Thesis for the degree of Doctor of Philosophy

Seaweed Invasions and Novel Chemical Defences

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The invasion paradox:

How can a species become widespread

and dominant in a community in which it

doesn't occur naturally and in which it

hasn't evolved?

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Abstract. Biological invasions pose a risk to the biodiversity and the functioning of ecosystems in invaded areas. The reasons why some introduced species become dominant and widespread in their new environments is still largely an unsettled question. It has commonly been predicted that introduced plants will invade when they are less affected by herbivores, since this will provide the introduced species with a competitive advantage over native plants. Furthermore, it has been suggested that introduced species with chemical defences that are novel to native herbivores in the new range are most likely to become successful invaders.

The scope of this thesis was to investigate ecological processes that underlie the successful invasion of plant/seaweed species and how chemical compounds mediate these processes, using the filamentous red alga *Bonnemaisonia hamifera* as a model organism. Having its origin in the Northwest Pacific, this alga has invaded large parts of the North Atlantic rocky shores and became dominant in many seaweed communities. Feeding preference experiments showed that native generalist herbivores explicitly preferred native seaweeds to the invader (paper I). Using a bioassay-guided fractionation, *B. hamifera* was found to be chemically defended against native herbivores by producing 1,1,3,3-tetrabromo-2-heptanone as the main feeding deterrent compound (paper I). The production of this compound was demonstrated to be costly, but also to increase the fitness of the invader by reducing the impact of pathogenic bacteria (paper IV) in addition to the shown reduced herbivory. Resource allocation to a chemical defence may also explain the relatively poor performance (in terms of growth) of *B. hamifera* in direct interactions with native seaweeds when herbivores were absent in experimental algal communities (paper II, III). In the presence of herbivores, however, the abundance of *B. hamifera* increased in the community as a result of both consumption of neighbouring algal competitors and an enhanced performance of the invader (paper III). In return, the invasive species was found to provide a superior refuge to herbivores from fish predation compared to native seaweeds, which may explain the previously observed rich species diversity and abundance of invertebrates associated with the alga. Overall, these results suggest that the invasion of *B. hamifera* has been facilitated by refuge-mediated apparent competition (paper III).

In conclusion, *B. hamifera* provides a remarkable example of how a novel chemical defence can drive different ecological processes in the new community and how this jointly contributes to the invasiveness of the introduced species. The further development of the invaded community is difficult to predict and depends on the ability of the native species to adapt to the chemical defence of the invader, as well as on the potential of the invader to respond to the novel selection regimes in the invaded area. Sufficient genetic variation is generally considered essential for the potential of adaptations. In Swedish waters, *B. hamifera* mainly propagates asexually by fragmentation, which suggests that the alga should be highly clonal with low genetic diversity within these introduced populations. Preliminary results from 83 amplified fragment length polymorphism markers analysed for 44 individuals indicated reduced genetic diversity in Swedish populations compared to populations from the native range in Korea. No clones were found in the Swedish population, although the low degree of differentiation and high similarity between the Swedish individuals suggests that the individuals belong to a single clonal lineage, that is well intermixed by fragment dispersal (paper V).

Populärvetenskaplig sammanfattning

Främmande växter finns i alla miljöer runt omkring oss exempelvis i trädgårdar, i skogar, vid vägkanter och i havet. I motsats till på land har de flesta introduktioner av främmande arter i marina system skett oavsiktligt. Ökad fartygstrafik och vattenbruk gör havet särskilt utsatt för nya invasioner. Det uppskattas att flera tusen arter transporteras mellan havets biogeografiska regioner vid varje tidpunkt. När en introducerad art får en stor utbredning och blir dominerande i ett samhälle klassificeras den som invasiv. Invasiva arter anses vara en risk för den globala biologiska mångfalden och ekosystemens funktion, men en allmän förklaring till varför vissa främmande arter kan bli invasiva saknas ännu.

Min doktorsavhandling syftar till att undersöka de ekologiska processerna som förklarar varför främmande arter kan utbreda sig till synes okontrollerat. För att testa specifika hypoteser kring detta har jag använt en liten rödalg med namnet japantofs (*Bonnemaisonia hamifera*) som modellorganism. Japantofsen har spridits kraftigt sedan den introducerades i Europa i slutet av 1800-talet och är numera en av de vanligast förekommande filamentösa alger i Sverige.

En hypotes att förklara framgången av främmande arter är den så kallade 'enemy release hypothesis'. Den antar att en främmande art som kommer till en ny miljö blir av med sina naturliga fiender och därför växer mycket bättre än i sitt ursprungsområde, samt även växer bättre än de inhemska växterna som har kvar sina fiender. De flesta betare i havet är dock inte särskilt kräsna när det gäller mat och de kan beta på många olika alger. Då infinner sig frågan varför de inte skulle äta invaderade arter? Jag kunde visa att japantofsen inte alls är omtyckt av de små men talrika betarna i algsamhället. Grunden för det beror på att algen har ett effektivt kemiskt försvar i form av ett kemiskt ämne 1,1,3,3-tetrabromo-2-heptanon, som inhiberar betning. Att detta ämne är så effektivt mot betning kan sannolikt förklaras med att det inte finns någon annan inhemsk art som har något liknande ämne, det vill säga att de inhemska betarna är evolutionärt naiva mot detta ämne.

Jag kunde också visa att även om betarna inte konsumerar algen får de ett bättre skydd mot fiskpredation när de befinner sig i japantofsen jämfört med andra inhemska alger. Genom att söka skydd i *B. hamifera* men beta på de kringliggande konkurrenterna, hjälper betarna till att japantofsen kan sprida sig. När jag tog bort betarna kunde *B. hamifera* inte öka i abundans på grund av att de andra inhemska algerna var mycket bättre konkurrenter och växte mer. Det beror antagligen på att det är kostsamt för japantofsen att producera sitt försvarsämne och då har den mindre resurser kvar till tillväxt.

Det är svårt att förutse hur samhällen invaderade av *B. hamifera* kommer att utvecklas. Primärproduktionen påverkades inte i experiment där vi undersökte effekterna av främmande alger på ekosystemfunktioner, men om japantofsen tillväxer på bekostnad av andra inhemska alger är det möjligt att den kommer att ha effekter på de inhemska betarna i längden. Det kommer i stor usträckning att bero på om betarna kommer att kunna använda arten som föda i framtiden. Det kräver dock att de inhemska betarna utvecklar resistens mot försvarsämnet i *B. hamifera*. Dessutom kommer det att bero på hur algen själv utvecklas, speciellt om den kan anpassa sig till ett högre betningstryck genom att producera högre halter av sitt försvarsämne. Även om min avhandling inte kan ge svar på dessa intressanta frågor har den genererat nya insikter som kan utgöra grunden för vidare studier.

List of papers

This thesis is a summary of the following papers:

Paper I: Enge, S., Nylund, G.M., Harder, T., and H. Pavia. 2012. An exotic chemical weapon explains low herbivore damage in an invasive alga. *Ecology*, doi.org/10.1890/12-0143.1.

Paper II: Sagerman, J., Enge, S., Pavia, H., and S.A. Wikström. (Manuscript). Divergent ecological strategies determine different impacts on community production by two introduced seaweeds.

Paper III: Enge, S., Nylund, G.M., and H. Pavia. (Manuscript, submitted). Native generalist herbivores promote invasion of a chemically defended seaweed via refuge-mediated apparent competition.

Paper IV: Nylund, G.M., Enge, S., and H. Pavia. (Manuscript, submitted). Costs and benefits of chemical defence in the red alga *Bonnemaisonia hamifera.*

Paper V: Enge, S., Pereyra, R., and H. Pavia. (Note). Preliminary insights into the diversity and population structure of the red alga *Bonnemaisonia hamifera* in its introduced and native ranges.

Contents

An introduction into the field of invasion ecology

1. What are biological invasions?

The phenomenon of biological invasions was already recognised by Darwin (1859) and the effects of biological invasions on native species, communities and ecosystems have been in focus of ecological research for decades (Elton 1958; Lodge 1993; Mack et al. 2000; Callaway & Maron 2006). Today, invasive species are considered to significantly contribute to the observed global environmental change (Vitousek et al. 1996) and to be the second largest cause of current biodiversity loss after habitat destruction (Wilcove et al. 1998; Sala et al. 2000; Sala & Knowlton 2006). A well-known example of an invasion caused by human activity is the Nile perch *Lates niloticus* into the Lake Victoria, which was introduced to compensate for diminishing fish stocks due to overfishing, but contributed to the extinction of more than 200 endemic fish species through predation and food competition. A prominent example from the marine environment is the invasion of the Mediterranean by a commercial aquarium strain of the green seaweed *Caulerpa taxifolia*. Only a few years after its introduction, the alga occupied about 6,000 ha and posed a severe threat to the sensitive native seagrass beds representing vulnerable nursery sites for other marine organisms.

Although these two cases are obvious examples of biological invasions, the meaning of the term 'biological invasion' remains controversial among ecologist (Davis & Thompson 2000; Colautti & MacIsaac 2004; Colautti & Richardson 2008; Valéry et al. 2008). In an ecological context, the term 'invasion' was first used by Goeze (1882) in his book "Pflanzengeographie für Gärtner und Freunde des Gartenbaus" to describe the spread of non-indigenous species (NIS) into new environments without any validation about their impacts (Rejmánek et al. 2002). It was used in this sense by ecologist during the first half of the last century. The publication of Elton's book 'The Ecology of Invasions by Animals and Plants' (1958) drew the attention to the increasing problems caused by NIS, but did neither provide a clear definition of the phenomenon (Richardson et al. 2000; Rejmánek et al. 2002; Valéry et al. 2008). From this point, invasion ecology progressively formed a research discipline of its own, although highly linked to general principles of community ecology theory (Rejmánek et al. 2002). Lacking a consistent definition, 'invasion' has been used to describe the spread of non-indigenous species *per se* (Colautti & MacIsaac 2004; Richardson & Pysek 2006), but has also been used in relation to the impact of invasions including both indigenous and non-indigenous invasive species (Davis & Thompson 2000). Recently, a mechanistic definition of biological invasions was proposed assuming that an overwhelming competitive advantage of the invader is always the reason behind an uncontrolled spread and this definition is independent of species origin (Valéry et al. 2008). The ecological processes resulting in the competitive advantage of invasive species are, however, still debated. Some theories suggest that the lack of shared evolutionary history between species provides the invader with a competitive advantage. Hence, it becomes clear that the criterion of non-indigenousness is essential for the definition of biological invasions. In my opinion, the term biological invasions should only be used for non-indigenous species in connection with a wide spread and high abundance in the new range, but without any validation about ecological or economic impacts. The term could be formulated as followed:

"Biological invasion is a process by which species with no historical record in an area breach biogeographic barriers and extend their range to become widespread and dominant in a new environment."

