassum muticum* (Yendo) Fensholt | 1987 | Koster, Bohuslän | Hittarp, Helsingborg (Hellfalk et al. 2005) |
| *Neosiphonia harveyi* (J. Bailey) M.-S. Kim, H.-G. Choi, Guiry & G.W. Saunders | early 1990's | Väderöarna (Athanasiadis 1996), Bohuslän | Limfjorden and the northern Kattegat (Nielsen 2005) |
| *Heterosiphonia japonica* Yendo | 2002 | Koster, Bohuslän (Axelius and Karlsson 2004) | Göteborg (Gustafsson in Wallentinus 2006) Limfjorden and the northern Kattegat (Nielsen 2005) |
| *Aglaothamnion halliae* (F.S. Collins) Aponte, Ballantine & J.N. Norris | 2003 | Strömstad, Bohuslän | Bua, the eastern middle Kattegat (Wallentinus 2006) |
| *Gracilaria vermiculophylla* (Ohmi) Papenfuss | 2003 | Rivö, Göteborg | Träslövsläge, the northeastern Kattegat (**Paper III**); Kiel, Germany (Schories and Selig 2006) |

## Species of special concern: *Gracilaria vermiculophylla*

The species emphasized in the second part of this thesis is *Gracilaria vermiculophylla* (Ohmi) Papenfuss, a west Pacific perennial red macroalga belonging to the family Gracilariaceae. It is one of the largest seaweed genera with over 150 species (Guiry and Guiry 2007). Several investigations have been made on different *Gracilaria* species, since many of them are harvested or cultivated as a source for agar (Tseng and Xia 1999) and food. In Sweden there are two native species of Gracilariaceae: *G. gracilis* (Stackhouse) Steentoft, L. Irvine & Farnham, which previously was recorded only from the Skagerrak (Karlsson et al. 1992) as *G. verrucosa;* (Steentoft and Farnham 1997; Nielsen 2005), but was in 2005 found in Bua, in the middle of Kattegat (Alsterberg and Wallentinus unpubl. obs; Ahlgren 2005b), and *Gracilariopsis longis-*

*sima* (Gmelin) Steentoft, L. Irvine & Farnham, also found in Bua (Alsterberg and Wallentinus unpubl. obs; Ahlgren 2005b), but the overall distribution of this species in Sweden is uncertain. The native distribution of *Gracilaria vermiculophylla* is east and south-east Asia, but as a result of unintentional introductions it can today be found in several other areas in the world (Figure 4). In Sweden, the species was identified on the west coast in September 2003 (Wallentinus and Jenneborg 2003) although seen already in the summer of 2003 (pers. obs.) which was later confirmed. The identity was verified by DNA-analyses (Rueness 2005).

| Continent | Countries/States | Reference |
|---|---|---|
| ***Asia*** | Japan | Ohmi 1956 |
| | Korea, China, Vietnam | Tseng and Xia 1999 |
| ***America*** | California, Mexico | Bellorin et al. 2004 |
| | Virginia/North Carolina | Thomsen et al. 2005; Freshwater et al. 2006 |
| ***Europe*** | Denmark (Wadden Sea & Belt Sea) | Nielsen 2005; Thomsen et al. in press-a; in press-b |
| | Germany (Wadden Sea & Kiel) | Schories and Selig 2006; Thomsen et al. in press-a |
| | France, the Netherlands, Spain, Portugal | Rueness 2005 |
| | Sweden (west coast) | Wallentinus and Jenneborg 2003; **Paper III** |
| ***Africa*** | Morocco | Christophe Destombe pers. comm. |

Figure 4. World distribution of *Gracilaria vermiculophylla.* Squares denote native areas and circles show the areas where it has been introduced. For details see text below the map.

Our findings of *G. vermiculophylla* in Sweden agree with the following descriptions given by Ohmi (1956; see also, Ahlgren 2005b for the morphology of Swedish specimens). It grows in the intertidal zone, in Sweden also in the upper subtidal, and attaches to the substratum (small stones, shells, mussels) with a discoid holdfast. The species also grows lying loose on sandy or muddy bottoms in shallow bays. It is irregularly branched, with three to four orders of branches, and can reach 1 m in length. It is quite common that germlings attach to the old plants as conspecific epiphytes (Ahlgren 2005b). The colour varies from purplish brown to dark brown and sometimes to greenish or yellow (Tseng and Xia 1999; pers. obs.). *G. vermiculophylla* has three different kinds of reproductive stages in the life cycle; tetrasporophytes, male and female gametophytes. In some specimens tetrasporangia and sexual organs occur together. Cystocarps are subglobose, protruding and up to 1200 µm diameter and scattered over the branches (Figure 5). The antheridia forms (25) 90-150 (270) µm deep and 45-120 µm wide cavities, which can be up to 300 µm long (Ahlgren 2005b) and they are scattered all over the surface of the fronds. The tetrasporangia are also scattered over the fronds.

***Latin synonyms*****:** *Gracilaria vermiculophylla* (Ohmi) Papenfuss, *Gracilariopsis vermiculophylla* Ohmi, *Gracilaria asiatica* Zhang & Xia (Guiry and Guiry 2007).
***Japanese name:*** Ogo-modoki (Ohmi 1956).
***Swedish names:*** Perukalg, grov agaralg.

Figure 5. Female gametophyte of *Gracilaria vermiculophylla* with protruding cystocarps.

## OBJECTIVES AND THE STRUCTURE OF THE THESIS

The general objective of this thesis was to increase the understanding of non-indigenous marine algae in general, and of alien species acting as habit modifiers, but also to provide data on a recently introduced alga, of which there was poor knowledge of its ecology in 2003. The first part of the thesis (**Papers I-II**) has a general focus exemplifying different types of impact and predicting introduction. The second part (**Papers III-IV**) focuses specifically on the Asian red alga *Gracilaria vermiculophylla*. In addition to **Papers I-IV**, data on the ecology of *G. vermiculophylla* (not included in the different papers) are given in the thesis summary. On the following pages I will give a brief overview of the papers included. For a more detailed description of the methods and results, I refer to the original papers.

**Paper I:** The aim of Paper I was to describe the impact of habitat modification caused by some non-indigenous species. Such changes are of advantage to the non-indigenous species themselves, but may also have a severe impact on native species.

**Paper II:** What determines the success of an introduction? In Paper II we investigated whether there are any common patterns of species traits that can increase the likelihood of a non-indigenous species being introduced into a new area and becoming invasive. 1) Is there a difference between the species traits of introduced and native macroalgal species and 2) is there a difference between the species traits of invasive and non-invasive introduced macroalgal species?

**Paper III:** The objectives of Paper III was to gain a quantitative data set of flora and fauna associated with the non-indigenous *Gracilaria vermiculophylla*, to compare the Scandinavian communities (Sweden and Denmark) with *Gracilaria* communities from the east coast of the United States and to document the distribution in Sweden.

**Paper IV:** The ambition with Paper IV was to construct a model for impact assessment of an introduced species on a native species in the same ecosystem. The model was then used to derive impact probabilities for the non-indigenous marine alga *Gracilaria vermiculophylla* on eelgrass, *Zostera marina*.

## ABOUT METHODS

The results presented in this thesis origin from laboratory experiments, field observations and reviewing publications. This section gives an overview of the methods used, a more detailed description is provided in the included papers. Additional data from tolerance experiments on *Gracilaria vermiculophylla*, not included in the attached papers, are given in this thesis summary. The experimental setup for those studies is thus described in some more detail.

### Habitat modification (Paper I)

Introductions of NIS are mostly discussed through their impact on biodiversity. However, NIS can also act as ecosystem engineers, influencing the habitat itself, positively or negatively, directly or indirectly, which should be included when making risk assessments. **Paper I** is a review on some of the marine and brackish water NIS causing habitat modifications, but not including trophic interactions between two species. Algae, plants and animals are exemplified. Several of the examples that are discussed in the paper are taken from field observations, while a few are results from experimental work or from modelling. The positive or negative impact of the NIS is mainly described from an ecosystem perspective leaving the exemplification of the economic impact to a future review. We have chosen not to include effects on man-made structures, since these structures themselves are contributing to a change of the habitat.

### Species traits of macroalgae (Paper II)

Once a species has been established it will be very hard or impossible to eradicate, and therefore predicting which species may become a risk would be highly valuable. Such a prediction could be accomplished by searching for common patterns of features that can increase the likelihood of a successful invasion. In **Paper II** we go to the depth of the importance of specific species traits for the success of non-indigenous and invasive species. The paper is based on data from the literature (scientific articles, books, floras and web pages). We applied quantitative ranking of species traits facilitating dispersal, establishment and ecological impact in marine ecosystems. We wanted to evaluate this on a large assemblage of marine macroalgae and therefore chose to study the 113 introduced macroalgae known in Europe at the time of the study. Native and introduced species were compared. The introduced species were further divided into invasive and non-invasive introductions. The native species (Anonymous 2000) were randomized from the same families as the introduced, since some traits (e.g. secondary metabolites and size) may differ widely between families.

Thirteen species traits (divided between the three main categories dispersal, establishment and ecological impact; Table 2) were quantitatively ranked by using interval arithmetic, a method for evaluating calculations over sets of numbers contained in intervals. For each category a scale from 0 to 1, divided into ten intervals was used (0 posing the lowest risk and 1 the highest). A value was obtained for each alga, some-where between 0 and 1, depending on the specific trait they possessed and the uncertainty involved in determining them. These values were finally summarized for each group of algae (Rhodophyta, Phaeophyceae and Chlorophyta). We also summed all categories to determine the species constituting the highest overall risk. In addition, we wanted to test if a quantitative arrangement of species traits could be used as a tool for risk assessment, for intentional introductions, or when establishing risk species lists.

Table 2. The three main categories and the 13 subcategories used for the quantitative ranking.

| Dispersal | Establishment | Ecological Impact |
|---|---|---|
| 1. Distribution | 4. Salinity range | 10. Size |
| 2. Probability of being transported | 5. Temperature range | 11. Morphology |
| 3. Survival time out of water | 6. Tolerance to pollutants | 12. Habitat effect |
| | 7. Reproductive mode | 13. Life span |
| | 8. Growth strategies, surface: volume | |
| | 9. Grazing and defence mechanisms | |

Clarification of **Paper II:** In the categories salinity (4) and temperature (5) the word "range" denotes the number of units that the species survives, not the actual (measured) salinity (psu) or temperature (ºC). Thus a salinity range of 3-6 denotes a stenohaline species, found in salinities of e.g. 28 (or 31) to 33, or 11 (14) to 16 etc., while a range of 27-30 denotes a euryhaline species found in very low salinities to almost normal seawater. Furthermore, the salinity category (4) is not included for the native species due to lack of data. For introduced species detailed information of where the species is found is easily assessed, while the data for native species usually just notifies in which countries or sea areas they are found, not giving a more precise description if they are found in estuaries or other areas with extreme salinities.

### Species traits ranking of *Gracilaria vermiculophylla*

The new discovery of *Gracilaria vermiculophylla* in Sweden made us curious to investigate how this species would be ranked compared to the other non-indigenous species in Europe. We therefore applied the same method as described in **Paper II**.

### *Gracilaria vermiculophylla* surviving emerged conditions

To gain more knowledge about the tolerance of *Gracilaria vermiculophylla* to emerged conditions, tetrasporophytes were collected on the west coast of Sweden on several occasions in September-October 2003 and in February-March 2004. The specimens were gently shaken, to shed excess water, and were thereafter stored in closed plastic bags (Figure 6) in darkness and out of water at 8 °C.

Figure 6. The storage of *Gracilaria vermiculophylla* in plastic bags.

The algae were stored for between 4 and 175 days. Two experiments were performed: In *experiment I* the resistance and tolerance to treatment of specimens collected at three different locations (Rivö N 57º39′4″; E 11º47′6″, Stora Amundön N 57º35′3″; E 11º54′8″, and Vallda N 57º29′0″; E 11º56′2″) were compared for two salinities (26 and 35). In *experiment II* the resistance and tolerance to treatment of different durations were compared at a salinity of 26. After treatment, 20 mm long shoot pieces were placed in Petri dishes in a climate chamber with a constant temperature of 11.5 °C ± 0.1 (StErr). The shoots were grown in f/2 medium (Guillard 1975), which was changed weekly. The irradiance was 265 µmol photons $m^{-2}s^{-1}$ ± 3 (StErr) and the shoots were cultivated under a 16:8 hour light:dark cycle, which together with the temperature of 11.5 °C, corresponds to late spring in Sweden. The experiments were terminated after 32 days due to the size of the shoots, since prolongation of the experiment could have resulted in space limitation. The lengths of the shoots were measured at start and end of the experiments and the relative growth rate was calculated according to Equation 1 with the unit $day^{-1}$, where $l_1$ is the initial length, $l_2$ is the length after t days, and $t$ is the duration of the experiment in days.

$$RGR\,(\%) = 100 \times \left( \frac{\ln\left(\frac{l_2}{l_1}\right)}{t} \right) \qquad (1)$$

## Salinity tolerance of *Gracilaria vermiculophylla*

To investigate the potential survival of *Gracilaria vermiculophylla* in the inner-most part of the Baltic Sea we decided to perform a salinity tolerance test. In late October 2003, plants of *Gracilaria vermiculophylla* were collected from a shallow soft bottom bay at Vallda (N 57º29′0″; E 11º56′2″) in the inner archipelago south of Göteborg, on the Swedish west coast. At the time of collection the water temperature was 10°C and the salinity 26. The collected algae were kept in a climate chamber, in seawater with a salinity of 26 and a temperature of 11.5°C. After a month, 20 mm long shoots were cut from tetrasporophytic plants. These were cultivated for 22 days at 11.5 °C ± 0.1 (StErr) in five different salinities; 2, 4, 6, 8 and 26. Three shoots were placed in each

Petri dish, and for each treatment five replicates were used. The shoots were grown in ESAW culture medium (Harrison et al. 1980), receiving additions of nutrients and vitamins according to f/2 medium (Guillard 1975). The medium was also enriched with carbon ($NaHCO_3$) to gain a carbon concentration equal to that of water with a salinity of 26 (1.66 mmol C $dm^{-3}$), to avoid carbon limitation. Furthermore, the carbon concentration in natural brackish water is higher than in seawater diluted with distilled water (McLusky 1989). The medium was changed once a week, and macroalgal epiphytes were gently removed. The algae lacking epiphytes were treated in the same way to eliminate epiphyte removal as a possible confounding factor. The shoots were cultivated under a 16:8 hour light:dark cycle at the average irradiance of 266 µmol photons $m^{-2}$ $s^{-1}$ ± 3 (StErr). To capture the growth of *G. vermiculophylla* in the different salinities the shoots were measured at start and termination of the experiment. Relative growth rates were calculated according to Equation 1.

**The spread of *Gracilaria vermiculophylla* (Paper III)**

Since we found the “first” sample of *Gracilaria vermiculophylla* in Sweden we got a good opportunity to follow its spread from start. During the late summers of 2003 to 2005 the archipelagoes of the eastern Kattegat and the Skagerrak (the Swedish west coast), between the Koster archipelago and the southern province of Halland (N 58º21′16″; E 11º24′33″ and N 57º03′49″; E 12º16′39″, respectively), were surveyed to document the spread of *G. vermiculophylla.* All the investigated locations were shallow (0 to 3 m) soft-bottom bays and the surveyed areas about 100 $m^2$ and were accessed trough wading or snorkelling.

