

Fucus radicans
– Reproduction, adaptation &
distribution patterns
by
Ellen Schagerström



Plants & Ecology

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Cover: *Fucus radicans* and *Fucus vesiculosus* together in a tank.
Photo by Ellen Schagerström

Summary

The Baltic Sea is considered an ecological marginal environment, where both marine and freshwater species struggle to adapt to its ever changing conditions. *Fucus vesiculosus* (bladderwrack) is commonly seen as the foundation species in the Baltic Sea, as it is the only large perennial macroalgae, forming vast belts down to a depth of about 10 meters. The salinity gradient results in an increasing salinity stress for all marine organisms. This is commonly seen in many species as a reduction in size. What was previously described as a low salinity induced dwarf morph of *F. vesiculosus* was recently proved to be a separate species, when genetic tools were used. This new species, *Fucus radicans* (narrow wrack) might be the first endemic species to the Baltic Sea, having separated from its mother species *F. vesiculosus* as recent as 400 years ago. *Fucus radicans* is only found in the Bothnian Sea and around the Estonian island Saaremaa. The Swedish/Finnish populations have a surprisingly high level of clonality. As much as up to 80% of the individuals on the Swedish side are clones, dominated by one female clone that has been found over a range of 550 km. In spite of this ability to asexual propagation, we do not find *F. radicans* further south than Öregrund in Sweden, and even further north in Finland. I attempt to find out why.

Sammanfattning

Östersjön anses vara en ekologiskt marginell miljö, där både marina och limniska arter kämpar för att anpassa sig till ständigt föränderliga förhållanden. *Fucus vesiculosus* (blåstång) ses ofta som foundation species i Östersjön, eftersom det är den enda perenna makroalgen och den bildar stora bälten ner till ett djup av cirka 10 meter. Salthalts-gradienten resulterar i en ökad salthalts-stress för alla marina organismer. Detta syns ofta hos många arter som en minskning i storlek. Vad som tidigare beskrivits som en dvärgform av *F. vesiculosus*, inducerad av låg salthalt, har nyligen visat sig vara en separat art, då genetiska verktyg användes. Den nya arten *Fucus radicans* (smaltång) kan vara den första endemiska arten i Östersjön. Beräkningar visar att den kan ha bildats ur *F. vesiculosus* så sent som kanske för bara 400 år sedan. *Fucus radicans* finns bara i Bottenhavet och runt den estniska ön Ösel. De svensk-finska populationerna har en förvånansvärt hög klonalitet. Så mycket som upp till 80 % av individerna på den svenska sidan består av kloner. Det är framförallt en kvinnlig klon som har återfunnits längs en sträcka på 550 km. Trots denna förmåga att föröka sig asexuellt, finner vi inte *F. radicans* längre söderut än Öregrund i Sverige och ännu längre norrut i Finland. Jag försöker ta reda på varför.

Introduction

It was recently discovered that what was previously thought of as a well-adapted morph of the brown macroalgae *Fucus vesiculosus* L. was indeed a new species (Bergström *et al.* 2005), one that might actually have formed sympatrically in less than a thousand years (Pereyra *et al.* 2009a), making it the first known endemic to the Baltic Sea. Here follows an introduction to how the new species *Fucus radicans* sp. nov. Bergström et Kautsky, differs from its mother species *Fucus vesiculosus*, and in what ways they are similar. Further, the different mechanisms of speciation are discussed leading on to dispersal and distribution related questions and the effects the eutrophication of the Baltic Sea might have on reproductive traits in *Fucus vesiculosus* and *Fucus radicans*.

The Baltic Sea- a marine marginal environment

The Baltic Sea is the world's largest brackish sea, with a surface area of 412 000 km² and a volume of 22 000 km³. The geographical limit of the Baltic Sea is not absolute, but differs from reaching all the way up the Swedish Skagerrak coast to the Norway border (HELCOM 1974) to including only the Kattegat Sea (Kautsky & Kautsky 2000) or stopping somewhere at the narrow sills in the Danish belts (Johannesson & Andre 2006), nowadays easily defined by the physical border of the Öresund bridge, which is the limit I will use here. For clarification, the term marine refers to a salinity of > 15 psu and brackish denotes salinity between 15 psu-1 psu. The surface salinity gradient ranges from 10 psu in the south to 0.5 psu in the north, making it an ecologically marginal environment. It is also a geographical limit for many of its species as well, which makes the Baltic Sea a truly marginal marine environment (Johannesson & Andre 2006). The sea has varied in size, shape and salinity over the last 12 000 years BP since it was formed, having both periods of higher salinity as well as periods of being a freshwater sea (Björck 1995). The latest larger influx of saline water occurred between 8000-4000BP, during the Littorina Sea period, when the Baltic Sea experienced a higher salinity than today (Russell 1985). The species of marine origin still present in the Baltic Sea today were mostly recruited during that era (Snoeijs 1999). The salinity has progressively decreased from 7500 BP until about 3000 BP, creating an increasingly brackish habitat (Fig. 1), to which but a few marine species have managed to adapt (Russell 1985). Today, one finds approximately 320 benthic macroalgae on the western coast (Kattegat) of Sweden, but only 90 in the Baltic proper. The number drops further north

up in the Bothnian Sea, where, on the other hand, many freshwater species are abundant (Nielsen *et al.* 1995).

