

LIFE STRATEGIES OF FILAMENTOUS ALGAE IN THE NORTHERN BALTIC PROPER

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Short lived filamentous algae are a major component of the rocky-shore macroalgal vegetation of eutrophic waters in the Baltic Sea. They show considerable variation in abundance both seasonally and from year to year. In this study the seasonal pattern of growth and reproduction is documented in six species to outline their life strategies. Five of the species studied were reproductive in summer or autumn, just after a period of active growth. *Pilayella littoralis* was the only exception. It grew fast in the spring but reproduction was successful only in winter, when only the basal parts of plants were left. The amount of filamentous algae was very low in winter. The only species which survived the winter period as macroscopic filaments was *Ceramium tenuicorne*. At least three species, *Cladophora glomerata*, *Dictyosiphon foeniculaceus* and *Ectocarpus siliculosus*, relied on microscopic stages to survive the unfavourable winter period. Responses of these filamentous species to variations in their physical environment are discussed.

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KEYWORDS: Life history; macroalgae; recruitment; seasonality; settlement.

INTRODUCTION

Short lived filamentous algae are the most variable part of the macroalgal vegetation in the tideless and brackish Baltic Sea. These algae grow fast and may disappear quickly. They can occasionally form summer mass occurrences which are connected in the present study area to the upwelling intensity (KIIRIKKI & BLOMSTER 1996). In addition to their varying contribution to biomass production, the dominant species are not always the same. This variation has been observed by Wærn (cited by WALLENTINUS 1974 and KAUTSKY 1989), who proposed that there might occur so-called 'green and brown algal years', according to the dominance of green or brown filamentous algae. To understand the mechanisms behind these fluctuations, detailed information on the biology of the main species is needed. The northern Baltic Proper offers a good opportunity for this kind of study because the brackish water has restricted the marine macroalgal flora to only a few species which can survive in salinities ranging between 5 and 7 psu (WÆRN 1952; HÄLLFORS & al. 1981; RUSSELL 1985, 1988).

Seasonal changes in macroalgal vegetation have been documented widely (MATHIESON 1989; MURRAY & HORN

1989). In addition to seasonal changes in the occurrence and dominance of species, their reproduction is often limited to a certain period of the year. Reproductive seasonality has been found both in the tropics and at high latitudes, and reproduction of a species is thought to be generally concurrent with its period of active growth (HOFFMANN 1987). However, it has also been proposed that the optimum conditions for the growth of thalli and settlement of propagules may not be identical. Successful recruitment of juveniles does not only depend on propagule production and release, but also on the availability of resources for the settling juveniles (SANTELICES 1990). Seasonality of reproduction may be an adaptation for utilising surfaces available only during certain periods of the year (DAYTON 1975; OJEDA & SANTELICES 1984; KENNELLY 1987) and this period may not necessarily be favourable for growth.

In this study, the seasonal nature of the occurrence of filamentous algal species is documented together with their reproductive seasonality. These data are used to outline their life strategies and to evaluate the response of the filamentous algal community to variations in their physical environment.

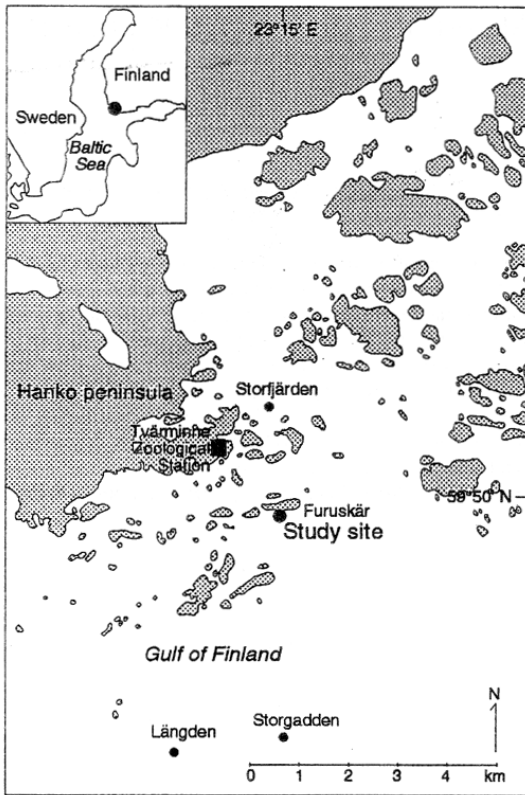


Fig. 1. The study site in the Tvärminne archipelago, northern Baltic Proper.