There is a wide agreement that invasions are largely a direct or indirect consequence of human activities. Many of the NIS were introduced intentionally (see examples above) to satisfy physical or social needs of humans, e.g. crops, game for hunting, ornamental flowers, or biological control agents. However, these examples of intentional introductions only account for a small part of todays invasions, with the vast majority of those being the result of accidental introductions due to an extensive global trade (Pimentel 2002; Wilson et al. 2009). Aquatic environments are especially vulnerable to biological invasions and it is estimated that at any time several thousand marine species are shuffled between biogeographic regions (Johnson & Chapman 2007). The majority of marine organisms are introduced as fouling organisms on ships or aquaculture organisms, but other introduction vectors are ballast water, fishing gear and aquarium trade (Carlton 1989; Reise et al. 2006; Schaffelke et al. 2006; Hewitt et al. 2007).

The global number of introduced seaweed is estimated to about 300 species, comprising about 10-40 % of the total marine NIS (Schaffelke et al. 2006; Williams & Smith 2007). In contrast to terrestrial plants of which many species were introduced to fulfil human needs, less than 3 % of the seaweed introductions were intentional (e.g. for aquaculture of the edible brown alga *Undaria pinnatifida*) and the vectors of introduction are only known for 60 % of all introduced seaweeds (Williams & Smith 2007). Most introduced seaweed species are either corticated or filamentous red algal species that are native to the NW Pacific or Indo Pacific, areas with the highest seaweed diversity in the world (Kerswell 2006; Williams & Smith 2007). By contrast, the Mediterranean and the Northeast Atlantic are the most heavily invaded oceanic regions (Williams & Smith 2007). Considering the intense shipping traffic between Asia and Europe (Drake & Lodge 2004; *nceas.ucsb.edu*), this geographic pattern of introduction may, however, not be surprising. The introduction and spread of *Caulerpa taxifolia* into the Mediterranean was probably the first case that raised the scientific and also public attention to seaweed invasions (Meinesz 1999). Since then, research on seaweed invasion has increased but is often lacking synthesis with terrestrial invasion ecology (Johnson & Chapman 2007).

1.1. The stages of biological invasions and their terminology

As outlined above, the terminology within the field of invasion ecology has been a source of confusion and miscommunication because the terms are often used differently and are prone to subjective interpretation. Additionally, the terminology and the concepts in invasion biology are affected by military metaphors (e.g. invasion, eradication, enemy release or novel chemical weapons). The use of this militaristic framework has the advantage that it draws attention to the problems caused by NIS, but I agree with Larson (2005) that it also poses a risk to lose scientific credibility and objectivity. However, since this is the common language and vocabulary in scientific communication within the field of invasion ecology, these terms are adopted in this thesis. By summarising different invasion models, Colautti and MacIsaac (2004) have presented a helpful illustration of the invasion process (see Figure 1) and suggested an adequate and neutral use of the terminology in the field, which I have adopted as a guideline in this thesis.

In general, biological invasions begin with the uptake of a resident species in a donor region (stage 0) into a transport vector (stage I), e.g. ship ballast water, and moved over a distance further than their natural biogeographical barriers. Propagules that survive the
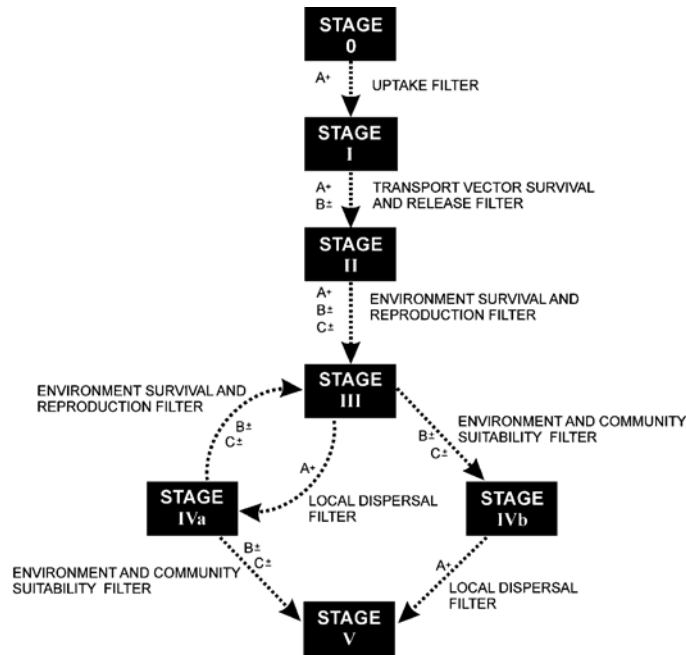
Figure 1 The stages of biological invasions according to Colautti & McIsaac (2004).
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transport are released and thus introduced into a new region (stage II). If the introduced species succeed to maintain a self-sustaining population independent of constant introductions of new propagules, but is still localised and numerically rare, the introduced species has been established in the new area (stage III). There are three classes of determinants that affect the probability to pass through the filters separating one stage from the next: (A) propagule pressure (i.e. the number of individuals released to a site in combination with discrete release events), (B) physicochemical requirements, and (C) community interactions (Figure 1). The filters may be unspecific allowing a random subset of species or genotypes to pass through, but can also be highly selective allowing only specific species or genotypes to enter the next stage. During the initial dispersal, propagule pressure and matching environmental conditions determine if a species will become introduced. During establishment, interactions between the introduced and resident species in the community should become increasingly important and determine if the NIS reach the next stages to become widespread but numerically rare (stage IVa), dominant but localised (stage IVb), or both widespread and dominant (stage V) in the new environment. NIS reaching stage V is commonly referred as 'invasive', a definition also used in this thesis.

2. How can biological invasions be explained?

During the last 50 years, research on species invasions has been aiming to identify general principles to explain establishment and invasion of introduced species (Elton 1958; Baker 1965; Blossey & Nötzold 1995; Rejmanek & Richardson 1996; Levine & D'Antonio 1999; Lonsdale 1999; Callaway & Aschehoug 2000; Davis et al. 2000; Keane & Crawley 2002; Lockwood et al. 2005). Despite these efforts, there is still poor general understanding of what explains biological invasions (Mitchell et al. 2006). Different processes are likely to be of importance at different stages of invasions and the factors determining the sensitivity of a community to the establishment of an introduced species may differ from factors that determine the invasiveness of a species. As a consequence, research on biological invasions

has divided into different directions focusing on propagule pressure, characteristics of the invader and the invaded communities, or on ecological and evolutionary processes.

2.1 Propagule pressure, traits of the invader and characteristic of the invaded community

Numerous studies tried to find common patterns in the traits of successful invaders (Baker 1965; Rejmanek & Richardson 1996; Van Kleunen et al. 2010b) and in the characteristics of communities most susceptible to invasion (Levine & D'Antonio 1999; Lonsdale 1999; Davis et al. 2000; Levine et al. 2004). Propagule pressure, disturbance, resource availability, and the species diversity of the recipient community are single factor hypotheses suggested to explain successful establishment of introduced species (Knops et al. 1999; Davis et al. 2000; Lockwood et al. 2005). Human transport may determine where, how often, and how many propagules of NIS will enter a new community. Propagule pressure has been demonstrated to be a good predictor for the variation in establishment success across both taxa and sites as large numbers of propagules and frequent release events will enhance the probability of an introduced species to survive and establish (Lockwood et al. 2005; Colautti et al. 2006). However, the propagule pressure needed for an introduced species to establish at a given location is influenced by the traits of the introduced species and by the characteristics of the environment (Lockwood et al. 2005). Based on niche theory, environments with high species diversity/richness have been assumed to provide biotic resistance to the establishment of NIS because of strong interspecific interaction (Elton 1958; Kennedy et al. 2002; Fargione & Tilman 2005). Diverse communities are likely to use available resources more completely and hence lack 'empty niches' that could be filled by NIS (Kennedy et al. 2002; Fargione & Tilman 2005). Although this assumption is logically appealing, no general pattern has been found in the correlation of species diversity and invasibility (Davis 2009; Bezemer & van der Putten 2007). It has also been proposed that temporally and spatially heterogeneous environments created by human disturbance will be highly susceptible to invasions mainly due to fluctuating resource availabilities (Davis et al. 2000; Thompson et al. 2001), and disturbance and higher resource availability seem to be robust predictors of the invasibility of communities at multiple spatial scales (Colautti et al. 2006). This pattern may also hold for marine communities (Byers 2002; Valentine et al. 2007), although in environments affected by anthropogenic activities disturbance, propagule pressure, resource availability and biodiversity are likely interrelated. For example, harbours are usually highly disturbed and eutrophicated areas with low species diversity, but also sites with the highest release of propagules (Drake & Lodge 2004). Knowledge about propagule pressure, disturbance, and resource availability may enable to predict which areas have an increased risk for the establishment of introduced species, but are less useful to understand the spread after establishment. This is more likely determined by the traits of introduced species and their ecological interactions with native residents in the new environment (Colautti et al. 2006).