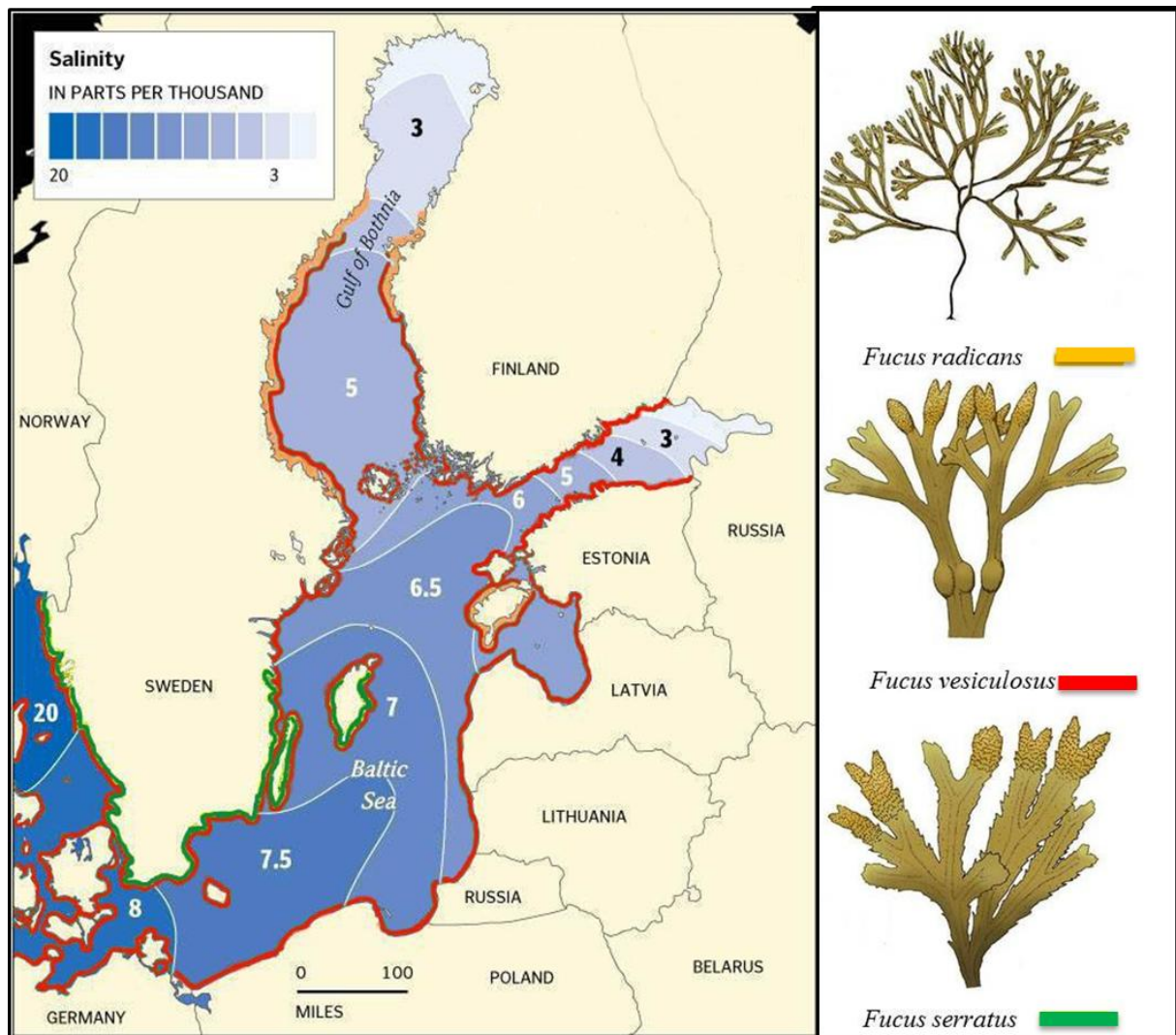


Figure 1. Surface water salinities (psu) and the distribution of Fucoids in the Baltic Sea. *Fucus serratus* (yellow) distribution is only shown along the Swedish coast. *Fucus vesiculosus* (red) can be found all along the Baltic coast in salinities greater than 4 psu. *Fucus radicans* (orange) has not been documented in salinities higher than 6.5 psu. It should be noted that it is not a continuous distribution of Fucus, but the map shows where the species may be found if rocky substrate is available.