MATERIAL AND METHODS

Monitoring of macroalgal vegetation

The study was carried out in the Tvärminne archipelago in the northern Baltic Proper. Monitoring of macroalgal vegetation took place on the wave exposed southern rocky shore of island Furuskär (Fig. 1). Effective Fetch, an exposure index of the shore is 50 km. Effective Fetch describes the average distance in which a wave can collect energy before it meets a shore (HAKANSON 1981). A comprehensive description of the hydrography of the study area can be found in NIEMI (1973).

Monitoring of macroalgal vegetation was conducted with 16 permanently marked 40 x 40 cm sample plots. The sample plots were organised into four groups of four replicate plots. They were situated at depths of 0.2 m, 3.0 m, 6.0 m and 8.0 m, relative to the average sea level, covering the whole depth range of the macroalgal vegetation of the shore (Fig. 2). The sample plots were inspected on average once a month for 3 years, 1992-1995. Algal samples were collected regularly to verify the identification of species. Access to the sample plots necessitated scuba diving, because the Baltic Sea is practically tideless and the sampling sites were permanently submerged. Diving times in waters which, for most of the year, are between 0 and 10 °C are constrained by coldness. As the effective diving time in cold water is around 30 min with a

conventional dry suit, all time-consuming methods for estimating cover (MEESE & TOMICH 1992) were out of the question. For that reason a simple visual percent cover estimate (scale: 1, 2, 3, 5, 7, 10, 15, 20, 30, 40...100 %) was used. In addition, the average canopy height of the species was estimated during the two last years. Visual cover estimate is the quickest method for the description of vegetation, but it is unreliable especially when estimates of several workers are used in the same data set (BAKER & LITTLE 1989). This problem was avoided by using the same estimator, the first author, throughout the study. However, worker variability is not the only problem which plagues this method. Visibility and light conditions may affect the estimate. To provide a reference for each estimate, the results of the previous investigation were available underwater on a waterproof piece of paper. Thus, every coverage estimate is based on a comparison of the previous coverage value with the present vegetation. This had the effect of providing more consistent data, making detection of any changes more conservative and decreasing the amount of variation caused by the estimation procedure.

Monitoring of settlement

The timing of propagule settlement was determined by using a sequence of regularly exposed artificial substrates, concrete blocks of 40 x 40 cm, on which new recruits were observed (Fig. 3). In summer, a new block was added to the set every week and in winter every month. The 'old' blocks were inspected every time a new block was added and algal samples were collected regularly to verify the identification of species. Both the cover and the canopy height of a species were estimated. The concrete blocks were fixed at a depth of 1.5-2.0 m, at the border of short lived and perennial parts of the vegetation, where most algal species were present (KIIRIKKI 1996b). This part of the study was carried out only during the last of the three years (1994-1995).

The present method allows the exact determination of the end of a settlement period, as a species cannot enter an artificial substrate which is exposed when its propagules are no longer available. The beginning of the settlement has to be evaluated, as a species can occupy substrates exposed during its period of settlement as well as older ones. The principle used to evaluate the beginning of settlement is demonstrated in Fig. 3. If the reproductive period of a species lasts e.g., for one month, the algae settled at the end of the period are younger than the ones settled at the beginning of the period. This can be seen as a decrease in their size towards the newer substrates. All the substrates which were present when the settlement started were colonised simultaneously and therefore algae growing on them are of the same size. Thus the beginning of settlement has occurred at the point where the size of the algae does not increase any more with the exposure age of substrates.

Search for microscopic epi- or endophytic stages

The only large algal species in the northern Baltic Proper is *Fucus vesiculosus* L. It may offer a favourable habitat for microscopic stages of some filamentous algae. On 10 August 1995, stipes of 10 *Fucus* individuals representing different size classes

