Macroalgae in the Baltic Sea
-responses to low salinity and nutrient enrichment
in Ceramium and Fucus

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2005

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Title: Macroalgae in the Baltic Sea – responses to low salinity and nutrient enrichment in *Ceramium* and *Fucus*.

Abstract: The brackish Baltic Sea is a marginal environment for both marine and freshwater species. The rate of ecological differentiation is presumably high due to strong selection pressure from a gradient of decreasing salinity that has been present in its current state for only about 3,000 years. Even more recently, increased nutrient loading due to human activities has affected the growth rate of species, with potential effects on their competitive interactions and responses to other regulating factors. I have investigated the potential effects of low salinity and nutrient enrichment on the distributional ranges of two marine macroalgae with a wide distribution in the Baltic Sea, the red alga *Ceramium tenuicorne* (Kütz.) Wærn and the brown alga *Fucus vesiculosus* L.

A field study in the northern Baltic Sea indicated a strong relationship between the community structure of macroalgae and abiotic factors even on a small, local scale. The abiotic factors are potentially modulated by eutrophication, which may have a strong effect on the depth distribution and abundance of macroalgae. On a regional scale, laboratory experiments suggested that nutrient enrichment is unlikely to affect the distribution of *Ceramium* and *Fucus* along the salinity gradient. Growth in *Ceramium* from the Baltic Proper was enhanced by nitrate and phosphate, but the response did not override growth constraints due to low salinity. *Ceramium* from the Gulf of Bothnia had an inherently lower growth rate that was not positively affected by nitrate and phosphate increase. In *Fucus vesiculosus*, reproductive performance was impaired by nitrate and phosphate levels corresponding to ambient levels in eutrophicated areas of the Baltic Sea, when measured by their effect on zygote attachment, germination, and rhizoid development.

The wide distribution of *Ceramium* in the inner Baltic Sea is probably related to local adaptation, rather than a generalized tolerance of different salinity levels. Ecotypic differences were observed when comparing strains from the Baltic Proper (salinity 7 psu) and the Gulf of Bothnia (4 psu). A high rate of vegetative reproduction was evident, although sexual reproduction was occasionally observed in salinity 4. In *Fucus vesiculosus*, genetic and morphological analyses of sympatric and allopatric populations of the common, vesicular, morphotype and a dwarf morphotype, characteristic for the Gulf of Bothnia, showed that the dwarf morphotype represents a separate evolutionary lineage. Also, vegetative reproduction was observed in *Fucus* for the first time, as supported by genetic and experimental data.

The results show that the biota of the inner Baltic Sea may have unique adaptive and genetic properties, and that it is highly relevant to consider subspecies diversity in Baltic Sea management.

**Key Words:** adaptation, asexual reproduction, Baltic Sea, Gulf of Bothnia, low salinity, marine macroalgae, nutrient enrichment, sexual reproduction, stress
Macroalgae in the Baltic Sea

- responses to low salinity and nutrient enrichment in *Ceramium* and *Fucus*

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Nearly every man who develops an idea works at it up to the point where it looks impossible, and then gets discouraged. That’s not the place to become discouraged.

Thomas A. Edison
List of papers

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


III. Bergström, L., Kautsky, L. Local adaptation in *Ceramium tenuicorne* (Ceramiales, Rhodophyta) within the Baltic Sea salinity gradient. *Manuscript*.


V. Bergström, L., Tatarenkov, A., Jönsson, B. R., Johannesson, K., Kautsky, L. Morphological and genetic differentiation of *Fucus vesiculosus* in the brackish Baltic Sea. *Manuscript* ¹


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¹ An other version of this manuscript is to be published in Journal of Phycology, Blackwell Publishing Ltd.
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Introduction

How far can species reach?

The geographic range of a species can be viewed as a spatial reflection of its ecological niche. Provided dispersal is not limiting, the distributional limit of a species is reached where it is excluded as a result of poor performance in response to the regulating abiotic and biotic environmental conditions (Brown and Lomolino, 1998). However, range limits are dynamic and may shift because of changes in the environmental factors, and also because species evolve new traits that influence the range limits (Case and Taper, 2000; Holt, 2003).

Because species tend to coexist in associations with similar ecological requirements, transitional changes from one community type to another often occur along strong environmental gradients. Communities in their marginal environment often have low species diversity in comparison to those in core habitats, but the species that are present may have high abundance and an increased local habitat range due to ecological release. The effects of ecological release in combination with strong natural selection make marginal habitats interesting in the study of stress responses and local adaptations.

Where do species come from?

Genetic and demographic variation within a species is called population diversity (Luck et al., 2003), and is a prerequisite for its sustained evolutionary potential and proper ecological function under environmental changes. Population diversity of one species may be high along environmental gradients due to both local adaptation and random genetic differentiation (Schilthuizen, 2000; Smith et al., 2001).

Local adaptation occurs when populations of the same species are subject to divergent ecological selection so that genetically differentiated ecotypes are formed. This is the first step in the process of ecological speciation, which occurs if the differentiating populations also evolve reproductive isolation (Schluter, 2001). Random genetic differentiation occurs when lineages diverge by genetic alterations that are not related to ecological selection, such as genetic drift or mutations, and is most likely to be significant in isolated and small populations (Turelli et al., 2001). Isolation increases the rate of genetic differentiation because it prevents the exchange of genes between diverging populations (Lenormand, 2002), but speciation may also occur in sympatric populations (Via, 2001). The precise mechanisms of differentiation are not easy to detect unless differentiation is relatively recent (Schliewen et al., 2001), and may in many cases be due to a combination of factors (Schluter, 2000).
Speciation is a slow process when it involves gradual accumulation of genetic differences that indirectly lead to reproductive isolation, but sometime only minor genetic or behavioral alterations are required to achieve reproductive isolation (Hendry et al., 2000; Johannesson, 2001; Ferguson, 2002). This will increase speciation rates significantly, and enable evolutionary dynamics to potentially occur on the same time-scale as ecological dynamics. Reproductive isolation may be achieved particularly rapidly in populations with a capacity for asexual reproduction, as novel genotypes, created by mutation or hybridization, can be efficiently fixed by cloning (Turelli et al., 2001; Kearney, 2003).

Figure 1. The Baltic Sea area, including the names of geographic areas mentioned in the text. Isohalines show major changes in salinity (arabic numerals) of the surface water. Circles refer to places where the studies presented in this thesis were performed; roman numerals = number of study; Qs and Qn = southern and northern area of the Northern Quark (see Table 2).
The Baltic Sea

The brackish Baltic Sea is a marginal environment for both marine and freshwater species, and an area with a potentially high rate of ecological and random differentiation. The Baltic Sea area is young from an evolutionary perspective, and most organisms are believed to have colonised the area within the last 8,000 years. Also, it has a strong environmental gradient of a gradually decreasing salinity from the entrance to the inner parts (Fig. 1). This gradient is clearly correlated with species richness, due to a gradual loss of marine taxa with decreasing salinity (Fig. 2).

