

**Genetic structuring in natural
populations – the influence of life
history strategies and asymmetric
migration**

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Doctoral Thesis



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Abstract

In this thesis I investigate aspects of genetic differentiation and factors influencing the structure of populations. This is done with a special focus on life histories and dispersal strategies common in the marine environment. Many marine organisms are planktonic or have a planktonic life stage and due to dispersal with ocean currents asymmetric migration between populations are thus a common occurrence. Here I present a method that makes it possible to calculate directional measures of genetic differentiation and relative migration. The method aims to advance measures of genetic differentiation and reveal more information in systems with asymmetric migration patterns. Knowledge about direction makes it easier to correlate gene flow to factors such as oceanographic connectivity. With the use of this method my coauthors and I have investigated the population genetic structure of the marine diatom *Skeletonema marinoi* and the two sibling species of macroalgae, *Fucus vesiculosus* and *F. radicans*, in the Baltic Sea area. We found that *S. marinoi* was genetically differentiated between all local populations along the salinity gradient from the Bothnian Sea to the North Sea entrance. The biggest difference was found between the two sides of the Danish Straits, thus this region indicates a major dispersal barrier. Local populations inside the Baltic Sea showed signs of adaptation to local salinities. Directional relative migration, calculated with our method, was found to be significantly correlated to oceanographic connectivity. Furthermore, asymmetric migration coming from the Baltic Sea coincided with the direction of the surface current. Many planktonic microalgae including *S. marinoi* form long-term resting stages that accumulates in the sediments. By constructing a simple genetic population model and also conducting a systematic literature review my coauthors and I have investigated if and how a life history strategy including resting stages can affect the genetic structure of a population. We found that resting stages can have an anchoring effect on local populations that can lead to genetic differentiation between adjacent populations despite ongoing gene flow. This anchoring effect may help explain how microalgae with huge dispersal potential can be found genetically differentiated on small geographical scales. When investigating the genetic population structure of *F. vesiculosus* and its newly evolved sister species *F. radicans* we found support for earlier conclusions of two reproductively isolated species. However, we conclude that the genetic pattern of these two species is very complex and that geographical differences are high.

Populärvetenskaplig sammanfattning

Med hjälp av genetik studerar jag i min avhandling hur populationer är strukturerade. Vad en population är, är inte helt lätt att definiera. Enkelt kan man säga att det är ett antal individer, av samma art som lever så nära varandra att det finns en möjlighet att de skaffar barn ihop. Ofta finns det strukturer inom en population, dvs. vem som skaffar barn med vem är inte helt slumpmässigt utan vissa individer har större chans att skaffa barn med varandra än andra har, vilket till exempel kan bero på att de bor närmare varandra. Populationsgenetiker studerar, med hjälp av genetik, hur mycket struktur det finns i populationer genom att mäta hur mycket den genetiska sammansättningen skiljer sig mellan individer från olika platser. Genom att kartlägga strukturen hos en population får man svar på hur mycket individer rör sig mellan olika områden. Om en population är helt eller delvis isolerad från andra populationer finns en möjlighet att den kan anpassa sig till den lokala miljön. Om förändringarna är stora och isoleringen hög så kan en ny art bildas. När man vill skydda en hotad art eller en population är det generellt bra att bevara så mycket genetisk variation som möjligt. Men i vissa fall kan det istället vara bättre att skydda populationer som innehåller mindre variation men som är genetisk anpassade till en specifik miljö. För att kunna göra sådana bedömningar behöver man information om populationens struktur. I havet har många arter möjlighet att sprida sig över stora områden, dels finns det inte några direkta stopp, dels har många arter ägg eller larver som sprids med strömmar. Forskare har därför tidigare dragit slutsatsen att populationer i havet inte är så strukturerade. Men genom ny forskning har man sett att många arter uppvisar genetiska skillnader mellan individer från närliggande områden. Växtplankton till exempel, är många och små, flyter med strömmar och har stora möjligheter att sprida sig över vida områden. Trots detta har flera studier hittat tydliga skillnader mellan individer från närliggande områden. Mönstren kan ha flera orsaker, en kan vara strömmarnas riktningar. När man mäter en genetisk struktur använder man sig ofta av ett mått som heter genetisk differentiering. När man räknat ut hur differentierad en population är kan man översätta det värdet till hur mycket gener som flödar mellan de olika delarna av populationen dvs. hur mycket migration som sker. De klassiska måtten som mäter genetisk differentiering antar att migration mellan och inom populationer sker i lika stor utsträckning åt alla håll. Men i ett system som styrs av strömmar är det troligt att migrationen är större i en riktning än i en annan, dvs. den är asymmetrisk. I denna avhandling presenterar jag en ny metod som kan räkna ut riktad genetisk differentiering och som ger information inte bara om hur mycket migration som sker mellan två

populationer utan också hur mycket som sker och i vilken riktning. Genom att statistiskt undersöka om skillnaden mellan olika riktningar är tillräckligt stor kan man bedöma om migrationen är asymmetrisk eller inte. Information om migrationens riktning gör det lättare att jämföra genetiska mönster med mönster hos riktade faktorer, som exempelvis strömmar, för att se om de överensstämmer med varandra. Ett intressant område för studier av lokala anpassningar och artbildning är Östersjön. I Östersjön har miljön förändrats mycket och snabbt. Under de senaste tiotusen åren har Östersjön gått från att vara en sjö till att bli ett hav och därefter till att bli det bräckta innanhavet det är idag. Många av de marina arterna som finns i Östersjön idag kom till området när salthalten var högre och har därför fått anpassa sig när salthalten under åren har sjunkit. Den snabba förändringen har lett till att många av Östersjöns arter lever på gränsen av vad de klarar av. I Östersjön växer exempelvis blåstång och dess systerart smaltång. Smaltången är en ny art som har bildats i Östersjön under de senaste tusen åren, dvs. väldigt nyligen i artbildningssammanhang. Tillsammans med mina medförfattare har jag undersökt den genetiska strukturen hos dessa två arter. Vi upptäckte att det på vissa ställen är större skillnad mellan individer på olika geografiska platser än mellan individer tillhörande de två olika arterna. Trots detta kan man tydligt se att de olika arterna skiljer sig åt även när de växer precis jämte varandra. Detta visar att det kan finnas svårigheter att definiera vad som är en population när arter är nära besläktade. I en annan studie undersöker vi ett växtplankton, kiselalgen *Skeletonema marinoi*, och visar att det finns en population av *Skeletonema marinoi* i Västerhavet och en annan i Östersjön. Vi visar också att Östersjöpopulationen verkar vara anpassad till en lägre salthalt. Bälten mellan Sverige och Danmark visar sig fungera som en tydlig barriär för migranter mellan dessa två populationer. Strukturen inom de två områdena är tydligt kopplad till strömmarnas mönster och vi ser att det finns en asymmetrisk migration ut ur Östersjön som följer samma riktning som ytströmmen. En orsak till att populationer av växtplankton kan skilja sig åt på korta avstånd, trots att de har stora spridningsmöjligheter, kan vara att många arter av växtplankton har en förmåga att bilda cystor. Cystor är ett vilostadium precis som växters fröer. När en art bildar cystor kan den överleva vilande under lång tid, vissa arter kan överleva ett helt århundrade. När cystor bildas faller de ner till botten där de samlas i sedimentet och bildar ett arkiv av gamla generationer. Detta arkiv är en genbank, från vilken cystorna kan kläckas och börja leva på nytt i vattnet. I avhandlingen presenteras en modell som undersöker vilken effekt cystorna har på en populations struktur. Vi visar att vilostadier kan ankra en population i ett område, detta gör att en genetisk struktur kan bildas eller förstärkas även när det finns pågående migration av individer mellan områden.