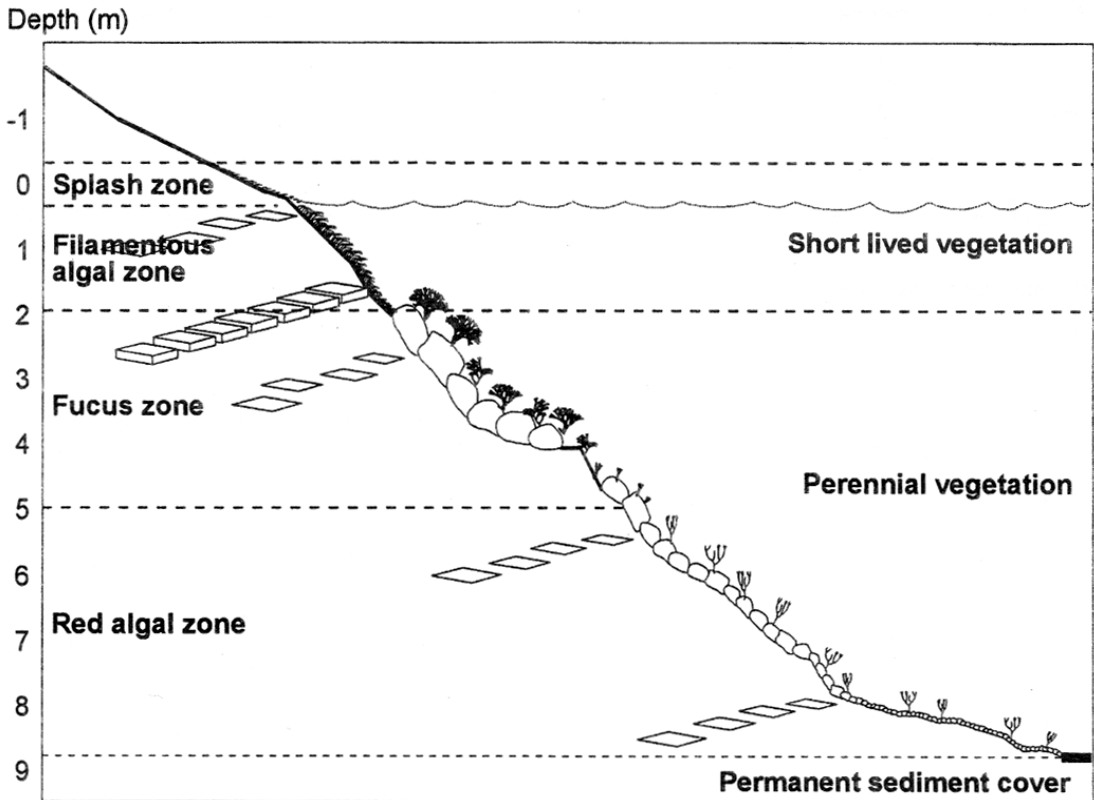


Fig. 2. Zonation of macroalgal vegetation on July 1994 in the study site, Tvärminne archipelago, northern Baltic Sea. Approximate location of the permanent sample plots is indicated by the skewed squares and the artificial substrates by skewed blocks. See also the zonation terminology of DU RIETZ (1930), WAERN (1952) and HÄLLFORS & al. (1981).

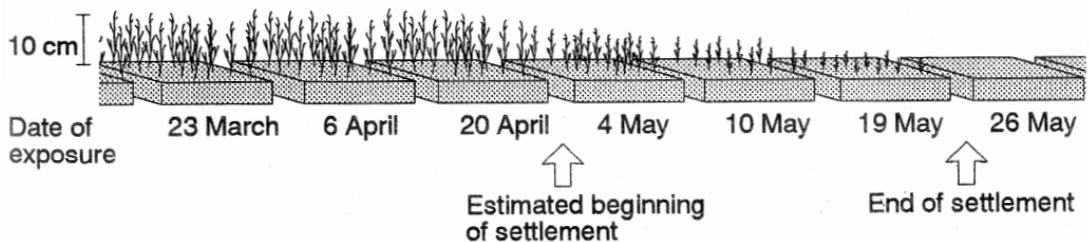


Fig. 3. Experimental set-up used to determine the reproductive seasonality of macroalgae. A new substrate was added to the set-up once a week in summer and once a month in winter. The figure describes part of the set-up on 6 July 1995. The algae growing on the substrates were *Dictyosiphon foeniculaceus*. The reproductive period of *D. foeniculaceus* had ended between 19 May and 26 May, because the last individuals were found on the substrate exposed on 19 May. These last settled individuals were only 2 cm high. The size of the algae grew towards the older substrates and the largest 10 cm high individuals were found on the substrates exposed on 20 April or before. The similar size of algae on these older substrates indicates that they were colonised simultaneously, which means that the period of propagule settlement had begun between 20 April and 4 May.

and growing depths were collected in the study area. The stipes were surface sterilised for 1 min in 100 % ethanol and rinsed 5 times in autoclaved sea water. The stipes were chopped into 2 mm thick disks, which were placed in tissue culture bottles filled with nutrient rich autoclaved culture medium (HÄLLFORS

& HÄLLFORS 1992) and incubated in a culture room at +15 °C, with 12:12 h light for 2 months. The algae - culture medium ratio was 1 disk per 5 ml. During the culture period all macroscopic thalli originating from *Fucus* discs were identified.