**The community associated with *Gracilaria vermiculophylla* (Paper III)**

When a NIS becomes abundant in a new surrounding it is important to study how it interacts with the native community. *Gracilaria vermiculophylla* was collected from nine locations on the west coast of Sweden, four locations in Denmark and four locations in Virginia on the east cost of the United States. Specimens of *G. vermiculophylla* were collected at a water depth between 0.1 and 1 m, and at each location loose-lying and attached (if found), specimens were collected by hand. The specimens were gently lifted up above the water and swiftly placed in separate plastic bags and kept cold until arrival at the laboratory. All organisms were identified to lowest possible taxa. Abundance of animal individuals (N), number of taxa (S), algal biomass, Pielou’s evenness (J’ = H’ / log S) and Shannon-Wiener diversity (H’ = - $\Sigma p_i * \ln p_i$) were calculated. Diversity and evenness were based on the animal assemblage only. Attachment status of *G. vermiculophylla* and associated flora and fauna were compared for the three countries. Correlation between number of species, number of individuals and the amount of associated algae and plants were analyzed with two-tailed Pearson’s correlation coefficient.

The sampling technique did not allow us to capture all motile animals. Alternative methods for future studies would be to use mesh bags under water or preferably drop traps (Pihl and Rosenberg 1982).

## Event tree describing potential impacts of *Gracilaria vermiculophylla*

To illustrate the risk of further dispersal and the potential impact of *Gracilaria vermiculophylla* on the ecosystem we used an event tree. An event tree enhances the possibilities to consider most of the likely ways in which an initiating event can affect a system. Event tree analysis is based on binary logic, in which an event succeeds or fails. It depicts consequences arising from an undesired event. Our tree begins with the initiating event of *G. vermiculophylla* being introduced into the Kattegat and/or the Belt Sea. The initiating event is followed through a series of possible paths, visualizing all the events. As the number of events increases, the picture fans out like the branches of a tree.

## Assessing the impact of *Gracilaria vermiculophylla* (Paper IV)

The most straightforward method to measure the impact of non-indigenous species is to perform competition experiments. However, these do not account for the many direct and indirect ways the species affect each other, and also it is less desirable to add a NIS to a system, even if it already exists there. A model for impact assessment that includes both direct and indirect effects of one species on another was developed in **Paper IV**. The model was applied on two sets of non-indigenous species with the population size of one native species each as the endpoint. These were the non-indigenous marine alga *Gracilaria vermiculophylla* affecting the native angiosperm *Zostera marina* Linnaeus and the non-indigenous freshwater plant *Nymphoides peltata* (SG Gmelin) O. Kuntze affecting the native macrophyte *Alisma wahlenbergii* (OR Holmberg) Juzepczuk. A conceptual model that depicts the major ways that the non-

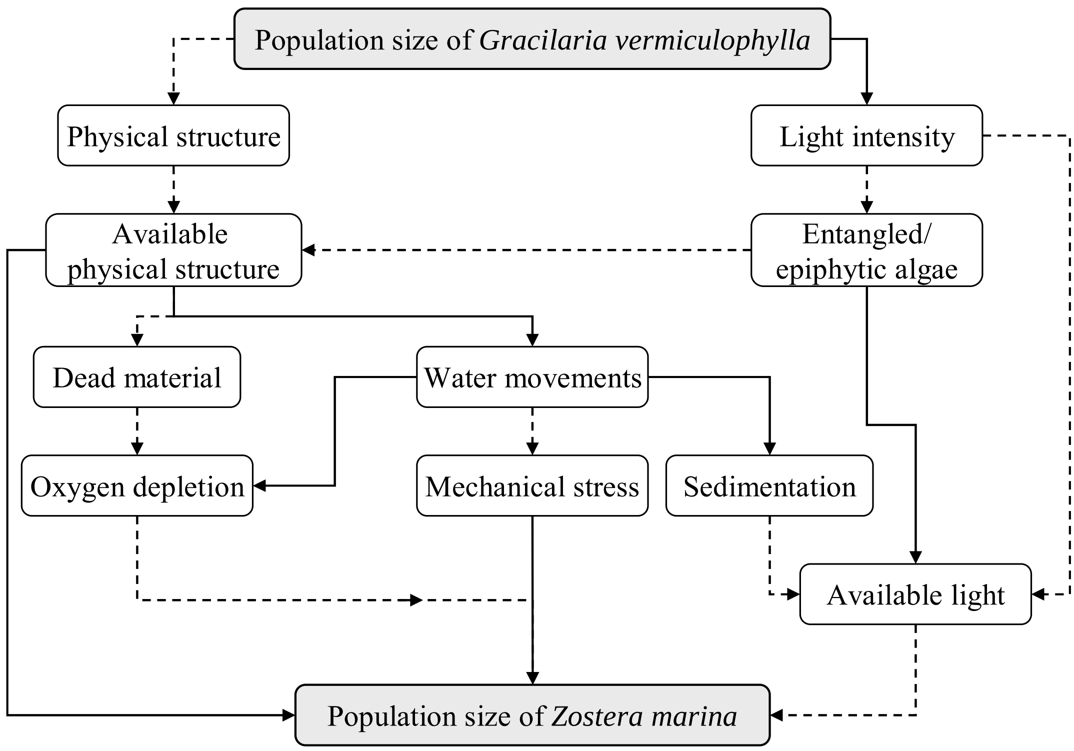



Figure 7. Conceptual model for *Gracilaria vermiculophylla*. Solid arrows denote negative causal links and dashed arrows denote positive causal links.

indigenous species affect the native species was constructed for each species pair. The conceptual model for *G. vermiculophylla* and *Z. marina* is shown in Figure 7. Both positive and negative links are depicted. E.g. if the water movement increases the mechanical stress will increase (positive link). If the mechanical stress increases the population size of *Z. marina* will decrease but if the mechanical stress decreases the population size will increase (negative link).

The two models were thereafter condensed to a single conceptual model with reduced complexity (Figure 8). The components distinguished in the common conceptual model most likely becoming affected by the NIS and causing an effect on the endpoint species were; light, water movements, sediment and epiphytic algae. The conceptual model was thereafter transformed into a quantitative model by giving all the causal relations functional expressions, ranging from mathematical functions (from established models), to simple functions expressing directions or categorical relations. Since the complexity of the model increases rapidly with the number of components, only the most obvious and well motivated components with possible generalisations for macroalgae and plants were included in the model. The impact was measured as change in abundance of the endpoint species. This was divided into three categories: unacceptable decrease, small decrease and an increase. For *Z. marina* the impact was set to be negative when exceeding a threshold of 10% decrease in biomass. Variability was included in the model as stochasticity in causal relationships and as daily variability in components. By running the model, with different sets of values for the components in Monte Carlo simulations, different densities of the non-indigenous species were gained. The outputs were impact curves depicting the relationship between the biomass of the non-indigenous species and change in the biomass of the native species.

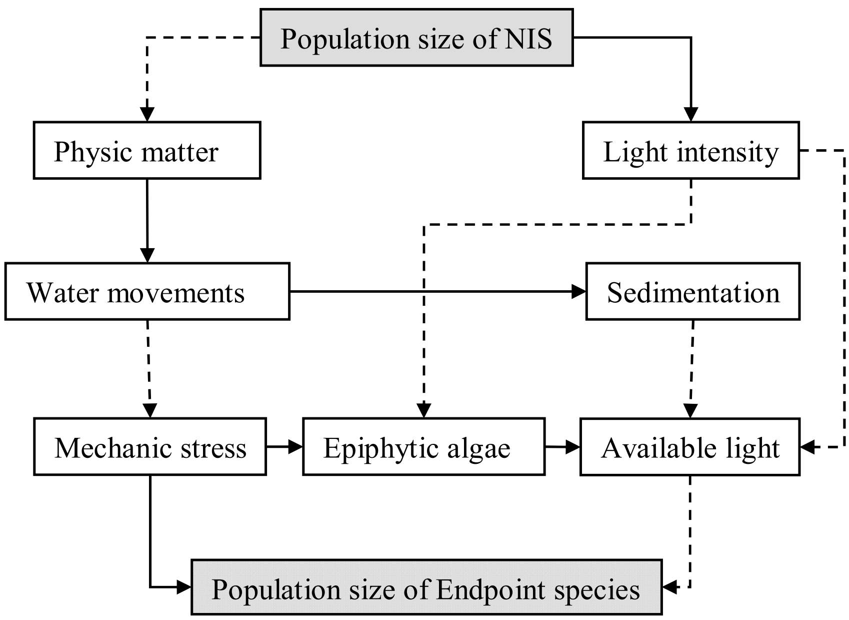



Figure 8. Combined conceptual model showing components and links that create a path from the NIS *Gracilaria vermiculophylla* to the endpoint *Zostera marina*. Solid arrows denote negative correlations and dashed arrows positive correlations.

## RESULTS

### Habitat modification (Paper I)

The habitat modifications of introduced species occur both on small and large scales. The physical and chemical changes of natural environments can roughly be divided into; 1) changes of the substrate, 2) changes of habitat architecture, 3) effects on foraging, 4) changes in light climate, 5) changes in nutrient availability and 6) changes due to allelopathy and toxic compounds (some effects are mentioned in Table 3).

1) There are several ways in which introduced species directly change the physical condition of the substrate. The most obvious modifications are by animals (crabs, polychaetes, mussels) digging burrows in the sediments, which also may cause erosion of shore banks. The digging by a NIS can also increase the bioturbation leading to oxygenation of anoxic sediments and hence better denitrification. Introduced plants stabilize sediments with their roots, giving protection from infrequent wave disturbance. The presence of rooted plants also increases the oxidizing capacity of sediments and enhances total microbial mineralization in comparison to in unvegetated areas. Other NIS indirectly change the physical condition of the substrate; among these are mat-forming macroalgae and saltmarsh species, which trap suspended and depositing particles, which can change the grain size of the sediment. Benthic microalgae also to a large extent stabilize the sediments, and if introduced by e.g. ballast sediment they may have an impact, although to my knowledge there is no published description of an introduced microalga doing so. Some introduced suspension-feeding gastropods have a very high food intake and considerably influences the biogeochemical cycle, through depositing biogenic silicate via faeces and pseudofaeces.

2) Many NIS (algae, plants and sessile animals) influence the architecture on both rocky and sandy bottoms. When large sessile organisms colonize previously unvegetated areas, they may change the water movements, which in turn can affect the substrate conditions, both physically and chemically. Depending on the morphology of the introduced algae they can transform a complex three-dimensional system into an almost two-dimensional one or vice versa. The establishment of one introduced calcareous crust alga makes it difficult for other algae to recolonize, which changes the dimensions of the ecosystem. Reef-building animals in general, including molluscs, are also obvious examples of organisms casing changes in the habitat. 3) Dense cover of algal NIS on previously more or less barren substrates, or in areas where vegetation easily permitted access to the sediments, can negatively affect the foraging of many animals. Dense belts or mats of NIS on the seabed may also, in general, reduce the amount of suspended particles from reaching the seabed, which could imply less food for benthic suspension- and deposit-feeders. 4) The large filtering capacities of introduced mussels have resulted in positive environmental effects by clearing water masses that were turbid before they established. On the other hand, dense belts or mats of introduced algae may imply a shading effect on other algae. 5) If long-lived introduced algae establish, they may decrease nutrient availability for other primary producer by storing nutrients and trace elements for longer periods. On the other hand,

algal NIS with large surface:volume ratios can influence nutrient availability by their rapid uptake rates. 6) Many introduced algae have toxic secondary metabolites, which directly affect other species, by causing chlorosis, necrosis, inhibit settlement and germination of various other algae, deterring settling of epibionts and inhibits settling of larvae.

Table 3. Examples of introduced organisms' action and their ways of modifying the habitat.

| Organism | Action | Effect/Result |
|---|---|---|
| **Algae** | 1) Toxic secondary metabolites and allelopathic substances | • Cause chlorosis and necrosis[1]<br>• Inhibit settling of larvae[2] |
| | 2) Buoyancy | • Move oysters/mussels to new areas |
| | 3) Mat formation and development of dense cover | • Trap sediment[3,4]<br>• Less amount of suspended particles reaches the seabed, leading to less food for benthic suspension- and deposit-feeders[3,5]<br>• Shading[6,7]<br>• Negatively affect the foraging of many animals[8] |
| **Algae & Plants** | 1) Growth | • Change the habitat from three-dimensional to almost two-dimensional or the opposite (in barren areas)[9,10,11,12] |
| **Plants** | 1) Growth | • Stabilize sediments with their roots[13]<br>• Increase the oxidizing capacity of sediments[5]<br>• Reduction of wave disturbances[13]<br>• Transformation of beaches to marshes[14-17] |
| **Mangroves** | 1) Growth | • Stabilize sediments with their roots and protect[18] against erosion, resulting in improved water quality[19] |
| **Algae, plants and filter-feeding bivalves** | 1) Absorption and storage of nutrients and trace elements (and bio-remediation)[20,21] | • Decrease nutrient availability for other primary producer<br>• Removal of pollutions (heavy metals, chemicals) |
| **Large sessile organisms** | 1) Blocks water movements | • Change in water movements<br>• Affect the substrate conditions both physically and chemically |
| **Molluscs** | 1) Presence | • Substrate for epibionts[22]<br>• Shelter[22] |
| | 2) Filtration[17,23] | • Removal of nutrients<br>• Clearer water<br>• Less turbidity<br>• Increased light penetration |
| | 3) Bulldozing | • Removing sediments[24] |
| | 4) Nutrients release from the sediment and the clams | • Promote phytoplankton blooms[25] |
| **Crabs, Polychaetes & Mussels** | 1) Digging | • Collapse and erosion of shore banks<br>• Increased bioturbation[26]<br>• Aeration of sediment |
| **Polychaetes** | 1) Reef-building | • Altered water flow[27]<br>• Altered sedimentation[27] |
| **Gastropods** | 1) Depositing biogenic silicate via faeces and pseudofaeces | • Influence the biogeochemical cycle[28] |
| **Ascidians** | 1) Creating dense three-dimensional matrices | • Modify the intertidal habitat structure[29] |

For complete references see the reference list in **Paper I;** [1]Guerriero et al. (1992), [2]Hellio et al. (2004), [3]Piazzi & Cinelli (2000), [4]Piazzi et al. (2005), [5]Gribsholt & Kristensen (2002), [6]Britton-Simmons (2004), [7]Sánchez et al. (2005), [8]Levi & Francour (2004), [9]Boudouresque (2002), [10]Wallentinus (2002), [11]Wallentinus (2006a), [12]Wallentinus (2006b), [13]Posey (1988), [14]Bruno (2000), [15]Bruno & Kennedy (2000), [16]Chen et al. (2004), [17]Cuddington & Hastings (2004), [18]Allen (1998), [19]Rönnbäck (1999), [20]Lindahl et al. (2005), [21]Schuenhoff et al. (2006), [22]Gutiérrez et al. (2003), [23]Hecky et al. (2004), [24]Bertness (1984), [25]Bartoli et al. (2001), [26]Olenin & Leppäkoski (1999), [27]Schwindt et al. (2004), [28]Ragueneau et al. (2005), [29]Castilla et al. (2004).