List of papers

This thesis is based on the following papers, referred to in the text by their roman numerals.

- I. **Sundqvist L.**, Sefbom J., Godhe A., Jonsson P. R. (Manuscript). The anchoring effect – long-term dormancy and genetic population structure.

- II. **Sundqvist L.**, Keenan K., Zackrisson M., Prodöhl P., Kleinhans D. (2016). Directional genetic differentiation and relative migration. *Ecology and Evolution*, 6(11): 3461-3475.

- III. Sjöqvist C., Godhe A., Jonsson P.R., **Sundqvist L.**, Kremp A. (2015). Local adaptation and oceanographic connectivity patterns explain genetic differentiation of a marine diatom across the North Sea-Baltic Sea salinity gradient. *Molecular Ecology*, 24(11): 2871-2885.

- IV. Ardehed A., Johansson D., **Sundqvist L.**, Schagerström E., Zagrodzka Z., Kovaltchouk N.A., Bergström L., Kautsky L., Rafajlovic M., Pereyra R.T., Johannesson K. (2016). Divergence within and among Seaweed Siblings (*Fucus vesiculosus* and *F. radicans*) in the Baltic Sea. *PLoS ONE*, 11(8): e0161266.

Other publications not in this thesis

- **Sundqvist L.**, Harkonen T., Svensson C.-J., Harding K. (2012). Linking Climate Trends to Population Dynamics in the Baltic Ringed Seal: Impacts of Historical and Future Winter Temperatures. *Ambio* 41(8): 865-872.
- Godhe A., Egardt J., Kleinhans D., **Sundqvist L.**, Hordoir R., Jonson P.R. (2013). Seascape analysis reveals regional gene flow patterns among populations of a marine planktonic diatom. *Proceedings of the Royal Society of London. Biological Sciences*, 280(1773): e20131599.
- Godhe A., Sjöqvist C., Sildever S., Seftom J., Hardardóttir S., Bertos-Fortis M., Bunse C., Gross S., Johansson E., Jonsson P.R., Khandan S., Legrand C., Lips I., Lundholm L., Rengefors K.E., Sassenhagen I., Suikkanen S., **Sundqvist L.**, Kremp A. (2016). Physical barriers and environmental gradients cause spatial and temporal genetic differentiation of an extensive algal bloom. *Journal of Biogeography*, 43(6): 1130-1142.

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Population genetics and the structuring of populations

The field of population genetics developed in the 1920s and 1930s, thanks to the work of Ronald A. Fisher, John B.S. Haldane and Sewall Wright. The establishment of this new field was the first step towards the modern evolutionary synthesis that merged Mendelian inheritance and Darwinian evolution into a unified theory of evolution. The modern synthesis emphasizes the genetic basis of evolution and defines evolution as changes in allele frequencies within populations over time (Huxley, 1944).

In an evolutionary perspective one can define a population as "a group of individuals of the same species living in close enough proximity that any member of the group can potentially mate with any other member" (Waples and Gaggiotti, 2006). A population can be more or less structured implying the some individuals are more likely to mate with each other than with other individuals within the population, thus mating is not completely random. The degree of structure can range from totally random mating (panmixia) to total isolation (Fig. 1).

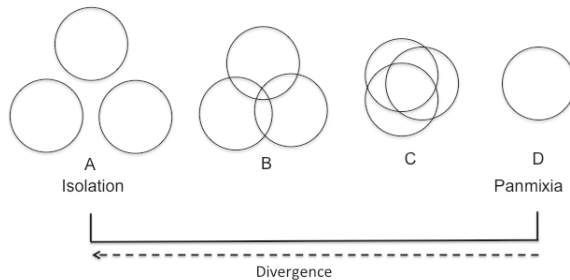


Figure 1: This figure is redrawn from Waples and Gaggiotti (2006) and illustrates population genetic differentiation. Each group is representing subpopulations, with varying degree of gene flow in between.

Studies of population genetic structure investigate differences in the genetic make-up of individuals in populations, in space or time, to find out if a species is genetically differentiated or not. Knowledge about a species genetic structure can answer questions about past and present demographic and evolutionary processes such as migration patterns, local adaptation or speciation (Hartl and Clark, 2007). In a conservation perspective, knowledge about genetic structure can be crucial for a threatened species or population as it makes it possible to direct efforts in such a way that essential genetic diversity can be maintained (Dunham et al., 1999; Bonin et al., 2007).

A structured population can be referred to as a metapopulation, divided into partly isolated subpopulations (Levins, 1969). In metapopulations source-sink dynamics may occur, meaning that some subpopulations might have a higher survival and or reproduction rate compared to others, which could lead to asymmetric migration between subpopulations (Hanski and Gaggiotti, 2004).

There are five factors that can change the distribution of alleles in populations over time: natural selection, sexual selection, mutations, genetic drift and migration (Hartl and Clark, 2007). To study these changes one need genetic information from individuals in populations. In the empirical studies included in this thesis genetic information have been collected with the help of microsatellite markers.

Life cycles and gene flow in the marine environment

Understanding both the life history of a species and its environment is important when interpreting data on its genetic structure. In the marine environment complex life cycles are common and many organisms have a planktonic phase during early stages of development. Releasing planktonic spores, eggs or larvae into the water is common, especially for sessile organisms (Cowen and Sponaugle, 2009). This reproductive strategy is often correlated with high fecundity and high potential for dispersal, where long-lived larvae can disperse long distances (Siegel et al., 2003). Many marine organisms like e.g. algae (Round et al., 1990), zooplankton (Decaestecker et al., 2009), sponges (Wulff, 1991) and corals (Richmond and Hunter, 1990) also have the ability to alternate between sexual and asexual reproduction. During favourable conditions vegetative reproduction often results in high population growth rate and for fast growing species this can result in vast population sizes. This is true for many planktonic species of microalgae as they can form massive blooms when nutrient and light is unlimited (Cloern, 1996).

When nutrient or light is depleted many species of microalgae and zooplankton have the ability to form resting eggs or cysts (Von Dassow and Montresor, 2010; Hairston, 1996). These resting stages can be stored in the sediment and form banks of genetic material that can stay dormant as long as decades or even centuries (Lundholm et al., 2011; Härnström et al., 2011). When studying the genetic structure of a species it is important to understand the whole life cycle of the organism as factors as dispersal rate and selection may change between different life stages

with different effects on the genetic structure of the population.