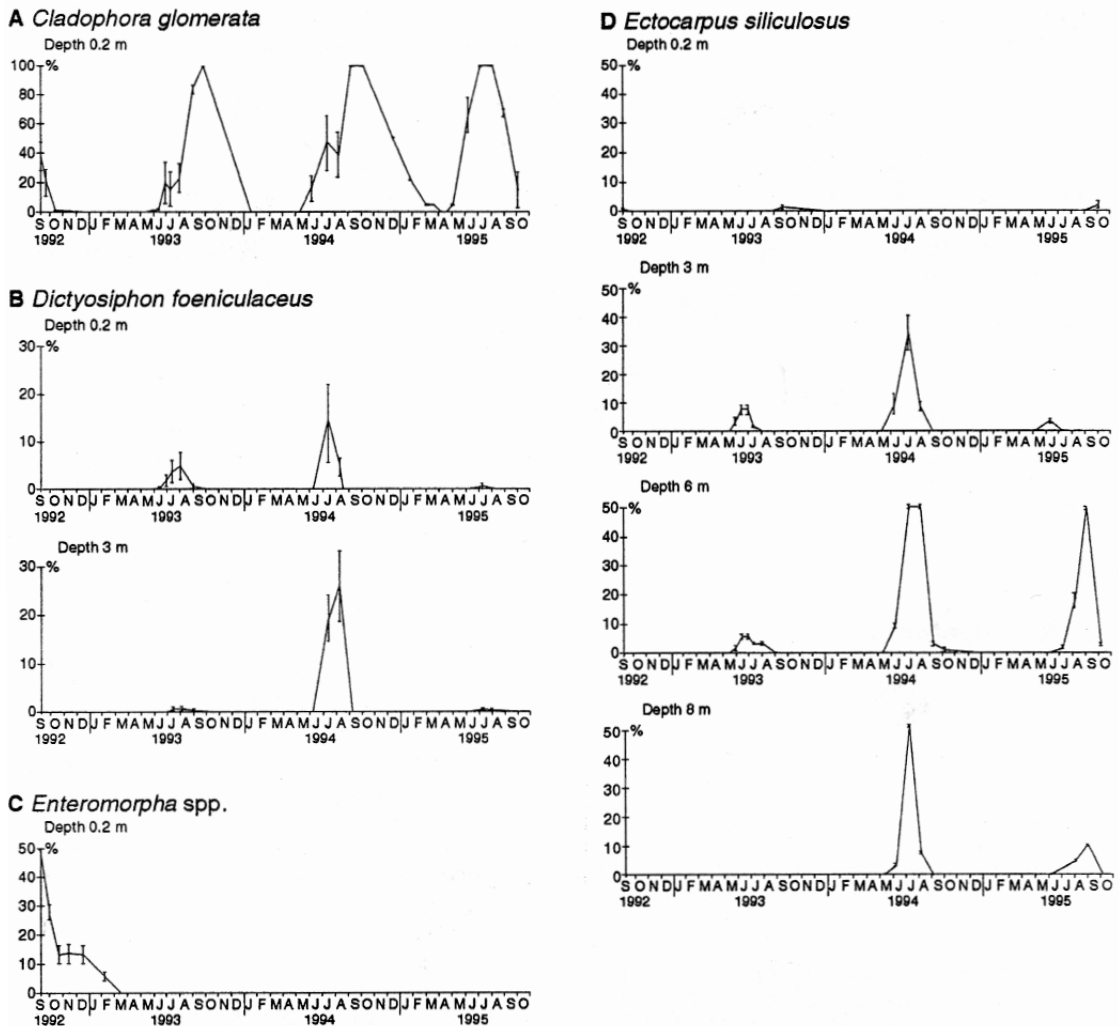


Fig. 4A-D. Cover fluctuations of filamentous algae in the northern Baltic Proper. Cover was monitored at four depth levels (0.2, 3, 6, 8 m) for three years. Variation of four replicate sample plots is given as a standard deviation.