## Species traits of macroalgae (Paper II)

In general, the results from the ranking of species traits showed that introduced species presented a higher risk (of being dispersed, becoming established and having an ecological impact) than natives, and introduced invasive a higher risk than introduced non-invasive species. Several interesting trends can be seen. The largest differences were found for transportation, geographical distribution and habitat impact, where introduced and introduced invasive species ranked high. Important traits, (common for many introduced species), that facilitate both dispersal and establishment is the ability to grow on a wide variety of substrates, from sand to artificial surfaces, as well as on live molluscs. Being able to grow on different substrates is also of importance for habitat effects. No differences were seen between introduced and native species in the categories survival time out of water, grazing and defence mechanisms, and life span. The results for the categories salinity range, temperature range and growth strategies showed no differences between introduced invasive and introduced non-invasive species. In contrast to the trend seen in all categories with a higher ranking for introduced and introduced invasive species, the category survival time out of water rendered introduced non-invasive species higher than introduced invasive species. Invasive species have a large impact on the habitat, through development of a dense cover, suppression of other species, and their distribution in a large depth range.

To check how well the qualitative ranking worked we summed all the categories to gain the species with the overall highest risk. This returned fifteen of the 26 introduced species listed as invasive among the 20 highest ranked. The top five most hazardous species when summarizing the categories were (in descending order) *Codium fragile* ssp. *tomentosoides, Caulerpa taxifolia, Undaria pinnatifida, Asparagopsis armata* and *Grateloupia doryphora* (valid name *G. turuturu*; Gavio and Fredrique 2002), all invasive.

## Ranking of *Gracilaria vermiculophylla*

When applying the same approach as in **Paper II** for *Gracilaria vermiculophylla*, and using the new information from tolerance experiments (this summary), *G. vermiculophylla* obtained the highest ranking among red algae in the category dispersal (0.83), shared second rank in the category ecological impact (0.74), but it was not among the eight highest ranked red algae in the category establishment (0.69). In total, of all the categories, it scored the highest (0.75) among the introduced red algae analysed, but ranked slightly lower than the two most invasive green algae, and was equal to the most invasive brown alga (for the ranking comparisons see Table 4 page 273 in **Paper II**). The score for each category is seen in Figure 9. *G. vermiculophylla* scored high in the categories: probability of being transported, survival time out of water, salinity range, reproductive mode and morphology.

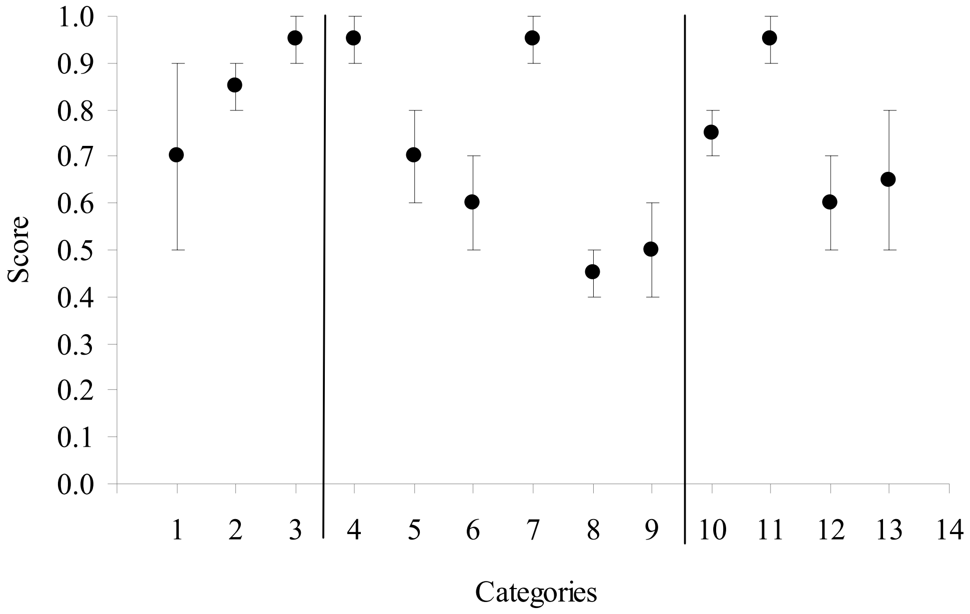



Figure 9. The ranking scores of *Gracilaria vermiculophylla* for dispersal (categories 1 – 3), establishment (4 – 9) and ecological impact (10 – 13), see Table 2 for categories. The symbol shows the average with minimum and maximum values.

### *Gracilaria vermiculophylla* surviving emerged conditions

In the storage treatment (in darkness and out of water) *Gracilaria vermiculophylla* had the same reddish-brown colour after, as it had before treatment. The shoots grew well, independent of treatment duration, and showed an exponential increase in size with time. The RGR for *experiment I* is shown in Figure 10. Comparison of growth between the three different locations (*experiment I*) in a two-way orthogonal ANOVA (with location as random and salinity as fixed factors) showed a significant difference between locations ($F_{2,54}$ = 50.983, p = 0.019) and a significant difference between salinities ($F_{1,54}$ = 21.599, p = 0.043), but no interaction was seen between location and salinity ($F_{2,54}$ = 0.532, p = 0.590). The significancy should be regarded with caution, since Cochran's test showed heterogeneity among variances and the data were not possible to transform. From day 17 of the experiment, fragmentation could be observed. The new fragments were 7.7 ± 0.6 mm long (mean ± StErr) the first time they were observed, and they all continued growing after they had been shed. The smallest fragment in this study was 0.9 mm. The average number of fragments produced from each shoot is also plotted in Figure 10.

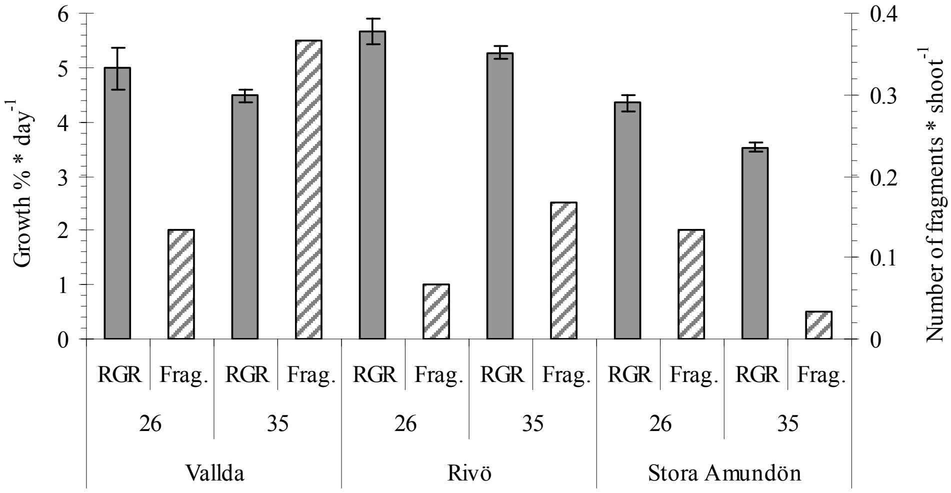



Figure 10. Relative growth rate in salinities of 26 and 35 of the shoots of *Gracilaria vermiculophylla* from Vallda, Rivö, and Stora Amundön treated for 40–47 days. The grey bars show the average value of the RGR ± StErr (n = 10). The average pooled number of fragments per shoot is plotted with striped bars (n = 30).

Cochran's test for *experiment II* showed homogeneity among variances and comparisons of algae stored for different durations with a one-way ANOVA (treatment time as a fixed factor) showed a significant difference in the growth ($F_{3,16}$ = 5.786, p = 0.0071). No correlation (r = 0.34) was seen with length of time. The RGR for the shoots treated for 4 to 175 days and average number of fragment per shoot are shown in Figure 11. Most fragments developed from the specimens that had been treated for 4 and 175 days.

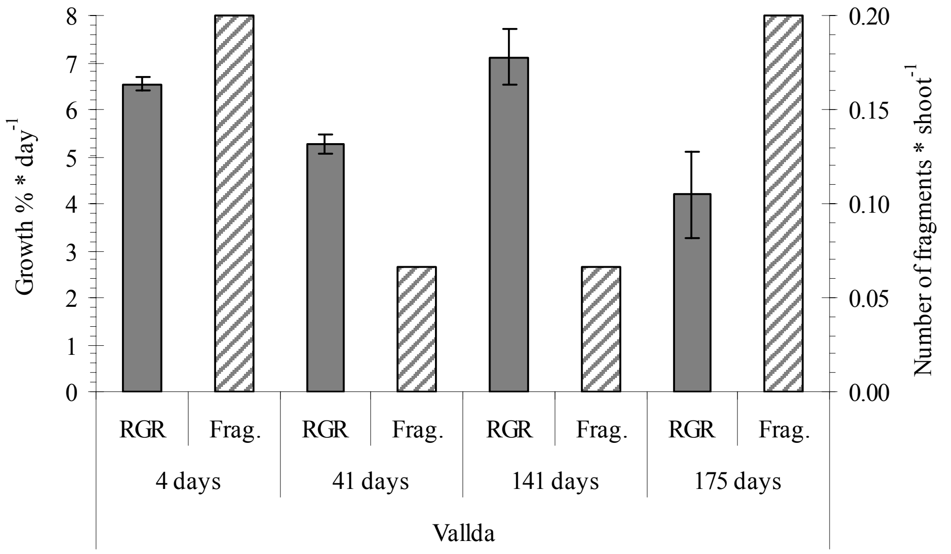



Figure 11. Relative growth rate for the four different treatment times for *Gracilaria vermiculophylla* from Vallda, grown in a salinity of 26. The grey bars show the average value of the RGR ± StErr (n = 5). The average pooled number of fragment per shoot is plotted with striped bars (n = 15).

After 14 days of growth, the shoots started to develop small discoid holdfasts at the base of their main frond (Figure 12). A small number of epiphytes were found on some of the algae; these were the green alga *Ulothrix* sp. (with cylindrical shaped cells, between 10.1 to 12.6 µm in length and width, and similar in morphology to the two *Ulothrix* species found in brackish water), the red alga *Colaconema daviesii* (Dillwyn) Stegenga, and diatoms.

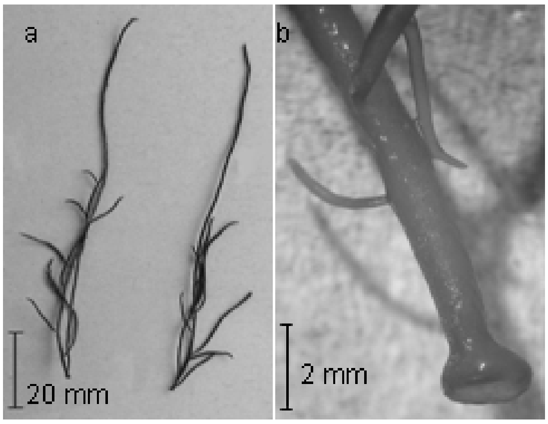



Figure 12. *Gracilaria vermiculophylla* after 32 days of growth in a salinity of 26. a) The small discoid holdfasts can be seen at the base of the shoots. b) Detail of holdfast.

### Salinity tolerance of *Gracilaria vermiculophylla*

The relative growth rates for *Gracilaria vermiculophylla* at the different salinities are given in Figure 13. The shoots grew in all tested salinities. Cochran's test showed homogenous variances. There was no significant difference between salinities (ANOVA, $F_{4,24} = 1.242$, $p = 0.325$). Some fragmentation was noted, on average 0.13 fragments $shoot^{-1}$.

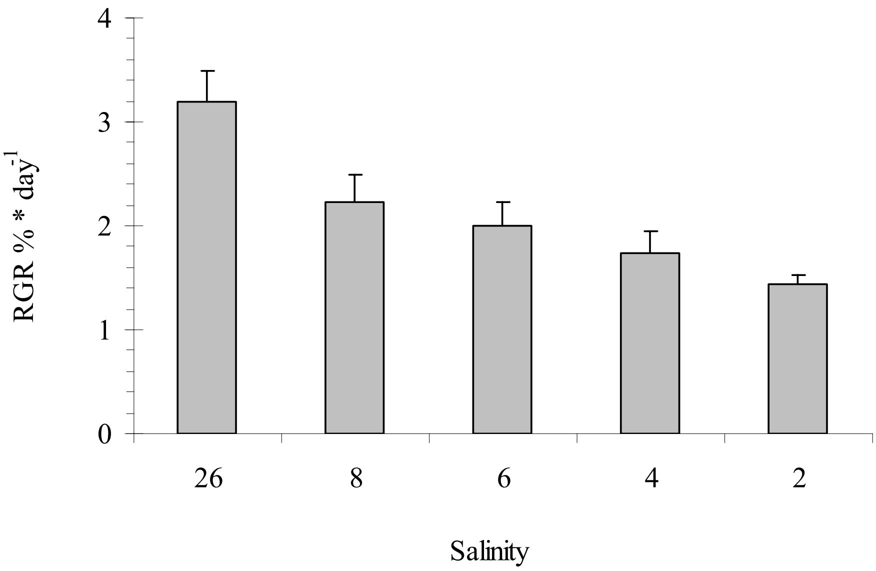



Figure 13. Average relative growth rate ± StErr (n = 5) for *Gracilaria vermiculophylla* grown in different salinities.

In the salinities 26 and 8 a few shoots died, probably due to bad conditions of the shoots at start. Also some necrosis occurred, mostly in the tips of the shoots and in some cases in the central parts. Necrosis occurred in the salinities of 26, 8 and 2 (Table 4). At start no epiphytes could be seen on the shoots, but during the experiment the green alga *Ulotrix* sp. (morphological characters as described in the previous section) developed rapidly with a gradient having the highest abundance in the highest salinity and least in the lowest salinity. The experiment was terminated due to the growth of the epiphytes.

Table 4. Number of dead shoots and shoots with necrosis of *Gracilaria vermiculophylla* in the different salinities (n=15).

| **Salinity** | **26** | **8** | **6** | **4** | **2** |
|---|---|---|---|---|---|
| Dead | 5 | 2 | 0 | 0 | 0 |
| Necrosis | 5 | 1 | 0 | 0 | 1 |

### The spread of *Gracilaria vermiculophylla* (Paper III)

In only two years time *Gracilaria vermiculophylla* had spread 80 km to the north and 70 km to the south, from its original discovery location in the Göteborg archipelago, Sweden (Figure 14). *G. vermiculophylla* was found in 35 of the more than 50 locations that were visited. It was primarily found in soft-bottom bays at depths of less than 1 m (however, it can also occur deeper). In 2003, the majority of the specimens were unattached, often developing dense mats, while in 2005, specimens attached to stones and mussels were almost as common. The unattached specimens were often partly covered with sand or mud. During the survey, both sexual (female and male gametophytes) and asexual individuals (tetrasporophytes) were found, as well as specimens with tetrasporangia in combination with either spermatangia or cystocarps.