![Figure 2](image)

**Figure 2.** Species number of macroalgae and macrofauna in different salinity regions of the Baltic Sea, 24 psu = Kattegatt, 7 psu = northern Baltic Proper, 5 psu = Bothnian Sea, 3 psu = Bothnian Bay. Figures for macroalgae are total number of marine and lacustrine species in each area according to Snoeijis (1999). Figures for macrofauna are total number of taxa below the halocline (15 m depth), where mainly marine taxa occur, according to Jansson (1972) and Bonsdorff (2004).

The geographical focus of this thesis is from the northern Baltic Proper to the southern and central Gulf of Bothnia (Fig. 1). This area has a surface salinity between 7 and 3 psu and corresponds to the inner distributional limit for some of the marine species most tolerant of low salinity in the Baltic Sea (Bergström and Bergström, 1999). The Gulf of Bothnia consists of four sub-basins, which are separated from each other by shallow straits. The two largest basins are the Bothnian Sea and the Bothnian Bay, which are separated from each other by the northern Quark strait (maximum depth ca 20 m). The southern Quark strait (maximum depth ca 40 m) separates the Bothnian Sea from the Åland Sea which, together with the shallow Archipelago Sea connects with the Baltic Proper (Omstedt and Axell, 2003). The Gulf of Bothnia differs from the Baltic Proper by having a stronger freshwater influence, but also by a shorter growth
season and lower productivity rates (HELCOM, 1996). The average number of ice days increases from 20-30 in the Baltic Sea proper, to 40-60 in the Åland Sea and 90-100 in the Gulf of Bothnia (Seinä and Peltola, 1991).

The macroalgal community of the southern Gulf of Bothnia was studied in detail by Wärn (1952). Quantitative analysis of coastal community structure have been performed mainly by H Kautsky (e.g. Kautsky et al., 1981; Kautsky, 1983; Kautsky et al., 1988; Kautsky, 1989). However, coastal systems of the Gulf of Bothnia are generally poorly investigated in comparison to many other areas of the Baltic Sea.

**Origin of the Baltic Sea and its species**

The recent geological history of the Baltic Sea area is governed by global increases in sea level and processes of land uplift following the retreat of the latest continental ice sheet (Ignatius et al., 1981, Andersen and Borns, 1997). This has resulted in repeated shifts in the level of connection between the Baltic Sea area and the North Sea (Fig. 3). Most of the marine organisms in the Baltic Sea are thought to have colonised from the west after the beginning of the Littorina Sea phase (8 000 years ago). Before this, the Baltic Sea area was a freshwater ecosystem (The Ancylus Lake) for a period of about 1 000 years. During the Littorina Sea phase, the connection to the North Sea was wider than today and the salinity was higher. This enabled the presence of more marine species in the Baltic Sea area than are currently present (Snöeijis, 1999). The connection to the North Sea then narrowed again, and the salinity of the Baltic Sea area decreased progressively until it reached approximately current levels 3 000 years ago (Andersen and Borns, 1997).

Today, salinity conditions are regulated by climate-related, stochastic changes in the inflow of sea water through the Baltic entrance, and by freshwater influx from the rivers, but are remarkably stable on a regional scale in the inner areas (Wallentinus, 1991; Omstedt and Axell, 2003). The rate of salinity decrease has been very low in the past 3 000 years due to a relatively cool climate, but it is conceived that global warming may enhance the rate of salinity decrease in the future through increased precipitation and freshwater influx (Meier, 2002).

Due to increased constraints from low salinity over time, many of the marine species that were once present in the Baltic Sea area are locally extinct today, and the low salinity imposes strong environmental pressure on the organisms that are present. The performance of some common species is reduced by salinity stress, as these have a lower growth rate or reproductive output in their local salinity conditions in the Baltic Sea than they do in higher salinity (Kautsky et al., 1990; Andersson et al., 1992). However, at least some level of local adaptation is also evident in many Baltic populations of marine species (Table 1). Many of these probably represent true brackish-water ecotypes of marine taxa (if Russell, 1985; Snöeijis, 1999), but there is currently no evidence that ecological speciation has occurred during the evolutionary short time period
at hand. Some of the marine species that are widely distributed in the Baltic Sea live in estuaries or in the intertidal zone in fully marine environments. These may have had some pre-adaptations to tolerate conditions of low salinity prior to colonisation. However, one important difference between low salinity in the tideless Baltic Sea and in these environments is that salinity is constantly low in the Baltic Sea, without temporal refuges.

Organisms of freshwater origin become increasingly common towards local freshwater outflows, and are also subject to selection pressure in the brackish water. For example, there are indications of strong ecological selection on freshwater diatoms in the Gulf of Bothnia (Snoeijis and Potapova, 1998). A number of Baltic taxa are also considered to be glacial relicts, representing lineages or species that once had a wide distribution in arctic marine and freshwater areas, but now mainly remain in refuge habitats such as the inner Baltic Sea (Väinölä and Hvilsom, 1991; Sell, 2003; Väinölä, 2003). By contrast, there are also numerous examples of recently colonised species, which are mainly accidentally introduced by man (Leppäkoski and Olenin, 2000).

**Figure. 3.** Geological history of the Baltic Sea. From Russell (1985).
Table 1. Adaptive differentiation of marine species in the Baltic Sea. Examples of experimental studies that show a shift in the salinity tolerance of Baltic populations when compared with populations of the same species from a marine environment.

<table>
<thead>
<tr>
<th>Species</th>
<th>Effect on</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Brown algae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chorda filum</em> (L.) Stackh.</td>
<td>Net photosynthesis</td>
<td>1</td>
</tr>
<tr>
<td><em>Fucus vesiculosus</em> L.</td>
<td>Growth</td>
<td>2</td>
</tr>
<tr>
<td><em>Fucus serratus</em> L.</td>
<td>Reproduction</td>
<td>3</td>
</tr>
<tr>
<td><em>Pilayella littoralis</em> (L.) Kjellm</td>
<td>Net photosynthesis</td>
<td>1</td>
</tr>
<tr>
<td><em>Scytosiphon lomentaria</em> (Lyngb.) Link</td>
<td>Reproduction</td>
<td>4</td>
</tr>
<tr>
<td><strong>Red algae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ceramium tenuicorne</em> (Kütz.) Wærn</td>
<td>Growth</td>
<td>7</td>
</tr>
<tr>
<td><em>Delesseria sanguinea</em> (Huds.) Lamour</td>
<td>Growth</td>
<td>8</td>
</tr>
<tr>
<td><em>Membranoptera alata</em> (Huds.) Stackh.</td>
<td>Growth</td>
<td>8</td>
</tr>
<tr>
<td><em>Phycodrus rubens</em> (L.) Batt</td>
<td>Growth</td>
<td>9</td>
</tr>
<tr>
<td><strong>Green algae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cladophora rupestris</em> (L.) Kütz.</td>
<td>Survival</td>
<td>5</td>
</tr>
<tr>
<td><strong>Fauna</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mytilus trossulus</em> (M. edulis L.)</td>
<td>Survival</td>
<td>10</td>
</tr>
<tr>
<td><em>Gadus morhua</em> L.</td>
<td>Osmoconforming gene</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Reproduction</td>
<td>12</td>
</tr>
</tbody>
</table>