RESULTS

Cladophora glomerata (L.) KÜTZ. (Figs 4A; 5)

Cladophora glomerata was the dominant species of the filamentous algal zone. It started to grow in May when the surface water temperature was rising fast. The first individuals appeared from small crevices and fissures of the ice-scraped rock surface. Within a few weeks, a more or less continuous canopy covered the filamentous algal zone. In July, the overwintered generation started to degenerate. Settlement was observed from late May to the end of August. There was a clear difference in the intensity of settlement between 1994 and 1995. In

1994 the artificial substrate exposed on 3 August had 6 weeks later a *Cladophora* cover of 50 %. In 1995, the *Cladophora* cover for a similar case was only 1 %.

Dictyosiphon foeniculaceus (HUDS.) GREV. (Figs 4B; 5) Settlement of *Dictyosiphon foeniculaceus* propagules was observed from the end of April to late May. The source of these propagules has to be a microthallus, because no macroscopic forms had been seen since the previous August. The propagules grew to a macrothallus which became visible at the end of May or beginning of June, only a bit later than the first filaments of *Cladophora*. The share of *Dictyosiphon* in the

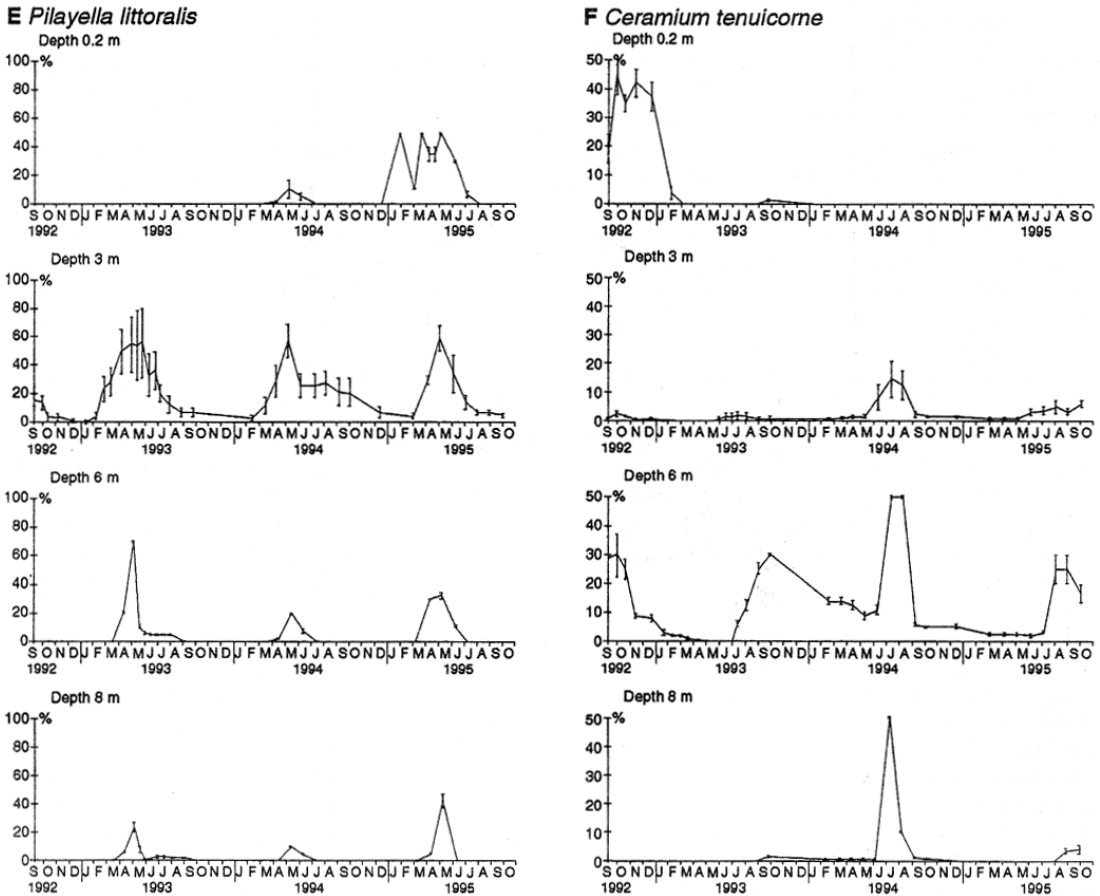


Fig. 4E-F. Cover fluctuations of filamentous algae in the northern Baltic Proper. Cover was monitored at four depth levels (0.2, 3, 6, 8 m) for three years. Variation of four replicate sample plots is given as a standard deviation.

