Marine Seaweed Invasions –
the Ecology of Introduced *Fucus evanescens*

Sofia A. Wikström

Department of Botany
Stockholm University
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Doctoral dissertation
Sofia A. Wikström
Department of Botany, Stockholm University
106 91 Stockholm, Sweden

Från läsidan, närbilder.

Blåstång. I det klara vattnet lyser
tångskogarna, de är unga,
man vill emigrera dit,
lägga sig raklång på sin
spegelbild och sjunka till
ett visst djup – tången
som håller sig uppe med
luftblåsor, som vi håller
oss uppe med idéer.

Tomas Tranströmer
(Östersjöar, 1974)

Abstract

Biological invasions are an important issue of global change and an increased understanding of invasion processes is of crucial importance for both conservation managers and international trade. In this thesis, I have studied the invasion of the brown seaweed *Fucus evanescens*, to investigate the fate and effect of a perennial, habitat-forming seaweed introduced to a coastal ecosystem. A long-term study of the spread of *F. evanescens* in Öresund (southern Sweden) showed that the species was able to expand its range quickly during the first 20 years after the introduction, but that the expansion has been slow during the subsequent 30 years. Both in Öresund and in Skagerrak, the species is largely restricted to sites where native fucoids are scarce. Laboratory experiments showed that the restricted spread of *F. evanescens* cannot be explained by the investigated abiotic factors (wave exposure and salinity), although salinity restricts the species from spreading into the Baltic Sea. Neither did I find evidence for that herbivores or epibiota provide biotic resistance to the invader. On the contrary, *F. evanescens* was less consumed by native herbivores, both compared to the native fucoids and to *F. evanescens* populations in its native range, and little overgrown by epiphytes. Instead, the restricted spread may be due to competition from native seaweeds, probably by pre-occupation of space, and the establishment has probably been facilitated by disturbance.

The studies provided little support for a general enemy release in introduced seaweeds. The low herbivore consumption of *F. evanescens* in Sweden could not be explained by release from specialist herbivores. Instead, high levels of chemical anti-herbivore defence metabolites (phlorotannins) could explain the pattern of herbivore preference for different fucoids. Likewise, the low epibiotic colonisation of *F. evanescens* plants could be explained by high resistance to epibiotic survival. This shows that colonisation of invading seaweeds by native herbivores and epibionts depends on properties of the invading species. The large differences between fucoid species in their quality as food and habitat for epibionts and herbivores imply that invasions of such habitat-forming species may have a considerable effect on a number of other species in shallow coastal areas. However, since *F. evanescens* did not exclude other fucoids in its new range, its effect on the recipient biota is probably small.

List of papers

The thesis is based on the following papers, which are referred to by their Roman numerals:

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

II. Wikström, S. A. & L. Kautsky (2004) Invasion of a habitat-forming seaweed: effects on associated biota. *Biological Invasions 6*: 141-150.

III. Wikström, S. A., M. B. Steinarsdóttir, L. Kautsky & H. Pavia (manuscript) Evaluation of the enemy release hypothesis for an invading seaweed.

IV. Wikström, S. A. & H. Pavia (2004) Chemical settlement inhibition versus post-settlement mortality as an explanation for differential fouling of two congeneric seaweeds. *Oecologia 138*: 223-230.

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Introduction

Biological invasions occur when organisms are transported outside their natural ranges, often into remote areas, where their offspring spread and persist. In a strict sense, invasions are neither a new nor an exclusively human-driven phenomenon. Changes in species' ranges occur constantly on all spatial scales due to rare long-distance dispersal events. During the last 20 million years, many episodes of mass interchanges has occurred due to tectonic activity (Vermeij 1991), and after the last glaciations many species have expanded their range dramatically from glacial refugia (Birks 1989, Cain et al. 1998).

Humans have however greatly accelerated the rate and geographical scale of invasions by breaking former barriers to dispersal. The number of species that have entered new areas through human activity has increased by several orders of magnitude during the past centuries, due to the expanding global transport and trade (di Castri 1989). Large-scale examples include construction of the Suez Canal, which enabled hundreds of marine species to enter the Mediterranean from the Red Sea (Por 1978). On a smaller scale, species are constantly transported over large distances and accidentally or deliberately released in new areas. Today virtually all habitats on earth have experienced invasions, and for most countries the number of documented introductions is within a range of 10^2-10^4 species (Lodge 1993).

Although most invaders seem to have only minor effects on the recipient biota, there are numerous examples where the effect of introductions has been dramatic (reviewed by Mack et al. 2000). In many areas, introduced species are among the greatest threats to native biodiversity and the functioning of natural ecosystems. Identifying invaders and following their pattern of spread is therefore regarded to be highly important for the development of policies to prevent introduction of species (e.g. Reichard & Hamilton 1997, Rejmánek 2000). Besides, studies of invasion processes and effects allow observations of community responses to perturbation on a scale not usually attainable with experimental manipulations. The ability of invasive species to become established in a community and the effect of the invasion on the recipient biota have provided information on general ecological issues such as community assembly theory (Wilson et al. 2000), evolutionary stability of ecological interactions (Bowers et al. 1992; Richardson et al. 2000; Trowbridge & Todd 2001), factors limiting species distributions (Richardson & Bond 1991) and the importance of species identities to ecosystem functioning (Vitousek & Walker 1989).

Factors affecting invader success

In this work, a *biological invasion* is defined as a geographical expansion of a species' range to an area where it has previously not been found. The definition includes range expansion following climatic change as well as long-distance dispersal, natural or human-mediated, but excludes species arrival during succession (at least secondary succession). I use the terms *introduced species* and *invader* to denote species that has established in an area outside its native range, without implying any negative or positive consequences of the invasion on the native biota.

A large number of species are transported between biogeographical regions and introduced to new areas, either intentionally or accidentally, but only a few of them are able to survive and establish a self-sustaining population in the new area. Whether a species will establish successfully depends on a number of factors, and how these factors interact with the characters of the introduced species (Fig. 1).

To be able to establish, a species has to sustain the climate and other abiotic conditions of the new area. As a consequence, most species that establish in new areas come from climatically similar regions, although there are exceptions to this pattern. For instance, despite its tropical origin, the green alga *Caulerpa taxifolia* has established successfully in the warm-temperate Mediterranean Sea (Meinesz et al. 1993). Another consequence is that species with broad ecological tolerance, i.e. ability to maintain relatively constant fitness over a range of environmental conditions ("general purpose genotype" sensu Baker 1965), could be predicted to have a higher probability to establish in new areas. Such niche breadth can be due to both individual phenotypic plasticity and population genetic polymorphism. For instance, the successful invasion of the weed *Verbascum thapsus* to a wide range of habitats in North America was explained by a high phenotypic plasticity for climatic tolerance (Parker et al. 2003). Finally, it could be predicted that harsh environments, where few species are able to survive, are difficult to invade and will receive few newcomers. This may explain the observed paucity of exotic species in dry, infertile and otherwise harsh environments (Crawley 1987, Rejmanek 1989, Harrison 1999, Lonsdale 1999).

The ability of a species to establish in a new area is also affected by interactions with other species (e.g. competitors, predators and pathogens). Biotic interactions may both inhibit and facilitate invasions and two alternative hypotheses have been put forward to predict their effects on introduced species. The *biotic resistance hypothesis*, first developed by Elton (1958), states that competition or predation from native species can prevent introduced species from invading a community. This is based on the notion that biotic factors interact with abiotic conditions to restrict a species' ecological niche
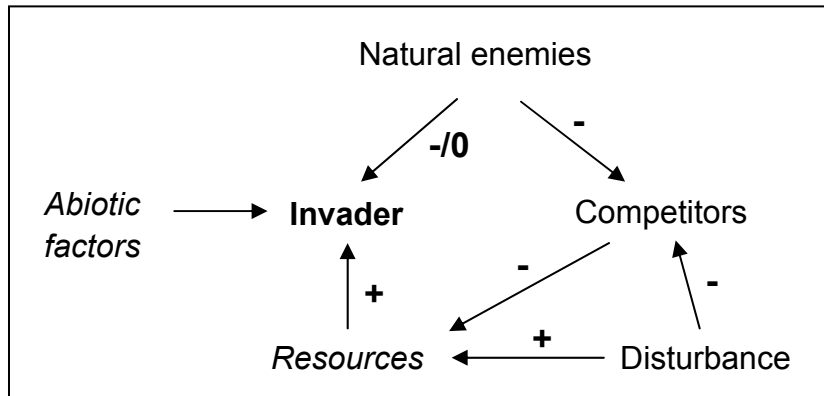
Figure 1. Conceptual model describing factors that may affect establishment and success of introduced species. The effect of natural enemies may be negative (*biotic resistance hypothesis*) or neutral (*enemy release hypothesis*). See the text for discussion.