Furoids in the Baltic Sea

Three species from the *Fucus* family are found in the brackish waters inside the Baltic Sea (Fig 1). These are often described as foundation species (Dayton & Hessler 1972; Virnstein 1977; Roff & Zacharias 2011) in the Baltic Sea. *Fucus serratus* (L.) is least tolerant of the brackish conditions, and is not found in salinities lower than 7 psu on the Swedish coast

(Malm *et al.* 2001). *Fucus radicans* and *Fucus vesiculosus* are the only perennial canopy-forming seaweeds that reach all the way into the Bothnian Sea down to salinities as low as 4 psu (Forslund *et al.* 2012), and reaching a depth of down to ~10 metres (Kautsky *et al.* 1986). Although the mere presence of these species does not indicate high species richness of associated flora or fauna, they host a high biomass of invertebrates, which in turn affects higher trophic levels, should the fucooids decline (Wikström & Kautsky 2007) since there is a positive correlation between animal abundance and habitat size of macroalgae (Christie *et al.* 2009)

Ecologically, *F. radicans* is most likely as important as the larger *F. vesiculosus*, often supporting a varied and rich associated fauna (Råberg & Kautsky 2007). Fucooids also serve as important substrate for several epiphytic algal species, in the Baltic Sea most commonly *Elachista fucicola* (Velley) Areschoug, *Ceramium tenuicorne* (Kützing) Waern and *Pilayella littoralis* (L.) Kjellm (Rönnberg *et al.* 1992), which, in turn, are grazed by several invertebrates, such as *Idotea baltica* Pallas, *Gammarus spp.* (Kotta *et al.* 2006) and various gastropods, mainly *Theodoxus fluviatilis* L., *Radix peregra* O.F. Müller and *Radix baltica* L. (Malm *et al.* 1999).

Morphological variation and a new species

The morphology of *Fucus serratus* is easiest to distinguish, with its serrated sides and lack of air bladders (Fig. 1). *Fucus vesiculosus*, however, has a very varied morphology (Waern 1952; Kalvas & Kautsky 1993), with several morphs living either attached or free floating, with or without airbladders (Norberg 1995) and differing widely in height, width and appearance due to i.e. wave exposure (Bäck 1993). However, Ruuskanen and Bäck (1999) concluded that a combination of four morphological characters (midrib width, thallus width, plant length and stipe length) was sufficient to distinguish between populations from different sites.

The dwarf morph of *F. vesiculosus*, commonly found in sympatry with the common morph in the Bothnian Sea, was believed to be caused by the low salinity of the area (Waern 1952; Ruuskanen & Bäck 1999). A similar morph was also found in a low-saline environment in Finland (Luther 1981). The high amount of irregular branching on this morph was believed to be a response to grazing (Van Alstyne 1989) or apical osmotic damage caused by freshwater pulses (Ruuskanen & Kiirikki 2000). Through the use of DNA microsatellites, Tatarenkov *et al.* (2005) discovered that an uncommonly large part of this dwarf morph was clonal, and

genetically separated from the common form of *F. vesiculosus*. Based on this, Bergström *et al.* (2005) described *Fucus radicans* as a new species, reproductively isolated from a truly sympatric population of common *F. vesiculosus*.

Sexual reproduction

The reproduction of fucoids differs from most other brown algae in that they do not have an alteration of generations. They have gametic meiosis, but lack zoospores and a gametophyte stage. The multicellular macroscopic thallus is diploid, although cases of polyploidy do occur within the Fucales (Coyer *et al.* 2006). There are both dioecious (*F. vesiculosus*, *F. serratus*, *F. radicans*) and hermaphroditic (*Fucus spiralis* L., *Fucus evanescens* C. Agardh) species within the family. The reproductive structures, the receptacles (Fig 2), develop apically at the tips of the branches. In the receptacles of those species that are dioecious, antheridia (male) or oogonia (female) are formed within cavities of the receptacle surface, called conceptacles (Fig 2). The oogonia each contain 8 haploid egg cells, the antheridia 64 laterally biflagellate spermatozoa (Hoek *et al.* 1993). Eggs are negatively buoyant, which makes them sink to the sea floor upon release. The fucoid sperm are negatively phototactic, actively swimming away from light (Brawley & Johnson 1992) and they are attracted to the eggs by pheromones released by the eggs (Maier & Müller 1986; Brawley *et al.* 1999).



Figure 2. Mature receptacles of *Fucus radicans* (left) and cut receptacles (right) displaying conceptacles filled with oogonia (top) and antheridia (bottom). Photos: E. Schagerström.

In the tidal waters of the marine coasts, the peak of gamete release in *Fucus* sp. is during the calmer periods of the tidal cycle. Release is first initiated by a period of desiccation during

low tide (Berndt *et al.* 2002). The synchronous release is then triggered by differences in hydrodynamic conditions that can be sensed by the algae (Pearson & Brawley 1997; Pearson *et al.* 1998; Brawley *et al.* 1999). This has been suggested as the mechanism for promoting fertilization success by minimizing gamete dilution by Pearson *et al.* (2004).