filamentous algal zone was highest in summer 1994 after the most severe winter, and lowest in 1995 after the mildest winter of the study period. The maximum annual cover was reached on average in July when the thalli were densely covered by unilocular sporangia. A short and weak second settlement period was observed in mid July. It is not clear whether these propagules originated from the overwintered microthalli or from the unilocular sporangia of the first summer generation. The degeneration of *Dictyosiphon* thalli was fast in late summer and the last thallus remnants were seen in late August. *Dictyosiphon* was also found as an epiphyte of *Fucus vesiculosus* L., where it showed similar seasonality as in the filamentous algal zone.

Enteromorpha spp. (Figs 4C; 5)

Because of the uncertain taxonomic status of the Baltic *Enteromorpha* species, all observations are treated to-

gether as *Enteromorpha* spp., though most of the plants resembled *Enteromorpha intestinalis* (L.) LINK. *Enteromorpha* was found in the sample plots of the filamentous algal zone (0.2 m) only in the first autumn (1992). The occurrence of *Enteromorpha* coincided with a high cover of *Ceramium tenuicorne* (KÜTZ.) WAERN and *Fucus* plantlets in the same zone. Outside the sample plots *Enteromorpha* was commonly found in adjacent rock pools throughout the year. Propagule settlement occurred during August and September. Single *Enteromorpha* individuals were also observed to emerge from surface sterilised *Fucus* disks.

Ectocarpus siliculosus (DILLW.) LYNGB. (Figs 4D; 5) *Ectocarpus siliculosus* was mainly an epiphyte of *Fucus* and the perennial red algae *Furcellaria lumbricalis* (HUDS.) LAMOUR. and *Phyllophora* sp. *Ectocarpus* appeared at the beginning of June reaching its maximum

cover in July or August. Propagule settlement was observed only in 1995, when it started at the end of June and continued till late September. The summer generation was found to grow sparsely in the filamentous algal zone in September, but no new individuals were found on *Fucus* or perennial red algae. When surface sterilised disks of *Fucus* were taken to cultivation in August 1995, a dense covering of *Ectocarpus* filaments appeared. Thus, it seems obvious that the new generation lives and overwinters as an 'microthallus' (RUSSELL 1983) without any macroscopic emergent filaments. This microscopic stage starts to produce macroscopic epiphytic filaments at the beginning of the following summer.

Pilayella littoralis (L.) KJELLM. (Figs 4E; 5)

Pilayella littoralis grew both on rock surfaces and as an epiphyte of perennial species, especially *Fucus*. It started to grow as early as in February. Maximum cover was reached at the beginning of May and degeneration and detachment of filaments occurred during late May and June. A second growth period was observed in September-October. This growth was only a slight increase in the length of the filaments, and it did not increase the cover values. *Pilayella* was found throughout the year only in the *Fucus* zone, where it remained on the rock surface below thick *Fucus* bushes during late summer and autumn. In the filamentous algal zone, the occurrence of *Pilayella* was highly variable. Maximum cover was reached in spring 1995 after an almost ice free winter and a spring without distinct periods of low sea levels.

Propagule settlement was observed in winter from late September till at least mid December. The artificial substrate of January was lost in a storm and it is not certain when the settlement ended. However, no settlement was observed on the artificial substrate exposed at the beginning of March. Nor were any new recruits found during spring when practically the whole studied zone was covered with *Pilayella*.

Ceramium tenuicorne (KÜTZ.) WAERN (Figs 4F; 5)

Ceramium tenuicorne was primarily an epiphyte of *Fucus vesiculosus*, *Furcellaria lumbricalis* and *Phyllophora* sp. It also grew occasionally on rock surfaces in the filamentous algal zone, where high cover was observed only in autumn 1992. This happened simultaneously with high cover of *Enteromorpha* and *Fucus* plantlets.