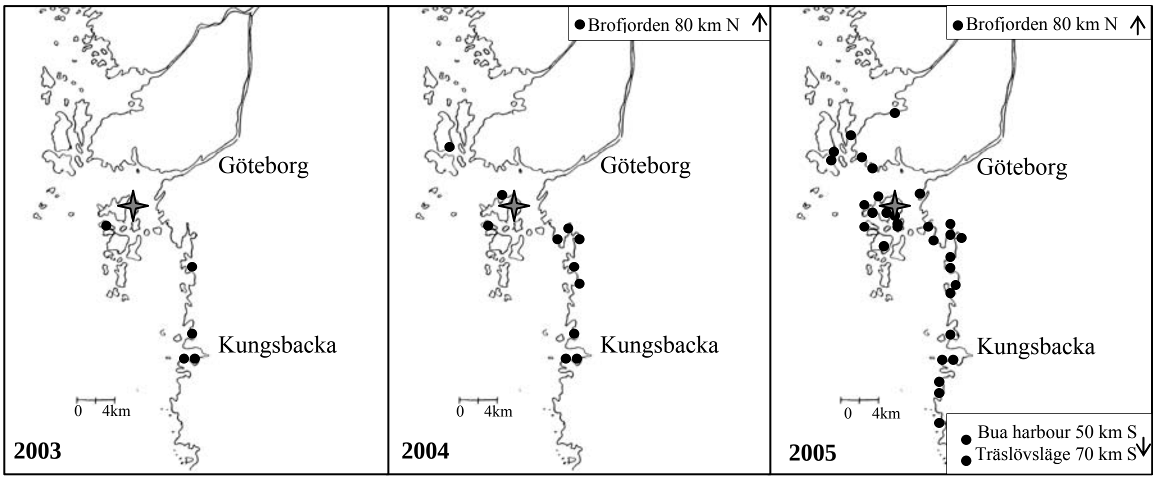



Figure 14. Spread of *Gracilaria vermiculophylla* on the Swedish west coast 2003-2005. Grey star denotes the first location of discovery from which the dispersal is measured. The northern-most report is from Brofjorden 80 km north and the southern-most is from Träslövsläge 70 km south. (Data from Brofjorden, L-H Jenneborg pers. comm. and the three northern-most records on the mainland in the Göteborg area from Ahlgren 2005a).

## The community associated with *Gracilaria vermiculophylla* (Paper III)

*Gracilaria vermiculophylla* was among the five most abundant macroalgae and plants at all 17 sampled locations in Sweden, Denmark and eastern USA, and was the most abundant at 14 locations. Both attached and loose-lying specimens were found but not at all locations. *G. vermiculophylla* was found attached to stones, gastropods, bivalves and a piece of glass. In Virginia all specimens were found incorporated into the tubes of the polychaete *Diopatra cuprea* (Bosc) (Thomsen and McGlathery 2005) and some of the specimens in Denmark were attached to mussels via byssal threads. The biomass of the unattached specimens was larger than for attached specimens.

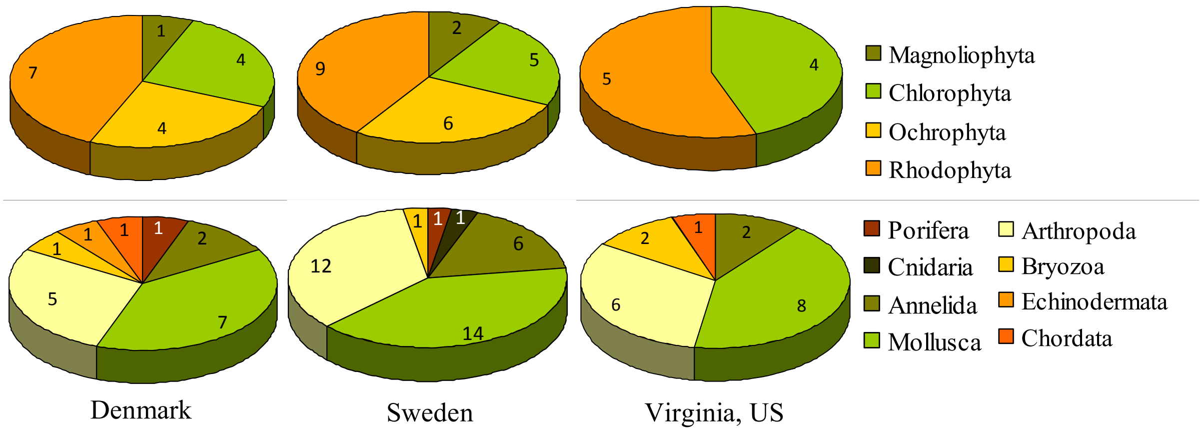



Figure 15. Number of taxa in each phylum for Denmark, Sweden and the United States.

A total of 92 taxa was found attached on or entangled in *G. vermiculophylla*. The associated primary producers with the largest biomasses were *Ulva* sp. (including former *Enteromorpha*), *Zostera marina*, *Fucus vesiculosus* Linnaeus and *Bryopsis plumosa* (Hudson) C. Agardh. The samples from Virginia contained significantly higher biomasses of associated algae and plants than the Scandinavian samples. For number of phyla and lower taxa see Figure 15. Of the 30 algal taxa found, only 9 were attached to the thallus of *G. vermiculophylla* and the rest were entangled. The most abundant animals were *Mytilus edulis* Linnaeus, Amphipoda, *Pusillina sarsi* Lovén and *Pagarus* sp. As expected, *G. vermiculophylla* from the three countries sustained different associated animal taxa. This study did not reveal any trends for the richness, diversity or evenness between attached and loose-lying *G. vermiculophylla*. The numbers of faunal individuals, the amount of associated primary producers and the number of taxa of flora and fauna were more numerous on non-fertile *G. vermiculophylla*, while the biomass of the *G. vermiculophylla* specimens were larger for the reproductive specimens.

## Event tree describing potential impacts of *Gracilaria vermiculophylla*

The event tree begins with the initiating event of *Gracilaria vermiculophylla* being introduced into the Kattegat and/or the Belt Sea (Figure 16). A plausible vector of dispersal is the ballast water of a ship, and for Göteborg the international dredgers used in the harbour cannot be ruled out, while mollusc movements seem less likely. It could

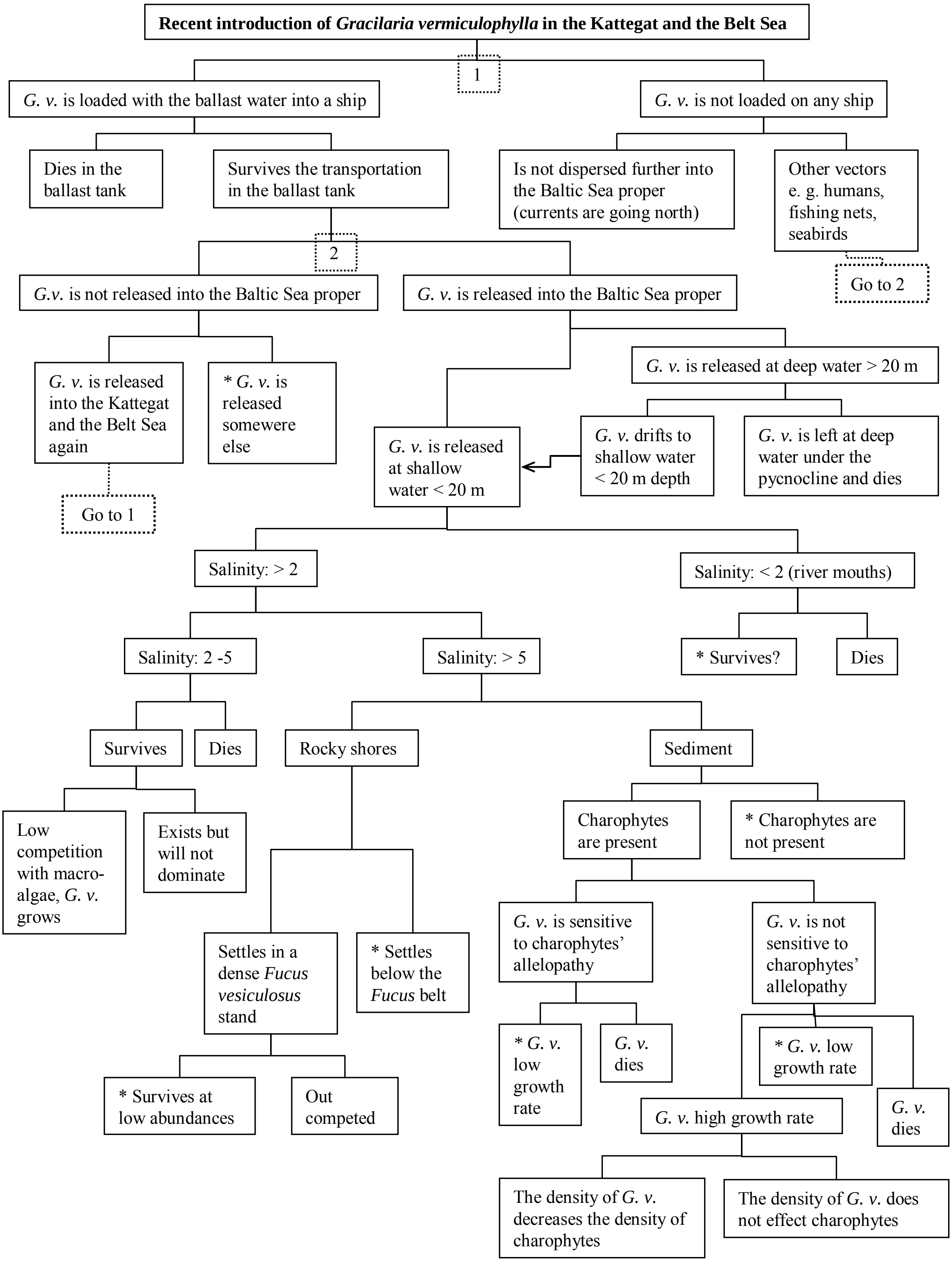



Figure 16. Event tree for the spread of *Gracilaria vermiculophylla* (*G.v.*) to the Baltic Sea proper and its consequences. Steps marked with a * can be developed further.

also be spread with any other human vector such as small boats, with currents or by migrating seabirds. If it survives the transportation, there is a possibility that it will be released into the Baltic proper, inside the sills of Darss and Limhamn, where it is not yet known to be present. A release at rocky shores and soft bottoms would have different outcomes. In both cases the salinity would have a determining role of the growth rate of the species. Suppose that *G. vermiculophylla* ends up in a stand of Charophytes. Provided that the salinity is not too low, and that *G. vermiculophylla* is not sensitive to the allelochemicals emitted from the Charophytes (Berger and Schagerl 2003; Mulderij et al. 2003), the new population could develop a dense cover which could shade and diminish the survival chances of the Charophytes, some of those being red-listed.

### Assessing the impact of *Gracilaria vermiculophylla* (Paper IV)

In **Paper IV** all steps for assessing impact by model simulations are shown; from the choice of endpoint, through conceptual model building and quantification of an assessment model, to the compilation of the output into an interpretable graph. The graphs of the impact (impact curves) caused by *Gracilaria vermiculophylla* on *Z. marina* showed that negative effects were likely at most abundances of *G. vermiculophylla*. The probability of an unacceptable impact on *Z. marina* increased rapidly with the increasing abundance of *G. vermiculophylla* (Figure 17a). Above a *G. vermiculophylla* biomass of 0.01 kg DW $m^{-2}$ negative effects were the most likely outcome. At lower abundances, *G. vermiculophylla* was not likely to affect *Z. marina.* Although the probabilities for positive effects were low, they existed at all abundances of *G. vermiculophylla.* A factor strongly influencing the result of the model was water velocity. When velocities were fixed, the probability of a negative impact increased (Figure 17b) and there was no positive impact.

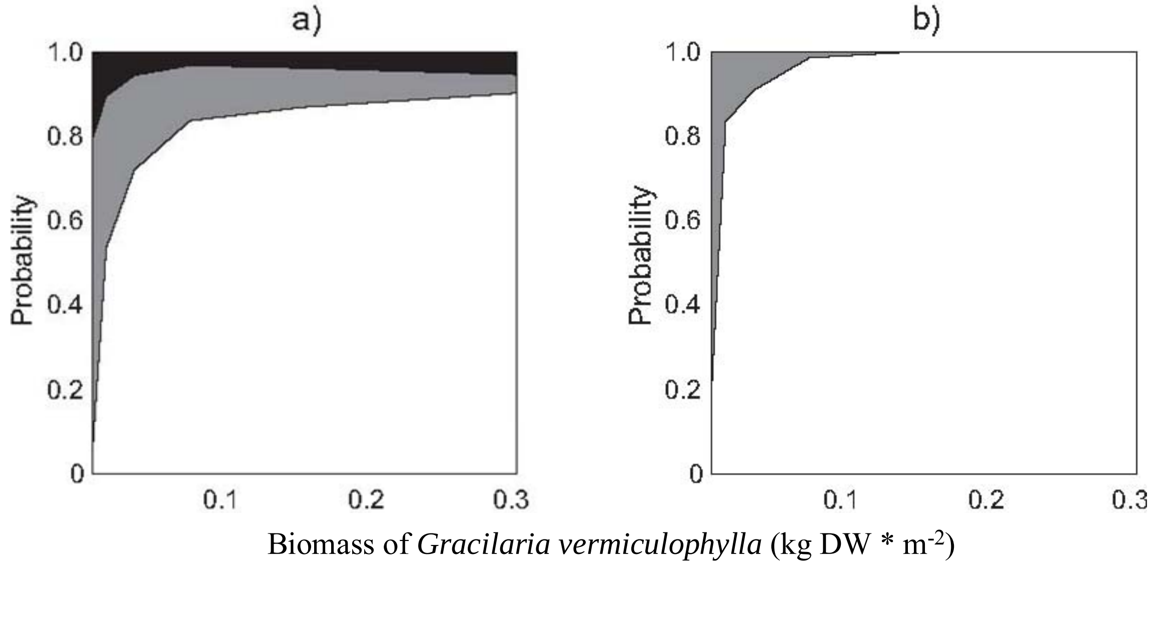



Figure 17. Impact curves showing the probability of a negative impact (white area), no impact (grey area) and a positive impact (black area) on *Zostera marina* caused by *Gracilaria vermiculophylla* using a) the full model and b) the model with fixed velocity.

The uncertainty of the impact curve was generally large but decreased for the negative impact with the increase of the biomass of *G. vermiculophylla.* Changing the threshold value in the impact definition, z, from 10% to 50% resulted in a less steep slope of the impact curve for a negative impact, and increased the uncertainty (Figure 18). The impact curves could, in accordance with dose–response curves, be used to find a highest acceptable NIS biomass in a region by determining an acceptable threshold for the probability of a negative impact. For instance, if the accepted risk is 50% (with z = 10%), the highest acceptable mean seasonal biomass of *G. vermiculophylla* is 0.02 kg DW $m^{-2}$. However, if we choose to account for the uncertainty and thus use the conservative bounds derived from maximum conditional probabilities, the highest acceptable biomass would be 0.01 kg DW $m^{-2}$.