(Hutchinson 1957). Several studies in terrestrial plant communities have documented that dense resident vegetation may restrict establishment of introduced plants, by pre-empting available resources (space, light nutrients etc; e.g. Burke & Grime 1996; Naeem et al. 2000). However, little is known about the potential of native predators and parasites to restrict invasion success.

On the other hand, the *enemy release hypothesis* (ERH) states that release from natural enemies (predators and pathogens) enables introduced species to become abundant in their new range. The hypothesis was first formulated by Darwin (1859) to explain why some introduced species that are rare in their native range become extremely abundant as invaders. The hypothesis is based on the assumptions that (a) the specialist enemies of the invader are absent in the new region, and/or (b) native enemy species are slow to include the invader in their diets. The invader thus experiences lower predation than the native competitors, which may give it a competitive advantage in the new range. Several studies of terrestrial plant invaders have given support for the enemy release hypothesis (reviewed by Keane & Crawley 2002, see also Wolfe 2002; Mitchell & Power 2003; Siemann & Rogers 2003). There are several examples of lower herbivore pressure on invading compared to native species (Olckers & Hulley 1991; Schierenbeck et al. 1994; Siemann & Rogers 2003) and on invading populations compared to native populations of the same species (Wolfe 2002). The successful biological control of invasive weeds by introducing specialist enemies from the native area of the plant (Van Driesche & Bellows 1996) also provides circumstantial evidence that release from specialist enemies may increase invasive success of terrestrial plants. However, the hypothesis has rarely been evaluated for other groups of organisms.

Finally, natural and anthropogenic disturbance are hypothesised to be important in facilitating invasions, particularly in plant communities, by increasing the amount of free resources available for the invader. Disturbance may increase resource availability by two separate mechanisms, it may reduce resource use by damaging or destroying the resident vegetation or it may increase resource supply, e.g. as a consequence of nutrient enrichment (Davis et al. 2000). The hypothesis is supported by observations of high numbers of established invaders in disturbed sites (e.g. McIntyre et al. 1988, Planty-Tabacchi et al. 1996) and by several experiments in grasslands (Hobbs & Atkins 1988, Huenneke et al. 1990, Burke & Grime 1996) and marine benthic communities (e.g. Arrontes 2002; Valentine & Johnson 2003).

Consequences of biological invasions

Biological invasions are regarded as one of the major agents of global change (Vitousek et al. 1996; Mack et al. 2000) and there are many documented cases of invaders having large ecological effects, both on population and ecosystem levels. Most examples of dramatic effects on native populations come from introductions of pathogens and predators, which interacts strongly with native species. One famous example is the introduction of the Asian Chestnut blight fungus, which has destroyed vast forests of American chestnut (*Castanea dentata*) in eastern USA. Another example is the predatory Nile perch (*Lates nilotica*), which has eliminated or gravely threatens more than 200 endemic cichlid fish species after its introduction to Lake Victoria (Goldschmidt et al. 1993).

Another category of invading species that may have a large ecological effect is species with important ecosystem functions, e.g. nitrogen fixing or sediment stabilisation, especially when they invade regions where species with similar functions are absent. There are several examples of invasive grasses that have altered the fire regime to more frequent and intense fires (D'Antonio & Vitousek 1992), and the invasion of Hawaii by the nitrogen fixing tree *Myrica faya* has completely transformed a formerly nutrient-poor ecosystem (Vitousek & Walker 1989). Similarly, invasion of habitat-forming species (e.g. trees and perennial seaweeds) may have a large impact on the native community by changing the life conditions for a number of other species.

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Seaweed invasions

In marine habitats, shipping and mariculture have dramatically increased the transfer of species between areas, resulting in a continuously growing number of species introductions (e.g. Carlton 1985, Norton 1992, Leppäkoski & Olenin 2001). In the same time, many coastal areas are currently in a process of rapid environmental change due to anthropogenic activities, altering biotic community composition and causing the decline of many species. Despite the growing concern for their possible effect on the coastal ecosystem, marine invasion processes and the impact of introduced species on the native biota are still poorly understood (Grosholz 2002).

Seaweeds are important components of marine benthic communities. Large, perennial seaweeds, e.g. members of the families Fucales and Laminariales, are particularly important by providing habitat for a diversity of other species. Long-lived seaweeds are often overgrown by epibionts, which use the hard and relatively stable surface of the seaweed as living space. They also provide habitat and sometimes food for a diverse assemblage of motile invertebrates and fishes. The faunal community in seaweed beds is dominated by small invertebrate herbivores, e.g. herbivorous crustaceans and gastropods, which are collectively termed mesoherbivores. They feed on host seaweeds and their epibionts and are in their turn important prey for many fish species (e.g. Edgar & Shaw 1995a; Edgar & Shaw 1995b), providing an important link between primary production and large predators in littoral food chains.

There is increasing evidence that native seaweeds may restrict colonisation of invaders. Several experiments have shown that removal of competitors facilitate establishment of invading seaweeds (Arrontes 2002; Valentine & Johnson 2003). However, few studies have addressed the interaction between introduced seaweeds and their natural enemies. In contrast to terrestrial herbivore faunas, which are dominated by insect species with a high degree of host specificity (Strong et al. 1984), most marine herbivores are relatively unspecialised in their food choice (Hay & Steinberg 1992). Release from herbivory has been proposed as an explanation for the successful spread of invading seaweeds, e.g. the rapid invasion of *Caulerpa taxifolia* in the Mediterranean (Boudouresque & Verlaque 2002), but the few studies of marine herbivore colonisation of new species have provided conflicting results. While the introduced *Caulerpa taxifolia* hosts fewer species of invertebrates than native seaweeds in the Mediterranean (Bellan-Santini et al. 1996), other introduced seaweeds, e.g. *Sargassum muticum* in Europe and North America and *Codium fragile* in New Zealand, have rapidly achieved diverse herbivore faunas (Norton & Benson 1983; Trowbridge 1995; Viejo 1999). No attempt has been done to compare herbivore pressure between the native and new ranges of invading species, preventing a rigorous evaluation of the enemy release hypothesis for marine seaweeds.

Even fewer studies have addressed the interaction between introduced seaweeds and epibiotic species. Epibionts may have a positive effect on the host, providing protection from herbivores or abiotic stress (Wahl & Hay 1995), but negative effects seems to be more common. An extensive epiphytic load may decrease seaweed productivity (Littler & Littler 1999), growth (Buschmann & Gómez 1993; Worm & Sommer 2000) and survival (D'Antonio 1985), and the negative effect of fast-growing epiphytic algae has been proposed as one factor explaining the decline of perennial macroalgae in nutrient-enriched areas (Vogt & Schramm 1991; Worm & Sommer 2000). Colonisation by epibiotic species may thus affect the success of introduced seaweeds. However, the stability of the interaction between macroalgae and their epiphytes is little studied except for a few cases (Seed & O'Connor 1981, Correa & McLachlan 1991, Lining & Garbary 1992), making it difficult to assess the probability of introduced species being released from epiphytes in the invaded community.

Objectives of the thesis

The general objective of this thesis was to investigate the establishment and ecology of the brown seaweed *Fucus evanescens* C. Ag. in Sweden, as a model for the invasion of a habitat-forming seaweed. The specific objectives have been to:

(1) Document the establishment and spread of *F. evanescens* in Sweden.