Ceramium overwintered as a macroscopic plant, but the cover of this overwintering generation varied considerably between years. The highest cover of overwintered epiphytic plants was observed in spring

1994 after a severe winter with long lasting ice cover. *Ceramium* started to grow in May or June and the highest cover was reached in July-August. Propagule settlement was observed only in 1995, when it started in mid July and lasted for approximately one month. No recruitment was observed in 1994 on the artificial substrates. However, at the beginning of August 1994 young recruits were found commonly growing on the apices of *Fucus*.

Overwintered and summer generations were clearly distinguishable from each other when they grew as epiphytes of *Fucus*. At the beginning of August the overwintered generation was degenerating fast and the summer generation had just appeared. These two generations inhabited different parts of the canopy, the summer generation the apices of *Fucus* whereas the overwintered plants grew deeper inside the canopy. *Ceramium* was able to creep and attach to neighbouring perennial algae, with the help of its rhizoids. Large individuals were often attached to several host algae or adjacent branches of the same alga and the original holdfast was difficult to find.

DISCUSSION

Seasonality of reproduction

The filamentous algae of the northern Baltic Proper have short reproductive periods. The length of a period of successful propagule settlement varied between 4 and 10 weeks. In late summer and autumn, several species had their propagules simultaneously in the water mass and interspecific competition for free surfaces was obvious. This probably caused the lack of observed recruitment, primarily of the epiphytic species *Ectocarpus* and *Ceramium* in summer 1994, when the recruitment of the dominant species *Cladophora* was highly successful. In winter and spring only one filamentous algal species was reproductive at a time. This observed pattern of the reproductive seasonality of the northern Baltic Proper filamentous algae is in good agreement with the conclusions drawn by HOFFMANN (1987): In cold temperate regions fertility tends to be restricted to summer and early autumn.

In the set of species studied, propagule release occurred during or just after the period of active growth in four species: *Ceramium tenuicorne*, *Cladophora glomerata*, *Ectocarpus siliculosus* and *Enteromorpha* spp. The most conspicuous disparity between growth and successful reproduction was observed in *Pilayella littoralis*. It showed rapid growth in early spring, degeneration and detachment of filaments in May, survival of its basal parts in summer and reproduction in the winter. *Pilayella* also produced sporangia in spring,

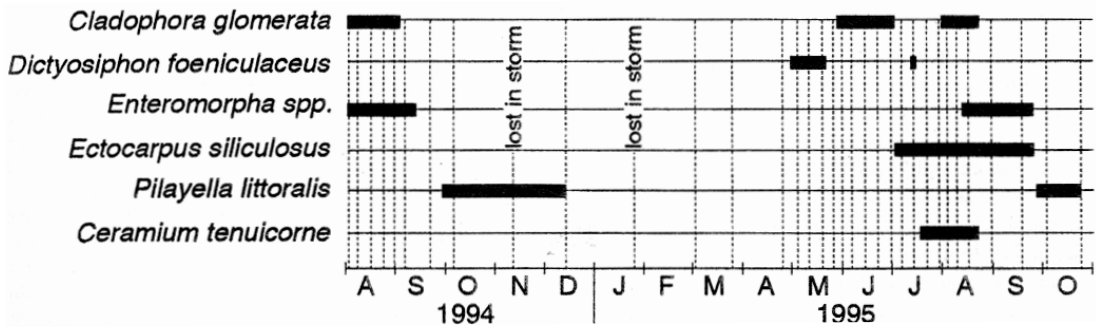


Fig. 5. Reproductive seasonality of filamentous algae in the northern Baltic Proper. Periods of propagule settlement on artificial substrates are indicated with black bars and the dates when artificial substrates were exposed with vertical hatched lines.

but no settlement and recruitment was observed even though practically no competing propagules were present at that time. This unsuccessful reproduction and rapid simultaneous detachment of filaments during the generally calm month of May raises an idea that it might be caused by an external physical or chemical factor. It is possible that *Pilayella* is not completely adapted to the eutrophic and estuary-like environment of the young Baltic Sea.

Green and brown algal years?

The observed variations in the cover of *Cladophora glomerata* and *Dictyosiphon foeniculaceus* in the filamentous algal zone fit well to the concept of green and brown algal years introduced by Wærn. After average winters with ice cover and ice scraping, these species compete for the dominance in the filamentous algal zone. The results of this competition depend on their individual overwintering strategies and winter conditions.