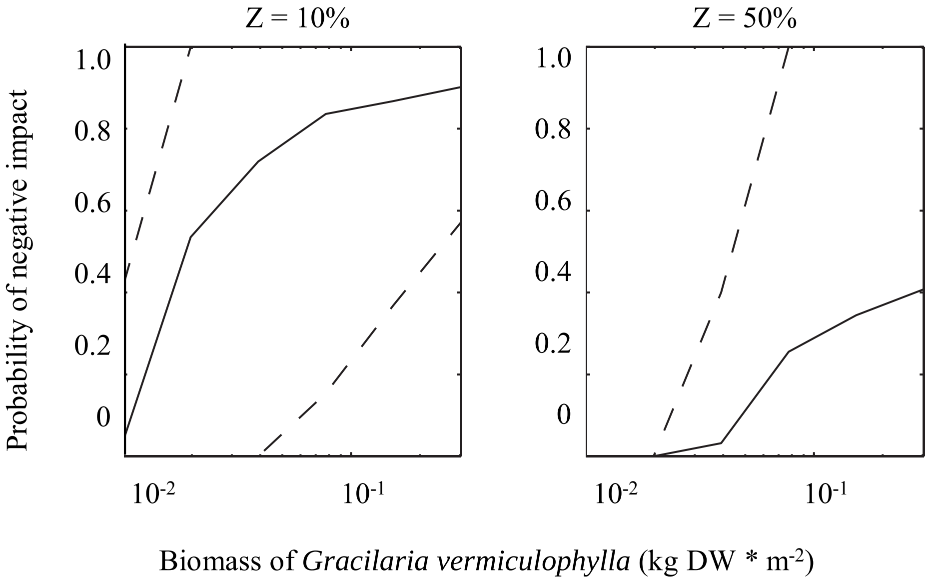



Figure 18. Impact curves for a negative impact by *Gracilaria vermiculophylla* on *Zostera marina* and different values of the threshold value z. The curves are the mean (solid line), the minimum and maximum (dashed lines) probability of a negative impact in each assessment. Note the logarithmical scale on the x-axis.

# DISCUSSION

The earth is shaped by human activities and one of them is non-indigenous species. This is the second of five serious threats to the present state of the ecosystem and biodiversity, induced by humans (Wilcove et al. 1998; Genovesi and Shine 2003). We are getting more and more aware that we have to act now, if we want to protect our planet from impoverishment. Except from changing our behaviour and implementing e.g. ballast water treatment it is desirable to be able to predict which species will invade and which habitats will be invaded by non-indigenous species. The optimal solution would be to prohibit intentional introduction of non-indigenous species but this is not realistic due to the great economical loss.

Marine macroalgae and plants, as well as sessile animals, have a profound importance for creating the architectural structure of the ecosystem in the photic zone, as well as along the shoreline. Hence, introduced species play a fundamental role, when occurring in high abundances and acting as habitat modifiers (**Paper I**). The presence of introduced algae in previous unvegetated soft-bottom areas provides habitats for a large variety of plants and animals. Also on rocky shores introduced macroalgae may be beneficial for native animals (Bulleri et al. 2006). Non-indigenous algal mats have been shown to cause considerable habitat modifications for the benthic faunal community. They also form physical barriers for many species by capturing settling larvae (Ólafsson 1988; Bonsdorff 1992), changing water movements, preventing light from penetrating down to the microphytobenthic communities in the sediment, and by reduceing the amount of food for animals depending on suspended or deposited particles. Also canopy species such as *Sargassum muticum* can change the composition of the infaunal communities (Strong et al. 2006).

The quantification of species traits with interval arithmetic in **Paper II** is an easy approach to obtain a value for comparing different species or groups. Another advantage is that it allowed us to incorporate different levels of uncertainties (Hayes et al. 2003). The intervals of the categories we defined, gave us ranks that placed most of the invasive species high in the ranking, thus stating that our suggested intervals are plausible. If a species will score high in many of the categories, and also has salinity and temperature survival ranges that encompass that of the geographical area of interest, it may pose a high risk of becoming invasive. Since **Paper II** was written there have been some new introductions and some changes in the nomenclature have occurred (see Table 5). Even though several of these introductions were earlier than when we made the analyses in **Paper II**, they were not known to us. Some of the introductions not verified to species were known, but it was not possible to collect data on species traits.

Table 5. Non-indigenous macroalgae introduced into Europe, not included in **Paper II**. Number in brackets denote year of introduction.

| Red algae | Brown algae | Green algae |
|---|---|---|
| *Hypnea musciformis* (Wulfen) J.V. Lamouroux [1] | *Botrytella* sp. (1919)[2] | *Codium vermilara* (Olivi) Chiaje (1993-1995)[9] |
| *Colaconema dasyae* (F.S. Collins) Stegenga, I. Mol, Prud'homme van Reine & Lokhorst (1953)[2] | *Myriactula* sp. (1980)[2] | *Caulerpa webbiana* Montagne (2002)[9] |
| *Acrochaetium densum* (K.M. Drew) Papenfuss (1967)[2] | *Elachista* sp. (1993)[2] | *Batophora* sp. (2002)[10] |
| *Grateloupia* sp. *(1985)[3, 4] | *Dictyota ciliolata* Sonder *ex* Kützing (1995)[8] | *Prasiola* sp. (2002)[11] |
| *Laurencia majuscula* (Harvey) A.H.S. Lucas (1983-84)[3] | *Sorocarpus* sp. (1996)[3] | |
| *Laurencia chondrioides* Børgesen (1990)[3] | | |
| *Laurencia caduciramulosa* Masuda & Kawaguchi (1991)[3], (2002)[5] | | |
| *Gracilaria vermiculophylla* (Ohmi) Papenfuss (1996)[6], (2003)[7] | | |

* Was later in France identified as *G. asiatica* Kawaguchi & Wang. [1]Mediterranean Spain, ICES WGITMO (2006); [2]the Netherlands, Wolff (2005); [3]Italy, Wallentinus (in press); [4] Thau Lagoon, France, Verlaque et al. 2005; [5]Mediterranean France, Klein and Verlaque 2005; [6]Brittany, France, Rueness 2005; [7]Göteborg, Sweden, this thesis; [8]South Atlantic and Mediterranean Spain, Rull Lluch et al. 2007; [9]the Azores, Cardigos (2006); [10]Taranto, Italy, ICES WGITMO (2003); [11]Venice, Italy, ICES WGITMO (2006).

The following species listed in **Paper II** have been revised and changed affinities according to Guiry and Guiry (2007); Red algae: *Grateloupia filicina* var. *luxurians* is now *G. subpectinata* Holmes (but see also Verlaque et al. 2005), *Polysiphonia harveyi* is now *Neosiphonia harveyi* (Bailey) Kim, Choi, Guiry & Saunders, *Prionitis patens* is now *Grateloupia patens* (Okamura) Kawaguchi & Wang; Brown algae: *Alaria grandiflora* is now included in *A. esculenta* (Linnaeus) Greville, *Laminaria japonica* is now *Saccharina japonica* (Areschoug) Lane, Mayes, Druehl & Saunders, *Laminaria ochotensis* is now *Saccharina ochotensis* (Miyabe) Lane, Mayes, Druehl & Saunders; Green alga: *Caulerpa racemosa* refers to *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque. N.B. The introduced red alga *Antithamnion pectinatum* is now considered to be *A. nipponicum* Yamada & Inagaki in the introduced areas (for details see Cho et al. 2005). *Caulacanthus okamurae* Yamada has recently been introduced in the United Kingdom (verified by molecular analysis, ICES WGITMO 2006) and it might be the same alga as *C. ustulatus* (Mertens *ex* Turner) Kützing reported elsewhere in Europe and on the Pacific coast of North America.

The categories, used in **Paper II**, do not include all categories that would be of interest to compare. The reason for this is that very little information was found for most species for the other categories. Other categories that would be interesting to include, in a larger study, are *survival time in darkness*, which is crucial for survival in the northern parts of Europe, and also for the survival in ballast water tanks and *presence of pathogens and parasites*. Another character, which probably is important, but more difficult to obtain data for, is the matching of temperature and day length, where a mismatch often leads to loss of fertility (Breeman et al. 1988; Guiry and Dawes 1992), but the species may still survive through fragmentation.

The high ranking of *G. vermiculophylla* (when applying the method in **Paper II**) indicates that this species might have a large impact on its new environment. It is euryhaline, surviving salinities from 2 to 60 (this thesis; Yokoya et al. 1999) and can reach a growth rate of 22% $day^{-1}$ (at 25°C and a salinity of 30) (Yokoya et al. 1999; for more results see Raikar et al. 2001; Rueness 2005). The significantly lower growth rate in my experiment was most probably due to the low temperature (11.5 °C). Generally, a decrease in salinity, besides loss of ions, results in an increase in cell volume and turgor with a need of osmotic adjustment, if the high turgor should not cause damage to membranes, organelles and enzymes (Kirst 1989). Since *G. vermiculophylla* survives and grows in a wide range of salinities, it must be very efficient to adjust the osmotic potential. Also other species of *Gracilaria* have been found to tolerate a wide salinity range (e.g. Yu and Pedersén 1990; Ekman et al. 1991). High activities of the enzyme Galase (an α-galactosidase which can break down floridoside), have been found in *Gracilaria* species when grown in low-saline media, suggesting that the enzyme may have a role in osmoregulation (Yu and Pedersén 1990). *G. vermiculophylla* also seems to be tolerant of being emerged, surviving a dehydration of up to 17 % without effecting the growth notably (Nyberg & Wallentinus, unpublished).

Growth and survival experiments with *G. vermiculophylla* have been performed in the irradiance interval of 20-266 µmol photons $m^{-2}s^{-1}$, with maximum growth at the higher irradiances (Yokoya et al. 1999; this thesis). All these laboratory irradiance levels are far below those experienced at less than 1 m water depth in spring to autumn in Sweden. Intertidal algae will experience even higher levels, when emerged during low-water periods, indicating a broader tolerance for light than seen in earlier studies. However, in an outdoor experiment we found that *G. vermiculophylla* had a lower growth rate in high irradiances (≈1000 µmol photons $m^{-2}s^{-1}$) and high UVA-radiation (20 W $m^{-2}$) compared to in the laboratory experiments in 266 µmol photons $m^{-2}s^{-1}$ which was probably due to the UV radiation. It tolerated these high solar irradiances significantly better than the native *G. gracilis* and equally as well as *Fucus vesiculosus* (Nyberg & Wulff unpublished). *G. vermiculophylla* would therefore be a strong competitor for space with these native species in shallow areas in Sweden.

Tolerance and resistance to darkness is also an advantage of *G. vermiculophylla*, which survived more than 5 months in darkness without any notable effect. In comparison, the gametophytes of *Undaria pinnatifida* (Harvey) Suringar can survive seven months in darkness (Kim and Nam 1997). Lüder and co-authors (2002) suggested that *Palmaria decipiens* (Reinsch) R.W. Ricker probably endured darkness by using accumulated floridean starch. This could also be a factor in the ability of *G. vermiculophylla* to survive a long time away from light and water. The tolerances to darkness and ”dehydration” indicate that *G. vermiculophylla* would survive long journeys entrapped in protected areas of a vessel with high air humidity. *G. vermiculophylla* is in other words a very tolerant species and this tolerance to environmental fluctuations and extremes, promotes the success of the species, when introduced into new areas and becoming established there. Another trait that facilitates the success of *G. vermiculophylla* is its ability to reproduce both sexually and asexually. On the west coast of Sweden tetrasporophytes and male and female gametophytes have been seen all year round (**Paper III,** pers. obs.). *G. vermiculophylla* also easily reproduces by developing fragments and these, even though as small as one millimetre, survives and continues growing after detachment. These results indicate that even small fragments carried in fishing nets, in ballast tanks, among diving equipment, or by migrating seabirds may lead to the introduction of the species into new areas. Grazing may increase the amount of produced fragments. Some of the native herbivores on the Swedish west coast graze *G. vermiculophylla*. These are: *Aplysia punctata* Cuvier, *Idotea granulosa* Rathke, *Littorina littorea* (Linnaeus) and nereid polychaetes (Gustafsson 2005; Thomsen et al. in press-a). Survival of thalli through the digestive system of the herbivores did not seem to be possible (Gustafsson 2005). Thus herbivores that do graze on *G. vermiculophylla* will not participate in the dispersal of the alga by its passage through their digestive systems.

The introduction of *G. vermiculophylla* adds structural complexity to a relatively homogenous system, which affects the soft bottom communities by providing new attachment sites, shelter and food for other organisms. This in turn may enhance the local diversity. The results in **Paper III** showed that *G. vermiculophylla* sustains a large taxonomic richness from primary producers to filter feeders, herbivores and predators. Many juvenile and young adult fish and crustaceans have been seen hiding and foraging in loose-lying bundles of *G. vermiculophylla* (Nyberg, pers. obs.), but were not documented in **Paper III** due to the sampling technique.

*Gracilaria vermiculophylla* was probably brought to Sweden by ships. Its further dispersal along the coast is most probably due to smaller vessels, such as fishing and leisure boats, releases from fishing tools, currents or by migrating seabirds. *G. vermiculophylla* has expanded its range in Sweden with 150 km in two years, which is quite rapid. It can be compared to 270 km in four years for the Japanese kelp *Undaria pinnatifida* along the south coast of England (Fletcher and Farrell 1998) and 15-17 km year$^{-1}$ for *Sargassum muticum* in Denmark (Stæhr et al. 2000). The spread of *G. vermiculophylla* will most certainly continue. According to the salinity experiments, *G. vermiculophylla* can easily survive the salinity along the coast of the Baltic Sea to the northernmost parts of the Bothnian Bay. Since the alga can survive in darkness for more than five months, the dark winters in the northern part of Scandinavia would probably not be a problem for its survival (nor would the capture in dark ballast tanks). Two abiotic factors that might limit the survival of the algae are the temperature and the ice coverage. However, it has survived several winters on the Swedish west coast. The results from using the method in **Paper II** and the results in **Paper IV** show that *G. vermiculophylla* have the potential to cause sever alterations in shallow ecosystem communities. According to these results and the state of *G. vermiculophylla* abroad it has the potential of becoming invasive in Sweden (Thomsen et al. in press-a).

Today no negative aspects of the introduction have been recorded in Sweden (but cf. Freshwater et al. 2006). However, since *G. vermiculophylla* often has been found growing in the same habitat as *Zostera noltii* Hornemann (Ahlgren 2005a), which is classified as ‘vulnerable’ (Gärdenfors 2005) and in eelgrass beds (*Zostera marina*, an important biotope for many species), there is an impending risk for future effects. Should *G. vermiculophylla* become established in the Baltic Sea, it may for example outcompete charophytes. Shallow-growing communities of sixteen charophytes are found in the Baltic Sea and in the Kattegat (Luther 1951; Blindow 2000). These species are already under major threat from eutrophication and pollution discharges (Blindow 2000). Two of the charophytes are red-listed as ‘endangered’, three as ‘vulnerable’ and one as ‘near threatened’ (Gärdenfors 2005). A topic worth addressing is that one of the red-listed species is the non-indigenous *Chara connivens*. This shows that after some time, in this case about 150 years, some non-indigenous species are regarded as native. In my opinion NIS that are abundant in there native area should not be included in the red-list.

In **Paper IV** we combined complex physical and biological processes into mathematical components described by measurable variables in order to acquire a quantitative model to predict the impact of a NIS on a native species. With this model it was possible to gain insight into the effect a NIS might have on a native species without knowing its direct effect on the endpoint species. The model was applied for two aquatic species with different growth strategies, but it could very well be parameterized for other species and environments. One of the purposes with the model in **Paper IV** was to evaluate if it was possible to create a model that could serve as a predictive tool for decision makers, since retrospective data on impacts often are absent. The impact-curve gained from the model functions as an excellent summary for risk evaluation. For future studies it would be interesting to evaluate the reliability of the model by using data from introductions where the impact is already known and measured in the field.