(2) Evaluate if abiotic factors (salinity and wave exposure) and biotic interactions (herbivory and epiphyte abundance) have the potential to affect the success of the invader.

(3) Investigate the mechanisms behind patterns of herbivory and epiphyte abundance on native and introduced species. I evaluate (a) the enemy release hypothesis by studying herbivore colonisation of invaded *F. evanescens* and (b) the effect of differential resistance to herbivory and epiphyte colonisation due to chemical defence.

(4) Assess impact on coastal ecosystems, by testing how the invasion of *F. evanescens* has affected the communities of species associated to the *Fucus* belt.

Methods

The results presented in this thesis are achieved from inventories, observational studies of associated biota and field- and laboratory experiments. This section provides an overview of the methods used, a more detailed description is provided in the included papers.

Study species

Fucus evanescens is a perennial brown seaweed belonging to the family Fucaceae. It is a common and often dominant species in its native range, forming a belt in the lower littoral (Jaasund 1965, Thom 1983, Chapman & Johnson 1990). The species is monoecious and self-fertile (Quatrano 1980) and has a maximum life-span of 2-3 years (Sideman & Mathieson 1983, Ang 1991a, 1991b). The native distribution of *F. evanescens* extends over the north Atlantic, the north Pacific and the Arctic oceans (Powell 1957a). In the East Atlantic it is native to Iceland, the Faeroes and northern Norway (north of the Trondheim fjord). It was introduced to Skagerrak (the Oslofjord) in the end of the 19th century, probably by ship traffic, and has since then spread southwards in southern Scandinavia and northern Britain (Fig. 2). In southern Scandinavia, *Fucus evanescens* invades habitats that are previously occupied by three seaweed species that are closely related and morphologically similar to the invader, *Fucus vesiculosus* L., *F. serratus* L. and *Ascophyllum nodosum* (L.) Le Jol.

Fucus evanescens has been regarded as a subspecies of *Fucus distichus* L. emend. Powell (Powell 1957a), but Rice and Chapman (1985) split *Fucus distichus* into *Fucus distichus* L. and *Fucus evanescens* C. Ag. based on morphometric analysis. Later, phylogenetic analysis of molecular data has shown that *Fucus distichus* and *F. evanescens* might not be monophyletic species (Serrão et al. 1999a). However, the two species are ecologically separated, *Fucus distichus* is found exclusively in rock pools and *Fucus evanescens* in the intertidal, and are probably reproductively isolated to a large degree in areas where they co-occur (Serrão et al. 1999a).

Despite its long invasion history in Scandinavia, rather little is known about how *F. evanescens* has established in most of the new range and no study have examined the effects of the invader on the native community. In the inner parts of the Oslofjord, where the establishment of *F. evanescens* has been followed since around 1940, the species has become the most common fucoid (Grenager 1957, Bokn & Lein 1978, Bokn et al. 1992). The increase in *F. evanescens* coincided with a general decline in the native fucoid species,

which was probably due to eutrophication (Bokn & Lein 1978). Also in the Baltic Sea region the native fucoids have declined in several areas, but here we lack data on the long-term success of *F. evanescens*.

The long invasion history of *F. evanescens* makes it possible to follow the long-term course of a coastal invasion. It is known from other systems that the nature of species interactions often changes considerably within the first years after an invasion. However, there are presently very few cases where the invasion of a marine organism has been followed over longer time periods than a few years (Grosholz 2002). For *F. evanescens*, the distribution along a coastal stretch of 120 km in Öresund was documented in 1966-72 (von Wachenfeldt 1975), about 20 years after the first known introduction of the species to this area (Lund 1949). This gives an unusual opportunity to picture the establishment of a macroalgal species in the Baltic Sea region. Since *F. evanescens* belongs to the brown seaweeds that are habitat-forming in the shallow littoral, it could also be used as model organism to study the effect of seaweed introductions, as well as the host specificity of epibiota and mesoherbivores among seaweed species.
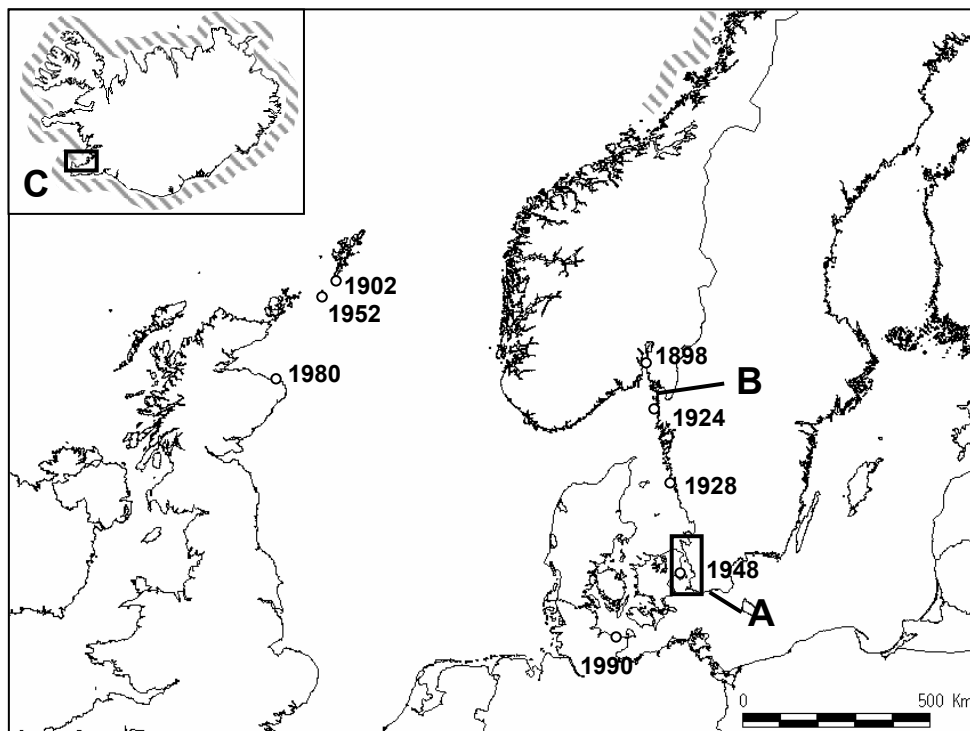

Figure 2. The expansion of *Fucus evanescens* in southern Scandinavia and the British Isles, illustrated by year of first record in different regions (data from Simmons 1898; Börgesen 1903; Hylmö 1933; Lund 1949; Powell 1957b; Powell 1981; Schueller & Peters 1994). The native range of *F. evanescens* is indicated with grey, broken line. The study areas of the thesis are indicated as (A) Öresund (Papers **I** and **II**), (B) Tjärnö (Papers **III** and **IV**) and (C) south-western Iceland (Paper **III**).

Study areas

The studies were performed in three areas (Fig. 2), Öresund (A) and the Tjärnö archipelago (B) on the Swedish west coast and the Reykjanes peninsula (C) in south-western Iceland. Both the Swedish west coast and south-western Iceland belong to the cold temperate region of the Northeast Atlantic and the floral and faunal communities are partly similar between the areas. However, the areas differ in some important aspects:

South-western Iceland has a truly marine environment with high salinity (30-35‰) and large tidal amplitude (4 m). The coast is open and dominated by shallowly sloping boulder fields. The shallow slope and the large tidal amplitude result in a broad intertidal zone, which is dominated by the fucoids *Ascophyllum nodosum*, *Fucus vesiculosus*, *F. evanescens* and *F. serratus* (Jónsson 1903).

The Swedish west coast is characterised by a strong salinity gradient, from high salinity in Skagerrak to brackish water at the border to the Baltic Sea. The small tidal amplitude, only 0.1-0.3 m, results in a narrow fucoid zone where the plants to a large extent grow constantly submerged. The native fucoids *F. vesiculosus*, *F. serratus* and *A. nodosum* often grow mixed, although *F. serratus* generally grow deeper than the others. *A. nodosum* has its southern distribution limit in northern Öresund, due to low salinity, but *F. vesiculosus* and *F. serratus* extend their ranges into the Baltic Sea (Nielsen et al. 1995).