The Baltic Sea has more or less annual cycles of high or low water levels caused by meteorological high- and low pressures, often resulting in low waters during early spring, and the daily tidal range is too small to have any effect. The trigger for gamete release in *F. vesiculosus* in the atidal Baltic Sea has instead been suggested to be tied to a circadian rhythm. This is incorporated into a fortnightly rhythm, timing the main releases to around full and new moon (Andersson *et al.* 1994). A relatively small number of eggs are shed about the same time every day, revealing a daily cycle, but the peak of the egg release in the Baltic Sea is somewhere between 18:00 and 22:00 in the evening, just before (terrestrial) dark (Serrão *et al.* 1996b). The periodicity does not seem to be affected by irregular variations in temperature or by high fluctuations in water level between days and egg release (Andersson *et al.* 1994).

Salinity plays a crucial role in successful fertilization for species with motile gametes, as the flagella that propel them through the water mass is driven by sodium ions. Sperm from *F. vesiculosus* growing in fully marine conditions (> 15 ppm) are unable to swim in salinities below 6 ppm, where Baltic *F. vesiculosus* sperm swim well (Serrão *et al.* 1996a), a clear adaptation to the low salinities of the Baltic Sea. However, a lowering of the ambient salinity reduces the velocity of sperm as well as the proportion of motile sperm for Baltic as well as marine *F. vesiculosus* (Serrão *et al.* 1999). Osmolality is a variation of molality that only takes into account solutes that contribute to a solution's osmotic pressure. Natural or anthropogenic changes in the areas of low salinity in the inner Baltic Sea that increase osmolality even the slightest could lead to an increase in successful fertilization since this might increase the sperm motility or prevent lysis of the egg (Pearson & Brawley 1996; Serrão *et al.* 1996a).

To locate and reach the egg, swimming sperm uses photic and chemical cues (Maier & Müller 1986), where the egg releases a pheromone to attract the sperm. This sexual pheromone system is identical for both dioecious and monoecious *Fucus* species (Müller & Gassmann 1985), and can therefore not be regarded as a pre-zygotic barrier to hybridization. Once the egg is fertilized it is vital that the egg is closed to all other sperm after the first one has penetrated. This polyspermy block is also facilitated by sodium ions (Brawley 1987, 1991). A

low concentration of sodium will thus lead to an increase in polyspermy, several sperm penetrating the same egg, which is fatal to the zygote (Serrão *et al.* 1999) as shown for *F. radicans*.

Several of the steps leading up to fertilization success in *Fucus* spp. are clearly affected by osmotic changes in the surrounding water. The cell wall created by the polyspermy block also protects the fertilized egg from lysis. At lower salinities (3-4 ppm), unfertilized eggs from areas with 6 ppm salinity rapidly swell and burst within 2 h (Serrão *et al.* 1999). This causes a narrow time window for sperm to reach the egg.

Salinity is thus considered to be the limiting factor for the northern distribution of *F. vesiculosus* in the Baltic Sea, since this correlates with the swimming ability of the gametes (Serrão *et al.* 1996a) as well as the double function of the polyspermy block (Serrão *et al.* 1999). The salinity requirements of the least tolerant life stage will most likely function as a physiological barrier to an expansion into more brackish waters for algae species. In another brown seaweed in the order Fucales, *Sargassum muticum* (Yendo) Fensholt, the salinity tolerance is lowest during fertilization and increases with germling age, preventing sexual reproduction in areas of too low salinity (Steen 2004).

The sexual reproductive cycle of *F. radicans* (Fig 3) does not differ from that of *F. vesiculosus*, as far as we know (Bergström *et al.* 2005). *Fucus radicans* does, however, supplement the salinity sensitive sexual reproduction with a high proportion of vegetative or clonal reproduction (Tatarenkov *et al.* 2005).

Clonal reproduction

Cloning by fragmentation is fairly common among marine macroalgae (Collado-Vides 2001) and is commonly used as main propagation method for aquaculture of commercially interesting species (Santelices 2001). A reduced sexual reproduction is not uncommon for marine macroalgal species living in marginal habitats (Dorken & Eckert 2001; Billingham *et al.* 2003). The entrance to the Baltic Sea through the Öresund and the Belts is both narrow and shallow, and has proved to be an effective barrier against genetic drift between Atlantic and Baltic populations for at least 20 marine species from different taxa, resulting in a loss of genetic diversity within the Baltic Sea populations (Johannesson & Andre 2006). This has favoured a selection of low-salinity adaptation traits, leading to Baltic Sea- specific ecotypes or variants. Perhaps the most striking difference in appearance between Baltic marine algae

and algae from N. Atlantic is their increasingly small stature as salinity decreases (Waern 1952; Luther 1981; Russell 1985). A reduction in thalli size can also be caused by, or in combination with, other stressors, most commonly wave exposure level (Ruuskanen & Bäck 1999, 2002; Wahl *et al.* 2011).

Several of the marine algal species present in the Baltic Sea today have adapted their life cycles to the low salinities by becoming more asexual, e.g. *Furcellaria lumbricalis* (Hudson) J.V. Lamouroux, *Ceramium tenuicorne* and *Pilayella littoralis* (Russell 1985; Alström-Rapaport *et al.* 2010).