Gene flow is a central process affecting the degree of genetic structure within a species distribution (e.g. Wright, 1943; Waples and Gaggiotti, 2006). The amount of gene flow is commonly restricted by different factors acting as barriers leading to partly isolated subpopulations (e.g. Orsini et al., 2013). Such barriers are often thought of as physical structures as mountains or rivers (e.g. Caplat et al., 2016). If restricting factors are absent, individuals will mate randomly and gene flow will homogenize the gene pool.

In the marine environment few absolute physical barriers to gene flow exist and as mentioned above, species are often characterized by having high dispersal, large population sizes and high fecundity/rapid growth rate. These characteristics may lead to weakly structured populations even across large geographical scales (Palumbi, 1994). However, even if dispersal potential and genetic differentiation is correlated for many taxa, high dispersal of a species does not necessarily mean that gene flow between populations is high (Bohonak, 1999). For instance, many species with planktonic larval dispersal have been found to recruit back to their source populations (Swearer et al., 2002). With increasing genetic information on structure in marine populations the paradigm of open populations in the marine environment have during the past decade been questioned (Hellberg, 2009). Even species of microalgae that share all of the above-mentioned characteristics and are passively moving with ocean currents their whole lives have been found to differ genetically on small geographical scales (e.g. Rynearson et al., 2006; Medlin, 2007; Godhe and Härnström, 2010; Lebret et al., 2012).

The accumulating results of structured marine populations indicate that even if absolute barriers often are absent other factors are potential drivers of genetic structure in marine species. For instance planktonic life stages permit passive movement by ocean currents resulting not only in potentially long distance dispersal but also in dispersal dependent on the paths produced by the currents, which often show consistent circulation patterns (e.g. Cowen and Sponaugle, 2009). Dispersal driven by oceanographic connectivity can lead to structured populations that deviate from a classic isolation by distance scenario since a distant population might receive more migrants than an adjacent depending on the direction of the currents between the populations. In systems driven by physical transport processes, such as wind or water currents migration patterns are often found to be asymmetric (Wares et al., 2001; Pringle et al., 2011).

Further, environmental conditions can lead to genetic differentiation despite dispersal simply because dispersed individuals may not survive in the new environment (Bohonak, 1999). In locally adapted populations maladapted migrants from other populations will have a lower survival rate which can produce a pattern of isolation by adaptation (Nosil et al., 2005). Abiotic factors as salinity or temperature or biological factors as for instance density of a foundation species may form spatial gradients or barriers to gene flow that can lead to isolation, thus varying environmental conditions can form locally adapted differentiated populations (Wang and Bradburd, 2014). Local adaptation is also a keystone in the monopolization hypothesis where the paradox of genetic structure for species with high dispersal potential is argued to originate from founder effects and being maintained by rapid local adaptation together with a buffering effect from resting stages (De Meester et al., 2002). A life history strategy including resting-stages could affect the genetic structure of a species as accumulation of dormant stages in the sediment can serve as a gene bank that can supply the planktonic population with "migrants from the past" (Templeton and Levin, 1979). In Paper I we investigate the effect of resting stages on the population structure of planktonic microalgae.

Seascape genetics

Linking genetic data to landscape features is called landscape genetics and the concept was introduced by Manel et al. (2003). Investigating if landscape features can explain some of the genetic structure found in populations is useful when disentangling evolutionary questions regarding gene flow and adaptation (Manel and Holderegger, 2013). Seascape genetics or marine landscape genetics is a field still in its beginning, in the first years of landscape genetics only 7% of the studies were performed in the marine environment (Storfer et al., 2010). As mentioned above marine environments differ in many aspects from terrestrial, e.g weak absolute barriers and the big influence of ocean currents. Accordingly seascape genetic studies have found ocean currents to partly explain population genetic structure in many marine groups e.g. corals (Galindo et al., 2006), fish (Teacher et al., 2013) and microalgae (Godhe et al., 2013). To perform these kind of studies where genetic data is correlated to a directional factor such as oceanographic connectivity directional information is needed. In this thesis I will present a new method that calculates directional genetic differentiation and directional relative migration (Paper II).

Life on the margin

The two empirical studies in this thesis were mainly conducted in the Baltic Sea, a young sea formed from a freshwater lake that was connected to the North Sea through the Danish Straights only 8000 years ago (Björck, 1995). Today the Baltic Sea is one of the worlds largest brackish water basins (Björck, 1995). Many of the marine species living in the Baltic Sea today are survivors from the more saline Littorina Sea period 8000 - 4000 BP (Ignatius et al., 1981; Johannesson and André, 2006). Since then a successive decline in salinity has occurred and today the Baltic Sea region has a salinity gradient ranging from 20-25 practical salinity units (PSU) at the North Sea entrance down to almost freshwater in the most northern and eastern parts (Fig. 2) (Feistel et al., 2010).

The Baltic Sea is both a geographical and an ecological marginal environment. Consequently, as is common for marginal environments, the Baltic Sea is low in species diversity and many Baltic Sea populations have also been found to have a low genetic diversity and to be genetically differentiated from populations outside of the Baltic Sea (Johannesson and André, 2006). Low genetic diversity and restricted gene flow is generally assumed to hamper adaptation to changing environments (Lande, 1988). However, a high gene flow from core populations to marginal environments is also expected to decreased potential for local adaptation (Kawecki, 2008).

Nevertheless many species in the Baltic Sea are locally adapted and even a case of rapid sympatric speciation have occurred within the last few thousand years resulting in the new Baltic Sea endemic species *Fucus radicans* (Bergström et al., 2005; Pereyra et al., 2009). Adaptation to marginal environments is interesting as it plays an important role in the evolution of ecological niches and species ranges (Kawecki, 2008). In the Baltic Sea the selection pressure has likely been strong on the marine species that have managed to persist in this ecosystem when the salinity has decreased (Russell, 1985). This makes the Baltic Sea a particularly interesting system for studies of evolutionary questions. Understanding the genetic structure and the migration patterns in this young marginal environment can help to understand mechanisms involved in range expansions, local adaptation and rapid speciation. In this thesis my coauthors and I have studied the genetic structure and migration patterns of three Baltic Sea species, the microalga *Skeletonema marinoi* (Box 1) and the two sibling species of the macroalgae *Fucus vesiculosus* and *Fucus radicans* (Box 2).