### *Laws and regulations*

Since NIS today are seen as one of the major threats to biodiversity they have become one of the primary concerns for biosecurity by many regulating authorities (Hewitt et al. 2005). The procedures to deal with NIS vary extensively and are often applied by each country individually even though species do not recognize the country boundaries that we humans have defined (Park 2004). To attain a sustainable environment in Sweden the Swedish Parliament has established 16 environmental quality objectives (see www.internat.naturvardsverket.se). Three of these objectives directly affect the marine environment and life therein. These are: “A balanced marine environment, flourishing coastal areas and archipelagos”, “Zero eutrophication” and “A rich diversity of plant and animal life”. In order to be able to fulfil the environmental quality objectives, the Swedish Environmental Protection Agency has decided on a policy for the control and management of NIS (Naturvårdsverket 1997). The Swedish legislation of NIS is today divided in different areas which main purposes are to protect agriculture, forestry, aquaculture, fisheries and human health. The Swedish Biodiversity Centre (CBM, Centrum för biologisk mångfald) has in a publication (CBM 2004) listed the rules and regulations of the European Union and Sweden and compared these to the guidelines of the Convention on Biological Diversity. Today there are no laws and regulations in Sweden that directly are written for the protection against non-native algae but the more generally written laws can be applicable for these as well (e.g. SFS 1998:179; SFS 1998:808; SFS 1998:899). For fish, crustaceans and molluscs there are several regulations that directly govern their introduction and use (e.g. FIFS 2001:3;

SFS 1994:1716; SFS 1994:1830; SJVS 2000:157). The Swedish Maritime Administration (Sjöfartsverket) is responsible for reducing the risks of introducing NIS with ballast water.

There are several international guidelines of how to attend the issue with introduced species and their impact. The Convention on Biological Diversity gives guidelines for the conservation of biodiversity (CBD 1992) and recommendations on how to prevent harm to biological diversity by invasive NIS is provided by the Bern Convention (Genovesi and Shine 2003) and the International Union for Conservation of Nature and Natural Resources (IUCN 2000). The International Council for the Exploration of the Sea has developed a code of practice for the introduction and transfer of marine organisms (ICES 2005). The document gives advice on the management of both intentional introductions and unintentional introductions associated with aquaculture species. The regulation of international commercial shipping, control and management of ballast water and sediments and the prevention of marine pollution is handled by the International Maritime Organization (IMO 2004). In a near future it will not be allowed to use antifouling paints containing organotin tributylin (TBT) on ships (IMO 2001) since this substance has a negative effect on oysters and whelks. The removal of TBT could lead to an increase of the amount of algae attached to the ship's hull and therefore also be a source of an intense spread of non-indigenous species.

### *Management aspects*

Intensive management actions with the intent to eradicate invasive species might work on short-term, but unless the entire species range is treated, there is a large risk for recolonization. If an eradication approach is taken it is also essential to deal with the vector responsible for the introduction (Schlaepfer et al. 2005). There are several examples of failed eradication efforts e.g. *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque in the Mediterranean (Ceccherelli and Piazzi 2005; Piazzi and Ceccherelli 2006). Due to the cost of eradications, especially if recolonizations are occurring, it is essential to perform a cost-benefit analysis. This process is reinforced if an interdisciplinary approach is used, involving biologists, ecologists, managers and national economists. Based on the results in this thesis, I think that *Gracilaria vermiculophylla* is here to stay (cf. Thomsen et al. in press-a). In areas of special importance, management should be undertaken to keep *G. vermiculophylla* at a low abundance. Due to the rapid and wide spread of *G. vermiculophylla*, a complete eradication would be a waste of resources. Nevertheless, would a mechanical eradication programme be used, the issue of fragmentation and regrowth of fragments need to be considered. Personally, I think that it would be valuable if unintentional introductions could be turned into something beneficial. In some countries *Gracilaria* species are cultivated and harvested for the agar industry (Chaoyuan et al. 1990). By integrating fish farming and *Gracilaria* cultivation a reduced nutrient waste and increased agar content in the algae are gained (Troell et al. 1997). This is an interesting thought to keep in mind if *G. vermiculophylla* would significantly increase its abundance in Sweden. However, the high salaries may render this aspect less plausible.

So, how should we respond to NIS? The Global Invasive Species Programme (GISP) has proposed an action plan divided into four major steps: 1) prevention, 2) early detection, 3) eradication and 4) control (assessment and management) (GISP 2001). The most efficient method to control NIS is to prevent their entry into a new area (IUCN 2000). If this does not work the second best option is an early detection. The early detection of potentially invasive species is crucial for the determination whether an eradication of the species is realistic or not (GISP 2001). Since many biological invasions are characterized by a relatively long lag time between initial introduction and subsequent population growth (Crooks 2005), the removal of a NIS population is most likely to succeed if control measures are undertaken at an early stage. However, in Sweden there are no monitoring programmes designed for detecting NIS, and hence early detection will only be achieved by the chance they turn up in other studies or are reported by the general public. Later, when the NIS have become more common, they might be recorded in other monitoring programmes.

Methods to remove/eradicate NIS involve mechanical removal (can be made by hand or with machines), chemical removal (e.g. using toxins, herbicides), biocontrol (e.g. grazing, parasites) and for vertebrates, hunting (GISP 2001). The mechanical method is the most target specific method but also the most labour intense. However, for several macroalgae and higher plants, which can reproduce asexually by fragments, there is also the risk of increasing the number of propagules when mechanical methods are used. An example of a successful removal is the heat treatment of *Undaria pinnatifida* on a sunken trawler off the New Zealand coast (Wotton et al. 2004). The chemical method is often efficient but costly and seldom target-specific. There is also a risk that the NIS would become resistant. An example of a successful chemical approach is the eradication of the invasive green alga *Caulerpa taxifolia* which was removed from a small lagoon in California by using chlorine and black plastic (Williams and Schroeder 2004; Anderson 2005). The biological method can be very successful, cost-efficient and self-sustaining but as with all living creatures there is never a hundred percent certainty that they will behave as we wish. There have been some success in tropical lakes for water hyacinth and the fern *Salvinia* by using specialized weevils as grazers (Pieterse et al. 2003), as well as for the Euroasian water milfoil in brackish and freshwater in North-America (Newman 2004). In freshwater also grass carp has been used to control nuisant aquatic plants (Santha et al. 1994). For the invasive tropical green alga *Caulerpa taxifolia* it was suggested to introduce Carribean ascoglossan snails to the Mediterranean Sea to control it (Meinesz 1997), but in a report to the French Minister it was suggested not to approve such an introduction (Thellier et al. 1997). If eradication is not possible, the final step in the action plan is to control the spread, density and abundance of the NIS to keep it below an acceptable threshold. The same methods that are used for eradication can be used for control (GISP 2001).

✧

To increase the knowledge of invasive non-indigenous species it is essential that research results are shared and communicated and that there is collaboration between researcher and authorities. Extensions of present monitoring programmes are essential to facilitate a fast discovery of new species. A cost-efficient way to solve the collection of information would be to involve school projects and the public. This is something I think many people would find exciting and, furthermore, they will be an important link in the monitoring process and make a contribution to the scientific progress.

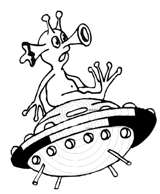
## QUESTIONS AND OUTLOOK FOR THE FUTURE

*Should we care about NIS?*
*How much resources should we use?*
*Are they after all impossible to prevent?*
*Are NIS a threat to the sustainable development?*

... these are some questions that still remain to be answered, and I do not believe that we have the answers today. With time, more and more species will be spread globally, with the potential result of a reduced, homogenized diversity world wide (McKinney and Lockwood 1999; Olden et al. 2004) and an alteration of the trophic structure of food webs (Byrnes et al. 2007). To understand the consequences of introductions and to perform risk assessments, it is essential to put more effort into collecting screening data through global monitoring. Future research also needs to incorporate all stages of the invasion process. It should further consider the ongoing climate change due to increasing amount of greenhouse gases in the atmosphere. The most discussed effect of the climate change is the increased temperature, which will have a large impact on attached species living near their tolerance limit (Laubier 2003). The climate change is also thought to have several effects e.g. stratification, raised sea level causing erosion and turbidity, alteration of currents, change in up-welling, storms (Steneck et al. 2002) as well as a decrease of the oceanic pH (Occhipinti-Ambrogi in press). Other anthropogenic effects, for example eutrophication and exploration of natural resources, are also important to take into account when studying introductions. The most important factor that needs to be incorporate into these studies is human behaviour. The more and more increasing knowledge about introductions is a major asset for future predictions, but the most challenging task for the future is to change the behaviour of humans…

*... after all, Homo sapiens is the most invasive species on this planet, leaving the largest and most severe footprints ...*

*... what the impact will be from the true aliens from outer space, we'll have to let the future tell ...*



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I also want to thank you who just read this page since this means that you in some way have shown interest for me and my thesis and that I truly appreciate!

# GLOSSARY

**Adventive species:** Species that is not native to, and that have not fully been established in a new habitat or environment (Mack and Barrett 2002b).

**Alien species:** See non-indigenous species.

**Allelopathy:** The production and release of organic compounds by an organism that causes detrimental consequences for its neighbours (Mack and Barrett 2002b).

**Arrival:** The process in which a species crosses a geographical barrier and comes to a recipient area (Sahlin 2003).

**Assessment:** The combination of analysis with policy-related activities such as identification of issues and comparison of risks and benefits (Suter 1993).

**Bayesian network:** Graphical model that represent relationships among uncertain variables (Burgman 2005)

**Biocontrol:** The intentional release of an organism that is intended to consume, infect, or debilitate a selected species to decrease its population size. Note: the possible limited specificity of biocontrol species is of concern as native species might be negatively affected (ICES 2005).

**Biosecurity threats**: Those matters or activities which, individually or collectively, may constitute a biological risk to the ecological welfare or to the well-being of humans, animals or plants of a country (IUCN 2000).

**Casual species:** Introduced species that may flourish and even reproduce occasionally in an area, but which do not form viable populations without being introduced repeatedly (Richardson et al. 2000).

**Conceptual models:** Models, diagrams, logic trees, or sets of mathematical equations representing components in a system, including input and output, flows, cycles, system boundaries and casual links (Burgman 2005).

**Conspecific:** Organisms belonging to the same taxonomic species.

**Cryptogenic:** Species of unclear or unknown origin (Carlton 1996).

**Cystocarp:** A small rounded structure on red algal female gametophyte, which contains the reproductive carpospores to be released.

**Decision trees:** Event trees in which one or more of the branch-points are decisions; a graphical representation of decision pathways (Burgman 2005).

**Deterministic model:** A model in which there is no representation of variability (Burgman 2005).

**Dispersal:** The scattering of propagules or individuals from a population (Sahlin 2003).

**Disturbance:** A temporary change/phenomenon that deviates from the normal.

**Donor region:** The geographical area from which an introduced species are imported or transferred from, before its arrival to the recipient region (Sahlin 2003).

**Ecological risk analysis:** Determination of the probability and magnitude of adverse effects of environmental hazards (chemical, physical or biological agents occurring in or mediated by the ambient environment) on nonhuman biota (Suter 1993).

**Ecological risk assessment:** The process of defining and quantifying risks on nonhuman biota and determining the acceptability of those risks (Suter 1993).

**Ecosystem engineer:** See habitat modifier.

**Effect:** A change in the state or dynamics of an organism or other ecological systems resulting from exposure to a chemical or other stressor (Suter 1993).

**Endpoint:** A quantitative or quantifiable expression of the environmental value considered to be at risk in a risk analysis (Suter 1993).

**Established species:** Species that can reproduce successfully without direct intervention by humans (or in spite of human intervention) and sustain a viable population (Richardson et al. 2000).

**Establishment:** A phase in which an introduced species reproduces and sustains a population in the recipient region (Sahlin 2003).

**Event tree:** A method for evaluating the reliability of complex systems. The event tree consists of an initiating event connected to all top events (endpoint events) by casual chains represented by a binary logic diagram. If the probabilities of the initiating event and the conditional events can be estimated, an event tree provides estimates of the risks of each top event (Suter 1993).

**Fault tree:** A method for evaluating the reliability of complex systems. The fault tree consists of a top event (the endpoint) and initiating events, connected by casual chains represented by a binary logic diagram. If the probability of each initiating event and the conditional events can be estimated, the risk of occurrence of the top event can be estimated (Suter 1993).

**Gametophyte:** The gamete-producing phase in algae characterized by alternation of generations.

**Habitat modifier:** Organisms that cause modification of habitats or creation of new habitats through direct or indirect control of resource availability (Jones et al. 1994). ***Synonym*:** Ecosystem engineer.

**Hazard:** A situation that in particular circumstances could lead to harm (Burgman 2005).

**Indigenous species:** Species that are living within their natural range (past or present), including the area that they can reach and occupy, using their natural dispersal systems. ***Synonyms***: not imported, native species (ICES 2005).

**Invasive species:** Species that have become abundant in a region and have negative impact on the environment and/or economy. ***Synonyms***: harmful, noxious, nuisance, pest, and weed (EPA 2001).

**Logic tree:** Diagrams linking all the processes and events that could lead to, or develop from, a hazard. See event tree and fault tree (Suter 1993).

**Logodds ratio:** The odds ratio of an event is a ratio of the probability that the event occurs to the probability that the event does not occur. The log of the odds ratio is a transformation of the probability to make it easier to understand (Frey and Patil 2002).

**Minimum viable population:** The smallest possible size at which a population can exist without facing extinction from natural disasters or demographic, environmental, or genetic stochasticity (from Wikipedia).

**Monte Carlo simulation:** A technique used to obtain information about the propagation of uncertainty in mathematical simulations models. It is an iterative process involving the random selection of model parameter values from specified frequency distributions, simulations of the system, and output of predictive values. The distribution of the output values can be used to determine the probability of occurrence of any particular value given the uncertainty in the parameter (Suter 1993).

**Native region:** The original geographical area of a species (Sahlin 2003).

**Non-indigenous species (NIS):** An individual, group, or population of a species, or other viable biological material that have been transported (intentionally or unintentionally) by humans from their native region to a new location, across major geographical barrier. ***Synonyms:*** alien, exotic, introduced, non-native (EPA 2001). Note: Secondary introductions can be transported by human-mediated or natural vectors (ICES 2005).

**p-bounds:** A modelling method which does not require specific guesses about distributional shape; "p-bounds" calculations bound arithmetic operations, making only those assumptions about dependencies, distribution shapes, moments of distributions, or logical operations that are justified by the data (Burgman 2005).

**Persistent species:** Species that do not have the possibility of becoming permanently established, since they can not reproduce successfully in the new area (Myers and Bazely 2003).

**Pest:** A species that is unwanted by humans in a specific area.

**Recipient area:** The geographical area to which a non-indigenous species arrives (Sahlin 2003). ***Synonym***: receiving area.