Furcellaria lumbricalis, one of the most common perennial red alga in the northern part of the Baltic Sea and the Bothnian Sea, can be found in salinities down to 3.6 psu. At the lowest salinities, *F. lumbricalis* does not form all phases or forms of its life cycle. These populations seem to reproduce only by spores and/or increasing levels of asexual fragmentation and reattachment, with the occasional sexual reproduction when salinities allow (Kostamo & Makinen 2006), similar to that found in *F. radicans*. Increasing within-population clonality in *F. lumbricalis* correlates with decreasing salinity. This indicates that thallus fragmentation and reattachment is more important in brackish populations existing at the range limit (Kostamo 2008).

Like in *F. lumbricalis*, there is a strong reduction in sexual reproduction in the filamentous red algae *Ceramium tenuicorne*, as the salinity decreases northwards in the Baltic Sea (Bergström *et al.* 2003). The Baltic Sea morph of *C. tenuicorne* was previously described as an own species, *Ceramium gobii* (Waern 1992) and considered endemic to the Baltic Sea, but this name has been reduced to synonymy through DNA analyses (Gabrielsen *et al.* 2003). In *C. tenuicorne* there can be seen a strong adaptation to local salinities, suggesting there are several ecotypes of this species within the Baltic salinity gradient. These ecotypes do not increase in growth when transferred to higher salinities (Bergström & Kautsky 2006).

The filamentous brown alga *Pilayella littoralis* found in the Baltic Sea has active growth at salinities as low as 1.5 psu, and is considered to be a subspecies to the marine *P. littoralis*, having its geographical limit near Copenhagen, where the salinity is about 8-9 psu (Russell 1994).

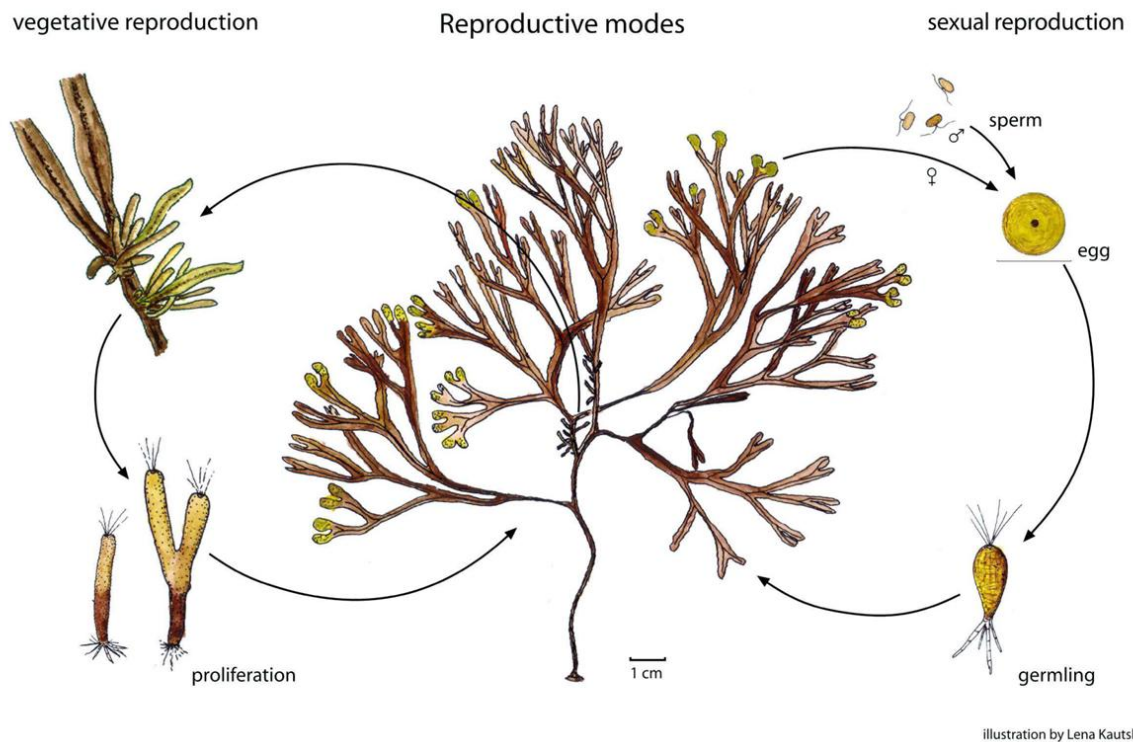


Figure 3. The life cycle of *Fucus radicans* showing the vegetative or clonal reproduction (left) and the sexual reproduction (right). Both modes are present in any one individual.