The Tjärnö archipelago is situated in northern Skagerrak and provides a varied environment with wave exposed cliffs alternating with sheltered bays. The salinity in the surface water typically fluctuates between 15-30‰, depending on the direction of ocean currents. The exact date of introduction of *F. evanescens* in this area is not known. It was first found around 1970 in the harbour of Strömstad (I. Wallentinus, personal comm.), but it has been present in Fjällbacka, 30 km south of Strömstad, since 1924 (Hylmö 1933).

Öresund is one of the straits joining the brackish Baltic Sea with the more saline waters of the Kattegat. This is the transition area between two partially different biota, where many marine species have their distributional limit due to the low salinity (Wallentinus 1991, Nielsen et al. 1995). The salinity in Öresund is very variable both in time and space, ranging between 8 and 30‰ in the coastal waters, the northern part having the highest salinity (Kornfeldt 1982). The coast is dominated by shallow sand and gravel bottoms, except for areas of emerging bedrock in the northernmost part. In this area, *F. evanescens* was first documented in the harbour of Copenhagen in 1948 (Lund 1949).

Inventories

During 1966-72 the distribution and abundance of *Fucus evanescens* in Öresund was investigated, as part of a comprehensive survey of the algal vegetation in the area (von Wachenfeldt 1975). To follow the continued spread of the species, we revisited all the shallow hard bottom sites at the Swedish side of the strait (in total 30 sites) in 2000 (Paper **I**). The present distribution and abundance of *F. evanescens* was investigated using the same method as in 1966-72. The algal flora was surveyed by snorkelling from 0-2 m depth throughout the extent of suitable substratum (rock or stone reefs) or, when the extent of suitable substratum was not restricted, along 20 m of the shore. The abundance of *F. evanescens* was estimated on a four-graded scale.

In 2000 I also investigated the small-scale distribution of *F. evanescens* in the archipelago around the Tjärnö laboratory. Sample sites were obtained from the nautical map, by spreading out a number of points approximately evenly in a restricted area (Fig. 3). At each site that had suitable substratum (rock or stones), the algal flora was surveyed as above, except that I did not estimate abundance. These data are not included in the papers.

Sampling of epiphyte and herbivore communities

The community of associated flora and fauna was compared between the introduced and the native fucoids to assess (1) consequences of the introduction for epibionts and free-living fauna in the *Fucus* community and (2) the ability of native epibionts and herbivores to switch to the invading species. In Papers **II** and **IV**, the introduced *F. evanescens* was compared to the native *F. vesiculosus*. In Paper **III**, *F. evanescens* was compared with *F. vesiculosus* and *Ascophyllum nodosum* both in Sweden and Iceland.

Plants of the seaweed species were collected randomly, using a fine-meshed bag to catch the motile fauna. In Sweden, all samples were collected at 0.5 m depth. In Iceland, the plants were collected from the mid intertidal during low tide. In Papers **II** and **III**, all macroscopic epibionts and free-living animals were removed and identified, after which their biomass and/or abundance were measured. In Paper **III**, we also counted the number of visible grazing marks on a part of the frond, to assess herbivore pressure in field populations. In Paper **IV**, only the number of attached *Balanus improvisus* was counted. Abundance and biomass of epibiota and free-living animals were corrected for the dry weight of the host plant. Differences in taxon richness and abundance/biomass of epibionts and motile fauna between seaweed species were analysed with univariate statistics. In addition, the epiphytic species composition of *F. evanescens* and *F. vesiculosus* was compared with

multivariate statistics, using detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) in CANOCO 4.0 (Paper **II**).

Experiments

A number of field and laboratory experiments were performed to (1) assess the effect of abiotic factors and biotic interactions potentially limiting the invasion success of *F. evanescens* and (2) investigate the mechanisms behind patterns of herbivory and epiphyte abundance on native and introduced species. All experiments were performed on the Tjärnö Marine Biological Laboratory (Sweden) and Sandgerði Marine Centre (Iceland).

Abiotic factors (Paper I)

The tolerance of *F. evanescens* to low salinity was evaluated in laboratory experiments, testing reproductive success of *F. evanescens* in different salinities. Reproduction has repeatedly been documented as the life-history stage most sensitive to salinity stress in fucoids (e.g. Serrão et al. 1999b, Malm et al. 2001), and successful reproduction seems to be the bottleneck for survival of these species in low salinity. Fertile fronds were collected from the Tjärnö area and acclimatised to different salinities (6, 8, 10, 12, 18 and 24 ‰) for 7 days before gamete release. Germination frequency was determined after 6 days and length growth after 14 days of culture in the different salinities.

Tolerance to wave exposure was assessed by comparing the attachment strength of *F. evanescens* plants to that of the native *F. serratus* and *F. vesiculosus*. Boulders with plants of the three *Fucus* species were collected from 0.5 m depth at two sites. The plants were attached to a force transducer and steadily pulled upward until either the holdfast detached from the rock or the stipe broke. The force required to detach the plant was recorded and the attachment strength was related to the size of the *Fucus* plant.

Grazing (Paper III)

To test the enemy release hypothesis, i.e. that introduced species are avoided by native herbivores in their new but not in their native range, corresponding preference experiments were performed with important herbivores in Sweden and Iceland. We tested the preference of three species, *Idotea granulosa* Rathke, *Littorina obtusata* L. and *L. littorea* L., that are known to feed on fucoid seaweeds and were found in considerable amounts on the seaweeds in the field studies. *L. littorea* is absent from Iceland and was only tested in Sweden.

Grazing preference of the herbivores was tested in choice experiments, comparing the three possible pairs of *Fucus evanescens*, *F. vesiculosus* and

Ascophyllum nodosum in both regions. Animals and seaweeds for the experiments were collected in the Tjärnö archipelago and in south-western Iceland, respectively. In Sweden the experiments were set up outdoors, in bottles with through-flowing filtered seawater, while in Iceland the experiments were performed in the laboratory with daily change of water. Herbivore consumption was measured as wet weight change of grazed seaweeds during the course of the experiment (3-4 days). Autogenic changes were controlled for by measuring weight change of ungrazed shoots from the same plants.

Barnacle settlement and survival (Paper IV)

To investigate the mechanism behind the low epibiotic abundance on *F. evanescens* compared to *F. vesiculosus*, I tested (1) if the pattern could be explained by differences in chemical inhibitors of epibiotic settlement and the potential role of phlorotannins as such inhibitors and (2) if the patterns could instead be explained by differential post-settlement mortality. Phlorotannins are polyphenolic secondary metabolites that are often present in high concentrations in fucoid seaweeds and have been proposed to function as a chemical defence against epibionts and herbivores. As test organism I used the barnacle *Balanus improvisus* L., which is a common epibiotic species in the shallow littoral zone.

The settlement of *B. improvisus* on fronds of the two *Fucus* species was tested in field and laboratory experiments. Colonisation of barnacles in the field was tested by transplanting *Fucus* fronds without epiphytes to an area with high barnacle abundance and recording the number of colonised barnacles after two weeks. In the laboratory, settlement of laboratory-reared barnacle larvae was tested in controlled choice as well as no-choice experiments in flow-through aquaria.

The effect of phlorotannins from both *Fucus* species on settlement of *B. improvisus* was tested in laboratory experiments. Crude extracts of the water-soluble substances in both species were prepared and one half of the extract was treated with insoluble polyvinylpolypyrrolidon (PVPP), in order to remove all phlorotannins. This procedure resulted in an extract containing all other compounds except phlorotannins, which was used as a control to specifically evaluate the effects of phlorotannins in settlement experiments. The crude and PVPP-treated extracts were diluted to a series of solutions with phlorotannin concentrations ranging from 0.1 to 100 μg ml^{-1} and their effect on settlement was tested in experiments with laboratory-reared larvae of *B. improvisus*.

Post-settlement mortality of newly metamorphosed barnacles on fronds of the two *Fucus* species was tested both in the laboratory and in the field.