**Risk:** Is the probability of an undesired effect (Suter 1993).

**Risk analysis:** Evaluation of the nature and extent of uncertainty (Burgman 2005).

**Risk assessment:** The identification and assessment of hazards (first step of the risk management process).

**Risk characterization:** The process of (a) integrating the exposure and effects assessments to estimate risks and (b) summarizing and describing the results of a risk analysis for a risk manager or for the public and other stakeholders (Suter 1993).

**Risk management:** The process of deciding what action to take in response to a risk (Suter 1993).

**Sensitivity analysis:** An analysis of how a model's output responds to changes in a variable or an assumption (Burgman 2005).

**Spermatangium:** A structure that produces spermatia in red algal male gametophytes.

**Spread:** The process of range expansion (Sahlin 2003).

**Stochastic:** Random; arising from a process that generates different values with some probability.

**Stressor:** An agent, condition, or other stimulus that causes stress to an organism.

**Tetrasporangium:** A unicellular sporangium found in most red algal tetrasporophytes in which four tetraspores are produced by meiosis.

**Tetrasporophyte:** The tetraspore-producing phase in red algae with alternating generations.

**Transformer:** A species that changes the character, condition, form or nature of ecosystems over a substantial area (Richardson et al. 2000).

**Vector:** Any living or non-living agent, that transports living organisms intentionally or unintentionally (ICES 2005).

**Weed:** A plant with high population densities that grows in sites, where they are not wanted, and which usually have negative impact on other plants valued by humans (Richardson et al. 2000).

# REFERENCES


Ahlgren H (2005a) Inventering av dvärgålgräs utmed göteborgskusten. Göteborgs Stad Miljöförvaltningen, Rapport 2005 (11): 1-22 http://www.miljo.goteborg.se/top/tryck/rapport/body_rapporter.htm Access date 27 October 2006

Ahlgren H (2005b) On the Gracilariaceae found in Sweden. M Sc thesis. Department of Marine ecology, Marine botany, Göteborg University. Contribution no. 266, 9 pp

Anderson LWJ (2005) California's reaction to *Caulerpa taxifolia*: A model for invasive species rapid response. Biological Invasions 7: 1003-1016

Anonymous (2000) European Register of Marine Species. Algae full detailed checklist. http://erms.biol.soton.ac.uk/lists/full/Algae.shtml Access date 12 November 2002

Athanasiadis A (1996) Taxonomisk Litteratur och Biogeografi av Skandinaviska Rödalger och Brunalger. Algologia, Göteborg. ISBN 91-630-4949-6

Axelius B, Karlsson J (2004) Japanplym, ny rödalg för Sverige (*Heterosiphonia japonica* new for Sweden). Svensk Botanisk Tidskrift 98: 268-273 (In Swedish with English legends).

Bedford T, Cooke R (2003) Probabilistic Risk Analysis Foundations and Methods. Cambridge University Press, Cambridge, 414 pp, ISBN 0-521-77320-2

Bellorin AM, Oliveira MC, Oliveira EC (2004) *Gracilaria vermiculophylla*: A western Pacific species of Gracilariaceae (Rhodophyta) first recorded from the eastern Pacific. Phycological Research 52: 69-79

Berger J, Schagerl M (2003) Allelopathic activity of *Chara aspera*. Hydrobiologia 501: 109-115

Blindow I (2000) Distribution of charophytes along the Swedish coast in relation to salinity and eutrophication. International Revue of Hydrobiology 85: 707-717

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83: 887-889

Bonsdorff E (1992) Drifting algae and zoobenthos - effects on settling and community structure. Netherlands Journal of Sea Research 30: 57-62

Boudouresque CF, Verlaque M (2002) Biological pollution in the Mediterranean Sea: invasive versus introduced macrophytes. Marine Pollution Bulletin 44: 32-38

Breeman AM, Meulenhoff EJS, Guiry MD (1988) Life history regulation and phenology of the red alga *Bonnemaisonia hamifera*. Helgoländer Meeresuntersuchungen 42: 535-551

Bulleri F, Airoldi L, Branca GM, Abbiati M (2006) Positive effects of the introduced green alga, *Codium fragile* ssp *tomentosoides*, on recruitment and survival of mussels. Marine Biology 148: 1213-1220

Burgman M (2005) Risk and Decisions for Conservation and Environmental Management. Cambridge University Press, Cambridge, United Kingdom., pp 488, ISBN 0-521-54301-0

Byrnes J, Reyholds P, Stachowicz J (2007) Invasions and extinctions reshape coastal marine food webs. Public Library of Science ONE 3: 1-7

Cardigos F, Tempera F, Ávila S, Gonçalves J, Colaço A, Santos R (2006) Non-indigenous marine species of the Azores. Helgoland Marine Research 60: 160-169

Carlton JT (1996) Biological invasions and cryptogenic species. Ecology 77: 1653-1655

CBD (1992) The Convention on Biological Diversity. UN Conference onEnvironment and Development, Earth Summit, Rio de Janerio. http://www.biodiv.org/default.shtml Access date 1 March 2007

CBM (2004) Sveriges genomförande av Konventionen om biologisk mångfald med avseende på främmande arter och genotyper. Centrum för biologisk mångfald, Uppsala, Dnr: 2004-02-22

Ceccherelli G, Piazzi L (2005) Exploring the success of manual eradication of *Caulerpa racemosa* var. *cylindracea* (Caulerpales, Chlorophyta): the effect of habitat. Cryptogamie Algologie 26: 319-328

Chaoyuan W, Minghuo J, Renzhi L, Xiaohang W, Sijian L, Zenian M, Jimin S (1990) Training manual on *Gracilaria* culture and seaweed processing in China. FAO Corporate document repository, http://www.fao.org/docrep/field/003/AB730E/AB730E00.htm Access date 21 March 2007

Cho TO, Won BY, Fredericq S (2005) *Antithamnion nipponicum* (Ceramiaceae, Rhodophyta), incorrectly known as *A. pectinatum* in western Europe, is a recent introduction along the North Carolina and Pacific coasts of North America. European Journal of Phycology 40: 323-335

Critchley AT (1983) The establishment and increase of *Sargassum muticum* (Yendo) Fensholt populations within the Solent area of southern Britain. I An investigation of the increase in number of population individuals. Botanica Marina 26: 539-545

Crooks JA (2005) Lag times and exotic species: The ecology and management of biological invasions in slow-motion. Ecoscience 12: 316-329

Davis M (2005) Invasibility: the local mechanism driving community assembly and species diversity. Ecography 28: 696-704

Ekman P, Yu SK, Pedersén M (1991) Effects of altered salinity, darkness and algal nutrient status on floridoside and starch content, α-galactosidase activity and agar yield of cultivated *Gracilaria sordida*. British Phycological Journal 26: 123-131

EPA (1992) Framework for Ecological Risk Assessment. Assessment Forum, U.S. Environmental Protection Agency. EPA/630/R-92/001.

EPA (1998) Guidelines for Ecological Risk Assessment. Fed Register 63: 26846-26924

EPA (2001) Gulf of Mexico Regional Panel. Aquatic Nuisance Species. Annual Report 2001

FIFS 2001:3 Fiskeriverkets föreskrifter (2001:3) om odling, utplantering och flyttning av fisk.

Fletcher RL, Farrell P (1998) Introduced brown algae in the north east Atlantic, with particular respect to *Undaria pinnatifida* (Harvey) Suringar. Helgoländer Meeresuntersuchungen 52: 259-275

Floc'h J, Pajot R, Wallentinus I (1991) The Japanese brown alga *Undaria pinnatifida* on the coast of France and its possible establishment in European waters. Journal du Conseil 47: 379-390

Freshwater DW, Montgomery F, Greene JK, Hamner RM, Williams M, Whitfield PE (2006) Distribution and identification of an invasive *Gracilaria* species that is hampering commercial fishing operations in southeastern North Carolina, USA. Biological Invasions 8: 631-637

Frey H, Patil S (2002) Identification and review of sensitivity analysis methods. Risk Analysis 22: 553-578

Friedlander M, Gonen Y, Kashman Y, Beer S (1996) *Gracilaria conferta* and its epiphytes. 3. Allelopathic inhibition of the red seaweed by *Ulva cf lactuca*. Journal of Applied Phycology 8: 21-25

Gärdenfors U (2005) Rödlistade arter i Sverige 2005 - The 2005 redlist of Swedish species, SLU, Uppsala, 496 pp

Gavio B, Fredrique S (2002) *Grateloupia turuturu* (Halymeniaceae, Rhodophyta) is the correct name of the non-native species in the Atlantic known as *Grateloupia doryphora*. European Journal of Phycology 37: 349-359

Genovesi P, Shine C (2003) European Strategy on Invasive Alien Species. Convention on the Conservation of European Wildlife and Natural Habitats, Council of Europe, Strasbourg. T-PVS/Inf (2004) 1. www.coe.int/t/e/Cultural_Co-operation/Environment/Nature_and_biological_diversity/Nature_protection Access date 1 March 2007

GISP (2001) Invasive Alien Species: A Toolkit of Best Prevention and Management Practices, CAB International. http://www.gisp.org Access date 1 Mach 2007

Gollasch S, Leppäkoski E (1999) Chapter 11. Are there special areas attracting invasions? In: Gollasch S, Leppäkoski E (eds) Initial Risk Assessment of Alien Species in Nordic Coastal Waters. Nordic Council of Ministers, Copenhagen, ISBN 92-893-0293-3

Gollasch S, MacDonald E, Belson S, Botnen H, Christensen J, Hamer J, Houvenaghel G, Jelmert A, Lucas I, Masson D, McCollin T, Olenin S, Persson A, Wallentinus I, Wetsteyn L, Wittling T (2002) Life in ballast tanks. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive Aquatic Species of Europe. Distribution, Impact and Management. Kluwer Academic Publishers, Dordrecht, the Netherlands, pp 217-231, ISBN 1-4020-0837-6

Goulletquer P, Bachelet G, Sauriau P, Noel P (2002) Open Atlantic coast of Europe - A century of introduced species. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive Aquatic Species of Europe. Distribution, Impact and Management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 276-290, ISBN 1-4020-0837-6

Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. Trends in Ecology & Evolution 17: 22-27

Guillard R (1975) Culture of phytoplankton for feeding marine invertebrates. In: Smith W, Chanley M (eds) Culture of Marine Invertebrate Animals. Plenum, New York, pp 29-60,

Guiry M, Guiry G (2007) AlgaeBase version 4.2. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org Access date 19 March 2007

Guiry MD, Dawes CJ (1992) Daylength, temperature and nutrient control of tetrasporogenesis in *Asparagopsis armata* (Rhodophyta). Journal of Experimental Marine Biology and Ecology 158: 197-217

Gustafsson T (2005) Can native herbivores, of the Swedish west coast, graze the introduced red alga *Gracilaria vermiculophylla*? M.Sc. Thesis. Department of Marine ecology, Göteborg University, Göteborg, Sweden, Contribution 288, 34 pp

Harrison P, Waters R, Taylor F (1980) A broad spectrum artificial seawater medium for coastal and open ocean phytoplankton. Journal of Phycology 16: 28-35

Hayes K, McEnnulty F, Sliwa C (2003) Ranking potential next pests. Third International Conference on Marine Bioinvasions, Scripps Institution of Oceanography, La Jolla, California, 57 p (Abstract)

Hayes KR, Sliwa C (2003) Identifying potential marine pests - a deductive approach applied to Australia. Marine Pollution Bulletin 46: 91-98

Heger T, Trepl L (2003) Predicting biological invasions. Biological Invasions 5: 313-321

Hellfalk M, Johansson L, Melin M, Lundgren V (2005) Inventering av grunda bottnar i Helsingborgs kommun, sommaren 2005, 69 pp, ISBN 91-976087-0-X

Hewitt CL, Campbell ML, McEnnulty F, Moore KM, Murfet NB, Robertson B, Schaffelke B (2005) Efficacy of physical removal of a marine pest: the introduced kelp *Undaria pinnatifida* in a Tasmanian Marine Reserve. Biological Invasions 7: 251-263

Hill K (2006) Success in establishment of invasive algal species: an evaluation of the importance of grazing. M.Sc. Thesis. Department of Marine ecology, Göteborg Univeristy. Contribution 300, 21 pp

ICES (2005) ICES Code of Practice on the Introductions and Transfers of Marine Organisms 2005. ICES, Copenhagen: 30 pp

ICES WGITMO (2003) Report of the Working Group of Introductions and Transfers of Marine Organisms, Vancouver, Canada, 26-28 March 2003. ICES CM 2003/ACME: 04, Ref.: E, F, Copenhagen. http://www.ices.dk/iceswork/wgdetailacme.asp?wg=WGITMO Access date 1 March 2007

ICES WGITMO (2006) ICES WGITMO (2006) Report of the Working Group of Introductions and Transfers of Marine Organisms, 16-17 March 2006, Ostende, Belgium. ICES CM 2006/ACME: 05, Copenhagen. http://www.ices.dk/iceswork/wgdetailacme.asp?wg=WGITMO Access date 1 March 2007

IMO (2001) IMO set to adopt convention on control of harmful anti-fouling systems for ships. http://www.imo.org Access data 1 March 2007

IMO (2004) International convention for the control and management of ships' ballast water and sediments. International Maritime Organization, BWM/CONF/36:1-36. http://www.imo.org Access date 1 March 2007

IUCN (2000) Guidelines for the prevention of biodiversity loss caused by alien invasive species. Prepared by the IUCN/SSC Invasive Species Specialist Group (ISSG) and approved by the 51st Meeting of the IUCN Council, Gland, Switzerland. http://www.iucn.org Access date 1 March 2007

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69: 373-386

Karlsson J, Kuylenstierna M, Åberg P (1992) Contribution to the seaweed flora of Sweden: New or otherwise interesting records from the west coast. Acta Phytogeographica Sueccia 78: 49-63

Keane R, Crawley M (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17: 164-170

Kim Y, Nam K (1997) Temperature and light responses on the growth and maturation of gametophytes of *Undaria pinnatifida* (Harvey) Suringar in Korea. Journal of Korean Fisheries Society 30: 505-510 (In Korean with English summary)

Kirst GO (1989) Salinity tolerance of eukaryotic marine algae. Annual Review of Plant Physiology and Plant Molecular Biology 40: 21-53

Klein J, Verlaque M (2005) *Laurencia caduciramulosa* Masuda et Kawaguchi (Ceramiales, Rhodophyceae), first recordedon the Mediterranean coast of France. Cryptogamie Algologie 26: 209-216

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16: 199-204

Laubier L (2003) Changement et vulnérabilité des peuplements marins côtiers. Comptes Rendus Geoscience 335: 561-568

Lowe S, Browne M, Boudjelas S (2000) 100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12 pp, http://www.iucn.org/places/medoffice/invasive_species/docs/invasive_species_booklet.pdf

Lüder U, Wiencke C, Knoetzel J (2002) Acclimation of photosynthesis and pigments during and after six months of darkness in Palmaria decipiens (Rhodophyta): A study to simulate Antarctic winter sea ice cover. Journal of Phycology 38: 904-913

Luther H (1951) Verbreitung und Ökologie der höheren Wasserpflanzen im Brackwasser der Ekenäs-Gegend in Südfinnland. II Specieller Teil. Acta Botanica Fennica 50: 1-370

Luther H (1979) *Chara connivens* in the Baltic Sea area. Annales Botanici Fennici 16: 141-150

Mack R, Barrett S (2002a) Evaluating predictive systems. In: Predicting Invasions of Nonindigenous Plants and Plant Pests. National Academy Press, Washington, D.C. Open book source http://darwin.nap.edu/books/0309082641/html

Mack R, Barrett S (2002b) Predicting Invasions of Nonindigenous Plants and Plant Pests. National Academy Press, Washington, D.C. Open book source http://darwin.nap.edu/books/0309082641/html, 194 pp

Maggs CA, Stegenga H (1999) Red algal exotics on North Sea coasts. Helgoländer Meeresuntersuchungen 52: 243-258

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14: 450-453

McLusky D (1989) The Estuarine Ecosystem. Blackie and Son Ltd, Glasgow., pp 215, Meinesz A (1997) Utilisation d'Ascoglosses pour la lutte biologique contre *Caulerpa taxifolia* de Méditerranée Dynamique d'Espèces Marines Invasives: Application à l'Expansion de *Caulerpa taxifolia* en Méditerranée. Académie des Sciences, Paris, pp 291-300, ISBN 2-7430-0236-0

Minchin D, Gollasch S, Wallentinus I (2005) Vector pathways and the spread of exotic species in the sea. ICES Cooperative Research Report 271: 1-29

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421: 625-627

Mulderij G, Van Donk E, Roelofs J (2003) Differential sensitivity of green algae to allelopathic substances from *Chara*. Hydrobiologia 491: 261-271

Munro ALS, Utting SD, Wallentinus I (1999) Status of introductions of non-indigenous marine species to north Atlantic waters 1981-1991. ICES Cooperative Research Report 231: 1-127, pp 1-43, ISSN: 0906-0596.