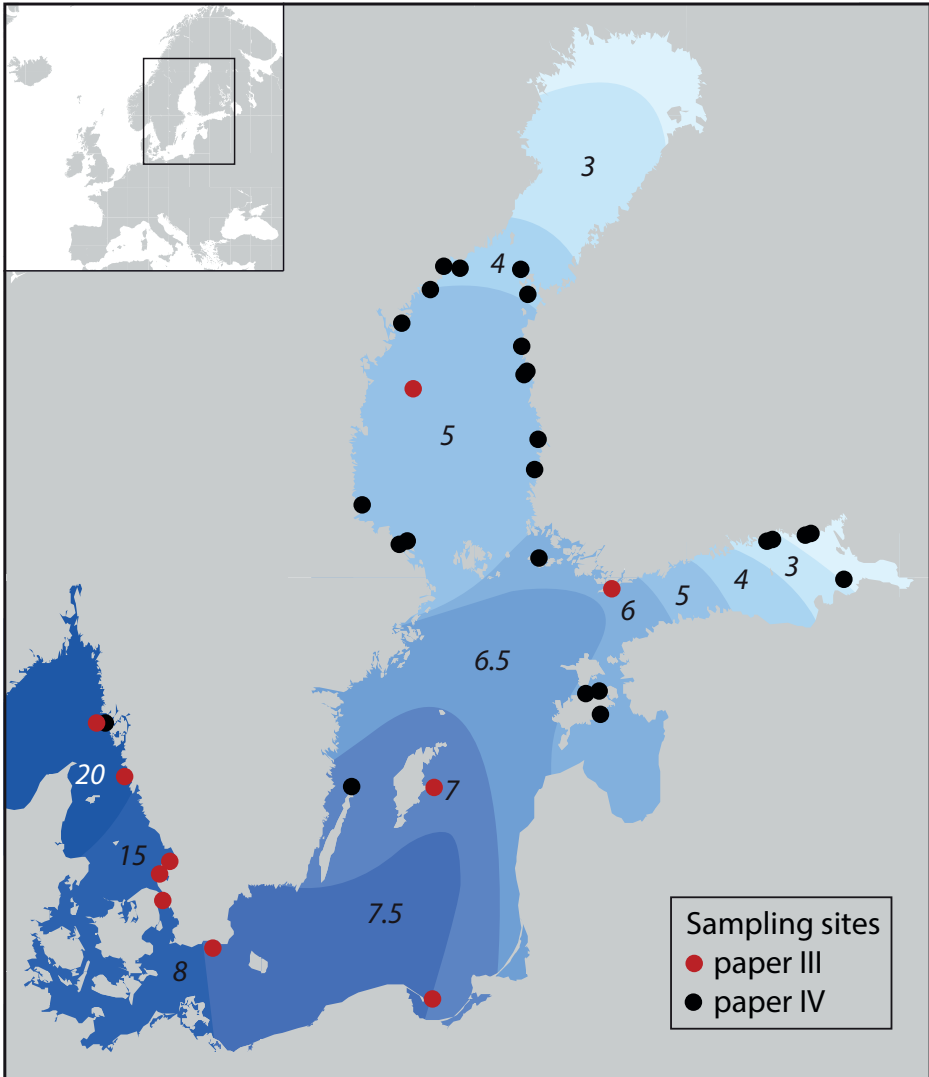


Figure 2: Map of the Baltic Sea, Kattegat, Skagerrak and the entrance to the North Sea, with the salinity gradient in PSU (shades of blue) and sampling sites from Paper III and IV as red and black dots.

Box 1. *Skeletonema marinoi*

Skeletonema is a cosmopolitan genus of centric chain-forming diatoms (Bacillariophyta). In Scandinavian waters *S. marinoi* is the exclusively dominant species (Kooistra et al., 2008). *Skeletonema marinoi* is an important primary producer found in the water all year round, during spring bloom (February, March) the species reach high abundances (about 10.000 cells ml^{-1}) (Saravanan and Godhe, 2010). *Skeletonema marinoi* mainly reproduce vegetatively through cell division at a rate of approximately one division per day (Taylor et al., 2009). Cell division in diatoms lead to a gradual reduction in cell size and at a critical size they undergo sexual reproduction to restore their original size (Round et al., 1990). Sexual reproduction can however also be triggered by environmental factors (Godhe et al., 2014). *Skeletonema marinoi* forms resting cysts that can be stored in the sediment at a density as high as 50.000 propagules per gram of sediment (McQuoid et al., 2002). These resting stages can survive for as long as a century (Härnström et al., 2011).



Figure 3: Vegetative cells of *S. marinoi*. Photo: Josefin Sefbom.

Box 2. *Fucus vesiculosus* and *F. radicans*

Fucus species (Phaeophyceae) are large brown algae found on rocky bottoms in the littoral and sublittoral zone. They function as foundation species as they provide habitat and shelter for other species (Dijkstra et al., 2012). *Fucus vesiculosus* is distributed all over the North Atlantic (Yarish et al., 1990). *Fucus radicans* was first believed to be a small morph of *F. vesiculosus* but through morphological and genetic analyses *F. radicans* has been established as a new species endemic to the Baltic Sea (Bergström et al., 2005). The two species live sympatric and can be found as close together as growing on the same rock (Fig. 4). The formation of *F. radicans* is a case of rapid sympatric speciation and the split from *F. vesiculosus* is believed to have occurred only some thousand years ago (Pereyra et al., 2009). Both species reproduce sexually by releasing female and male gametes from different plants. Surprisingly, in the Baltic Sea both species have been found to also reproduce asexually something that has never been found in fucoids in other regions (Tatarenkov et al., 2005).

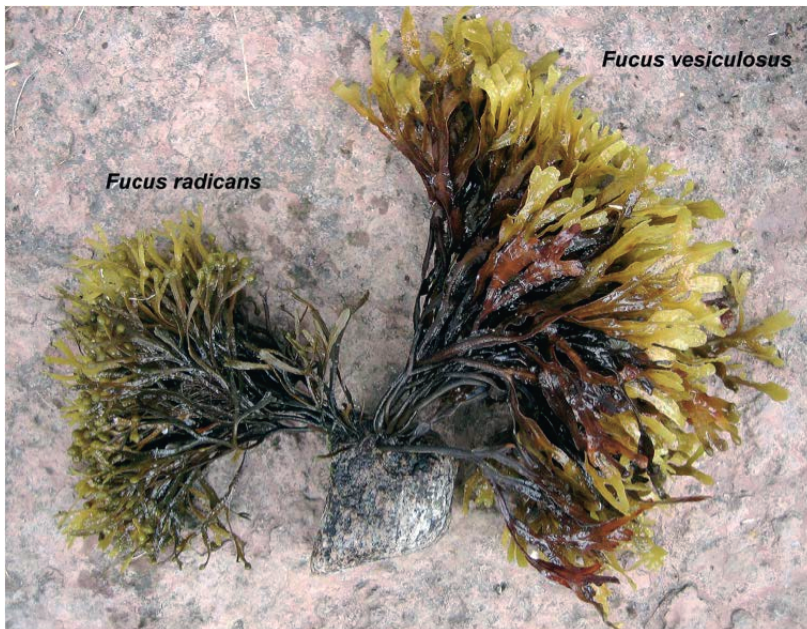


Figure 4: *Fucus vesiculosus* and *F. radicans* attached to the same rock. Photo: Lena Kautsky.