Laboratory-reared cyprids of *B. improvisus* were allowed to settle on the fronds, which were then transplanted to outdoor flow-through aquaria and to a field site with a well developed *Fucus* canopy. Survival was assessed after two weeks by counting the number of live barnacles.

Chemical analyses

Phlorotannin content was measured in *Fucus evanescens*, *F. vesiculosus* and *Ascophyllum nodosum* in Iceland and Sweden (Paper **III**) and in *F. evanescens* and *F. vesiculosus* in Sweden (Paper **IV**) to assess their potential role for explaining patterns of herbivore preference and epiphyte abundance. Plants for the analyses were collected from 0.5 m depth in Sweden and from the mid intertidal in Iceland. In Paper **III**, the plants were collected from three different sites in each region to assess the spatial variation in phlorotannin content. Phlorotannins were quantified colorimetrically using the Folin-Ciocalteus method (van Alstyne 1995). Phloroglucinol (1,3,5-trihydroxybenzene, art. 7069; Merck, Darmstadt, Germany) was used as a standard.

Results and discussion

Spread and present distribution

The long-term study of the spread of *Fucus evanescens* in Öresund (Paper **I**) showed that the species expanded quickly during the first 20 years after the introduction. In 1972, the species had established in a number of sites throughout the 100 km coastal stretch, dominating the algal vegetation at some of the sites. It was mainly found in sheltered sites inside harbours and small marinas. During the subsequent 30 years the expansion has continued, but at a lower rate, in the northern part of the area. In the southern part *F. evanescens* has instead disappeared from several of the sites that were occupied in 1972.

The distribution pattern of *F. evanescens* in the Tjärnö Archipelago in northern Bohuslän is shown in Fig. 3. The species was found in 16 of the 51 investigated sites, sometimes dominating the vegetation. Apart from the harbour of Strömstad, where it grew on a stone jetty, it was restricted to relatively sheltered sites, growing attached to stones or blue mussel shells. It was never observed on rock bottoms, which is a common substratum for the native fucoids in Sweden as well as for *F. evanescens* in its native range. It was also restricted to the northern part of the studied area. This distribution pattern may be due to that the species is spreading from a point introduction, maybe in the harbour of Strömstad where it was first documented in this area.

The fast initial spread of *F. evanescens* in Öresund is remarkable, given the lack of apparent mechanism for long-distance dispersal in *F. evanescens*. Seaweed gametes generally have dispersal shadows in the magnitude of meters (Santelices 1990; Kendrick & Walker 1995; Arrontes 2002) and other mechanisms are thought to account for long-distance dispersal in these species. The fast spread of the invasive seaweed *Sargassum muticum* along European and North American coast has been attributed to drift of whole plants with currents (Deysher & Norton 1982; Critchley et al. 1990). In contrast to *S. muticum*, *F. evanescens* plants lack air bladders. It is possible that the reproductive tissue, which becomes inflated upon maturation (Powell 1957a), may act as floating device for reproductive plants. However, the primarily occurrence in harbours and marinas in 1966-72 suggests that the main mechanism for long-distance dispersal was transport of reproductive plants with boats or fishing equipment. Since *Fucus evanescens* is monoecious and self-fertile, one fertile plant is enough to found a new population.

Figure 3. Distribution of *Fucus evanescens* in the Tjärnö Archi-pelago. Filled dots represent occurrences of *F. evanescens* and empty dots investigated sites where the species was absent. The site of first record in the area (the harbour of Strömstad) is indicated by a larger dot.

Apart from the fast spread between harbours in the Öresund area the first decades after the introduction, the spread of *F. evanescens* has been restricted, both in Öresund and in Skagerrak. The restricted spread could be compared with the fast expansion of *Sargassum muticum*, which was introduced to Sweden around 1985 with drifting plants, spread along the Swedish Skagerrak and Kattegat coasts within 10 years from the introduction and is today common along Swedish coasts (Karlsson & Loo 1999). At larger spatial scales, the slow expansion of *F. evanescens* may be explained by lack of a natural long-distance dispersal mechanism. However, the restriction to harbours in Öresund and stone bottoms in Skagerrak suggests that at the smaller scale, the expansion of *F. evanescens* is limited by abiotic or biotic factors.

Factors affecting the invasion

Abiotic factors

Among the major abiotic factors affecting the distribution and abundance of seaweeds are salinity and wave action. Salinity affects marine organisms by affecting osmotic pressure and the concentration of essential ions. True marine species are well adapted to a salinity around 30-35 ‰ and for most of these species, lower salinity provides a barrier to colonisation. However, the salinity tolerance experiment (Paper **I**) shows that *F. evanescens* is able to grow and produce viable offspring over a wide salinity spectrum, from 24 to at least 12‰. Such broad salinity tolerance is common in intertidal species (review in Lüning 1990), which are commonly exposed to low salinity from freshwater outlets or precipitation during emersion. Occupation of a habitat with fluctuating salinity may have pre-adapted *F. evanescens* for invading regions with low and fluctuating salinity, such as the Swedish coastal area.

Despite its broad salinity tolerance, low salinity may be a restricting factor for *Fucus evanescens* in the southern part of Öresund. At 12‰ salinity, germination frequency of *F. evanescens* was lowered and below 10 ‰ the species was not able to produce any viable offspring. The results should be compared with the median salinity of 8-9 ‰ in southernmost Öresund. Likewise, the incapacity for reproducing in low salinity will probably restrict *F. evanescens* from expanding into the Baltic Sea proper. The only observation of *F. evanescens* in the Baltic Sea is from the western part (the Danish straits and the Kiel Bight; Schueller & Peters 1994) where the salinity is 12‰, compared to only 6-8 ‰ in the Baltic Sea proper (Andersson et al. 1992).

Wave action is a major cause of mortality for seaweeds and other sessile organisms and has been documented to have a strong influence on species composition in coastal communities. However, the test of attachment strength (Paper **I**) did not indicate that wave exposure can explain the restriction of *F. evanescens* to sheltered sites. We found no difference in attachment strength between adult plants of *F. evanescens* and the native *Fucus* species, when plants of the same size were compared. The tolerance to wave action is congruent with the distribution of *F. evanescens* in the native range, where the species is found together with other *Fucus* species on relatively exposed shores (e.g. Thom 1983, Chapman & Johnson 1990).

Biotic factors

Since *F. evanescens* does not seem to be limited by abiotic factors, except for salinity in the southernmost part of its distribution, biotic interactions with native competitors or enemies could be predicted to explain its restricted spread. However, my studies do not support that native enemies provide biotic

resistance to the invasion of *F. evanescens*. On the contrary, *F. evanescens* was in general less utilised by herbivores than the native seaweeds in Sweden. It hosted fewer species and generally lower abundances of herbivores (Papers **II** and **III**) and had less visible grazing damage (Paper **III**). Besides, all investigated herbivore species (*Littorina obtusata*, *L. littorea* and *Idotea granulosa*) avoided to feed on the invader when given a choice with the native species (Paper **III**).

The observed avoidance of *F. evanescens* by native herbivores in Sweden contrasts with the pattern in the native range. In Iceland, the herbivore community was similar between *F. evanescens* and the other fucoids and the species was a preferred food choice for both *Littorina obtusata* and *Idotea granulosa* and showed high levels of grazing damage (Paper **III**). Similarly, previous studies in the north-west Atlantic, where *F. evanescens* is also native, have shown that the species often is heavily grazed (e.g. van Alstyne 1990; Worm & Chapman 1998) and that it is ranked high in the preference hierarchy for both periwinkles (Barker & Chapman 1990) and amphipods (Denton & Chapman 1991). Thus, rather than supporting the biotic resistance hypothesis, the results from Paper **III** suggest that *F. evanescens* is released from herbivory in the new range.