Fucus radicans is named for the ability of its adventitious branches to re-attach to the substratum and form new thalli after having come loose from the mother plant (Fig. 3), thus serving as vegetative propagules (Bergström *et al.* 2005; Tatarenkov *et al.* 2005). These new, clonal thalli should be described as **ramets**, according to the definition by Herben *et al.* (1994), since the high level of clonality within the species (Johannesson *et al.* 2011) makes the use of “genet” inappropriate (Scrosati 2002). *Fucus radicans* has a very high level of vegetative propagation or clonality. Some populations are almost considered monoclonal, with > 90% of a population being the same genetic individual (Johannesson *et al.* 2011). This trait is likely to have contributed in large to the quite successful geographical dispersal of *F. radicans*, considering the estimations by Pereyra *et al.* (2009a) of the time of speciation divergence. One clone in particular, a female, seems to have very high fitness in this regard, as it has been found in populations ranging over 550 km of the Swedish coast of the Bothnian Sea. In Finland, the populations seem to be dominated by two male clones (Johannesson *et al.* 2011). There are no reports of clonality in *F. vesiculosus* in marine habitats, but this might well change with the availability of more microsatellite loci for genetic comparison of *Fucus*

DNA (Engel *et al.* 2003). There were however some clones of *F. vesiculosus* found in the northern Bothnian Sea, but then only within populations (Johannesson *et al.* 2011).

There are as of yet no data on what triggers the adventitious branches of *F. radicans* to form rhizoids and reattach to a substratum. It is previously known that several furoid species can survive as detached, loose-lying forms (Lee 1989), but the results of Tatarenkov *et al.* (2005) showed a high level of reattachment in *F. radicans* (dwarf morph), and some of the adventitious branches of *F. vesiculosus* (common morph) also attached. It was speculated if reattachment could be facilitated by extended periods of calm conditions in the Baltic Sea (i.e. ice cover and/or no diurnal tidal movement of the water mass). Other triggering factors might be temperature, light, need for a period of calm conditions or the chemical properties of the substratum. Trials have been made with several different treatments, (i.e. different salinities, auxin, light /dark) but so far none have given any conclusive results (Forslund pers. comm.). Reattachment might also be somehow connected to salinity, induced by low levels or suppressed by high salinity. Such a trigger might explain why there are as of yet no clones found in the Estonian populations of *F. radicans* (Johannesson *et al.* 2011) where salinity is around 6 psu, compared to 4-5 psu in the Bothnian Sea. Nor do the Estonian populations of *F. radicans* form the rich amount of adventitious branches typical of the species in Finnish and Swedish populations (pers. obs.). An increase of asexual reproduction will reduce genetic variation within populations, thus increasing the risk of inbreeding depression and ultimately risks a complete population collapse (Charlesworth & Charlesworth 1987).

Speciation

The theory of sympatric speciation was first published by Darwin (Darwin 1859), and the fight has been going on ever since on whether or not this is possible (see i.e. review by Mallet (2008). Speciation is classically divided into allopatric, peripatric, parapatric and sympatric speciation (Coyne & Orr 2004), but this has been found as too rigid, leaving little room for the changing nature and mechanisms of speciation (Mallet 2007; Butlin *et al.* 2008). It is therefore perhaps more ecologically correct to consider allopatric and sympatric speciation as the very ends of a continuum of initial levels of gene flow between diverging populations (Butlin *et al.* 2008).

I here use the term **species** as on a genetic level, based on the reasoning by Mallet (1995) that defines species as a distinguishable group of genotypes that remains distinct, regardless of potential or actual hybridization and gene flow.

The prezygotic factors acting in the earliest part of the life cycle, before hybridization, restrict gene flow more than postzygotic, that are acting after hybridization. Prezygotic isolation can therefore be said to restrict a current gene flow more than postzygotic isolation for sexually reproducing diploid organisms (Turelli *et al.* 2001).

The suggested time of speciation for *F. radicans* is between 400-1500 YBP (Pereyra *et al.* 2009a), which is fast, but not unnaturally so. Speciation through polyploidy occurs over only one generation, since polyploidy causes a postzygotic isolation due to chromosomically based hybrid sterility (Turelli *et al.* 2001). Polyploidy can sometimes, but does not always produce offspring that are physically bigger (*gigas*) than the parents, due to larger cells, particularly if the original diploid is strongly heterozygous (Stebbins 1950).

Hybridization is known to occur between *Fucus* species, often in overlapping zones, resulting in hybrids of intermediate morphology (Coyer *et al.* 2002). An intrinsic sterility barrier between dioecious *Fucus* species was concluded by Bolwell *et al.* (1977), but natural crossings have been found between dioecious and hermaphroditic species, where the hermaphrodite provides the egg and the dioecious provides the sperm (Coyer *et al.* 2007).

Forslund and Kautsky (2012) had higher (>90%) rates of successful fertilization of hybrids when crossing *F. radicans* with *F. vesiculosus* *in vitro* than for within species crossings of *F. vesiculosus* (80%). Few germling survived after two weeks for both hybrids and within species crossings, so no conclusions as to lowered hybrid fitness could be made. However, the sperm attractant hormone is the same for all *Fucus* species (Müller & Gassmann 1985), so perhaps hybrids created in laboratory conditions does not reflect the natural rate of hybridization. So far, only one hybrid between *F. vesiculosus* and *F. radicans* have been found through genetic microsatellite analysis in the field, at Öregrund (Johannesson pers. comm.), which indicates that natural hybridization between these two species does not occur very often in the field. This particular site, however, has been shown by Johannesson and Andre (2006) to be a genetic bottleneck, related to a strong salinity gradient.