With the intent to elucidate what defines the invasiveness of an introduced species, functional traits related to increased plant performance, e.g. physiological tolerances, biomass allocation, size, growth rate and reproduction modes, have been compared between invasive, non-invasive, and native species (Daehler 2003; Pyšek & Richardson 2007; Van Kleunen et al. 2010a, 2010b). The results from such comparisons have been mixed for terrestrial plants (Daehler 2003; Van Kleunen et al. 2010b), and likewise no common traits generally explaining invasiveness were found for seaweeds (possible exception might be asexual reproduction and large growth form) (Nyberg & Wallentinus 2005). These findings reflect

that different traits may enable invasion of natural or human-disturbed communities (Sakai et al. 2001). Even when invasive species share common attributes, it still has to be demonstrated that these specific traits confer invasiveness (Colautti et al. 2006). Especially for species that have been intentionally introduced to satisfy human needs (e.g. ornamental plants with large flowers) common traits can be artefacts.

2.2 Ecological processes

Different traits of introduced species are likely to match different environments and the ecological interactions in the new community determine whether an introduced species will become invasive or not. Competition and natural enemies are the main factors that structure plant communities (Tilmann 1982; Huntly 1991; Hulme 1996). Consequently, several hypotheses suggest that ecological interactions are the drivers of invasion success and failure (Mitchell et al. 2006). The idea that biotic interactions and especially natural enemies are crucial factors that determine invasion success dates back to Darwin (1859). Impeded establishment or failed invasions have often been attributed to the biotic resistance exerted by the receiving community, i.e. competition with native residents, herbivory and diseases (Elton 1958; Maron & Vilà 2001; Levine et al. 2004; Mitchell et al. 2010), while invasion success of introduced plants has been explained by the release from natural enemies (i.e. the enemy release hypothesis, ERH). The rationale behind the ERH is that natural enemies, i.e. herbivores and pathogens, are important direct regulators of plant populations. In its classical sense, the ERH states that on introduction into a new region introduced plants escape the regulation by their co-evolved specialist enemies, which will result in an uncontrolled proliferation of the introduced population in their new region. The lack of biotic resistance from natural enemies in the introduced community were later included into the predictions of the ERH by Keane and Crawley (2002), who argued that introduced plants do not only escape their specialist enemies, but are also less affected than the resident species by enemies in the new range. Therefore, enemies are predicted to have increased negative effects on the performance of native species, which in turn decrease their competitive ability and releases the introduced plants from competition. This release enables for increased population growth and invasion success of the introduced species (Keane & Crawley 2002). Empirically, the ERH has been tested using two different approaches: *i)* biogeographic comparisons assessing differences of enemy impact on the plant population in its native and introduced ranges, and *ii)* community studies assessing enemy impacts on introduced compared to native species in the new community. While biogeographic comparisons have often supported the ERH showing reduced diversity, abundance and impact of herbivores on the introduced population compared to the native, the results from community studies are much more equivocal ranging from lowered to increased damage of introduced species compared to native species by local natural enemies (Agrawal & Kotanen 2003; Colautti et al. 2004; Parker & Hay 2005; Mitchell et al. 2006; Parker & Gilbert 2007). Only a few studies have assessed enemy release for introduced seaweeds. In comparison to terrestrial systems, there is a low degree of host specialisation among marine herbivores (Hay & Steinberg 1992). Consequently, the positive effects of escaping specialist herbivores should be less pronounced in marine systems in comparison to terrestrial systems and low impacts of generalist enemies should be even more important for the invasion success in aquatic environments. For example, the introduced species *Fucus evanescens* harbours reduced diversity and abundance of generalist herbivores and is of low preference to these generalists compared to native congeners in the introduced ranges, which was in opposite to the finding in its native range (Wikström et al. 2006; Forslund et al. 2010). Low feeding preference of generalist herbivores was also stated for the

red alga *Gracilaria vermiculophylla* (Nejrup et al. 2012) and reduced herbivore pressure was shown for non-native seaweeds in Hawaii (Vermeij et al. 2008). A comparison between invasive and non-invasive seaweeds has further indicated that invasive red and green algae generally exhibit only low herbivore damage (Nyberg & Wallentinus 2005).

In close linkage to the ERH, the invasion success has also been explained by evolutionary changes in the introduced plants towards larger growth and higher fecundity (Blossey & Nötzold 1995). The evolution of increased competitive ability hypothesis (EICA) predicts that natural selection should favour genotypes with reduced resource allocation to defence in the absence of enemies, but improved competitive abilities by maximised vegetative growth and reproduction (Blossey & Nötzhold 1995). The EICA-hypothesis was explicitly developed in the context of 'the dilemma of plants: to grow or defend' (Herms & Mattson 1992), which assumes that the production of secondary metabolites is costly and that there is a trade-off between defence production and growth or reproduction. Even though earlier studies provided inconsistent evidence (Bergelson & Purrington 1996), the common view today is that chemical defences in terrestrial vascular plants generally are costly (Purrington 2000; Heil & Baldwin 2002; Strauss et al. 2002; Cipollini et al. 2003, Walter & Heil 2007). In contrast to vascular plants, algal cells are less differentiated and do not form distinct parts such as roots, stems and leafs. Furthermore, internal transport mechanisms for nutrients and photosynthetic products are poorly developed and most parts of the thallus are capable to photosynthesise and absorb nutrients instead (Cole & Sheath 1990; Lobban & Harrison 1996). These features may make production and allocation costs different in macroalgae compared to vascular plants. Only a few previous studies have focused on the costs of chemical defences in seaweeds. Inferred from negative phenotypic correlations between growth and levels of defence metabolites, significant costs have been found for the brown algal phlorotannins (reviewed by Pavia et al. 2012). In addition, a study by Dworjanyn et al. (2006) demonstrated costs for brominated furanones in the red algae *Delisea pulchra* by experimentally manipulating the production of the defence compounds.

Even though there is now consensus about the costs of defences for vascular plants, support for the EICA has been equivocal and there are only a few studies being fully consistent with the predictions of the hypothesis (see Bossdorf et al. 2005 for references; Joshi & Vrieling 2005; Müller & Martens 2005; Meyer et al. 2005; Franks et al. 2008; Zou et al. 2008; Caño et al. 2009; Cripps et al. 2009; Orians & Ward 2010). Both the ERH and EICA rest on the logic that the introduced plants are not recognised by neither specialist nor generalist enemies in the new range. However, as mentioned above, empirical tests of the ERH have demonstrated that introduced plants do not generally escape herbivory by generalists (Parker & Hay 2005). Accordingly, more recent studies on the EICA-hypothesis have concluded that it is necessary to distinguish between chemical defences against generalist and specialist enemies and that protection against generalist enemies is important even in the plant's new range (Joshi & Vrieling 2005; Müller & Martens 2005; Wikström et al. 2006; Forslund et al. 2010; Huang et al. 2010). By redefining the predictions, Müller-Schärer et al. (2004) tried to preserve the validity of the EICA. Arguing for the existence of differences and trade-offs between resistance against generalist herbivores and protection from specialised enemies, they proposed that the observed increases in vigour and resistance against generalist could be explained by resource reallocation from defences against specialist to both growth and defences against generalists. According to this idea, the release from specialist enemies may select for a lowered level of quantitative defences (i.e. highly concentrated and large molecules that are costly to produce), which act as a digestibility-reducing defence against specialists. In addition, the lack of specialist herbivores allows increased qualitative defences (i.e. usually small molecules with relatively low production

costs), which are attractive to specialists but toxic to generalist enemies (Åström & Lunberg 1994; Müller-Schärer et al. 2004). In the plant's native range trade-offs between deterrence of generalist and attraction of specialists and between resistance to specialist and competitive ability should select for intermediate levels of these compounds. In the new range where specialist herbivores are absent but generalists present, the introduced plant is expected to evolve low levels of quantitative defence (but a higher growth than in the native area) and high levels of qualitative defences.

In contradiction to the EICA that explains the increased competitive ability with resource allocation from defence compounds to growth, the novel weapon hypothesis (NWH) attributes a competitive advantage of invaders over native plants to the production of bioactive secondary metabolites. The NWH was initially developed for plant-plant allelopathic interactions and states that introduced plants will get a competitive advantage over natives when they possess novel chemicals towards which native species are evolutionary naïve (Callaway & Aschehoug 2000; Hierro & Callaway 2003; Callaway & Ridenour 2004) (Figure 2). This hypothesis has later been expanded to include plant-herbivore, plant-pathogen and plant-soil biota interactions (Cappuccino & Carpenter 2005; Cappuccino & Arnason 2006; Verhoeven et al. 2009). Positive correlations between invasiveness and unique chemical compounds or unique chemical profiles have been used to support the NWH (Cappuccino & Arnason 2006; Barto et al. 2010). Co-evolved plants, fungi and herbivores in the native range of the spotted knotweed *Centaurea stoebe* were more resistant than naïve plants, fungi or herbivores in the introduced region (Callaway et al. 2008, 2011, 2012; Schaffner et al. 2011). No marine study has specifically addressed the NWH (but see paper I), although some have indicated the importance of the chemical defence in the invasion process of seaweeds (Amade & Lemée 1998; Wikström et al. 2006; Forslund et al. 2010). The highly invasive seaweeds *Caulerpa taxifolia, Sargassum muticum*, and *Codium frafile* spp. *tomentosoides* have been stated to be non-preferred food sources for native herbivores and to have effects on their growth and reproduction (Schaffelke & Hewitt 2007; Valentine et al. 2007; Williams & Smith 2007). At least *C. taxifolia* and *C. fragile* spp. *tomentosoides* are known to produce secondary metabolites that are suggested to have feeding deterrent effects on native herbivores (Amade & Lemée 1998; Lyons et al. 2007).

The NWH stresses evolutionary novelty to be a key advantage of introduced plants since enemies including competitors have not been selected to resist or tolerate the chemicals of the introduced plant. The NWH equate novelty with effectiveness in the mode of action of the secondary compounds. This has recently been challenged by Lind and Parker (2010), who found no indication that the chemical defences of introduced plants are generally more effective than the defences of native species.