Main factors regulating Baltic macroalgae

**Low salinity**

Marine species in low salinity are subject to hypoosmotic stress. They have to avoid excess water influx, which occurs if the osmotic potential within their cells is continuously higher than in the surrounding water. Algae do not have the capacity to expel excess water, but respond to hypoosmotic stress by passively tolerating an increased cell volume, or by reducing the concentration of osmotically active solutes in the cell (Kirst, 1990; Lobban and Harrison, 1994). This may result in decreased performance of the alga due to increased metabolic costs, changes in cellular ultrastructure, or consequential deficiency of ions or metabolites in the cell (Kirst, 1990). Brackish water may also directly impose ion deficiency, for example deficiency of dissolved carbonate, which is available in lower concentration in low salinity (Raven and Samuelsson, 1988), or deficiency of ions associated with transports across the cell membrane (Kirst, 1990; Raven, 1999, Fig. 4).
Salinity stress may also affect reproductive mechanisms, imposing the largest constraints on the performance of gametes and on fertilization (Raven, 1999; Serrão et al., 1999). In red algae, an increased dominance of tetrasporophytes, which is the diploid life stage, may be observed towards marginal areas (de Wrede and Klinger, 1988; Maggs, 1998). It has been suggested that diploid stages may have a higher fitness and adaptability to new environments than haploid stages, because they can carry a larger pool of alleles (Mable and Otto, 1998).

Figure 4. Effects of low salinity on marine macroalgae in the Baltic Sea. This thesis is focused on aspects relating to the encircled responses (e.g. Kirst, 1990; Lobban and Harrison, 1994; Middleboe et al., 1997; Raven, 1999; Serrão et al., 1999). Potential ecological consequences are related to loss of species diversity and, possibly, loss of genetic diversity due to increased asexual reproduction (e.g Hughes and Stachowicz, 2004). Potential evolutionary consequences are mediated by ecological selection, increased isolation between diverging populations due to constraints on sexual reproduction, and possibly by effects of asexual reproduction on the rate of genetic recombination (e.g Eckert, 2001). Also, relaxed biotic interactions due to loss of species may increase the ecological range of present taxa (e.g Pedersen and Snoeijis, 2002), which may develop ecological adaptations to new habitats.
Another feature that has been attributed to low salinity stress on marine species in the Baltic Sea is the appearance of populations with a reduced thallus or cell size, so called pauperization (Krok, 1869; Warf, 1952). However, this feature varies among different taxa, and is probably not always related to environmental induction (Warf, 1952; Russell, 1985).

Salinity tolerance is commonly measured by the effect of different salinity levels on growth rate, survival, photosynthesis and respiration (Kirst, 1990). Estimations of growth rate are ecologically relevant, because they reflect the balance between photosynthesis and respiration, and, thus, the ultimate performance of an organism. However, reproduction and the performance of early life stages are the most critical for population maintenance, and may often be more sensitive to external stress than adult stages (Wright and Reed, 1990; Raven, 1999; Steen, 2004).

**Nutrient enrichment**

Whereas the current salinity environment of the Baltic Sea has been present for about 3 000 years, a more recent factor structuring Baltic communities is nutrient enrichment. Increased winter concentrations of nitrate and phosphate have been seen in all regions of the Baltic Sea during the past 40-60 years, due to increased mobilization of these nutrients by human activities (HELCOM, 1996, 2003).

The main ecological effect of nutrient enrichment is eutrophication, which may be defined as the enhanced supply rate of organic matter into the ecosystem due to increased primary productivity (Nixon, 1995). Nutrient enrichment favours the productivity of fast growing algae (Fig. 5), which has effects on species interactions at all trophic levels, on the balance between primary production and consumption, and on biogeochemical processes (Bonsdorff et al., 1997; Cloern, 2001). One ultimate consequence of eutrophication is ecosystem instability due to an increased rate of nutrient and carbon cycling (Schramm, 1996). However, the level of response may be highly dependent on system-specific attributes, for example coastal topography and local grazing activity (Worm et al., 2002; Rönberg and Bonsdorff, 2004).

The main pathways of how eutrophication affects coastal ecosystems are rather well recognised today, but less is known about mechanisms that underlie specific responses and ecological links. One aspect of nutrient enrichment is its potential interactions with additional stress factors (Cloern, 2001). Moderate increases of nitrate or phosphate may be conceived to enhance growth conditions and thereby reduce the negative effects of e.g. low salinity stress on a species (Kirst, 1990; Kamer and Fong, 2001). This would be consistent with early observations that Fucus vesiculosus had an enhanced distribution close to local nutrient sources in the inner Baltic Sea (Warf, 1952; Pekkari, 1973; Luther, 1981). In order to accurately predict the potential effects of environmental changes on coastal zone biota, it is important to be able to link any observed changes in the distribution of species to particular environmental features.
Figure 5: Main effects of nutrient enrichment on algae. Fast growing microalgae and macroalgae are directly favoured over perennial macroalgae by a higher growth rate (represented by the thickness of the horizontal arrows). Indirect effects are mediated by an increased competition between species and changes in the quality of ambient environmental factors (vertical arrows). The magnitude of effect is enhanced by an increasing turnover rate of nutrients and carbon, because fast growing algae have a shorter generation time. Generalized from Schramm (1996), Snoeijs (1999), and Berger et al. (2004).

Objectives of this thesis

The general objective of this thesis was to study how conditions of low salinity and nutrient enrichment may affect the distributional ranges of marine macroalgae in the inner Baltic Sea. More specifically, I have studied:

1. The community structure of macroalgae in relation to local abiotic factors (Paper I)
2. Reproductive characteristics in low salinity (Papers II, VI)
3. Potential effects of nutrient enrichment (Papers III, IV)
4. Levels of population differentiation (Papers III, V)
Box. Macroalgae

The noun “alga” is an arbitrary name for organisms of various origin that are often only remotely related to each other. By coarse definition, any photosynthetic or heterotrophic eukaryote organism that is not a bryophyte or a vascular plant may be considered an alga (Palmer *et al.*, 2004).