A shift in reproductive timing is an effective means of reinforcing a reproductive isolation for broadcast spawners such as *Fucus*. This is shown by Monteiro *et al.* (2012) to occur between sympatric *Fucus spiralis*, *Fucus guiryi* G.I.Zardi, K.R.Nicastro, E.S.Serrão & G.A.Pearson (selfing hermaphrodites) and *F. vesiculosus* (dioecious), who grow more or less adjacent but with very low levels of hybridization.

In the Bothnian Sea, the Swedish and Finnish populations of *F. radicans* and *F. vesiculosus* live sympatrically (Forslund *et al.* 2012), with no apparent difference in receptacle maturation or gamete release triggers. In Estonia, however, there is a clear difference in time of reproduction of approximately 2-3 months between *F. vesiculosus*, which reproduces in May, and *F. radicans* that reproduces in late August –September, which, incidentally, overlaps with the reproductive period of the autumn reproducing morph of *F. vesiculosus* in Sweden (Forslund & Kautsky 2012). Such a shift in spawning synchrony might be the mechanism behind the rapid speciation, if the Estonian population is regarded as the origin of the species. It is also interesting to note that there is a (modelled) gene flow barrier between Estonia and the Bothnian Sea (Jacobi *et al.* 2012), isolating populations of organisms with a long larval stage from each other. Will this barrier exist long enough to enhance further divergence (Turelli *et al.* 2001), creating yet another species endemic to the Baltic Sea?

What factors might be limiting the southern distribution of *Fucus radicans*?

The northern distribution of fucoid species in the Baltic Sea is limited by the low salinity, but it is not known why *F. radicans* is not found further south on the Swedish coast, or why it is only found north of Poori/Björneborg in Finland (Fig. 1). Inventories around the outer archipelago of Rauma made in 2011 found vast belts of *F. vesiculosus* in both broad and narrow morph, but no *F. radicans* (pers. obs.). This might be an indication of intraspecific competition, where *F. radicans* is simply outcompeted by the larger *F. vesiculosus*, or that dispersal against the counter clockwise surface current in the Baltic Sea (Nehring & Matthäus 1991) is limiting the spread southwards.

Experiments performed so far indicate that neither the reproductive stages nor the growth in *F. radicans* is limited by salinities higher than 6 psu. Trials with reproduction on a salinity scale of 2 psu to 33 psu even show an increase in successful fertilization with increasing salinity (Schagerström and Kautsky in prep).

The isopod *Idotea baltica*, a common grazer on *Fucus spp.* in the Baltic Sea (Salemaa 1979), prefers *F. radicans* over *F. vesiculosus* (Forslund *et al.* 2012). Grazing by *I. baltica* has been known to cause major declines in *Fucus* populations in the Baltic Proper (Kangas *et al.* 1982; Vogt & Schramm 1991; Engkvist *et al.* 2000; Nilsson *et al.* 2004) and the northernmost limit for *I. baltica* overlaps with the southern limit for *F. radicans* on the Swedish coast (Leidenberger *et al.* 2012). Grazing might not be the sole reason for the southern limit, but might well work in synergy with other unknown factor(s) (Fig 4).

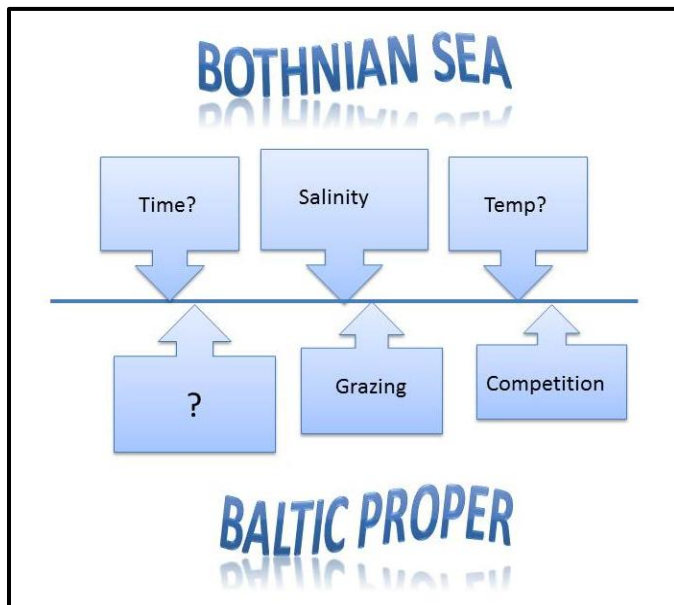


Figure 4. Factors favouring a distribution of *Fucus radicans* further south (top) and factors preventing it (bottom).