A missing co-evolutionary history of the introduced and members of the new community has also been used to explain the susceptibility of introduced plants to generalist herbivores (Parker et al. 2006). Verhoeven et al. (2009) argued that evolutionary novelty leads to mismatches in interactions between the introduced plant and its novel environment, but depending on the mode of action these mismatches can either be beneficial for the introduced plant, thereby promoting invasion, or can be disadvantageous and result in biotic resistance of the community.
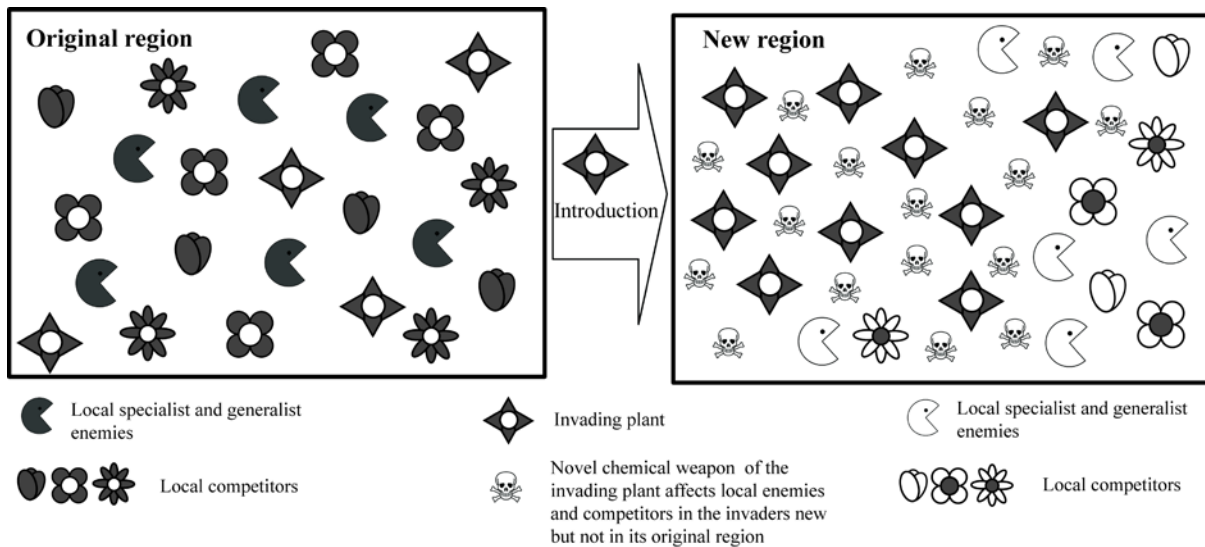
Figure 2 Illustration of the Enemy Release Hypothesis (ERH) and Novel Weapon Hypothesis (NWH). In the native region all plants suffer from their generalist and specialized enemies as well as from interspecific competition. On introduction to a new region, the non-indigenous plant escapes regulation by its enemies as predicted by the ERH. The introduced plant will be less attacked by local enemies than native plants due to its effective chemicals as predicted by the NWH. As a consequence, the non-indigenous plant will gain a competitive advantage and become invasive in the new region. © Oxford 2012

2.3 Invasion genetics

In addition to the ecological paradox of species invasion, i.e. that introduced species not adapted to the new environment can be more successful than native species that have evolved in this environment, there is also a genetic paradox of species invasions (Allendorf & Lundquist 2003; Frankham 2005). The colonisation of new areas by introduced species is usually considered to cause severe population bottlenecks as the number of initial released individuals is often small. The genetic variation in the founder populations is likely to be further reduced due to increased genetic drift (Sakai et al. 2001; Allendorf & Lundquist 2003; Frankham 2005). The reduced genetic variation is predicted to limit the ability of species to adapt to novel environments (Fisher 1930; Sakai et al. 2001; Lee 2002) and can also lead to inbreeding depression and an increased risk for extinction (Lande 1988; Brook et al. 2002). All this leads to the genetic paradox of invasions, i.e. how bottlenecked populations with typically low genetic diversity, low evolutionary potential and sometimes even low reproductive fitness can become successful in their new ranges.

Inbreeding depressions can be circumvented by means of asexual reproduction or self-fertilising (Sakai et al. 2001; Allendorf & Lundquist 2003; Frankham 2005). Clonal reproduction seems to be a common feature of some introduced terrestrial and aquatic plants (Liu et al. 2006; Roman & Darling 2007), and may especially in combination with high phenotypic plasticity give rise to invasive populations consisting of only one highly successful clonal genotype (Sakai et al. 2001; Ren et al. 2005). In striking contrast to the examples of extreme low genetic diversity in invasive populations, repeated introductions and admixture of the same species from different source populations have been shown to generate invasive populations that are genetically more diverse than the single source populations (Sakai et al. 2001; Bossdorf et al. 2005; Sax et al. 2007). If multiple introductions causing equal or increased genetic diversity of introduced compared to native populations are

exceptions or and the rule of plant invasions is not fully understood. Regarding seaweeds, asexual reproduction is a common feature of all algal divisions (Collado-Vides 2001) and most of the investigated seaweed species have shown reduced genetic diversity in their new range compared to the native range (McIvor et al. 2001; Provan et al. 2004; Andreakis et al. 2007, but see Andreakis et al. 2009).

A commonly observed feature of invasions is a lag time between the initial establishment and the range expansion of the invader (Sakai et al. 2001). These lag times have often been explained with the time needed for the introduced species to evolve adaptations to the new environment (Sakai et al. 2001). Some theories in invasion ecology, i.e. the EICA-hypothesis including its refinements (Blossey & Nötzold 1995; Müller-Schärer et al. 2004), consider adaptive evolution as more important than the degree of preadaptation necessary for an introduced species to establish (Sakai et al. 2001). These theories assume that the genetic variation in introduced populations at the time of their establishment is sufficient to allow for adaptive evolution in the new environment, because the lag times are usually too small to explain evolution through mutation or genetic drift (Fitzpatrick et al. 2011). Differences in resistance traits and growth between introduced and native individuals grown under common environmental conditions have been usually interpreted as adaptive evolution in the introduced populations (see Bossdorf et al. 2005; Van Kleunen et al. 2010a). However, it is difficult to distinguish between adaptive evolutionary changes, i.e. responses to selection, and non-adaptive genetic changes due to founder effects (Bossdorf et al. 2005; Van Kleunen et al. 2010a). The identification of the source population and its invasion history should thus be fundamental for the understanding of genetic changes occurred in introduced populations. For this purpose, molecular markers represent helpful tools in invasion ecology to identify NIS (e.g. cryptic introductions) and their source populations, to track invasions in space and time, to assess molecular genetic diversity and to uncover possible hybridisation with indigenous species (Booth et al. 2007).

Generally, the genetics and evolution of invasive species have received far less attention than their ecology, and questions about biological invasions have only recently been approached by a combination of ecological work with population genetics and ecological genomics (Bossdorf et al. 2005).

3. What effects do biological invasions have on communities and ecosystems?

Introduced species can alter community structure (species diversity and composition) and ecosystem processes through a variety of mechanisms at different spatial and temporal scales, and with different degrees of impact (Levine et al. 2003; Strayer et al. 2006; Hejda et al. 2009; Ehrenfeld 2010; Vilà et al. 2011). The impacts of plant invaders can be categorised into: *i)* effects on individual plant species (e.g. through hybridisation), *ii)* effects on community composition and diversity (e.g. local extinctions), *iii)* effects on higher trophic levels and food webs, *iv)* effects on the physical environment (e.g. fire regimes, hydrology, hydrodynamics, sedimentation), and *v)* effects on ecosystem processes (e.g. net primary production, biogeochemical cycling of elements) (Levine et al. 2003; Ehrenfeld 2010; Vilà et al. 2011).

The introduction of a new plant species will inevitably alter the composition of the local community, but the degree of the impact can be highly variable. A dominating and widespread (i.e. invasive) introduced species will per definition have a higher impact on the community structure than a numerically rare introduced species (i.e. non-invasive). In most

cases, the spread and dominance of an introduced species involves the decline of native species and is therefore considered as a threat to biodiversity. After habitat destruction, the introduction of NIS is often stated to be the second most important cause of current global biodiversity loss, but it should be noted that an increase of net diversity for specific regions and localities followed by the introduction of NIS have also been observed (Vitousek et al. 1996; Wilcove et al. 1998; Sax & Gaines 2003, 2008; Gurevitch & Padilla 2004). Effects on biodiversity have often been explained with direct competitive effects of the introduced species on growth and reproduction of native competitors (Vilà & Weiner 2004; Vilà et al. 2011). However, it is often difficult to distinguish whether introduced species are drivers of biodiversity loss or passengers of human mediated habitat degradation since correlations between native species loss and invasive species dominance do not necessarily reflect causality (Didham et al. 2005; MacDougall & Turkington 2005; Powell et al. 2011).

Despite the fact that invaded communities have frequently been shown to have a reduced biodiversity (Blossey et al. 2001; Vilà et al. 2006, 2011), primary production and standing biomass increase for invaded communities, which is in contrast to the notion that more diverse ecosystems are more productive (Loreau et al. 2001; Liao et al. 2008; Vilà et al. 2011). Although, no specific trait has been identified that can generally explain invasions success (see section 2.2), ecophysiological and morphological traits have a central role in explaining species-ecosystem relationships. Accordingly, these traits of introduced species have been suggested to provide a predictive framework for the impacts of introduced species on ecosystems.

Introduced plants have not only been reported to affect the plant community, but have also been shown to have bottom-up effects on higher trophic levels by changing the composition, diversity and behaviour of consumers and decomposers (Levine et al. 2003; de Groot et al. 2007; Gerber et al. 2008; Vilà et al. 2011). The effects on higher trophic levels partly depend on the degree the introduced plant is used as a food source by consumers, but can also be a result of altered habitat properties, e.g. refuge from predation or access to nesting sites (Schmidt & Whelan 1999; Pearson 2008; Vilà et al. 2011).