In this thesis, the word “macroalga” denotes multicellular algae that are visible by eye (Tolstoy and Österlund, 2003). The main groups of marine macroalgae are traditionally named by their colour as brown, red, and green macroalgae.

- “Brown macroalgae” (class Phaeophyceae) are marine seaweeds within the monophyletic group Heterokonta, which also includes for example diatoms (Andersen, 2004). This group may be equally distant from red and green macroalgae as they are from animals (Palmer *et al.*, 2004).

- “Red macroalgae” is an ancient and highly diverse group that has a common origin with the green algae around 1 500 Ma. The red algae are referred to as subkingdom Rhodoplantae by Saunders and Hammersand (2004).

- The traditional “green algae” (Division Chlorophyta) are currently included in Kingdom Chlorobionta together with the Charophytes and embryophytes (land plants), thus emphasising the close phylogenetic relationship between green algae and land plants (Lewis and McCourt, 2004).

Study species

The experimental studies are focused on two species of marine origin that have a wide distribution in the Baltic Sea, the red alga *Ceramium tenuicorne* (Kütz.) Wern and the brown alga *Fucus vesiculosus* L., and on aspects of their reproduction (Figs 6-8). In terms of responses to eutrophication, *C. tenuicorne* represents the group of filamentous algae, which are generally considered to be favoured by eutrophication, whereas the perennial *F. vesiculosus* is currently threatened by eutrophication in many areas of the Baltic Sea (reviewed by Schramm, 1996). Both *Ceramium* and *Fucus* are highly variable genera, which make them taxonomically complex (Kjellman, 1890; Du Rietz, 1930; Powell, 1963; Maggs *et al.*, 2002; Gabrielsen *et al.*, 2003; Wallace *et al.*, 2004).

At least eight different species of *Fucus* are currently recognised (Powell, 1963; Wynne and Magne, 1991). *Fucus vesiculosus* is among the widely distributed of these and shows high morphological variability. This variation is probably
often attributed to environmental plasticity (Burrows and Lodge, 1951; Ruuskanen, 1997), but it has also been speculated that some of its form variation may be inherent (Wärn, 1952; Luther, 1981; Evans et al., 1982). Some level of adaptation to low salinity has previously been reported in both Ceramium and Fucus from the Baltic Sea (Table 1).

The most abundant Ceramium taxon in the inner Baltic Sea was described as a separate species, C. gohii, by Wärn (1992). However, this view was not supported neither by genetic analyses, nor by crossing experiments between C. tenuicorne, C. gohii Wärn and C. strictum sensu Harvey, which showed that these taxa are not reproductively isolated, and that they may all be referred to C. tenuicorne (Rueness, 1978; Gabrielsen et al., 2003).

Figure 6. Life history and early reproductive stages in the genus Fucus. The sexual life cycle is gametic; the free-living stage is diploid, and the only haploid stages are the gametes. The gametes (1) are produced in the receptacles, from which they are then released and fertilization is external. After fertilization, the egg produces an adhesive by which it attaches to the substrate (2). The egg polarizes according to the prevailing light direction, is attached further by a rhizoid cell that develops by the first cell division (3), and develops into a germling (4). Fucus vesiculosus is dioecious (female at the left and male at the right in the picture). Gametic life cycles occur within the Fucales, whereas in most other brown algae a free-living diploid stage alternates with a free-living haploid stage (South and Whittick, 1987; Kropf, 1997). Scale bar = 1 mm for phases 1-3, and 15 mm for adult individuals. Drawing by L. Kautsky.
Figure 7. Life history of the genus *Ceramium*. The sexual life cycle is a triphasic *Polysiphonia*-type life cycle. A free-living diploid tetrasporophyte stage alternates with a dioecious haploid gametophyte stage and a diploid carposporophyte stage, which develops on the female gametophyte after fertilization. Meiosis occurs in tetrasporangia on the tetrasporophyte. Fertilization occurs by direct contact between female and male gametophytes. The carposporophyte releases carpospores, which produce the new sporophyte generation. The dispersal range is often low as there are no motile life stages. This type of life cycle is characteristic for most red algae within the class Florideophyceae (South and Whittick, 1987; Saunders and Hammersand, 2004). Drawing by L. Kautsky.

Figure 8. *Ceramium tenuicorne* may also reproduce asexually by vegetative propagules (sometimes called paraspores or monospores), which may be formed laterally or apically in any life stage. Also, vegetative fragments of the thallus may re-attach by secondary rhizoid formation (Eriksson, 2002; Rueness *et al.*, 2002). Pictures of lateral parasporangia, drawn by L. Kautsky from photos by Rueness *et al.* (2002), Tolstoy and Österlund (2003).
Description of the studies

Community structure (Paper I)

The community structure of macroalgae at the border between the Baltic Proper and the Gulf of Bothnia was studied in relation to environmental factors that change with depth. The study was performed in an area that provides one of the longest time-series of studies on vegetation structure in the Baltic Sea (Wäern, 1952; Kautsky et al., 1986; Eriksson et al., 1998). These studies show that the depth distribution of *Fucus vesiculosus* has decreased substantially during the past 60 years, most probably due to external changes at a larger scale, as there are no local sources of pollution in the area. It is assumed that the decrease reflects a decreased light penetration into the water due to eutrophication, but the relationship between the depth distribution and potentially regulating environmental factors has not been assessed previously. To achieve this, we recorded the depth distribution of individual species and vegetation zones at ten sites in the area, and collected samples for the determination of species biomass composition at four depths at each site (4, 6, 8, and 10 m). All sites had similar substrate (rock) and salinity (5 psu), but differed in the degree of wave exposure. The vegetation data was analysed in relation to data on ambient sediment cover and cartographic indices describing aspects of topography, wind exposure and light penetration, using multivariate analyses.