Likewise, there is no indication that competition from epiphytic algae provides biotic resistance to the invasion of *F. evanescens*. In Sweden, the abundance and biomass of epibiota was lower on *F. evanescens* compared to both the native *F. vesiculosus* (Papers **II**, **III** and **IV**) and *Ascophyllum nodosum* (Paper **III**). Also in sites where the native fucoids were heavily overgrown by epibionts, *F. evanescens* was almost clean. Multivariate analysis also showed that the epiphytic community on *F. evanescens* differed from that on *F. vesiculosus*, mainly by being less diverse (Paper **II**). The abundance of epiphytes was low also on Icelandic *F. evanescens* (Paper **III**), suggesting that the pattern of epibiotic abundance reflects species-specific quality of the seaweeds rather than release from specialised epibionts in the new range.

While herbivores and epiphytes seem to provide little biotic resistance, competition from the native vegetation may explain the restricted spread of *F. evanescens* in Sweden. Field experiments have shown that fucoids are sometimes excluded from potential habitats by competition from other perennial species (e.g. Lubchenco 1980; Chapman 1990; Worm & Chapman 1996), suggesting that competition between perennial seaweeds can be an important structuring factor in intertidal communities. As the depth range of *F. evanescens* in Öresund overlaps those of the native fucoid species in the zonation (Paper **I**), competition probably occurs and could possibly prevent the invading species from colonising sites with a rich cover of large macroalgae. The principal establishment of *F. evanescens* in harbours in Öresund might be due to lower abundance of other fucoids at these sites. In

harbours in the southern part of the area, where *F. evanescens* is absent, the native fucoids are scarce and the algal community mostly consists of filamentous algae. Likewise, the restriction of *F. evanescens* to sheltered bays in the Tjärnö area may be due to the lower abundance of other fucoids in this habitat, compared to the dense canopy on rocky bottoms. In these sites, *F. evanescens* often grow attached to the shells of blue mussels (*Mytilus edulis* L.), which provide continuously new supply of substratum due to shell growth.

In marine benthic communities, competition for space is often intense, implying that biotic resistance from competitors may be important in many marine invasions. Species diversity was also shown to restrict success of an introduced ascidian by increasing the spatial and temporal occupation of space (Stachowicz et al. 2002). Likewise, many studies have shown that colonisation and survival of both introduced and native species is enhanced by disturbance that creates free space to colonise (e.g. Chapman & Johnson 1990; Arrontes 2002; Valentine & Johnson 2003). It is possible that availability of free space is particularly important for colonisation of invading species that could be expected to involve a low number of propagules from a single long-distance dispersal event.

Disturbance

If competition from native seaweeds is an important mechanism restricting the establishment of *F. evanescens*, disturbance may facilitate the invasion by opening space to colonise and releasing the invader from competition. It is possible that disturbance of the native fucoid communities, due to pollution (e.g. from toxic anti-fouling paints), nutrient enrichment or physical disturbance, has allowed the species to establish successfully in harbours in Öresund. Also in Great Britain, *F. evanescens* have mostly colonised harbours (Powell 1957b) and the fast expansion of the species in the Oslofjord has been connected with a simultaneous decline in native fucoids due to eutrophication (Bokn & Lein 1978). This supports the notion that disturbance makes a community more susceptible to invasions (e.g. Elton 1958, Burke & Grime 1996) and implies that the present large-scale changes in benthic vegetation occurring in many coastal areas may increase the risk for seaweed invasions.

It is also possible that *F. evanescens* is actually favoured in nutrient-enriched areas. Increased nutrient load has been shown to favour the growth of epiphytic algae, resulting in lower growth rate of the host and possibly in the decline of fucoids in eutrophicated areas (Vogt & Schramm 1991; Worm & Sommer 2000). The low abundance of epiphytes on *F. evanescens* (Papers **II** and **III**), may thus translate into a weaker effect of nutrient-enrichment on the invader compared to the native fucoids. Besides, laboratory experiments have shown that increased nutrient levels had a stronger positive effect on growth and survival of young plants of *F. evanescens* compared to *F. serratus* (Steen

& Scrosati 2004). Nutrient-enrichment may thus induce a change in the seaweed community by affecting competitive interactions between the *Fucus* species. Eutrophication-driven changes of seaweed communities from dominance of perennial to ephemeral species are well documented (e.g. Cloern 2001), but this may represent a dominance shift within the group of perennial seaweeds, which are generally regarded to respond in a similar way to increased nutrient loads in coastal waters.

Mechanisms behind patterns of herbivory and epibiont abundance

This thesis provides the first explicit evaluation of the enemy release hypothesis (ERH) for marine seaweeds. Due to the taxonomic similarity of herbivore communities between the native and new regions, herbivory on introduced *F. evanescens* was not affected by the absence of specialist herbivores, which is one of the predictions of the ERH. The situation may be different for seaweeds introduced to regions that differ strongly in herbivore community composition compared to their native region. However, the degree of host specialisation is low in marine herbivores, in contrast to terrestrial plant-herbivore systems (Hay & Steinberg 1992), questioning the potential of specialist herbivores to affect the outcome of seaweed invasions.

One reason for the absence of some herbivore species from *F. evanescens* in Sweden may be the low amount of epiphytes on the invader. The abundance and biomass of free-living fauna was positively correlated with biomass of epiphytes (Papers **II** and **III**), suggesting that the epiphytes play an important role in providing a suitable habitat for motile epifauna. Macroepiphytes increase the substrate complexity and also constitute the most preferred food source for some species (e.g. *Littorina littorea*, Watson & Norton 1985; *Gammarus locusta*, Pavia et al. 1999), and several studies have documented a positive effect of algal epiphytes on mesoherbivore abundance (e.g. Martin-Smith 1993, Worm & Sommer 2000). Thus, the amount of epiphytes may be a determining factor for the colonisation of introduced seaweeds by native herbivores.

While the low herbivore diversity and abundance on *F. evanescens* in Sweden may in part be due to low epiphytic load, the low preference for the species in the feeding choice experiments (Paper **III**), indicates that at least some herbivore species avoid *F. evanescens* because of its quality as food. Low feeding preference for *F. evanescens* compared to *F. vesiculosus* was also seen for the herbivorous isopod *Idotea baltica* in another recently invaded area (western Baltic Sea, Schaffelke et al. 1995). The avoidance of Swedish *F. evanescens* may be due to local adaptation to native seaweeds, preventing herbivores from colonising the invader. Local adaptation of herbivores is well

documented for terrestrial insect herbivores (Mopper & Strauss 1998), but there are no documented examples of local adaptation in marine herbivores.

An alternative explanation is that invading populations of *F. evanescens* are more resistant to herbivory than native populations. *F. evanescens* populations in the new region had twice as high phlorotannin content as populations in the native region (Paper **III**). Several studies have documented a negative correlation between phlorotannin concentration and herbivore preference for many herbivore species, for instance *Littorina littorea* (Geiselman & McConnell 1981) and *L. obtusata* (Pavia & Toth 2000). There was also generally a high concordance between phlorotannin content and herbivore preference (particularly for *Littorina* spp.) for the four fucoid species in both regions, supporting the connection between phlorotannins and herbivore preference. For instance, Icelandic *A. nodosum* was little grazed and contained high phlorotannin content, while the opposite was true for the Swedish populations.

Thus, although it is not possible to completely exclude that the release from herbivory in introduced *F. evanescens* is due to local adaptation of the studied herbivores, the release from herbivory in *F. evanescens* is more likely due to differential resistance to grazing in native and introduced populations. Similarly, high resistance to grazing may be the reason for the low herbivory on the invasive green seaweed *Caulerpa taxifolia* in the Mediterranean (Amade & Lemée 1998; Boudouresque & Verlaque 2002). This suggests that enemy release should not be generally expected in all invading seaweeds but that colonisation of invading seaweeds by native herbivores depends on the properties of the invading species.

Neither could the low epibiotic colonisation of introduced *F. evanescens* be explained by release from specialised epibionts. Most species that were found epibiotic on both the invader and the native fucoids are not obligate epibionts but are found on a diversity of substrates, including stones and man-made constructions. Besides, the low amount of epiphytes also on Icelandic *F. evanescens* suggests that the low epiphytic overgrowth reflects some species-specific character making the plant surface a less suitable substratum for epibiota compared to other fucoids.