Marine seaweeds represent a significant component of all marine NIS taxa. A total number of 277 non-indigenous seaweeds have been reported but their ecological impacts have been investigated for only 17 species (Williams & Smith 2007). Most of the work has concentrated on the four invasive seaweeds *Caulerpa taxifolia, Codium fragile* spp. *tomentosoides*, *Sargassum muticum* and *Undaria pinnatifida* (see Schaffelke & Hewitt 2007 for references). Invasive macroalgae are considered to have serious effects on ecosystem structure and processes through space monopolisation and alteration of food webs (Schaffelke & Hewitt 2007). The predominant effects reported are a reduced biomass and decreased diversity of native seaweeds in invaded communities, which has commonly been related to a superior competitive ability of the invasive seaweeds (see Schaffelke & Hewitt 2007 for references). Furthermore, effects on the abundances of native fish and invertebrate fauna have also been demonstrated (see Schaffelke & Hewitt 2007 for references). Much less is known about the effects of introduced seaweeds on ecosystem processes (e.g. primary and secondary production, nutrient cycling). For example, it is not known if introduced seaweeds increase the net primary production in invaded communities, which seems to be a general pattern in terrestrial plant invasions. The only published study on impacts of seaweed invasion on community production showed that the invasive brown alga *S. muticum* had a negative effect on the standing biomass of the invaded community since the growth of the introduced species could not compensate for the biomass loss of native understory species through shading (White & Shurin 2011). Increased productivity of the community in

terrestrial systems may be explained with the intentional introduction of plants selected for high growth rates. In contrast, this sampling effect should be less common for seaweeds since these have commonly been accidentally introduced.

Aim of the thesis

A fundamental question in plant invasion biology is how plants can invade natural communities in which they have not occurred previously and should thus be less well adapted than native species to the abiotic and biotic conditions. Several of the most influential invasion hypotheses, e.g. the ERH, EICA, NWH, or biotic resistance hypothesis, attribute invasion success to novel ecological interactions between introduced and native species in the new community. Especially, plant-herbivore interactions have repeatedly been suggested as an important determinant in plant invasion. However, key factors affecting the outcome of these new interactions between introduced and native species are not sufficiently understood. The aim of this thesis was to identify ecological interactions and mechanisms underlying the invasibility of introduced species by using the red alga *Bonnemaisonia hamifera*, which is highly invasive in large parts of the North Atlantic, as a model organism.

This thesis consists of five separate studies with specific objectives, which are briefly presented here.

Paper I: Based on the prediction of the ERH/EICA, the objective of paper I was to examine if *B. hamifera* is less affected by native generalist herbivores in comparison to native filamentous red algae, and to further investigate the mechanism behind the low preference for this invasive alga. The NWH predicts that plants should become invasive if they possess novel chemical defences towards which native species are evolutionary naïve. Since the feeding preference for native seaweeds by the generalist herbivores was not due to structural differences between the native and the invasive species, the presence of a chemical defence in *B. hamifera* was investigated.

Paper II: Primary producers form the basis for food webs, but the effects of seaweed invasions on ecosystem functioning are poorly understood. The aim of paper II was to examine the effects of *B. hamifera* and *Heterosiphonia japonica,* which is also an introduced and abundant seaweed on the Swedish west coast, on the biomass production of the invaded community, under two possible scenarios. One scenario simulated that the introduced species competitively exclude a native species leading to unaltered species diversity; the other scenario was that the invader and native species co-exist leading to increased species diversity. These two scenarios were chosen as natural communities are traditionally thought to be species saturated and a new species cannot be added without the loss of existing ones (Stachowicz & Tilman 2005; Sax et al. 2007). Species introductions have, however, also been shown to increase biodiversity on regional scales, suggesting that co-existence rather than competitive exclusion may be the rule (Davis 2003; Gurevitch & Padilla 2004). Since changes in primary production and biomass availability can further have cascading effects on the next trophic levels, we examined the value of the biomass produced of the invasive species for one of the most common native herbivores, the isopod *Idotea granulosa.*

Paper III: The results of paper II indicated that *B. hamifera* is not a superior competitor in comparison to native filamentous species. Therefore, to explain the prevalent dominance of this species in the study area, we hypothesised that the feeding preference of native

generalists provide the well-defended introduced species with a competitive advantage over the equally or faster growing native competitors. Increased herbivore damage does not always result in decreased performance of native plants since they may have evolved tolerances (e.g. compensatory growth) towards their common herbivores and, hence, feeding preferences does not have to relate to community effects (Chun et al. 2010). Additionally, the degree to which a plant species is consumed in the field does not solely depend on the food quality, but also on trade-offs between food acquisition and predation risk for the consumer (Duffy & Hay 1991; Pavia et al. 1999). Much of the evidence concerning the traits of invaders that may explain invasions has been obtained from correlations of e.g. growth rate, size or seed production between invasive versus natives or invasive versus non-invasive species (van Kleunen et al. 2010b). While these studies indicate which traits may be related with invasive species, they do not provide evidence that these traits are the causal drivers of invasions. The objective of paper III was to investigate the causal relationship between the low preference of native generalists for *B hamifera* (due to its chemical defence) and the invasion success in terms of increasing abundances in the red algal community. This study specifically addressed a recently published theoretical model (Orrock et al. 2010), which showed how introduced species may be able to invade a community via refuge-mediated apparent competition.

Paper IV: The costs of defence productions and the evolutionary trajectories of chemical defence levels in introduced plants are commonly discussed topics in studies testing the EICA-hypothesis. While there is ample evidence that chemical defences of vascular plants are costly, there are only a few studies that have addressed this question for seaweeds and are almost exclusively based on correlative data. The primary objective of paper IV was to experimentally investigate if the production of defensive secondary metabolites incurs a cost for *B. hamifera*.

Paper V: Due to population bottlenecks, introduced populations are usually expected to have a reduced genetic diversity compared to their source population and to possess an increased risk of inbreeding depression (Sakai et al. 2001; Allendorf and Lundquist 2003). Additionally, genetic drift is considered to limit the potential for adaptations to novel selection regimes in the new range (Sax et al. 2007; Roman and Darling 2007). Some invasions hypotheses such as the EICA assume that adaptive evolutionary changes provide introduced plants with a competitive advantage over native species, and thus rely on the assumption the genetic variation in introduced populations at the time of their establishment is sufficient to allow for adaptive evolution. Using the amplified fragment length polymorphism (AFLP) technique, the objective of paper V was to gather preliminary insights into the genetic diversity and population structure of *B. hamifera* in its introduced Swedish range compared to the native range in Korea.

Methods

This chapter describes the study area, the model organism, and the chemical and molecular techniques that were used in the studies of this thesis.

Study area and field collection

All laboratory experiments were performed at the Sven Lovén Centre for Marine Sciences – Tjärnö (former Tjärnö Marine Biological Laboratory) under stable conditions in the laboratory or on a mesocosm scale in outdoor tanks. The field station is situated on the Swedish Skagerrak coast next to the Kosterhavet Marine National Park. This area harbours the highest marine biodiversity in Sweden due to the influence of Atlantic water masses. Furthermore, it is characterised by a large proportion of rocky shores, a small tidal range of 0.2-0.3 m and an average salinity of 28 psu between 0-30 m. All material used in the experiments were collected in the archipelago around the field station by snorkelling or SCUBA.

The invasive red alga *Bonnemaisonia hamifera* (Hariot)

Bonnemaisonia hamifera was first described by Hariot (1891) from Yokosuka on the Isle of Honshu in Japan. The life cycle of the species was not completely clarified until the late 1940s (Breeman et al. 1988; Chen et al. 2007), but it is now known that *B. hamifera* has a heteromorphic life cycle where a multiseriate, haploid gametophyte alternates with a uniseriate, diploid tetrasporophyte (Figure 3). Before the life cycle was fully understood (Harder & Koch 1949), the two phases were considered as two separate species, *B. hamifera* and *Trailliella intricata*. Since the life cycle is adapted to the temperature and light conditions in the NW Pacific, this region is considered to be the native range of *B. hamifera* (Breeman et al. 1988). Both life stages grow epiphytically, whereby the gametophyte entangles to other seaweeds by means of its species specific hook and grows more shallow (intertidal to shallow subtidal) than the tetrasporophyte .