Ceramium tenuicorne

Reproductive characteristics (Paper II)

The reproductive characteristics of *Ceramium tenuicorne* (hereafter *Ceramium*) were studied quantitatively along a salinity gradient ranging from south to north in the northern Baltic Sea. *Ceramium* was collected from 0-1m and 2-3 m depths in regions of 7, 5, and 4 psu salinity (Fig. 1). In Baltic *Ceramium*, tetraspores are readily observable under a stereo microscope, whereas the gametangia of the male and female gametophytes are cryptic. The abundance of tetrasporo-bearing individuals in the collected material was used to estimate the frequency of the diploid life stage, and the abundance of carposporophytes was used to estimate the relative frequency of successful sexual fertilization. The results were related to growth experiments in the laboratory. The salinity tolerance range of different life stages (tetrasporophyte, male and female gametophyte) was tested on a strain of *Ceramium* isolated from the Baltic Proper, and the germination potential of field-collected tetraspores and carpospores was observed.
Local adaptation (Paper III)
The effect of low salinity and nutrient enrichment on natural populations of Ceramium was tested in paper III. Laboratory growth experiments were performed on Ceramium tetrasporophytes sampled in two different regions: the Baltic Sea proper (7 psu) and in the central Gulf of Bothnia (4 psu). Four experiments were performed, assessing:

1. The growth of strains from each region in water from both regions
2. The growth of strains from each region in very low salinity
3. Variation in the growth response among strains from the same site
4. Effects of nutrient enrichment on the tolerance of strains to very low salinity

All growth experiments were performed using freshly cut vegetative tips produced in treatment conditions after step-wise acclimatization. Growth rate was estimated from length increase after 7-10 d. In addition, the effect of low salinity on cell size was evaluated in paper II, and the effect on biomass increase in paper III. The methods were based on a protocol developed by Bruno & Eklund (2003), and are presented in more detail in each of papers II and III.

Fucus vesiculosus

Effects of nutrients on early life stages (Paper IV)
The early development after fertilization is critical for the recruitment of Fucus, and typically involves a high rate of mortality. The effect of nitrate and phosphate enrichment on the early reproductive stages of Baltic Fucus vesiculosus was tested in paper IV, with respect to the rate of attachment of zygotes, germination success, and the development of the primary rhizoid (Fig. 6). The tested nutrient concentrations correspond to ambient levels in eutrophic to severely eutrophic waters in the Baltic Sea (HELCOM, 1996, 2003). The experiments were performed using F. vesiculosus from the Baltic Proper and local seawater (salinity 7 psu). Gamete release from male and female receptacles and fertilization were induced in the laboratory. Treatment effects were assessed as the number of attached egg at 6, 12, 18, 24 and 48 h after fertilization, the number of surviving germings after 10 d, and the length of the primary rhizoid after 17 d.

Population differentiation (Paper V)
The main canopy-forming macroalga in the Gulf of Bothnia is a morphotype of Fucus that is clearly dwarfed in comparison to Fucus vesiculosus from the Baltic Proper and marine areas. Its dwarfed habit is commonly assumed to be a result of physiological constraints due to low salinity, so called pauperisation (Warn, 1952; Hällfors et al., 1981). However, dwarf and common morphotypes occur in sympatry in the southern Gulf of Bothnia, which implies that a genetic
component rather than environmental induction may explain their morphological differences. In paper V, we studied morphological variability and the level of genetic differentiation between sympatric populations of common *F. vesiculosus* and the dwarf morphotype. The results were related to the level of corresponding differentiation among other, geographically separated populations of *Fucus* along the Swedish coast. Random genetic differentiation was assessed by comparison of five microsatellite loci identified by Engel *et al.* (2003).

**Vegetative reproduction (Paper VI)**

Molecular analyses in connection to the study described in paper V unexpectedly revealed a high level of clonality in *Fucus* populations from the northern Baltic Sea. Paper VI describes the extent of clonality in more detail, together with experimental observations on how vegetative reproduction might be achieved in *Fucus*. Long distance dispersal by means of vegetative fragments that may re-attach has been observed in other macroalgae, for example in *Ceramium tenuicorne* (Eriksson, 2002; Qvarfordt, 2004). In order to explore if this mechanisms is also possible in *Fucus*, loose vegetative parts of *Fucus* thallus were placed on granite discs, and allowed to grow in natural brackish water and low temperature conditions (5 psu, 10°C). The development of the wounded surface was followed and the rate of re-attachment by secondary rhizoid formation was noted after 7 weeks. The vegetative parts tested were adventitious branches, apical tips and scrapes of adult thallus surface.

**Results & Discussion**

**Community structure (Paper I)**

A close relationship was observed between vegetation community structure and local abiotic factors in the northern Baltic Proper (Paper I). The results imply that vegetation structure is highly predictable in the area, and linked to factors that are modulated by eutrophication.

Depth distribution of the vegetation is commonly used as an indicator of water quality in coastal waters, because of its negative correlation with turbidity. Depth distribution is also an ecologically important aspect, because it is directly related to the amount of vegetation present, and thus, to the function of coastal ecosystems. The depth distribution of *Fucus vesiculosus* remained modest in the study area. Belt-forming *Fucus* occurred down to maximally 7 m depth, compared with 10 m in the 1940s (Wärn, 1952). The lower limit of the *Fucus* belt was most strongly correlated with sediment cover, probably because sediment infers with the attachment of zygotes and survival of germings (Chapman and Fletcher, 2002; Berger *et al.*, 2003). The lower limit of belt forming red algae and
*Sphacelaria arctica* was mainly correlated with light penetration, which was modelled using the clarity index (Kiirikki, 1996). These species are all capable of vegetative propagation in the study area, which may make their recruitment less sensitive to inference from sedimentation (Eriksson, 2002). The most common red algae were *Polysiphonia fucoides*, *Rhodomela confervoides*, and *Fucellaria lumbricalis* (see also table 2). The lower depth limit of individual *F. vesiculosus* was also best correlated with light, probably representing individuals that had successfully settled in sediment-free patches or very old individuals.

Environmental variables explained 50-61% of the variation in species composition at 4-10 m depth, increasingly with increasing depth, according to redundancy analysis (RDA). We did not evaluate the contribution of biotic interactions to community structure. Biotic interactions may account for part of the unexplained variance in the analyses. Also, the observed effects of abiotic factors may be mediated by biotic interactions, for example if some significant grazer species is more active on sheltered than on exposed sites. Experimental studies are needed to evaluate the specific mechanisms involved.

The dominant macroalgal species in the southern Gulf of Bothnia according to paper I are also observed further north (Table 2). Main part of the species are probably capable of vegetative reproduction by fragmentation or by asexual spores (South and Whittick, 1987), but studies of their reproductive performance in the inner Baltic Sea are rare. Of the marine species, sexual reproduction has only been observed in *Ceramium* (paper II), and *Fucus* (Serrão et al., 1999). One other important property of the vegetation further north is that the upper distribution limit of perennial species at exposed sites is forced downwards by ice erosion in the winter.

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**Table 2** (next page). Main macroalgal taxa in the northern Baltic Proper according to paper I (*Ph*), and their distribution in the southern and northern Northern Quark in the Gulf of Bothnia (*QS* and *Qn*, respectively) according to Bergström & Bergström (1999). All sites were exposed to semi-exposed rocky shores. **Origin**: *M* = marine, *L* = lacustrine. **Frequency**: figures denote the number of sites in which the species was observed, total n = 10 in each area. *X* = not quantified in paper I but occurs in the area according to personal observations and/or Wærn (1952). **Reproduction**: **Type**: letters denote reproductive features observed in the area, G = sexual reproduction, T = tetrasporangia, A = asexual sporangia, S = sporangia of undetermined type, SS = recruitment by spores, V = recruitment by vegetative fragments. **References**: 1 = Wærn (1952), 2 = Serrao (1999), 3 = Eriksson (2002), and papers I, II, VI. The nomenclature follows Nielsen *et al.* (1995).