Genetic differentiation

To measure the degree of population genetic structure measures of genetic differentiation are widely used. Zero genetic differentiation indicates that allele frequencies among populations are equal and values larger than zero represent increasing differences. Generally measures of genetic differentiation are calculated from two parameters, namely the mean heterozygosity in the total population (H_t) and the mean heterozygosity in the individual populations (H_s) (Meirmans and Hedrick, 2011). Genetic differentiation was first introduced by Wright with his fixation index (F_{st}) (Wright, 1943). As new genetic techniques have developed over the years adjustments to the original F_{st} have been required. Nei's G_{st} , was developed to handle more than two alleles per locus (Nei, 1973). More recently F_{st} and G_{st} have been found to be dependent on genetic diversity and the use of G'_{st} (Hedrick, 2005) or D (Jost, 2008) has been proposed.

Gene flow

A particularly useful feature of measures of genetic differentiation is that assuming an island model of population structure, they can be used to estimate migration among populations (Wright, 1931, 1949). The island model being defined as "the simplest model in which the total population is assumed to be divided into subgroups, each breeding at random within itself, except for a certain proportion of migrants drawn at random from the whole" (Wright, 1943). However, the island model is based on a number of assumptions that are likely to be violated in natural populations (Whitlock and McCauley, 1999). For instance it assumes migration to be symmetric (i.e. equally likely to occur among any subpopulation, in any direction). Using regular measures of genetic differentiation to calculate migration gives only one measure of migration between two populations. Nonetheless in nature, and especially in the marine environment, migration is often asymmetric and might occur in only one direction or at different rates in different directions between populations. There are methods available to calculate asymmetric migration from genetic data, for instance BayesAss and MIGRATE-N. However, these build on complex mathematical models using maximum-likelihood or Bayesian approaches (Wilson and Rannala, 2003; Beerli, 2009). These models are therefore often used as *black boxes* implying that users, due to the complexity of these analytical approaches, typically only have a limited understanding of the underlying models and their assumptions.

Aim of thesis

The overall aim of this thesis is to investigate aspects of genetic differentiation and factors influencing the structure of populations, with a special focus on life histories and dispersal strategies common in the marine environment. I present a method that makes it possible to calculate directional measures of genetic differentiation and relative migration. This method aims to make measures of genetic differentiation more useful in systems where asymmetric migration is common and to make it easier to correlate gene flow to directional factors as oceanographic connectivity. By using this new method we investigate the population genetic structure of the marine diatom *Skeletonema marinoi* and the two sibling species of macroalgae, *Fucus vesiculosus* and *F. radicans*, in the Baltic Sea. Further, we investigate if these species show genetic patterns that can be linked to the directions of prevailing ocean currents. Furthermore, many planktonic microalgae including *S. marinoi* form long term resting stages that accumulate in seed banks, we investigate if resting stages can have an anchoring effect on local populations leading to genetic differentiation between adjacent populations despite ongoing gene flow.

Paper I

This paper analyses the effects a life history strategy, including long-term dormancy, may have on the population genetic structure of planktonic microalgae. With the help of a simple genetic population model we investigate the effect of resting stages on time to fixation for one allele and genetic differentiation between populations connected with migration. In addition, a systematic literature review was performed with the aim to investigate if differences could be found in already published data between species forming and not forming resting stages concerning the strength of genetic differentiation.

Paper II

This paper presents a new method that aims to make it easier to investigate migration patterns and find asymmetries in natural populations. In contrast to classic measures of genetic differentiation our method calculates directional differentiation and migration. By providing information on direction we aim to make it straightforward to correlate gene flow to environmental factors that are expected to produce asymmetric migration patterns.

Paper III

The purpose of this study was to investigate the genetic structure of a marine planktonic microalgae, *S. marinoi*, along a salinity gradient. We wanted to find out if local populations were differentiated and if gene flow could be linked to dispersal barriers and oceanographic connectivity and, furthermore, if signs of local salinity adaptation could be found.

Paper IV

With this paper we further disentangle the genetic patterns found between and within *F. vesiculosus* and its newly evolved sister species *F. radicans* within the Baltic Sea. Earlier studies have shown a primary division into two geographic groups and thereafter a secondary division into *F. vesiculosus* and *F. radicans* within each geographic cluster (Pereyra et al., 2013). We investigate new geographical sampling sites in-between the previously investigated sites to see if individuals in these show an intermediate position in genetic analyses.

Genetic differentiation and long-term dormancy

Life history strategies including long-term dormancy can be found in many different groups of organisms (e.g. Lundholm et al., 2011; Lennon and Jones, 2011; Brendonck and De Meester, 2003; Vitalis et al., 2004). Paper I investigates how resting stages may affect the population structure in species where resting stages can accumulate in sediment and form banks with genetic material. High abundances of resting stages in sediment are common for many species of microalgae (McQuoid et al., 2002). We hypothesized that the ability to stay dormant for long periods could have a part to play in the high genetic differentiation recently revealed in many species of microalgae (e.g. Rynearson et al., 2006; Medlin, 2007; Godhe and Härnström, 2010; Lebet et al., 2012, Paper III). Strong differentiation on small geographical scales is surprising for microalgae since they are small in size and have a planktonic life style, which is expected to result in high gene flow between populations.

We formulated a simple genetic population model to compare a scenario with a life history strategy where blooms were partly inoculated from a seed bank, that was built up by previous blooms, with a scenario where blooms were solely inoculated from last year's bloom. Figure 5 shows that genetic differentiation (Jost's D) is significantly higher when blooms have a medium or high connection to the sediment. Even when migration is as high as 20% per season populations can stay differentiated for many seasons when sufficiently connected to previous blooms through a local seed bank.

To find out if the pattern we found through the model also could be found in natural populations we performed a systematic literature review. We collected all published studies that had used microsatellite markers to calculate genetic differentiation (measured by F_{st}) between populations at different geographical locations. This gave us information from 13 species that were divided into two categories (i.e. forming and not forming resting stages). When genetic differentiation (F_{st}) was correlated to geographical distance (km) we found a significant difference in the regression lines for the two different categories. Species forming resting stages showed higher genetic differentiation throughout the geographical range (Fig. 6). We conclude that a long-term resting stage is likely to have an "anchoring effect" on the genetic population structure, leading to possible high genetic differentiation despite ongoing gene flow between active planktonic populations.

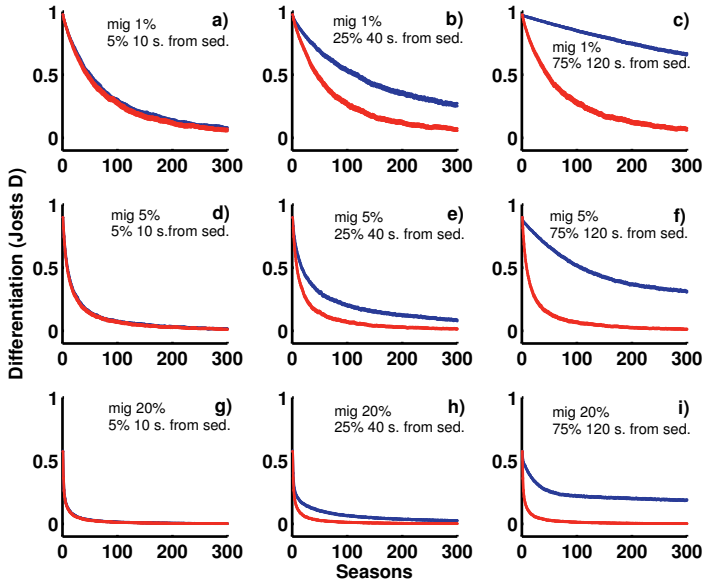


Figure 5: Changes in genetic differentiation (Jost's D) over time between two populations linked by migration. Blue lines show results for populations with a life history strategy including resting stages while red lines show results for populations that does not include resting stages. Solid lines show the mean calculated from 1000 simulations and the 95% confidence intervals is only visible as thickening of the solid line (from Paper I).