What effect might eutrophication have on reproductive traits in *Fucus*?

The large-scale eutrophication of the Baltic Sea has led to an increase in primary production (Bonsdorff *et al.* 1997) and thus to an increase in sedimentation. Sedimentation on hard bottoms has been shown to reduce the recruitment of fucooids, hindering the fertilized eggs from reaching the substratum for settling (Råberg *et al.* 2005). Experiments with clearing areas from sediment showed an increased density and survival of juvenile *F. vesiculosus* compared to areas exposed to natural sediment conditions. Sedimentation in the upper sublittoral zone is sparse due to wave action. The negative effects of sedimentation on recruitment success will therefore increase with depth and be part of setting the lower limit for the *Fucus* belt (Eriksson & Johansson 2003; Eriksson & Bergström 2005). Comparative studies of long-term changes of macroalgal vegetation in the Baltic Sea and between the Baltic Sea and the Skagerrak coast show a significant decrease in the depth distribution of several macroalgal species, partly correlated to an increase in sediment load (Eriksson *et al.* 2002). The variation in sediment load over time is an important factor for determining the abundance and distribution of a species, thus affecting the entire structure of the biota of these habitats (Eriksson & Johansson 2005). The increased levels of deposited matter in the Baltic Sea proper (Fig 1) might also be a hindering factor for the establishment of *F. radicans*

further south. Fertilized eggs of *F. vesiculosus* had very low (less than 1%) survival on substrates containing sediment (Berger *et al.* 2003).

The eutrophication has also led to increasing amounts of filamentous algal cover, which effectively prevents *Fucus* zygotes from reaching the substrate and attach (Kraufvelin *et al.* 2007). The settling of *F. vesiculosus* germlings is reduced by the physical presence of *P. littoralis* on the substrate. Also, even low concentrations of *P. littoralis* exudates negatively affects germination and rhizoid formation in the *F. vesiculosus* zygotes (Råberg *et al.* 2005).

Baltic *F. vesiculosus* along the Swedish coast exhibits two reproductive strategies; The first, previously thought the only one, has receptacle initiation triggered by the short days in the autumn and the reproductive peak in early summer (May-June), whilst the other strategy initiates receptacles cued by the longer days in early spring, with receptacle maturation later in the season, during autumn (September) (Berger *et al.* 2001). Tatarenkov *et al.* (2007) found no genetic differentiation between the summer- and autumn-reproducing morphs of *F. vesiculosus*. However, the summer- reproducing morph showed a high genetic similarity within one area, but pronounced genetic differences between different areas. This differs from the autumn- reproducing morph, whose genetic differentiation within an area is almost on the same the level of differentiation as that between areas (Tatarenkov *et al.* 2007). Two separate reproductive periods have also been found in *F. serratus* populations in the Baltic Sea (Malm *et al.* 2001), and strategy of having two reproductive periods can also be found in other members of the *Fucus* genera, for example in *Sargassum horneri* (Turner) C. Agardh, in Hiroshima Bay, Japan (Yoshida *et al.* 2004). The reasons behind this shift in the Baltic Sea might be the higher availability of substrate later in the season (Kiirikki & Lehvo 1997; Berger *et al.* 2001; Berger *et al.* 2003). There are, however, no reports of autumn reproducing *F. vesiculosus* in Finland, where it reproduces in June (Kraufvelin *et al.* 2012).

Repeating the survey of Berger *et al.* (2001) after 14 years found the previously summer reproducing localities around Gotland now all having 30 -100% of autumn reproductive individuals. Some populations even seemed to have individuals that were reproducing both in early summer and autumn (Schagerström *et al.* in prep) which, since this is previously unreported in Phaeophyceans, needs further investigation.

The occurrence of two separate sexually reproductive periods has not yet been observed in *F. radicans*, but might well be found. The initiation of receptacles seems to be triggered by short day photoperiod (pers. obs.), same as the early summer reproductive *F. vesiculosus* (Berger *et al.* 2001). The receptacles of *F. radicans* mature in late May-June at the southern dispersal limit, and during late July-mid August at the northern limit along the Swedish coast, same as the sympatric *F. vesiculosus*. The temporal difference in receptacle maturation is influenced by the gradients of temperature and light (Bird & McLachlan 1976). In Estonia, however, the timing of reproduction differs between the sympatric populations of *F. radicans* and *F. vesiculosus*, creating a pre-zygotic reproductive barrier between the two species (Forslund & Kautsky 2012). The Estonian *F. vesiculosus* reproduces in early summer, same as Swedish *F. radicans* and *F. vesiculosus*, while *F. radicans* in Estonia reproduces in the autumn, during late August- September. Such a prezygotic isolation might have led to this rapid speciation, if the Estonian population might be regarded as the “origin” population.

It would be interesting to find what mechanisms that has caused the speciation to take place, in order to determine if this speciation has indeed taken place within the time frame suggested by the model by Pereyra *et al.* (2009b) thus confirming the first endemic algae in the Baltic Sea.

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