Since seaweeds are often negatively affected by an extensive epibiotic colonisation, it could be expected that they would gain from evolving an effective anti-fouling defence. The presence of such a defence has been proposed to explain why some seaweed species have very little epibionts on their surface (e.g. Schmitt et al. 1995; Littler & Littler 1999). The defence could be either mechanical, as the shedding of the outer surface layer in some brown seaweeds (e.g. Filion-Myklebust & Norton 1981), or chemical, involving secondary compounds that deter settlement or survival of the

epibionts. Chemical mediation of host-epibiota interactions has been proposed to be a common phenomenon in marine systems (Steinberg & de Nys 2002) but there are still few studies evaluating the importance of chemical inhibition for abundance of epibiotic organisms.

Apart from their role as anti-herbivore defence, phlorotannins have been suggested to function as an anti-fouling mechanism. Earlier studies have also shown a negative effect of phlorotannins on settlement of invertebrate larvae (Lau & Qian 1997; Lau & Qian 2000). Accordingly, my study showed that phlorotannins from both *F. evanescens* and *F. vesiculosus* inhibited settlement of *Balanus improvisus* larvae (Paper **IV**). However, phlorotannins from *F. vesiculosus* was more effective settlement inhibitors than those from *F. evanescens*. Settlement of barnacles on intact fronds was also lower on *F. vesiculosus* compared to *F. evanescens*, both in the laboratory and in the field. Thus, although phlorotannins may act as settlement inhibitors, at least in some situations, this cannot explain the low abundance of *B. improvisus* on *F. evanescens* compared to *F. vesiculosus*.

The survival experiments showed that mortality of barnacles was high on *F. evanescens* both in laboratory experiments and in the field (Paper **IV**), indicating that the low barnacle abundance on this species is due to increased juvenile mortality rather than settlement inhibition. The rate of detachment of young barnacles was also higher from *F. evanescens* fronds compared to the other substrata. From our experiments it is not possible to deduce whether detachment occurred after the barnacles were dead for other reasons, or if the mortality was due to detachment of live barnacles. However, living barnacles were often observed to detach from the *F. evanescens* fronds during handling, suggesting that the increased mortality of barnacles on *F. evanescens* is due to a high detachment rate. The results from this study emphasises the importance of post-settlement processes for the abundance pattern of seaweed epibiota, which has been less studied than the process of colonisation. Further studies are required to understand the mechanism behind the high mortality of newly settled barnacles and to assess if this mechanism is acting generally towards all epibiotic organisms, explaining the low abundance of both epiphytic algae and sessile invertebrates on *F. evanescens*.

Consequences of the invasion

Since seaweeds act as hosts for many other species, changes associated with the introduction and establishment of a new species may have many indirect effects on the biota. The magnitude of these effects depends, at least in part, on the suitability of the introduced species as substratum for epibiotic organisms and free-living fauna, compared to the native species it replaces. As discussed above, the field studies of epiphyte abundance on *F. evanescens*

(Papers **II**, **III** and **IV**) shows that the abundance and diversity of epibiota was lower on *F. evanescens* compared to the native *F. vesiculosus* and *Ascophyllum nodosum*. This suggests that the invader constitutes an inferior substratum compared to some of the native fucoids and that a dominance shift from e.g. *F. vesiculosus* to *F. evanescens* would decrease the surface available for colonisation by epibiota. However, since most of the epibiotic species in the present studies are able to colonise rocks or other hard substrata as well (Paper **II**), the effect on populations of these species would probably be small.

Low epiphytic abundance may disfavour many free-living animals, which are dependent on epiphytes for food and habitat. Furthermore, the feeding-choice experiments suggest that *F. evanescens* is also an inferior food source for herbivores that consume fucoid tissue (Paper **III**). This suggests that *F. evanescens* plants provide less food for herbivores and an inferior habitat for free-living animals compared to *F. vesiculosus* and *A. nodosum*. This might translate into effects on higher trophic levels, e.g. fish populations feeding in the *Fucus* belt. However, further studies comparing the abundance of free-living fauna between sites with different degree of *F. evanescens* dominance are needed to conclude that a shift from *F. vesiculosus* to *F. evanescens* actually affects faunal populations in invaded regions.

The effect of the introduction on the littoral community will also depend on to what degree *F. evanescens* replaces other fucoid species. The inventories (Paper **I**, this thesis) suggest that rather than extruding other fucoids, *F. evanescens* mostly establishes where other species are rare or absent. If *F. evanescens* is able to sustain higher levels of nutrient enrichment than the native fucoids, it may play an important role as perennial, habitat-forming species, adding structural diversity to sites that would otherwise be dominated by annual, filamentous algae. This implies that the invasion of *F. evanescens* may in fact have a positive effect on local diversity and ecosystem function in disturbed sites.

Conclusions

The results presented in this thesis provide an emerging picture of the factors affecting the establishment and success of *F. evanescens* in Southern Scandinavia (Fig. 4). On a large scale, the restricted spread of the species could be explained by lack of long-distance dispersal mechanisms. Besides, the low salinity is probably restricting the species from colonising the Baltic Sea. On a smaller scale, I suggest that the spread of *F. evanescens* is restricted by biotic interactions. The restriction of *F. evanescens* to areas with sparse cover of native fucoids indicates that competing fucoids affects invasion success, probably by decreasing availability of important resources (e.g. space, light and nutrients). On the other hand, *F. evanescens* is less overgrown

by epibiotic organisms than the native fucoids, implying that it is released from competition with epiphytic algae compared to the native fucoids. This may be particularly important in areas affected by anthropogenic nutrient-enrichment, where the anti-fouling resistance of *F. evanescens* could provide a competitive advantage compared to the native fucoids.

The low amount of herbivory recorded on introduced *F. evanescens* suggests that although the species is not released from specialist herbivores in the new range (i.e. no classical enemy release), the native herbivores have low potential to provide biotic resistance to the invasion. Since introduced populations of *F. evanescens* are more resistant to herbivory than the native fucoids, herbivores may even favour the invader by having a stronger negative effect on competing seaweeds. Species-specific resistance to herbivory may generally be a more important determiner of seaweed invasion success than release from specialised or locally adapted herbivores, due to the low host specificity of herbivores.

Despite its restricted spread, *F. evanescens* has established stable populations both in Öresund and in Skagerrak and has certainly become a permanent
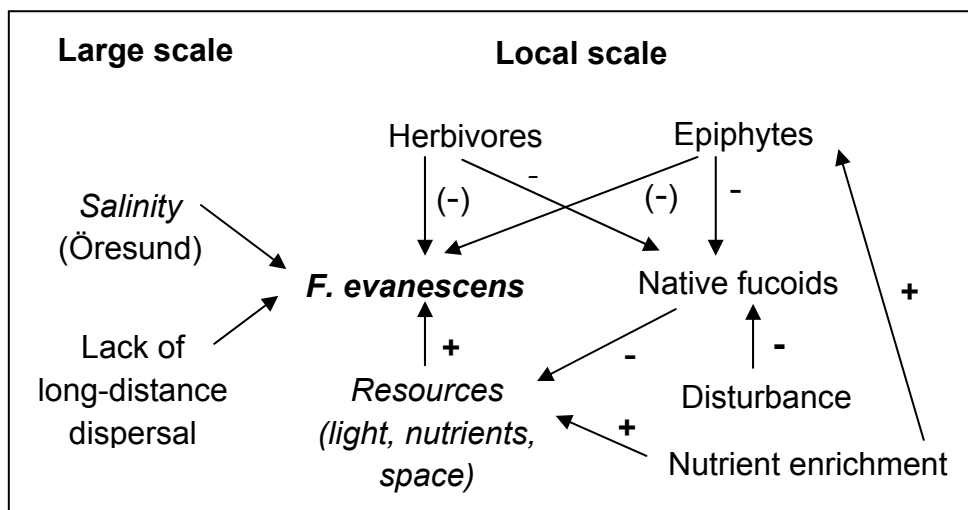

Figure 4. A simple conceptual model describing the factors restricting the spread of *F. evanescens* in Sweden. Salinity tolerance (Paper **I**) and lack of long-distance dispersal mechanism may explain the restricted spread on a large scale. On a local scale, herbivores and epiphytes do not seem to provide biotic resistance, since they utilise the invader little compared to native fucoids (Papers **II**, **III** and **IV**). I suggest that native fucoids provide biotic resistance to the invasion, by pre-emption of resources, and that disturbance may facilitate invasion by increasing the amount of available resources (light, nutrients and/or space). Anthropogenic nutrient enrichment may favour the invader indirectly, by increasing competition from epiphytic algae that are predicted to affect native fucoids more than the invader.

addition to the seaweed flora of the region. The fact that the invader differs from native habitat-forming seaweeds in its quality as host for epibionts and herbivores implies that the invasion may alter biodiversity and productivity at higher trophic levels. However, since the invader does not seem to competitively exclude native seaweeds, the effect of the invasion on Swedish coastal ecosystems is probably small.