(a) Quantified together with *P. littoralis* in paper I
(b) Possibly also *Phylllophora pseudoceranoides* (Gmel.) Newroth & Taylor

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22
<table>
<thead>
<tr>
<th>Species</th>
<th>Origin</th>
<th>Frequency</th>
<th>Reprod.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Salinity (psu)</strong></td>
<td></td>
<td><strong>PI</strong></td>
<td><strong>Qs</strong></td>
</tr>
<tr>
<td><strong>Brown algae</strong></td>
<td></td>
<td><strong>5-6</strong></td>
<td><strong>4-5</strong></td>
</tr>
<tr>
<td><strong>Chordia filum</strong> L. Stackh.</td>
<td>M 3</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><strong>Dictyosiphon foeniculaceus</strong> (Huds. Grev.)</td>
<td>M X 4</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><strong>Ectocarpus siliculosus</strong> (Dillw.) Lyngb.</td>
<td>M X 1</td>
<td>0</td>
<td>S</td>
</tr>
<tr>
<td><strong>Elachista fucicola</strong> (Vell.) Aresch.</td>
<td>M X 3</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><strong>Fucus vesiculosus</strong> L.</td>
<td>M 10</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td><strong>Pilayella littoralis</strong> (L.) Kjellman</td>
<td>M 10</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td><strong>Sphacelaria spp.</strong> (S. arctica Harv.)</td>
<td>M 10</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td><strong>Stictyosiphon tortilis</strong> (Rupr.) Reinke sensu Rosenv.</td>
<td>M 4 4 0</td>
<td>“V”</td>
<td></td>
</tr>
<tr>
<td><strong>Red algae</strong></td>
<td></td>
<td><strong>M 5</strong></td>
<td><strong>0</strong></td>
</tr>
<tr>
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<td>1</td>
</tr>
<tr>
<td><strong>Ahnfeltia plicata</strong> (Huds.) Fr.</td>
<td>M 0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
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<td>M 10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td><strong>Coccotylus truncatus</strong> (b) (Pall.) Wynne &amp; Heine</td>
<td>M 6 2 3</td>
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<tr>
<td><strong>Furcellaria lumbricalis</strong> (Huds.) Lamour</td>
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<td>7</td>
<td>4</td>
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<td><strong>Hildenbrandia spp.</strong> (H. rubra (Sommerf.) Menegh.</td>
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</tr>
<tr>
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<tr>
<td><strong>Polysiphonia tibillosa</strong> (Dillw.) Spreng</td>
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<tr>
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<td>5</td>
<td>0</td>
</tr>
<tr>
<td><strong>Rhodomela confervoides</strong> (Huds.) Silva</td>
<td>M 10</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><strong>Green algae</strong></td>
<td></td>
<td><strong>M/L X 1</strong></td>
<td><strong>6</strong></td>
</tr>
<tr>
<td><strong>Chaetomorpha bottnica</strong> nom. provis. Wærn</td>
<td>M/L X 1 6</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td><strong>Cladophora aegagropila</strong> (Dillw.) Harv. in Kütz.</td>
<td>L X 3 10 V</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td><strong>Cladophora glomerata</strong> (L.) Kütz.</td>
<td>L 10</td>
<td>10</td>
<td>9</td>
</tr>
<tr>
<td><strong>Cladophora rupestris</strong> (L.) Kütz.</td>
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<td>9</td>
<td>1</td>
</tr>
<tr>
<td><strong>Enteromorpha spp.</strong> (E. intestinalis (L.) Nees)</td>
<td>M/L 8 5 5 S</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td><strong>Ulothrix spp.</strong> (U. penicilliformis (Roth) Aresch.</td>
<td>M/L X 3 4 G</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td><strong>Urospora spp.</strong> (U. zonata (Weber &amp; Mohr) Kütz.</td>
<td>M/L X 1 2</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>
Reproductive characteristics (Papers II and VI)

The field study of reproductive stages of *Cerium tenuicorne* indicated that sexual reproduction is rare in the Gulf of Bothnia, and rather common in the Baltic Proper (Paper II). However, sexual reproduction may occur down to a salinity of at least 4 psu. Sexual reproduction is not a critical stage in the life cycle of *Cerium*, as it is also highly capable of vegetative dispersal (Fig 8), and the fitness of any genotype may be directly related to its capacity for vegetative propagation. Vegetative fragments of *Cerium* have been observed to settle on new substrates in colonization studies in both the Baltic Proper (Qvarfordt, 2004), and the southern Gulf of Bothnia (Eriksson, 2002).

An increased dominance of *Cerium* tetrasporophytes was observed towards the northern areas. This supports previous suggestions that the tetrasporophyte, which is diploid, may be more tolerant of extreme environments than the haploid gametophyte (Mable and Otto, 1998). However, the growth experiments of paper II indicated that both the tetrasporophyte and the gametophytes are highly tolerant of low salinity, down to 1-2 psu. Indeed, the performance of the different life stages may differ in some aspect that was not studied. Alternatively, an increased dominance of tetrasporophytes in the northern area may be explained by a relatively shorter season of growth in the north. The gametophyte generation typically develops from tetraspores in late summer, and a short growth season might prevent full alternation of generations within the same year. Also, ice erosion may prevent *Cerium* from being adequately established in the shallow zone. It appeared from the study that sexual reproduction is confined to shallower areas.

Genetic analyses revealed a high rate of clonality in northern populations of *Fucus vesiculosus*, indicating that vegetative reproduction may be widespread also in *Fucus* in the northern Baltic Sea (Paper VI). Laboratory experiments showed that vegetative fragments of *Fucus* from the area in which clonality was widely observed were capable of re-attaching to the substrate by secondary rhizoid formation. Re-attachment occurred mainly in the treatment with detached adventitious branches. Different populations of *Fucus* varied in their capacity for re-attachment. This indicates that the capacity for vegetative reproduction is genetically determined, and may be viewed as an adaptive response to low salinity. However, it remains to be assessed whether vegetative reproduction is possible in only some or in all individuals of a certain population, and also to which extent asexual reproduction may be induced by environmental factors. Vegetative reproduction has previously been observed in *Fucus vesiculosus* in that new fronds may regenerate from an existing holdfast, and adventive embryony has been observed to occur in rhizoidal filaments in laboratory cultures of germings (McLachlan and Chen, 1972; South and Whittick, 1987). These two mechanisms may enable vegetative dispersal over short distances. The finding that detached adventitious branches may act as vegetative propagules is novel in *Fucus*, and explains how even longer distance dispersal could be achieved.
An increased rate of vegetative reproduction in marine macroalgae in the inner Baltic Sea confirms with a general pattern that asexual reproduction tends to increase in dominance at the geographical margins of species’ ranges (Peck et al., 1998; Kearney, 2003). One obvious advantage of asexual reproduction in marginal environments is that it may allow populations to persist in habitats where sexual reproduction is impaired. It has also been suggested that many environments in which parthenogenesis is common have a reduced level of biotic interactions, and that this would confirm with the idea that one important advantage of sexual reproduction is that it enhances the capacity of organisms evolve in response to biotic interactions with competitors, predators, and parasites (Kearney, 2003).