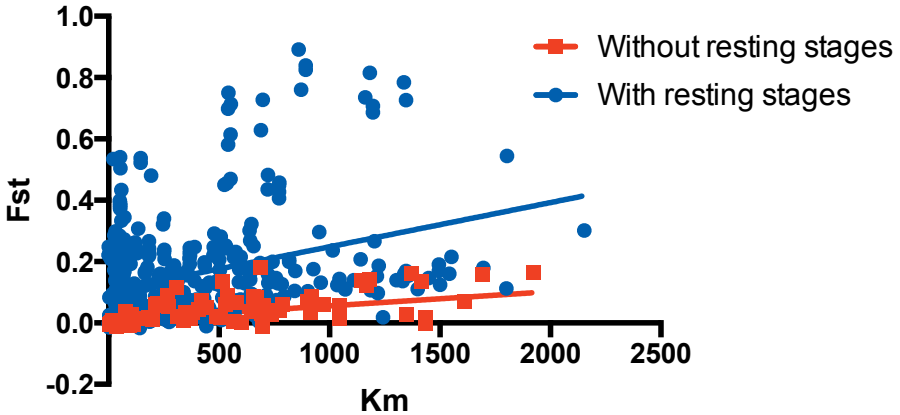


Figure 6: Regression analysis of genetic differentiation (F_{st}) and geographic distance (km) for species with a life history strategy including (blue) and not including resting stages (red), using published F_{st} -values. The regression line for species forming resting stages has an r^2 -value of 0.11 and the regression line for species that do not form resting stages has an r^2 -value of 0.28. The slopes of the two lines are significantly different with a p-value of 0.002 (from Paper I).

Directional genetic differentiation and asymmetric migration

In Paper II we present an extension to regular measures of genetic differentiation that makes it possible to calculate directional genetic differentiation and relative migration. This makes measures of genetic differentiation more useful in systems with asymmetric migration patterns. By providing information on direction this method makes it straightforward to correlate gene flow to environmental factors that are expected to produce asymmetric migration patterns. This new approach builds on defining a hypothetical pool of migrants between two populations in pairwise comparison. Alleles only present in one of the populations is assumed not to participate in migration, further the proportion of alleles in a population is expected to be reflected in the migrants. To fulfill these requirements the allelic composition of the hypothetical pool, $f(a, b)$, is inferred from the two populations in pairwise comparison (A and B).

$$f_i(a, b) = \gamma \sqrt{a_i b_i} \quad \forall i \quad (1)$$

Where i represent different alleles, $\gamma = (\sum_i \sqrt{a_i b_i})^{-1}$ and the vector of allele frequencies for the hypothetical pool is composed of the geometrical means of the allele frequencies (a_i and b_i) from populations A and B. To calculate directional measures of genetic differentiation the allele frequencies of population A and B can then be compared to the calculated frequencies of the hypothetical pool of migrants $f(a, b)$.

By calculating gene flow from the directional measures of genetic differentiation one can investigate the migration between pairs in relation to all investigated populations. To make it easy for users we present a web-application called divMigrate-online where directional relative migration can be calculated and visualised by network plots. Figure 7a shows directional relative migration between populations calculated from a simulated dataset where migration was simulated in a circular stepping stone model. Bootstrap calculations, makes it possible to investigate if one of the directions between a pair is significantly higher than the other (i.e. if migration is asymmetric). Figure 7b shows the directions that were found to be significantly higher. In figure 7c values below 0.5 have been filtered out using the filter threshold function available in divMigrate-online and shows the simulated migration pattern.

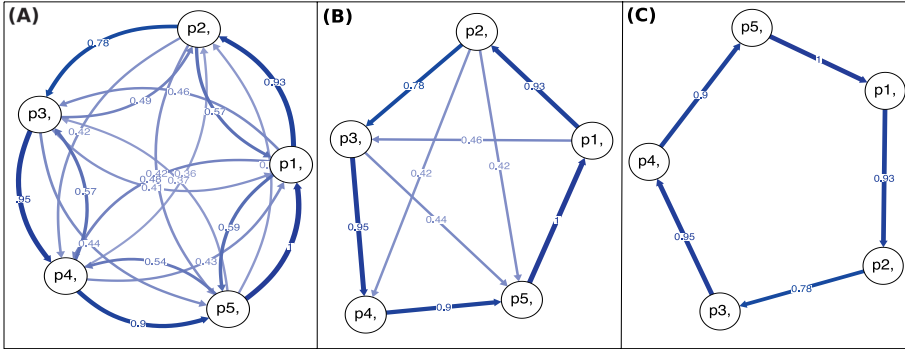


Figure 7: Directional relative migration calculated by divMigrate-online for a simulated circular stepping stone model with unidirectional migration. (A) Illustrates the calculated migration values. (B) Only includes the values found to be asymmetric, that is they are statistically higher in the shown direction. In (C), the filter threshold for the asymmetric values was set to 0.5 (from Paper II).

To test the performance of our new method we simulated unidirectional and bidirectional migration between two populations. The bidirectional migration was either asymmetric with 3/4 of the migrants going one direction and 1/4 of the migrants going in the opposite direction or symmetric with an equal proportion of migrants going in both directions. The method was tested for different sample sizes, number of loci and migration rates. Figure 8 shows the result for unidirectional migration calculated for different sample sizes. As for the other tested scenarios the method performed best when migration rates were medium corresponding to a migration rate of 0.005 and an F_{st} -value of 0.05.

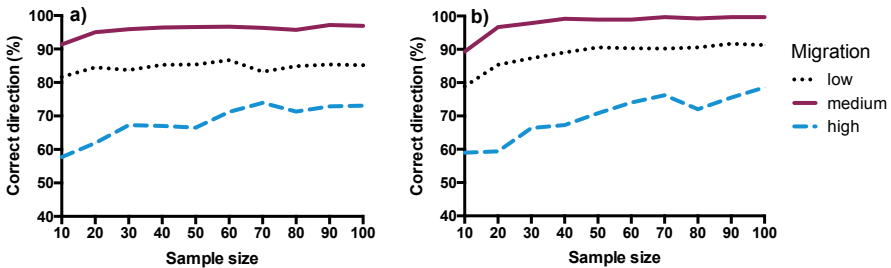


Figure 8: Unidirectional migration: percent correct directions as a function of sample size calculated using D (a) and G_{st} (b). Increasing sample size was evaluated at high (0.05), medium (0.005), and low (0.00025) gene flow. The number of loci was kept fixed at 50 (from Paper II).