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Svensk sammanfattning (Swedish summary)

Spridning av främmande arter anses idag vara ett av de största hoten mot jordens biologiska mångfald. Att organismer lyckas sprida sig och etablera sig i nya områden är i och för sig en naturlig process, men under de senaste århundradena har vi fått bevittna hur ett ständigt ökande antal arter med människans hjälp förflyttats till områden dit de knappast kunde ha spridit sig på egen hand. Många arter transporteras avsiktligt till nya områden för att planteras in för jakt eller odling, medan andra "liftar" med exempelvis transporterat gods eller i lastfartygens barlastvatten.

Det finns många exempel på att introduktionen av en ny art kan få stora ekologiska och ekonomiska konsekvenser. Främmande arter kan hota den biologiska mångfalden genom att tränga ut inhemska arter och kan i vissa fall förändra hela ekosystem. Ett närliggande exempel är den nordamerikanska minken, som introducerades till Sverige för pälsdjursuppfödning på 1920-talet och idag hotar sjöfågelbeståndet i många svenska kustområden. I vissa fall ställer introducerade arter också till problem för människan. Ett exempel på en problematisk art är den släta havstulpanen (*Balanus improvisus*) som har introducerats till Östersjön i historisk tid och orsakar stora kostnader genom att sätta sig fast på båtskrov och kylvattenintag.

För att på sikt minska risken för oönskade introduktioner är det viktigt att utveckla riktlinjer för transport, odling och utsättning av arter i nya områden. Detta kräver en ökad kunskap om hur främmande arter sprider sig, hur de påverkas av den nya miljön och vilken effekt de kan få på inhemska ekosystem.

Syftet med denna avhandling har varit att studera etableringen av en främmande tångart i ett kustekosystem. Tång är stora, fleråriga brunalger som dominerar algvegetationen på grunda klippbottnar i tempererade havsområden. De har stor betydelse för den biologiska mångfalden i grunda kustområden genom att erbjuda en unik livsmiljö för många andra arter. Fastsittande organismer, både alger och djur, lever på tångens yta ("påväxtorganismer") och många djur söker mat och skydd bland de stora tångplantorna. På grund av tångens stora betydelse för kustekosystem kan spridningen av en ny art tänkas ha stor påverkan på många andra organismer, men dagens bristande kunskap om främmande tångarter gör det svårt att bedöma risken för allvarliga konsekvenser.

Den främmande tångart jag har studerat är ishavstång (*Fucus evanescens*), som ursprungligen hör hemma i nordligaste Atlanten och Stilla havet (Nordnorge, Island, Grönland och Kanada). Ishavstången upptäcktes första

gången utanför sitt normala utbredningsområde i Oslofjorden 1898, dit man tror att den transporterats med båttrafik. Den har sedan spritt sig söderut i södra Skandinavien och på Brittiska öarna. Det första fyndet i Sverige gjordes 1924 i Fjällbacka (Bohuslän). Idag finns arten längs hela den svenska västkusten ner till Öresund, men har inte lyckats etablera sig i svenska Östersjön.

I en jämförande studie av ishavstångens utbredning i Öresund år 1972 och 2000 (ca 20 respektive 50 år efter att den introducerades till regionen) visar jag att ishavstången först expanderade snabbt men att spridningen varit begränsad under de senaste decennierna. Arten uppträder framför allt i hamnar och marinor, vilket antingen kan bero på att den sprids med båtar, eller att den har svårt att etablera sig i naturliga miljöer. Även i Bohuslän, där ishavstången funnits ända sedan 20-talet, är dess utbredning fortfarande begränsad.

Det finns inget som tyder på att den begränsade spridningen kan förklaras av miljöfaktorer som hindrar ishavstången från att överleva eller reproducera sig. Ishavstången är väl anpassad till att klara den låga och fluktuerande salthalten vid den svenska västkusten. Däremot klarar den inte av riktigt låga salthalter, vilket förmodligen hindrar den från att sprida sig in i Östersjön. Inte heller tycks tångens "naturliga fiender", växtätande snäckor och kräftdjur ("betare"), begränsa ishavstångens spridning. Tvärtom undviker djuren i Sverige att äta av ishavstång om de kan välja de inhemska tångarterna blåstång (*Fucus vesiculosus*) och knöltång (*Ascophyllum nodosum*). Det innebär att växtätande djur istället kan gynna ishavstångens etablering indirekt, genom att orsaka skador på dess viktigaste konkurrenter. Ishavstången är också mindre övervuxt av alger och djur än andra tångarter, vilket förmodligen gynnar den i områden påverkade av näringsutsläpp från mänsklig aktivitet, där andra tångarter drabbas hårt av konkurrens från snabbväxande påväxtalger.

Eftersom betare och påväxtorganismer visade sig ha liten effekt på etableringen av ishavstång i Sverige är det troligt att den viktigaste begränsande faktorn istället är konkurrens från andra tångarter. Ishavstången har framför allt etablerat sig på platser där inhemska tångarter saknas eller är sällsynta, antingen av naturliga orsaker eller på grund av mänsklig störning. Den huvudsakliga etableringen av ishavstång i störda miljöer visar att dagens storskaliga miljöförändringar i havet, som bland annat påverkar vegetationen i grunda kustområden, kan öka risken för att främmande arter ska lyckas etablera sig.

Ett skäl till att betare undviker att äta den nyinvandrade arten kan vara att de är evolutionärt anpassade för att utnyttja inhemska arter. Detta anses vara skälet till att vissa landväxter blir så framgångsrika när de etablerar sig i nya områden, där deras egna "naturliga fiender" saknas. För att undersöka om även främmande tångarter kan gynnas av att lämna sina naturliga fiender

bakom sig jämförde jag vilka betare som utnyttjar ishavstången i Sverige och på Island (ett område där den ursprungligen hör hemma). Island skiljer sig inte mycket från Sverige i vilka arter av betare som lever i klippsträndernas tångskogar. Trots detta visade det sig att isländska betare, till skillnad från de svenska, gärna äter ishavstång. Detta skulle kunna förklaras av att betarna är lokalt anpassade till att äta de tångarter de känner till. En mer trolig förklaring till att ishavstången äts på Island men inte i Sverige är dock att tångens motståndskraft mot betare skiljer sig mellan områdena. Introducerad ishavstång innehåller höga halter av florotanniner, en grupp kemiska substanser som har visats fungera som försvar mot betare.

Florotanniner från ishavstång och den närbesläktade blåstången visade sig även förhindra etablering av havstulpanen *Balanus improvisus*, en vanlig påväxtorganism, och kan således fungera som försvar mot påväxt. Florotanninernas hämmande effekt kan dock inte helt förklara att ishavstången är så litet överväxt av alger och djur. En trolig bidragande mekanism, åtminstone när det gäller etableringen av havstulpaner, är att djuren lättare lossnar från ishavstångens yta.

Sammanfattningsvis visar resultaten att ishavstången utgör en dålig värd eller föda för många betare och påväxtarter. Om ishavstången skulle ersätta de inhemska tångarterna kan det således tänkas påverka biologisk mångfald och energi- och materialflöden lokalt. Men eftersom arten inte tycks tränga undan inhemska tångarter, utan snarast etablerar sig i områden där det finns utrymme, är effekten av introduktionen förmodligen liten.