**Effects of nutrient enrichment (Papers III, IV)**

Growth experiments on *Ceramium tenuicorne* in low salinity indicated that nutrient enrichment affects its growth rate, but not its salinity tolerance range (Paper III). However, the magnitude of response varied among strains, plausibly depending on their level of adaptation to low salinity.

The strains were not able to utilise added nitrate and phosphate if they were repressed by low salinity. Growth in the two strains from the Baltic Proper was mainly controlled by salinity, which explained 66 and 97% of the variation between treatments. The effect of nutrient enrichment was smaller but generally positive. In strains from the Gulf of Bothnia, salinity explained only 14 and 17% of the total variation. The applied levels of nitrate and phosphate had a negative or no effect on growth rate in ambient salinity conditions (4 psu), but had a positive effect in low salinity (1.5 psu). However, growth rate was mainly affected by the presence or absence of trace elements, which explained 58 and 66% of the total variation. All strains performed best in the complete culture medium of nitrate, phosphate and trace elements. The applied levels of nitrate and phosphate addition were 3 and 5 times higher than those applied on *Fucus* in paper IV, respectively.

The attachment rate of *Fucus vesiculosus* zygotes and the survival of germlings was clearly impaired by nitrate and phosphate enrichment (Paper IV). Rhizoid development in juveniles that did survive the first 17 d was moderately negatively affected by nitrate. The results indicate that Baltic *F. vesiculosus* is sensitive to sustained nutrient enrichment.

*Fucus vesiculosus* is typically exposed to low nutrient concentrations in its natural habitat. Under such conditions, a capacity to rapidly take up and store nutrients when available would be a competitive advantage. Plausibly, if there is excess nutrient uptake, an increased conversion of nitrate or phosphate into storage compounds in the cell may delay any other metabolic processes, such as the production of adhesives for attachment, or result in secondary deficiency of some other nutrient required for storage, for example trace elements or carbon. A similar response was observed in the sea grass *Zostera marina* in mesocosm
experiments (Burkholder et al., 1992). Excess nitrate could also result in toxic effects of ammonium, which is the product of nitrate reduction (cf. Kevekordes, 2001). These hypotheses should be studied further, but are supported by that a very low nitrogen use efficiency was suggested for *Fucus* in the Gulf of Bothnia due to an inherently low metabolic rate (Raven and Samuelsson, 1988).

One ecological effect of the observations is probably that excess nitrate and phosphate may induce metabolic stress on *Fucus* recruits, which may further increase their susceptibility to other stress factors, such as competition with other species, or decreases their attachment capacity in areas affected by high rates of sedimentation (Paper I, Fig. 5).

**Population differentiation (Papers III, V)**

*Ceramium tenuicorne* shows characteristics of a generalist species by having a relatively high growth rate and flexible reproductive strategies (Paper II, Figs 7-8). However, the results of paper III indicate that local adaptation, rather than a generalized tolerance of low salinity explains its wide distribution in the inner Baltic Sea.

Growth studies on *Ceramium* indicated that populations from the Gulf of Bothnia and the Baltic Proper represent different salinity ecotypes, so that strains from the Gulf of the Bothnia are better adapted to endure low salinity. Previous studies on *Ceramium tenuicorne* have shown that there is a gradual transition between Baltic and Atlantic salinity ecotypes at the Baltic entrance (Rueness and Kornfeldt, 1992; Düwel, 2001). Altogether, these results suggest that the salinity optimum of *Ceramium* may change gradually with decreasing salinity along the Skagerrak-Baltic Sea gradient. The presence of multiple, locally adapted genotypes along the salinity gradient may be explained by that salinity is relatively constant on a regional scale in the Baltic Sea (Wallentinus, 1991). By contrast, selection for a single genotype that tolerates a wide range of salinity conditions might be expected in areas with high local salinity fluctuations, such as tidal estuaries, where periods of higher salinity may provide temporal refuges to recover from hypoosmotic stress.

Studies on populations of the dwarf morphotype and common *Fucus vesiculosus* showed that these were morphologically distinct even when present in complete sympatry, and were highly genetically differentiated from each other (Paper V). The two investigated populations of the dwarf morphotype showed genetic and morphological similarity although separated by a geographical distance of 400 km. The results suggest that the dwarf morphotype represents a separate evolutionary lineage, and its taxonomic status is currently being assessed. However, further studies are needed in order to clarify whether the dwarf morphotype may be endemic to the Baltic Sea, or if the two lineages have diverged outside the Baltic Sea and represent two independent colonization events.
The level of genetic differentiation was also high between common *F. vesiculosus* from the site where it was sympatric with the dwarf morphotype and common *F. vesiculosus* from the other investigated sites. Possibly, this is a reflection of high genetic drift in what may be viewed as a marginal population of common *F. vesiculosus*, where the effective population size may be reduced by constraints of low salinity on sexual reproduction (Serrão *et al.*, 1999).

Vegetative reproduction and a low dispersal range of gametes are likely to have enhanced genetic isolation of the two *Fucus* lineages, and perhaps also the rate of local adaptation in *Ceramium*. It is suggested that one ultimate factor limiting the distribution of a species is that local adaptation in peripheral populations is counteracted by gene flow from adjacent, suboptimally adapted populations (Mayr, 1963; Lenormand, 2002). The genetic analyses indicated that vegetative reproduction was widespread in the dwarf morphotype, but did also occur in Baltic populations of common *Fucus vesiculosus*. 
Conclusions

1. The wide distribution of *Ceramium* and *Fucus* in the inner Baltic Sea may be explained by adaptive responses to low salinity.

   Adaptation is seen in a shift towards a lower salinity tolerance range in *Ceramium* from the Gulf of Bothnia, reflecting local salinity conditions, and by a high rate of vegetative reproduction in both *Ceramium* and *Fucus*.