Genetic differentiation of a marine diatom across a salinity gradient

Many macro-organisms in the Baltic Sea have shown patterns of reduced genetic diversity and have been found to be genetically differentiated compared to populations in the North Sea (Johannesson and André, 2006). In Paper III we aimed to find out if the same pattern could be found in a microorganism and investigated the diversity and population genetic structure of the marine diatom *Skeletonema marinoi*, along the salinity gradient from the Baltic Sea to the North Sea transition. Further we wanted to investigate if we could find indications for local salinity adaptation along the salinity gradient and if patterns of genetic differentiation could be linked to physical barriers and oceanographic connectivity.

The diversity was, as expected, found to be lower inside the Baltic Sea compared to the population in the North Sea. Genetic differentiation analyses showed significant differences between the genetic make-up of all local populations of *S. marinoi*. The biggest differences were found between the two sides of the major dispersal barrier in the region, the Danish Straits. In agreement a STRUCTURE-analysis clustered the samples from inside the Baltic Sea as one population and the samples from the North Sea as another. The relative migration analysis further strengthened this pattern as the highest gene flow was found within these two populations (Fig. 9a). When reaction norms were assessed along a salinity gradient, algae from local populations inside the Baltic Sea showed highest growth rate at or close to their native salinity.

This indicates that local populations inside the Baltic Sea are adapted to the low salinities. Directional relative migration was found to be significantly correlated to oceanographic connectivity almost the year around. Interestingly two significantly asymmetric migration rates were found, both between sites located at different sides of the most prominent physical barrier, the Danish Straits. Both had a significantly higher rate out from the Baltic Sea, which is the same direction as the surface current (Fig. 9b). According to theory, populations in marginal environments and populations with a high proportion of asexuality may show reduced capacity for adaptation to local conditions (Kawecki, 2008). However, both in Paper III and Paper IV we find indications of locally adapted populations despite the fact that we also find a high degree of asexuality inside this marginal environment. Populations in marginal environments are expected to behave as sink-populations and thus have a reduced po-

tential for local adaptation, due to swamping from maladapted migrants from central source populations (Kawecki, 2008). The asymmetric dispersal out of the Baltic Sea found for *S. marinoi* is thus interesting as it goes against the general pattern expected in marginal environments and indicates that populations inside the Baltic Sea instead behave as source populations. This reversed source-sink dynamics driven by asymmetric migration caused by oceanographic connectivity might actually promote adaptation to a less favorable environment as shown in theory by Kawecki and Holt (2002).

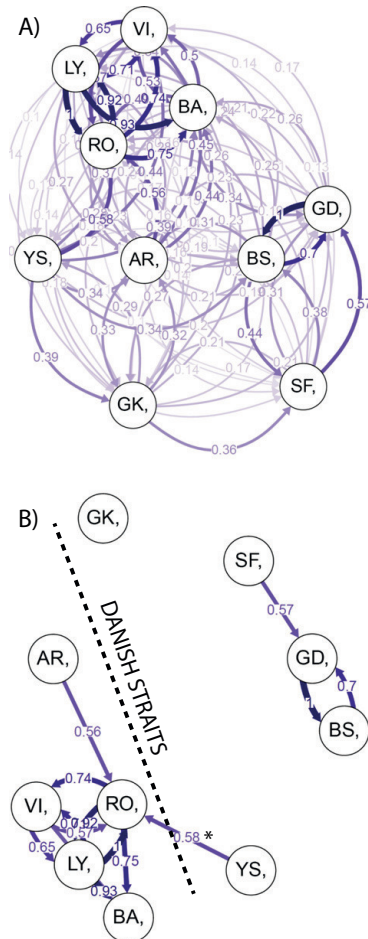


Figure 9: (A) The directional relative migration network including all relative migration values indicates stronger gene flow within the subareas than between. (B) Directional relative migration network displaying relative migrations above 0.5. The direction of the relative migration between RO and YS was significantly asymmetric (*CI 95%) (from Paper III).

Divergence within and among seaweed siblings

In Paper IV we continue to investigate the genetic patterns of the two sibling species *Fucus vesiculosus* and *F. radicans* within the Baltic Sea. New sites in the East Bothnian Sea, the Archipelago Sea and Gulf of Finland are analysed together with earlier data from N-W Bothnian Sea and Estonia (Pereyra et al., 2009, 2013; Johannesson et al., 2011; Ardehed et al., 2015). Earlier studies have found an isolation-by-distance effect within species that have resulted in a primary division into two geographic groups (one for Estonia and one for N-W Bothnian Sea), and thereafter a secondary division into *F. vesiculosus* and *F. radicans* within each geographic cluster (Pereyra et al., 2013). We hypothesised that the new sites investigated in this paper would show an intermediate position based on genetic analyses. But instead we found the genetic structure to be even more complex.

When samples along the Finnish, Russian and Estonian coasts were analysed we found an overall grouping according to species and local geographical area, supporting a division between the species. However, in the Gulf of Finland the species division was much less clear. Individuals from four of the sites inside the Gulf of Finland, those close to the Finnish coast (R, S, T, U), could not be assigned to species based on their morphological characteristics. Accordingly, individuals from these sites formed a separate group in all analyses, as can be seen in the directional relative migration network (Fig. 10). At the site close to the Russian coast of Gulf of Finland *F. vesiculosus* and *F. radicans* were sampled at the same locations (V1 and V2) and were found to group together and to be clearly separated from the individuals from R,S,T,U even if these sites are geographically close (Fig. 10).

High levels of asexual recruitment has previously been found in the northern Baltic Sea for both *F. vesiculosus* and *F. radicans* and have been explained by negative effects on the egg-sperm interaction from low salinities (Serrão et al., 1996; Johannesson et al., 2011; Ardehed et al., 2015). We therefore expected to find a high degree of asexually recruited individuals at the most eastern parts of the Gulf of Finland where salinities are low. Surprisingly we found that in three of five sites individuals were mainly sexually recruited despite a salinity of about 3 PSU in this area. These findings show that the genetic structure of Baltic Sea *Fucus* is complex and that divergence within species with the potential of rapid local adaptation can complicate the separation between closely related species.