After the introduction of *B. hamifera* into European waters, which likely occurred by ship traffic or shellfish import, the species became widely distributed and abundant from Norway to the Azores (Breeman et al. 1988; Maggs & Stegenga 1998; Thomsen et al. 2007). The species is also considered invasive on the NE Atlantic coast (Harris & Tyrrell 2001). In Europe, the tetrasporophyte was first reported in 1890 from the English Channel, followed by the description of female gametophytes in 1893. Both life stages can propagate vegetatively by fragmentation (Breeman et al. 1988), and observations of male gametophytes and fertilised cystocarps on females on the coasts of Helgoland, Brittany and Norway (Kornmann & Sahling 1962; Floc'h 1969; Haugen 1970) indicate that the species can reproduce sexually at least in some parts of the introduced range. However, the degree of recombination remains unknown for most parts of the introduced area and on both sides of the North Atlantic the tetrasporophyte is the dominant and invasive life stage (Johansson et al. 1998; Harris & Tyrrell 2001; Thomsen et al. 2007). In Scandinavian waters, the tetrasporophytic phase of *B. hamifera* is now one of the most common filamentous algae where it forms dense mats on rocky shores and dominates local communities (Johansson et al. 1998; Thomsen et al. 2007; Karlsson 2007).
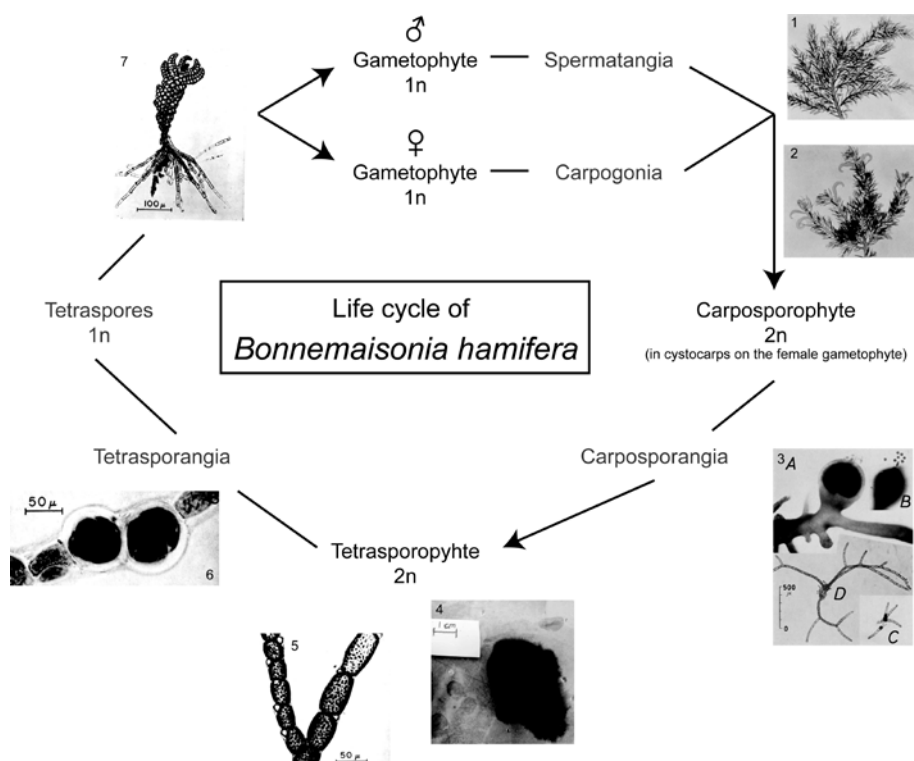
Figure 3 Illustration of the life cycle of *Bonnemaisonia hamifera*. Pictures 1, 2, and 3 used with the permission of Kornmann & Sahling 1962 © Springer 1962; pictures 5, 6, and 7 used with the permission of Chen et al. 2007 © Wiley 2007
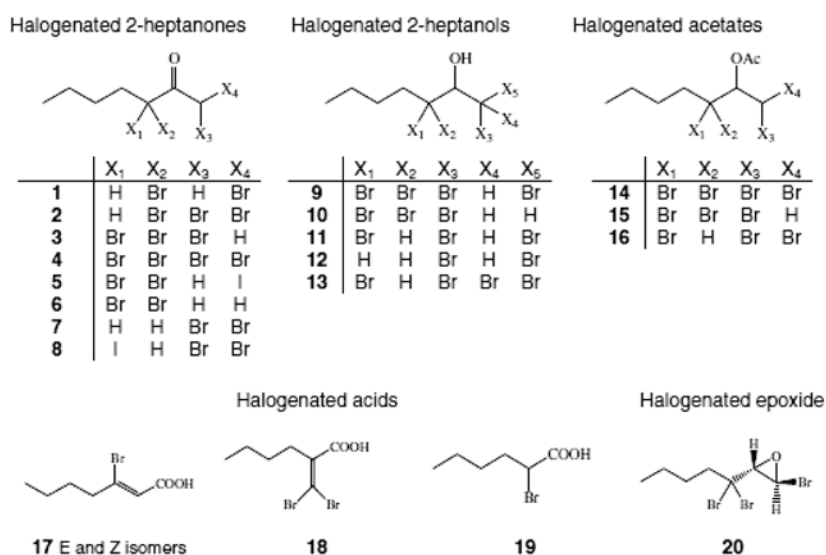

Figure 4 Halogenated metabolites of *Bonnemaisonia hamifera* from Kladi et al. 2004

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Bioassay-guided fractionation and analytical techniques

The identification of biological active compounds is necessary to evaluate the novelty of a compound in the introduced range, and to investigate seasonal and spatial changes to follow its evolutionary trajectories. The identification requires the separation of the active compounds from thousands of others present in the organism. A common approach to isolate the compounds is a so-called bioassay-guided fractionation. Hereby, an extract of the organism is prepared and then step-wise fractionated according to the physiochemical properties of the compounds, usually by liquid partitioning or liquid chromatography. The generated fractions are then tested for their activity in bioassays. Active fractions are further separated and subsequently bioassayed until, in the ideal case, one pure compound is obtained. As a final step the structure of the active compound is determined by spectroscopic techniques such as mass spectrometry (MS) and nuclear magnetic resonance spectrometry (NMR). Bioassay-guided fractionation is a straightforward approach to identify and assess biological active compounds. Depending on the size and character of the compound, the purification and structural identification may be a difficult process.

In this study, a bioassay-guided fractionation was used to identify the feeding deterrent compound in *B. hamifera*. The structural identification of the feeding deterrent compound was facilitated by the fact that mass fragments matched with a secondary metabolite that had already been described for *B. hamifera* (Siuda et al. 1975; Jacobsen & Madsen 1978; McConnell & Fenical 1980).

Amplified Fragment Length Polymorphism (AFLP)

The AFLP is a PCR based genetic tool for DNA fingerprinting. The advantage of this technique is that no *a priori* knowledge about the genome of the investigated species is required and that it produces a high number of dominant markers at moderate costs after a short start-up time (Bensch and Åkesson 2005). The procedure consists of five steps (Figure 5). In the first step, the complete genome is digested by two different restriction enzymes, one frequent and one seldom cutter, e.g. MseI and EcoRI enzymes. In the next step, adaptor pairs are ligated to the sticky ends of the restriction fragments. In the pre-selective amplification a subset of these fragments is amplified and of these an even more specific subset is amplified during the selective amplification. For the selective amplifications a fluorescent labelled primer is used, which allows the visualisation of the fragments after the electrophoretical separation on a sequence analyser.
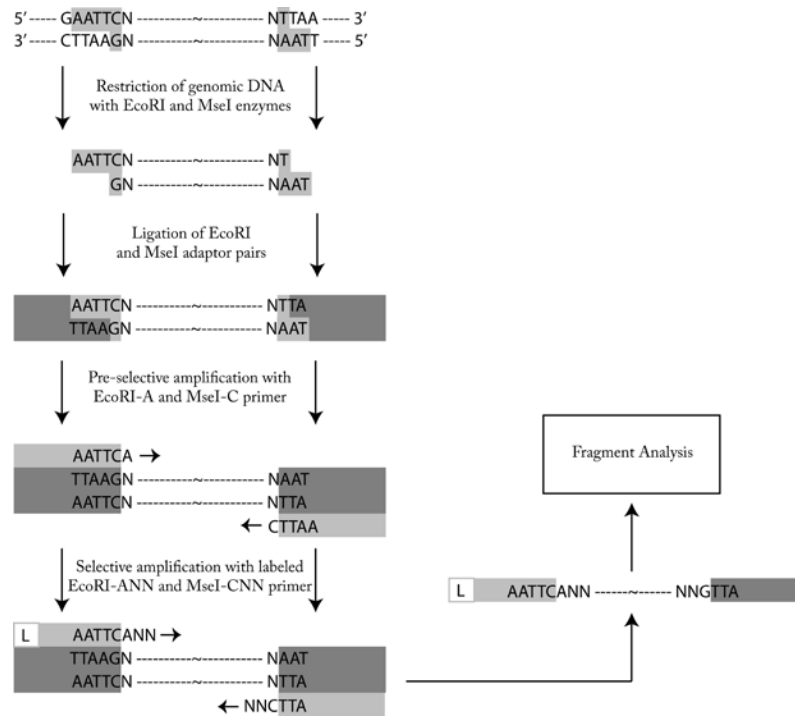
Figure 5 Schematic illustration of the AFLP procedure.