   Since both these taxa are well established in low salinity, it is not unlikely that their current salinity tolerance ranges may evolve further. Range expansion is theoretically unlimited in a gradually changing environment, such as that of the Baltic Sea, if gene flow is not too high and population density not too low (Kirkpatrick and Barton, 1997). However, the rate of future environmental changes is probably decisive, for example possible changes in salinity due to global warming.

2. The dwarf morphotype of *Fucus*, which is characteristic for the Gulf of Bothnia, represents an evolutionary lineage that is genetically separated from common *F. vesiculosus*.

   The lineages are also likely to differ in their ecological properties. This should be studied further, as the dwarf morphotype is the only large structural macroalga in the inner Baltic Sea, has reproductive traits that are unique for the genus *Fucus* (a mix of clonal and sexual reproduction), but is hitherto little studied.

3. Ecological effects of eutrophication should be assessed separately for different regions of the Baltic Sea.

   My results support established pathways of eutrophication effects (Fig. 5), suggesting more specifically that:

   - Nutrient enrichment does not enhance the salinity tolerance of *Ceramium* and *Fucus* in the Baltic Sea.
   - The level of adaptation of a species to low salinity may infer with its capacity to utilize nutrients.

   Macroalgae may be unlikely to adapt directly to novel nutrient regimes, because nutrients resources are highly variable in the field. Possibly, populations may respond to changes in biotic interactions that are mediated by indirect effects of eutrophication. For example, seasonal variation in factors that regulate recruitment may lead to a shift in reproductive season in *Fucus vesiculosus* (Berger et al., 2004, Fig. 8).
Figure 9. Potential pathways for negative effects of nutrient enrichment on *Fucus vesiculosus*. Juvenile and adult stages are affected by different pathways. The strength of different pathways may vary with season, and may, thus, have different impact on the survival of *Fucus* depending on whether it reproduces in summer or autumn. Fertilization and early post-settlement stages are a significant natural bottleneck for *Fucus* populations (Vadas et al., 1992; Serrão, 1996). Populations of *F. vesiculosus* have their main reproductive period in either summer or autumn in the Baltic Proper and on the Swedish west coast (Berger et al., 2001; Jönnsson, 2004). From Berger et al. (2004)
Acknowledgements

I thank Lena Kautsky, Lars Ericson, Erik Bonsdorff and Ulf Bergström for helpful comments on this thesis, and my co-authors for good cooperation in the projects on which this thesis is based. The studies were financially supported by Umeå Marine Science Centre, the Gunnar and Ruth Björkman foundation, the J.C. Kempe memorial foundation, “Bertil Lundmans fond för botaniska studier”, “Uddenberg-Nordinska stiftelsen”, WWF Sweden, MISTRA and the Swedish Environmental Protection Agency. The practical studies were to main part performed at Umeå Marine Science Centre, the Askö Laboratory, the Department of Botany at Stockholm University, and Tjärnö Marine Biological Laboratory.
References


Svensk sammanfattning (Summary in Swedish)

Många arter i Östersjön lever nära sin utbredningsgräns. Östersjöns vatten är bröckt (en blandning av sötvatten och havsvatten), och varken sötvattenerarter eller marina arter är helt anpassade för att leva i denna miljö. Marina arters tillväxt och förökning är ofta nedsatt på grund av fysiologisk stress i den låga salhalten. Östersjön är även starkt påverkad av näringsbelastning från land och hav, vilket förändrar arternas tillväxthastighet och konkurrenserna mellan arter.


Arbete 1 är en dykinventering av algvegetationen på gränsen mellan egentliga Östersjön och Bottniska viken. Algernas djuputbredning och sammansättning visade ett tydligt samband med sådana egenskaper i miljön som förändrars till följd av övergödning. Ljusstigningen, men även mängden löst sediment på de klippor och stenar där algerna växer tycks vara avgörande för deras djuputbredning. Resultatet stämmer överens med att man tidigare sett att algernas djuputbredning har minskat kraftigt i området under de senaste 60 åren, i takt med att övergödningen har ökat.

Arbete 2 och 3 beskriver förökning och tillväxt hos rödalen ullsleke. Resultaten visade att ullsleke växer bra ner till en salthalt på 1-2 promille, och förör sig både känligt och könlöst i Östersjön. Algen är i hög grad anpassad till sin lokala miljö. Ullsleke från Bottniska viken tålde låg salthalt bättre än ullsleke från egentliga Östersjön, men tålde ökad näringshalt sämre.

I arbete 4 studerade vi hur förplantningen hos blåstäng i Östersjön påverkas av näringsämnenas nitrat och fosfat. Resultaten visar att ägg av blåstäng som utsätts för hög halt av dessa näringsämnen dels fäster till substratet långsammare, dels har sämre överlevnad. Troligtvis är blåstängen så anpassat till låga näringshalter i sin naturliga miljö att den inte kan hantera den högre näringsstillgång som användes i experimentet, och som motsvarar näringsstillgången i många delar av Östersjön från vilka blåstäng har försvunnit.

I arbete 5 analyserade vi den morfologiska och genetiska variation hos blåstäng i Östersjön, framför allt hos en typ av tång som är vanlig i Bottniska viken. Denna "Bottniska viken-tång" är tydligt mindre och buskigare än vanlig blåstäng och har aldrig blåor. Man har ansett att detta är en följd av att den är stressed av låg salthalt, men våra resultat visar att skillnaden snarare är genetisk.
Skillnaden är så stor att Bottniska viken tången sannolikt representerar en helt annan art med egna ekologiska egenskaper.

Hos många arter är det främst den könliga förökningen som begränsas av låg salthalt. Vi upptäckte att tången i norra Östersjön har anpassat sig till den låga salthalten genom att komplettera könlig förökning med könlös förökning. Först såg vi att de genetiska analyserna visade identiska genuppsättningar hos separat växande individer av tång. Sedan såg vi i laboratorieexperiment att lösa bitar av tång kan vidfästa på nytt på sten. Detta ger en förklarande mekanism till den könlösa förökningen, eftersom man tidigare ansett att tång bara kan föröka sig könligt, genom att avge ägg och spermatozoer som befrukas i vattnet. Vidfästningen var effektivast hos adventivgrnar, en typ av småskott som är vanliga på tång i Bottniska viken.

Resultaten av min avhandling visar att marina alger i Östersjön kan ha en hög grad av anpassning till låg salthalt, men en begränsad kapacitet att utnyttja ökade näringshalter. Både genetiska och ekologiska egenskaper kan variera mellan alger som idag anses tillhöra samma art. Inomartsvariation och skillnader mellan olika regioner av Östersjön bör beaktas både i frågor som gäller arternas framtida anpassningsförmåga och deras omedelbara reaktioner på förändringar i miljön.