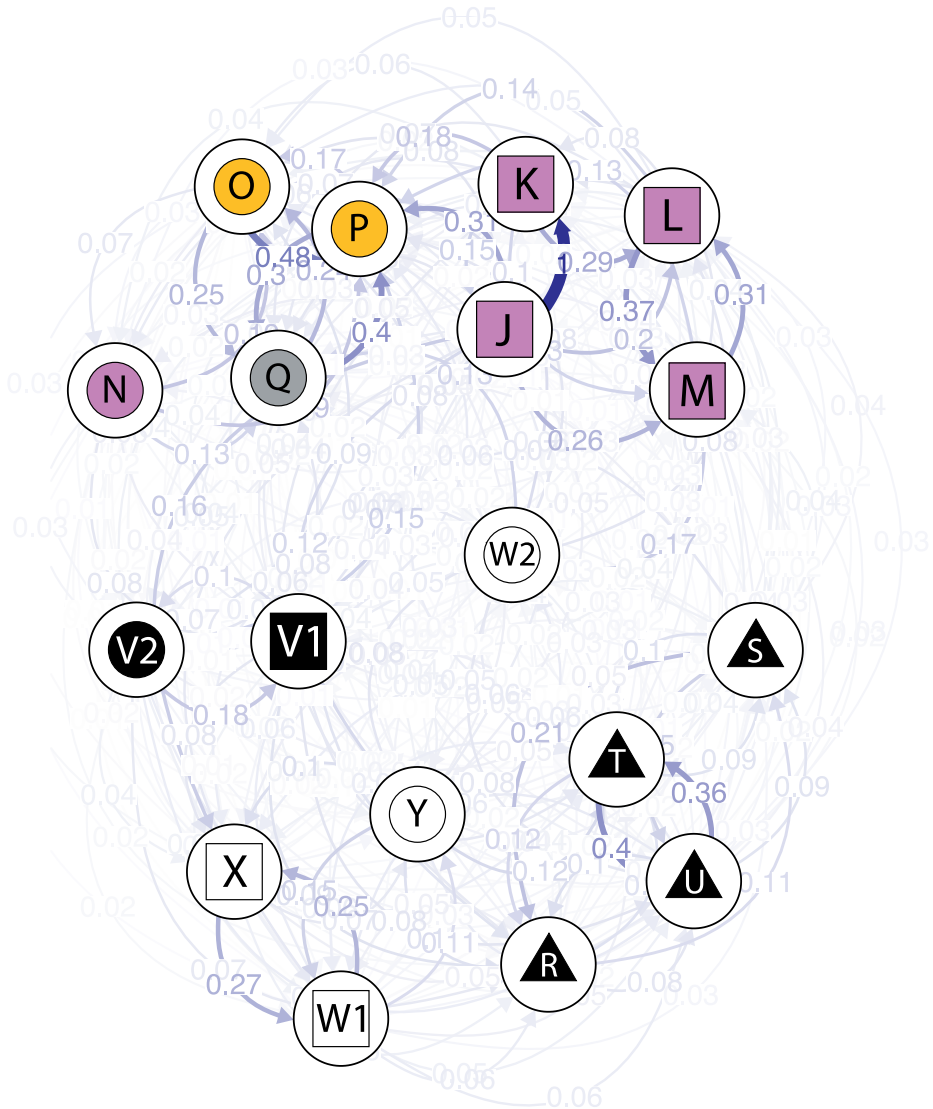


Figure 10: Directional relative migration network of Finnish, Russian and Estonian *Fucus* populations. *F. vesiculosus* (circles), *F. radicans* (squares), unassigned (triangles). Colours indicate different regions (white = Estonian coast; purple = north Bothnian Sea; yellow = east Bothnian Sea; grey = Archipelago Sea and black = Gulf of Finland). Population positions indicate relatedness from the perspective of gene flow. Arrows indicate the direction of gene flow, and numbers (and arrow shading/thickness) show the values of directional migration relative to the highest value in the analysis (in this case from population J to population K) (from Paper IV).

Conclusions and future perspectives

This thesis investigates aspects of genetic differentiation and factors influencing the structuring of populations, with a special focus on life histories and dispersal strategies common in the marine environment. In Paper I the influence of the ability to form long-term resting stages on population genetic structure is investigated. We conclude that resting stages accumulated in local seed banks may have a strong anchoring effect on populations, that can lead to genetic differentiation even when gene flow is present. This result can help explain the surprisingly high genetic differentiation found in many species of microalgae. The role of resting stages on the population genetic structure is complex and little is known about the key parameters driving the effect shown by our model. More research with a focus on what is to be found below the active populations in the water column is necessary in order to get a deeper understanding of the adaptive potential and dynamics of these species. In Paper II a new method calculating directional genetic differentiation is introduced. The method can be used to get information on the direction of gene flow between populations. Further asymmetries in migration patterns can be detected. This is useful especially in systems driven by physical processes such as ocean currents or in river networks. The method presented here is in its simplest form, and future adjustments to handle more complex scenarios, such as uneven population sizes and populations not being in drift/migration equilibrium, would make the method even more useful. Directional relative migration as calculated by the method makes it straightforward to investigate the correlation between migration patterns and directional factors, such as oceanographic connectivity. This is done in Paper III where the migration patterns of the microalgae *Skeletonema marinoi* are found to be significantly correlated to oceanographic connectivity. Further asymmetric migration out of the Baltic Sea is found for *S. marinoi* indicating that the Baltic population of *S. marinoi* functions as a source-population and does therefore not conform to theory, as populations in marginal environments are expected to behave as sink-populations. This reversed source-sink dynamics driven by asymmetric migration might promote adaptation to the conditions in the Baltic Sea. It would thus be interesting to investigate if asymmetric migration out of the Baltic Sea following the surface current across the Danish Straits could be found also in other species that show signs of local adaptation. One interesting example would be *Fucus vesiculosus*, which in Paper IV is shown to have a complex genetic structure, with indications of local adaptation, together with its sibling species *Fucus radicans*.

Author contributions

- I. The anchoring effect – long-term dormancy and genetic population structure.

AG initiated the study. **LS** and JS designed the study. **LS** designed and constructed the model with comments from PJ, JS, AG. **LS** ran the simulations. **LS** and JS performed the systematic literature review. **LS** wrote the paper with contributions from JS and review and editing from JS, AG and PJ.

- II. Directional genetic differentiation and relative migration.

DK conceived the study. KK, **LS**, MZ designed the simulations with comments from PP. KK wrote the simulations and **LS** ran the simulations. KK made the program. **LS** wrote the paper with contributions from DK and KK and review and editing from DK, KK, MZ and PP.

- III. Local adaptation and oceanographic connectivity patterns explain genetic differentiation of a marine diatom across the North Sea-Baltic Sea salinity gradient.

CS, AK, AG conceived and designed the study, CS and AG performed field sampling and molecular work, CS conducted experiments. CS, **LS**, PJ, AG analysed the data. CS wrote the paper with contributions, review and editing from AK, AG, **LS** and PJ.

- IV. Divergence within and among Seaweed Siblings (*Fucus vesiculosus* and *F. radicans*) in the Baltic Sea.

KJ, RTP conceived the study. AA, RTP, KJ designed and AA, **LS**, MR, RTP, KJ conceptualized the study. AA, DJ, RTP, KJ, NAK, LB, LK, ES performed field sampling. AA, ZZ performed molecular work. AA, DJ, **LS**, RTP analysed the data, AA, KJ wrote the paper with review and editing from DJ, **LS**, ES, LB, LK, MR, RTP.

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