Results and Discussion

The highly invasive red alga *Bonnemaisonia hamifera* was of very low preference to generalist herbivores in the invaded range (paper I). In fourteen out of sixteen pair-wise feeding preference experiments the generalist herbivores significantly favoured the native competitors over *B. hamifera* (Figure 6). These findings are consistent with the ERH, which predicts that invasive plants should experience little damage by native herbivores in their new environments. However, as outlined in section 2.2, the ERH provides no logical reason to why generalist herbivores in the new range should not recognise the introduced species as a suitable host/food. Consequently, it cannot explain why some introduced plants are rejected whereas others are readily consumed, or even preferred, by native generalists (Colautti et al. 2004; Parker & Hay 2005; Parker & Gilbert 2007). We could show that the low preference of native generalists for *B. hamifera* was due to a chemical defence, which was tracked down to the secondary metabolite 1,1,3,3-tetrabromo-2-heptanone by using a bioassay-guided fractionation. These findings are in accordance with the NWH, which attributes invasion success to the presence of phytochemicals that are novel in the invaded range. Support for the NWH had previously been based on circumstantial evidence, but paper I provided direct evidence that a novel chemical compound is responsible for the low degree of attack by herbivores in the new range. Our conclusion about the novelty of the compound was based on the fact that there are no reports (in scientific journals or chemical compound databases) showing the production of this compound in other organisms. Furthermore, all related members of family Bonnemaisoniacea produce different and species-specific secondary metabolites (Kladi et al. 2004). Thus, it is highly unlikely that herbivores in the native range have been exposed to 1,1,3,3-tetrabromo-2-heptanone before the introduction of *B. hamifera*, which can explain its effectiveness as a grazer deterrent.
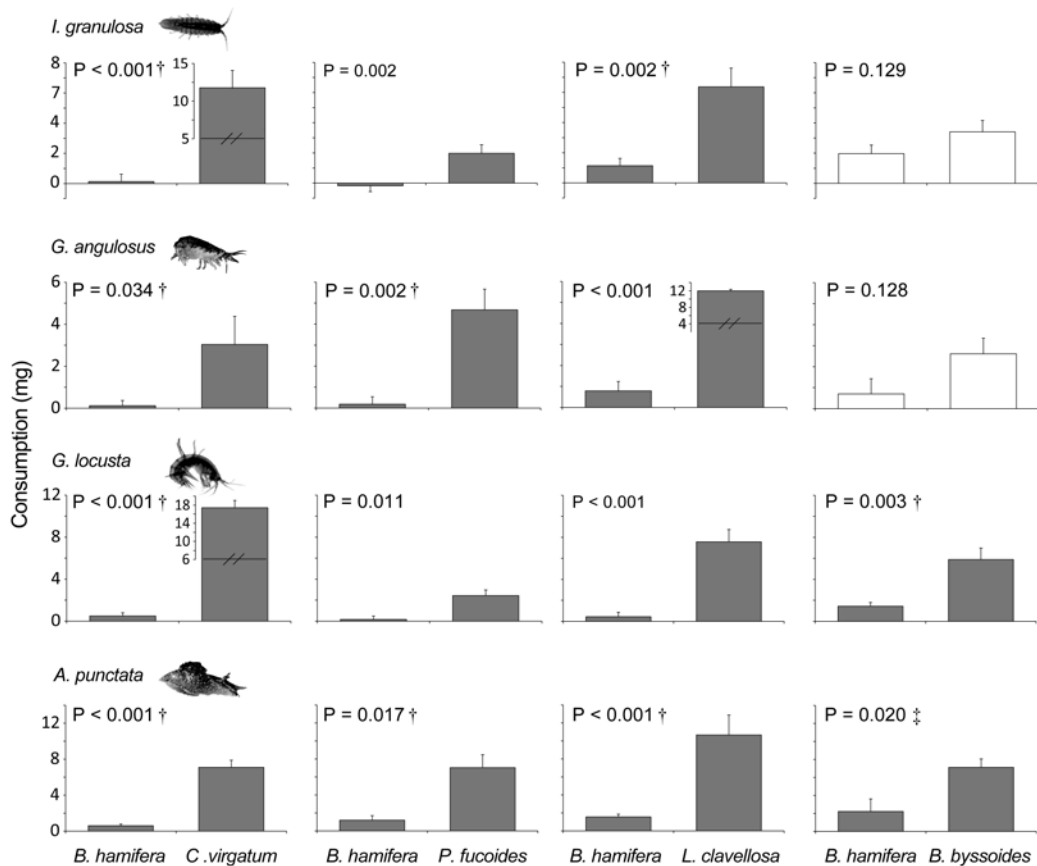
Figure 6 Feeding preferences of the generalist herbivores (*Idotea granulosa, Gammarellus angulosus, Gammarus locusta*, and *Aplysia punctata*) offered the choice between the invasive alga *Bonnemaisonia hamifera* and native algal species (*Ceramium virgatum, Polysiphonia fucoides, Lomentaria clavellosa* and *Brongniartella byssoides*). Bars show mean consumption of the two food types. Error bars show +1SE (n=10). Feeding deterrence is indicated by grey bars and p-values < 0.05. Numbers specify what data have been used in the statistical analysis: no symbol, untransformed; †, log transformed; ‡, data with heterogeneous variances.

Paper II investigated the effects of two introduced red algae, *Heterosiphonia japonica* and *B. hamifera,* on the primary production of the red algal community in the introduced ranges under two different scenarios: co-existence of native and introduced species or competitive exclusion of one random native species. Chemical defences are generally regarded to confer a cost, and trade-offs between growth and defence should result in comparatively slow growth rate of well-defended species, such as *B. hamifera*. In support of the notion that chemical defences are costly, the growth rate of *B. hamifera* was relatively slow compared to that of native filamentous red algae, and it did not affect the total primary production. In contrast, the more recently introduced and spreading species *H. japonica* showed an extraordinary high growth rate, causing an almost four-fold increase in the total biomass production of the receiving community. The increased biomass production will most likely change carbon fluxes with unknown consequences for the system (Ehrenfeld 2010). Interestingly, all polycultures of the red algae showed generally a decreased yield compared to what was expected from the yields of each species in the separate monocultures. However, the presence of the introduced species did not strengthen this effect. Strong interference interactions between the red algae may explain this unexpected result, which is in direct

contradiction to the biodiversity-ecosystem functioning hypothesis, but in accordance with other results from macroalgal polycultures (Russell 1992). Further examination of the value of the produced biomass for one of the most common and abundant native herbivore species, *I. granulosa,* showed that, in addition to the previous findings of a low preference for *B. hamifera* due to its chemical defence (paper I), juvenile isopods cannot grow and have high mortality on a diet of this seaweed (Figure 7).

The survival of the isopods on a diet of *H. japonica* was equally good as on a diet of the native species, but the isopods grew significantly less on *H. japonica* than on two of the four tested native algal species. This experiment was not designed to test for effects on the herbivore community, but the results clearly show that *B. hamifera* is of very low food quality to native grazers, thereby supporting the findings of paper I. Given that *B. hamifera* is expanding its distribution and abundance at the cost of more palatable native algae, *B. hamifera* may have a negative impact on secondary production in the recipient community in the long run. In contrast, the increased biomass provided by *H. japonica*, which offered a diet that allowed for the survival and growth of the isopods in our experiment, may support a larger herbivore population. However, feeding preference assays also indicate that this introduced species is not a preferred food compared to native filamentous red, green and brown algae (J. Sagerman et al. unpublished). In summary, two morphologically similar species invading the same community can have very different effects on primary production of the native filamentous red algal community (paper II). Furthermore,
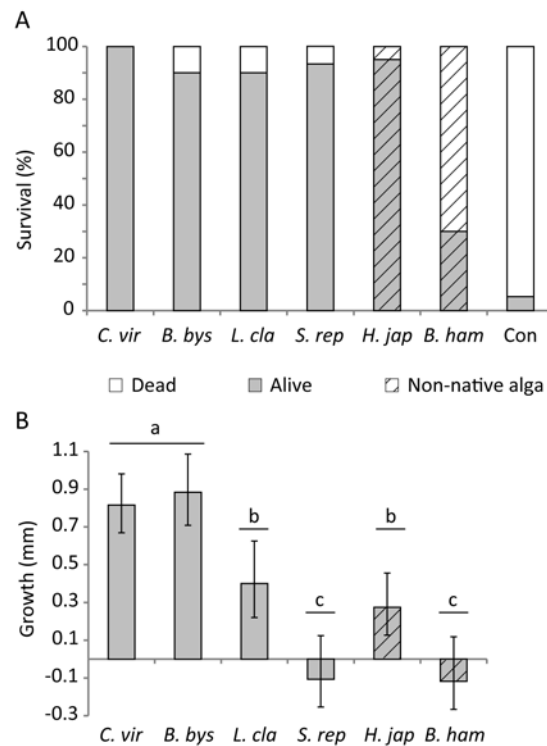

Figure 7 Survival (A) and growth (B) of juvenile *Idotea granulosa* on diets of two introduced (*Heterosiphonia japonica, Bonnemaisonia hamifera)* and four native red algae species (*Brongniartella byssoides, Ceramium virgatum, Lomentaria clavelosa* and *Spermothamnion repens)* and a control treatment with no food (n = 20 at the start of the experiment). Values in figure (B) are means $\pm CI_{95}$, means with a mutual letter in the figure is not significantly separated in pairwise comparisons (Tukey´s HSD test).

their different impacts can be linked to their divergent ecological strategies (extraordinary fast growth versus potent chemical defence), which are also likely to explain the invasion success of these two introduced seaweeds. This supports the notion that invasive species may possess traits that make them relatively unique among species in the native community, such as having novel weapons or novel resource use (Powell et al. 2011).

From papers I and II it became clear that *B. hamifera* has an effective chemical defence against generalist herbivores and that at least one of the most common and abundant generalist herbivores, the isopods *I. granulosa*, has a low survival and insignificant growth when this introduced seaweed is used as a food source. Paper II also showed that *B. hamifera* has a relatively slow growth rate, indicating that it is a poor competitor compared to native algal species in the absence of herbivores. In order to explain its remarkable success in the new area with a novel chemical defence, the consistently low preference of local generalist consumers for the invader should provide *B. hamifera* with such a strong advantage that it can outweigh its slower growth rate. Furthermore, to increase its growth in the presence of herbivores, the introduced species should be able to capitalise from the resources freed by the herbivores (Keane & Crawley 2002; Orrock et al. 2010). Paper III provided evidence that *B. hamifera* is inferior in direct competitive interactions with the native seaweeds, but that it gains competitive dominance in the presence of herbivores, and this effect is strengthened with increasing herbivore densities (Figure 8). The effective chemical defence of *B. hamifera* thereby enables a shift in competitive dominance towards the invader. The increased abundance of the introduced alga was a result of increased consumption and reduced performance of the native algae, but was also due to an increased growth rate of *B. hamifera* itself. The increased growth demonstrates that the invasive alga can capitalise from resources released by herbivores and/or from decreased competition by native seaweeds. Paper III further tested the hypothesis that the shift in competitive dominance in the presence of herbivores is promoted by refuge-mediated apparent competition, as suggested by a theoretical model of Orrock et al. (2010). By constituting a refuge to shared consumers, introduced plants are predicted to increase the consumer pressure on neighbouring plants, which in turn decreases their ability to compete for shared resources that can then be used by the invader. Fish are the most significant predators on small crustaceans in marine systems (Choat 1982; Diehl 1992), and refuge from fish predation is crucial for the survival of small invertebrates (Huang et al. 2008; Henninger et al. 2009). *Bonnemaisonia hamifera* was demonstrated to have a higher capacity to shelter herbivores against fish predation compared to native red algae, which may also explain the previously observed high diversity and richness of faunal organisms associated to the invader (R.J. Svensson & H. Pavia, unpublished). A few previous studies have also demonstrated the presence of apparent competition between introduced and native plants (Sessions & Kelly 2002; Meiners 2007; Orrock et al. 2008; Dangremond et al. 2010; Dutra et al. 2011). However, these studies focused on altered consumer behaviour or densities in the presence of an invasive plant and how this affected the distribution and abundance of native plants, but did not evaluate if apparent competition explains the invasiveness of the introduced species.