Myers J, Bazely D (2003) Ecology and Control of Introduced Plants. Cambridge University Press, Cambridge, 313 pp, ISBN 0-521-35778-0

Naturvårdsverket (1997) Naturvårdsverkets policy för introduktion och spridning av främmande organismer. Naturvårdsverket förlag, Stockholm, 67 pp, ISBN 91-620-1182-0

Newman RM (2004) Invited review - Biological control of Eurasian watermilfoil by aquatic insects: basic insights from an applied problem. Archiv für Hydrobiologie 159: 145-184

Nielsen R (2005) Danish seaweeds – Distributional index. http://www.botaniskmuseum.dk/BOT/seaweeds.htm Access date 5 April 2006

Nielsen R, Kristiansen A, Mathiesen L, Mathiesen H (1995) Distributional index of the benthic macroalgae of the Baltic Sea area. Acta Botanica. Fennica 155: 1-51

Occhipinti-Ambrogi A (in press) Global change and marine communities: Aliens species and climate change. Marine Pollution Bulletin (2007), doi:10.1016/j.marpolbul.2006.11.014

Ohmi H (1956) Contributions to the knowledge of Gracilariaceae from Japan. II. On a new species of the genus *Gracilariopsis* with some considerations on its ecology. Bulletin of the Faculty of Fisheries 6: 271-279

Ólafsson EB (1988) Inhibition of larval settlement to a soft bottom benthic community by drifting algal mats - an experimental test. Marine Biology 97: 571-574

Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution 19: 18-24

Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. Frontiers in Ecology and the Environment 2: 131-138

Park K (2004) Assessment and management of invasive alien predators. Ecology and Society 9 (2): Article 12, 17 pp

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3-19

Pheloung PC, Williams PA, Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57: 239-251

Piazzi L, Ceccherelli G (2006) Persistance of biological invasion effects: Recovery of macroalgal assemblages after removal of *Caulerpa racemosa* var. *cylindracea*. Estuarine Coastal and Shelf Science 68: 455-461

Pieterse AH, Kettunen M, Diouf S, Ndao I, Sarr K, Tarvainen A, Kloff S, Hellsten S (2003) Effective biological control of *Salvinia molesta* in the Senegal River by means of the weevil *Cyrtobagous salviniae*. Ambio 32: 458-462

Pihl L, Rosenberg R (1982) Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden. Journal of Experimental Marine Biology and Ecology 57: 273-301

Prinzing A, Durka W, Klotz S, Brandl R (2002) Which species become aliens? Evolutionary Ecology Research 4: 385-405

Puth L, Post D (2005) Studying invasion: have we missed the boat? Ecology Letters 8: 715-721

Råberg S, Berger-Jönsson R, Björn A, Granéli E, Kautsky L (2005) Effects of *Pilayella littoralis* on *Fucus vesiculosus* recruitment: implications for community composition. Marine Ecology Progress Series 289: 131-139

Radford I, Cousens R (2000) Invasiveness and comparative life-history traits of exotic and indigenous *Senecio* species in Australia. Oecologia 125: 531-542

Raikar S, Iima M, Fujita Y (2001) Effect of temperature, salinity and light intensity on the growth of *Gracilaria spp*. (Gracilariales, Rhodophyta) from Japan, Malaysia and India. Indian Journal of Marine Sciences 30: 98-104

Reise K, Gollasch S, Wolff W (2002) Introduced marine species of the North Sea coasts. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive Aquatic Species of Europe. Distribution, Impact and Management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 260-266, ISBN 1-4020-0837-6

Ribera Siguan MA (2002) Review of non-native marine plants in the Mediterranean Sea. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive Aquatic Species of Europe. Distribution, Impact and Management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 291-310, ISBN 1-4020-0837-6

Richardson D, Pyšek P, Rejmánek M, Barbour M, Panetta F, West C (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6: 93-107

Rodríguez-Prieto C, Gacia E, Delgado O, Sant N, Ballesteros E (1996) Seasonality in the productivity of Mediterranean *Caulerpa taxifolia* (Vahl) C. Agardh in relation to light and temperature: January and April 1994. In: Ribera M, Boudouresque C, Gómez A, Gravez V (eds) Second International Workshop on *Caulerpa taxifolia*, Publicasions Universitat Barcelona, Barcelona, pp 197-201, ISBN 84-475-1382-3

Rueness J (2005) Life history and molecular sequences of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta), a new introduction to European waters. Phycologia 44: 120-128

Rull Lluch J, Ballesteros E, Barceló MC, Gómez Garreta A, Ribera Siguan MA (2007) *Dictyota ciliolata* Sonder *ex* Kützing (Phaeophyceae, Dictyotales) in the Mediterranean Sea. Cryptogamie Algologie 28: 89-97

Sahlin U (2003) Risk analysis of alien species. Introductory paper no 152. Department of Ecology, Lund, 49 pp, ISSN 1100-1844

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305-332

Santha CR, Martyn RD, Neill WH, Strawn K (1994) Control of submersed weeds by grass carp in waterlily production ponds. Journal of Aquatic Plant Management 32: 29-33

Schaffelke B, Smith JE, Hewitt CL (2006) Introduced macroalgae - a growing concern. Journal of Applied Phycology 18: 529-541

Schlaepfer MA, Sherman PW, Blossey B, Runge MC (2005) Introduced species as evolutionary traps. Ecology Letters 8: 241-246

Schories D, Selig U (2006) Die Bedeutung eingeschleppter Arten (alien species) für die Europäische Wasserrahmenrichtlinie am Beispiel der Ostsee. Rostocker Meeresbiologische Beiträge 15: 147-158

SFS 1994:1716 Förordning (1994:1716) om fisket, vattenbruk och fisknäringen

SFS 1994:1830 Förordning (1994:1830) om införsel av levande djur m.m.

SFS 1998:179 Artskyddsförordning (1998:179)

SFS 1998:808 Miljöbalk (1998:808)

SFS 1998:899 Förordningen (1998:899) om miljöfarligverksamhet och hälsoskydd

Silva P (1957) *Codium* in Scandinavian waters. Svensk Botanisk Tidskrift 51: 117-134

SJVS 2000:157 Föreskrifter om ändring i Statens jordbruksverks föreskrifter (SJVFS 1995:125) om införsel av fisk, kräftdjur och blötdjur och produkter därav

Stæhr PA, Pedersen MF, Thomsen MS, Wernberg T, Krause-Jensen D (2000) Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. Marine Ecology Progress Series 207: 79-88

Steentoft M, Farnham WF (1997) Northern distribution boundaries and thermal requirements of *Gracilaria* and *Gracilariopsis* (Gracilariales, Rhodophyta) in Atlantic Europe and Scandinavia. Nordic Journal of Botany 17: 87-93

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29: 436-459

Strong JA, Dring MJ, Maggs CA (2006) Colonisation and modification of soft substratum habitats by the invasive macroalga *Sargassum muticum*. Marine Ecology Progress Series 321: 87-97

Suter G (1993) Ecological Risk Assessment. CRC Press LLC, Boca Raton, Florida, pp 538, ISBN 0-87371-875-5

Thellier M, Echaubard M, Kloareg B, Laubier L, Pave A (1997) Propositions d'actions de recherches. Report to the French Minister for the environment concerning the alga *Caulerpa taxifolia* in the Mediterranean Dynamique d'Espèces Marines Invasives: Application à l'Expansion de *Caulerpa taxifolia* en Méditerranée. Académie des Sciences, Paris, pp 345-352, ISBN 2-7430-0236-0

Thomsen M, Gurgel C, Fredericq S, McGlathery K (2005) *Gracilaria vermiculophylla* (Rhodophyta, Gracilariales) in Hog Island bay, Virginia: A cryptic alien and invasive macroalga and taxonomic correction. Journal of Phycology 42: 139-141

Thomsen MS, Staehr P, Nyberg C, Schwærter S, Krause-Jensen D, Silliman B (in press-a) Gracilaria vermiculophylla in northern Europe, with emphasis on Danish conditions, and what to expect in the future. Aquatic Invasions

Thomsen MS, Wernberg T, Stæhr P, Krause-Jensen D, Risgaard-Petersen N, Silliman B (in press-b) Alien macroalgae in Denmark - a national perspective. Marine Biology Research

Thomsen MS, McGlathery K (2005) Facilitation of macroalgae by the sedimentary tube forming polychaete *Diopatra cuprea*. Estuarine, Coastal and Shelf Science 62: 63-73

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421: 628-630

Troell M, Halling C, Nilsson A, Buschmann AH, Kautsky N, Kautsky L (1997) Integrated marine cultivation of *Gracilaria chilensis* (Gracilariales, Rhodophyta) and salmon cages for reduced environmental impact and increased economic output. Aquaculture 156: 45-61

Tseng C, Xia B (1999) On the *Gracilaria* in the western Pacific and the southeastern Asia region. Botanica Marina 42: 209-217

Verlaque M (2001) Checklist of the macroalgae of Thau Lagoon (Hérault, France), a hot spot of marine species introduction in Europe. Oceanologica Acta 24: 29-49

Verlaque M, Brannock PM, Komatsu T, Villalard-Bohnsack M, Marston M (2005)The genus *Grateluopia* C. Agardh (Halymeniaceae, Rhodophyta) in the Thau Lagoon (France, Mediterranian): a case study of marine plurispecific introductions. Phycologia 44: 477-496

Vitousek PM, Dantonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: A significant component of human-caused global change. New Zealand Journal of Ecology 21: 1-16

Wallentinus I (1999) *Sargassum muticum* (Yendo) Fensholt, 1955. In: Gollasch S, Minchin D, Rosenthal H, Voigt M (eds) Exotics Across the Ocean. Case Histories on Introduced Species prepared by Members of the European Union Concerted Action on Testing Monitoring Systems for Risk Assessment of Harmful Introductions by Ships to European Waters (MAS3-CT-97-011). Lagos Verlag, Berlin, pp 21-30, ISBN 3-89722-248-5

Wallentinus I (2002) Introduced marine algae and vascular plants in European aquatic envronments. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive Aquatic Species of Europe. Distribution, Impact and Management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 27-52, ISBN 1-4020-0837-6

Wallentinus I (2006) Sprider sig de främmande algerna och äts de av några? In: Lindblom R, Lindegarth M, Pettersson K (eds) Havsmiljön 2006. Kontaktgrupp Hav, Göteborg, p 16

Wallentinus I (in press) Introductions and transfers of plants. In Status of introductions of non-indigenous marine species to North Atlantic and adjacent waters according to national reports considered at meetings of the Working Group on Introductions and Transfers of Marine Organisms. In: Gollasch S, Kieser D, Minchin D, Wallentinus I (eds) ICES Cooperative Research Report 284

Wallentinus I, Jenneborg L-H (2003) Introducerad rödalg? In: Carlberg A, Lindblom R, Nilsson P, Pettersson K (eds) Havsmiljö september 2003, Kontaktgrupp Hav, Göteborg, p 23

Walters LJ, Brown KR, Stam WT, Olsen JL (2006) E-commerce and *Caulerpa*: unregulated dispersal of invasive species. Frontiers in Ecology and the Environment 4: 75-79

Wikström S, von Wachenfeldt T, Kautsky L (2002) Establishment of the exotic species *Fucus evanescens* C. Ag. (Phaeophyceae) in Öregrund, southern Sweden. Botanica Marina 45: 510-517

Wikström SA, Steinarsdóttir MB, Kautsky L, Pavia H (2006) Increased chemical resistance explains low herbivore colonization of introduced seaweed. Oecologia 148: 593-601

Wilcove D, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48: 607-615

Williams SL, Schroeder SL (2004) Eradication of the invasive seaweed *Caulerpa taxifolia* by chlorine bleach. Marine Ecology Progress Series 272: 69-76

Williamson M (2006) Explaining and predicting the success of invading species at different stages of invasion. Biological Invasions 8: 1561-1568

Williamson MH, Fitter A (1996a) The characters of successful invaders. Biological Conservation 78: 163-170

Williamson MH, Fitter A (1996b) The varying success of invaders. Ecology 77: 1661-1666

Wolff W (2005) Non-indigenous marine and estuarine species in The Netherlands. Zoologische Mededelningen 79: 1-116

Wotton D, O'Brien C, Stuart M, Fergus D (2004) Eradication success down under: heat treatment of a sunken trawler to kill the invasive seaweed *Undaria pinnatifida*. Marine Pollution Bulletin 49: 844-849

Yokoya NS, Kakita H, Obika H, Kitamura T (1999) Effects of environmental factors and plant growth regulators on growth of the red alga *Gracilaria vermiculophylla* from Shikoku Island, Japan. Hydrobiologia 399: 339-347

Yu S, Pedersén M (1990) The effect of salinity changes on the activity of α-galactosidase of the red algae *Gracilaria sordida* and *Gracilaria tenuistipitata*. Botanica Marina 33: 385-391

Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole ecosystem context. Trends in Ecology & Evolution 16: 454-459

Zenetos A, Çinar ME, Pancucci-Papadopoulou M, Harmelin J, Furnari G, Andaloro F, Bellou N, Streftaris N, Zibrowius H (2005) Annotated list of marine alien species in the Mediterranean with records of the worst invasive species. Mediterranean Marine Science 6: 63-118

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**II** Nyberg CD & Wallentinus I (2005) Can species traits be used to predict marine macroalgal introductions? Biological Invasions 7: 265-279

**III** Nyberg CD, Thomsen MS & Wallentinus I (submitted) Are there species using the new habitat provided by *Gracilaria vermiculophylla*?

**IV** Sahlin U, Larson D & Nyberg CD (submitted) Dose–response impact assess-ment of non-indigenous aquatic plants and algae — a modelling approach.



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