One assumption repeatedly used for the interpretation of the results from the experiments in this thesis was that the chemical defence confers a cost for *B. hamifera*. A large number of studies have shown that chemical defences are generally costly for terrestrial vascular plants (Purrington 2000, Heil & Baldwin 2002, Strauss et al. 2002, Cipollini et al. 2003, Walters & Heil 2007). However, due to structural and functional differences between vascular plants and macroalgae these studies do not necessarily reflect the costs of defence production in macroalgae. The small amount of knowledge that exists about resistance costs
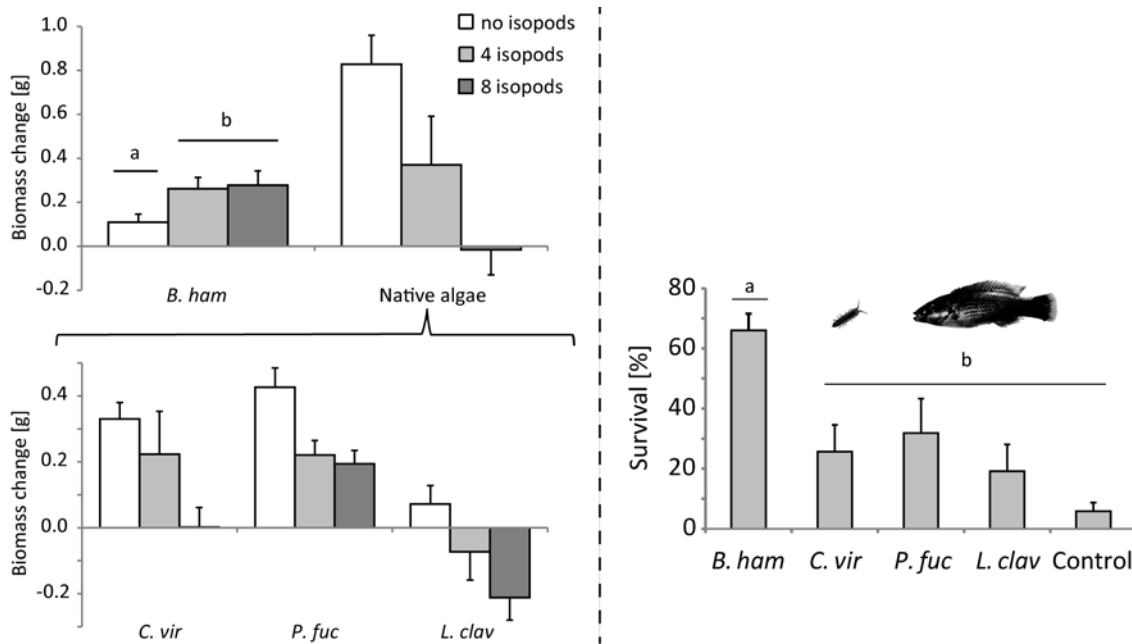
Figure 8 Left side: Change in the biomass of *Bonnemaisonia hamifera* compared to the native algal competitors *Ceramium virgatum, Polysiphonia fucoides* and *Lomentaria clavellosa* at different densities of the native generalist herbivore *Idotea granulosa* (Isopoda). Error bars show + 1SE (n=8). Significant differences are indicated by a, b (SNK-test, α = 0.05)

Right side: Survival of the isopod *Idotea granulosa* associated to the invasive alga *Bonnemaisonia hamifera* in comparison to the survival of isopods associated to the native red algae *Ceramium virgatum, Polysiphonia fucoides and Lomentaria clavellosa,* or to the control mesh. Error bars show + 1 SE (n=12). Significant differences are indicated by a, b (SNK-test, α = 0.05).

in macroalgae has been attained from phenotypic correlations, while direct experimental tests have rarely been used. In paper IV, the defence production in *B. hamifera* was experimentally manipulated to examine if there is a trade-off between defence production and growth. We further tested if the defence provides fitness benefits (in addition to herbivore deterrence) by reducing harmful bacterial colonisation of the alga. Experimental manipulations of chemical defence production by preventing the access to bromine are particularly well suited for red algae, where bromine is commonly incorporated into secondary metabolites (Kladi et al. 2004), but considered to be non-essential for growth and primary metabolism (Fries 1963; Dworjanyn et al. 2006). Such culture manipulations offer a powerful way to examine costs of chemical defences in macroalgae, for which poor mechanistic knowledge of chemical defence production restricts the use of chemical elicitors or transgenic strains, i.e. methods that have been successfully used in studies of costs of chemical defences in terrestrial plants (e.g. Baldwin 1998, Zavala et al. 2004). The results of paper IV showed significantly higher growth for individuals of *B. hamifera* individuals with impaired production of defence metabolites in the absence of natural enemies. After four weeks in culture, individuals with impaired defence metabolite production had grown on average 20 % more than individuals with normal metabolite production, when the bacterial growth was controlled by external addition of 1,1,3,3-tetrabromo-2-heptanone. Individuals with impaired defence metabolite production were, however, unable to control its epibacterial load. At the end of the experiment in which no 1,1,3,3-tetrabromo-2-heptanone was externally added to the media,

individuals cultured without bromine suffered from high bleaching and grew significantly less compared to the controls. This finding is consistent with our second hypothesis that the chemical defence provides fitness benefits by protecting against harmful bacterial surface colonisation. The effectiveness of 1,1,3,3-tetrabromo-2-heptanone in inhibiting or adjusting surface bacterial colonisation was also shown by Nylund et al. (2008). Furthermore, a recent study found allelopathic effects of this compound against spores of algal competitors (Svensson et al. in press). Paper IV clearly showed that the chemical defence of *B. hamifera* is costly, but the multiple ecological benefits of this compound shown in this thesis and by others (Nylund et al. 2008; Svensson et al. in press) most likely outweigh this cost.

When a novel chemical defence and the ecological benefits this provides are the underlying mechanism promoting the invasion of plants, it should be a trait under selection during establishment and invasion in the new range. The potential to adapt to novel environmental regimes, e.g. altered selection pressure by herbivores, highly depends on the genetic variation in the introduced populations. Due to population bottlenecks and founder effects, introduced populations are usually expected to have a reduced genetic diversity compared to their source population (Sakai et al. 2001; Allendorf and Lundquist 2003). There is, however, increasing evidence that many invasive populations do not show a significant loss of diversity and that it can even be increased through genetic admixtures of multiple source populations (Lavergne & Molofsky 2007; see Sax et al. 2007 for references). Due to population bottlenecks and the high degree of vegetative reproduction in Scandinavian waters, introduced populations of *B. hamifera* were expected to have only a low degree of genetic diversity. Preliminary results of the analysis of 83 AFLP loci from individuals from seven Swedish populations and four Korean populations indeed showed reduced genetic diversity in the introduced compared to native populations, which is in accordance to other findings for seaweeds (e.g. *C. fragile* and *P. harvenji*) (McIvor et al. 2001; Provan et al. 2004). However, given that the alga is considered to predominantly reproduce asexually in Swedish waters, the genetic diversity within the Swedish populations was unexpectedly high. From this limited number of samples, it could be stated that the Swedish populations of *B. hamifera* consist of several different genotypes, rather than a single clone, which may allow for adaptive responses to the novel selection regimes in its new range.

Conclusions and future perspectives

The overall conclusion from this thesis is that the ecological interactions in the new community, particularly plant-herbivore interactions between introduced seaweeds and native generalists, can explain the invasion success of introduced species. However, the results highlight that comparisons of herbivore abundances on introduced and native species alone can result in erroneous conclusions about herbivore impact on plant performance and competitive interactions. This is because herbivore abundances do not necessarily correlate to damage and plant performance, especially in situations when plants provides other functions than food, such as refuge from predation. In accordance with predictions of the ERH, EICA and NWH, *B. hamifera* experiences little damage by native herbivores its new range provided. However, the ERH/EICA do not specify the mechanism that explains why some introduced are rejected whereas others are readily consumed and the notion that generalist enemies do not recognize introduced species *per se* seems unjustified. In contrast, the results of this thesis demonstrated, that a chemical compound that is evolutionary novel to native herbivores is the mechanism behind the release from generalist herbivores, which supports

the NWH. Consequently, I conclude that effective chemical defences provide an explanation for the varying impact of generalist herbivores on introduced plants and the varying invasion success of introduced species. Future studies should preferably include biogeographic comparisons of the effectiveness of the chemical compounds against herbivores in both native and introduced ranges.

It can further be concluded that the generalist herbivores do not only have a low impact on introduced species with a novel chemical defence, but actually promote invasion through an increasedr impact on native competitors. Due to their superior capacity to shelter herbivores from predation, herbivores may preferable associate to some introduced species but still primarily feed on their neighbouring competitors. This can release resources that can be used by the invader and thereby strongly contribute to invasion success. Without these interactions that are governed by the novel chemical defence, *B. hamifera* would most likely not have become invasive as it is poor competitor in direct interactions with natives. The poor competitiveness of *B. hamifera* is likely explained by the cost of chemical defence production. Introduced species with costly chemical defences are unlikely to have high growth rates and should therefore not be expected to strongly affect the primary productivity of the recipient community, but are instead more likely to have significant effects on the second trophic level. This remains to be more thoroughly investigated in future studies in both marine and terrestrial systems.

My studies on the invasive red alga *B. hamifera* provide a clear example how the interactions between species with novel chemical defences and generalist herbivores in the new range can promote invasion. However, I do not claim that novel chemical defences explain every single successful invasion. Each invasion will be somewhat idiosyncratic since it will depend on unique combinations of traits of the invader and of the native community. Although management effort tries to prevent accidental introductions, we will still have to accept that native and non-native species intermingle in future communities. The more relevant question is if communities have the ability to 'cure' themselves from a dominance of an introduced species. In this context, future research should focus more on the potential of adaptations of the invaded community and the invader itself. When chemical defences are important for the invasion success they should be highly selected traits. The combination of genetic tools and ecological experiments may reveal how important adaptive changes are during establishment and spreading in the invasion process of introduced plants. Such approaches may also show if native herbivores can adapt to the chemical defence of invasive plants and thereby reduce their invasiveness.

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