Ageing *Cladophora* filaments start to produce thick-walled resting spores, akinetes in autumn (ROSEMARIN 1985). These unicellular stages attach to rock surfaces and can survive at least moderate ice scraping in fissures of the rock surface. *Dictyosiphon* survives the unfavourable season with the help of its microscopic filamentous generation. This microthallus produces plurilocular sporangia at low temperatures 0–8 °C and a rise of temperature in spring is the stimulus needed for release of propagules (PETERS & MÜLLER 1985). The habitat of this microthallus is not known, but as a multicellular organism, it probably survives only in fissures or below the ice scraped zone.

The intensity of ice scraping together with the texture of the rock surface determines the proportion of these species in the vegetation. *Dictyosiphon* recruits

can be found only on the most intensively ice scraped smooth surfaces or as a separate zone above *Cladophora*, where periods of low sea level have killed the overwintering akinetes in winter (KIIRIKKI 1996b). These two species utilise microscopic stages for overwintering. It has been proposed that these kinds of stages may form a 'seed bank' of an alga like the buried seeds of land plants (HOFFMANN & SANTELICES 1991, SANTELICES & al. 1995). These seed banks of microscopic forms seem to be important for species inhabiting the hazardous filamentous algal zone.

Ice free winters

Only the winter 1991–1992 preceding the three-year monitoring study was completely ice free in the present study area. When the sample plots were first visited in September 1992, the vegetation in the filamentous algal zone differed clearly from the following three autumns. In addition to the dominant species *Cladophora glomerata*, also *Enteromorpha* spp. and *Ceramium tenuicorne* were present with high covers. Furthermore, small recruits of *Fucus vesiculosus* grew sparsely among the filamentous species. It is not evident whether the *Enteromorpha* and *Ceramium* were overwintered plants or recruits of the same year. However, at least the recruits of *Fucus* in the filamentous algal zone have been connected to ice free preceding winters (RÖNNBERG & al. 1992).

It is possible that ice free winters make the overwintering of scraping intolerant species more successful, leading first to a filamentous algal community of higher diversity. In the case of several successive ice free winters, *Fucus vesiculosus* starts to invade the filamentous algal zone (WALLENTINUS 1979) and controls the filamentous algae by its whiplash effect (KIIRIKKI 1996a).

Epiphytes of perennial species

The main summer epiphytes *Ectocarpus siliculosus* and *Ceramium tenuicorne* differ in their strategy for overwintering. *Ectocarpus* stays the whole autumn and winter hidden as a microthallus (RUSSELL 1983) growing epi- or endophytically in the thalli of *Fucus*. This is again an example of a 'seed bank' which helps a species to survive the unfavourable season. *Ceramium* lacks the ability to establish a seed bank and it overwinters as macroscopic filaments. In winter, *Ceramium* filaments are vulnerable to the force of storms and this may explain the high variation in the numbers of their overwintering filaments. The severe winter of 1993-1994 with its long lasting ice cover was most favourable for overwintering. Probably ice cover sheltered the epiphytes from the effects of the winter storms. In summer, the reverse is true. The robust filaments and several attachment points of rhizoids help the basal parts of *Ceramium* to survive wave action. Summer gales often detach complete *Ectocarpus* individuals from their single attachment point (KIIRIKKI & BLOMSTER 1996).

Influence of sediment cover

The Baltic Sea has become increasingly eutrophic over the last decades. The spring diatom blooms are getting more intense, which can be seen as a decreasing trend in dissolved silicate (NIEMI & ÅSTRÖM 1987; RAHM & al. 1996). Most biomass produced during the spring bloom is not consumed in the water column and it sediments out during early summer (HEISKANEN & LEPPÄNEN 1996). Thus the increased primary production has been proposed to increase sedimentation (CEDERWALL & ELMGREN 1980; ELMGREN 1989).

Even small amounts of sediment on a hard substrate greatly reduces the settlement success of macroalgal propagules (DEVINNY & VOLSE 1978; NORTON 1978). It has been proposed by KANGAS & al. (1982) that there may be problems in the reproduction of *Fucus vesiculosus*, when sediment cover is abundant over rocky surfaces. It seems possible that increase in summertime sediment cover could induce changes in the composition of the macroalgal vegetation by benefiting species which release their spores in autumn and winter, when storms clean the rock surfaces of loose sediment. A shift from *Fucus* dominated bottoms towards the dominance of *Pilayella* has already been reported by several authors (HÄLLFORS & al. 1984; MÄKINEN & al. 1984; JUMPPANEN 1992). *Fucus* reproduces in May and June (BÄCK 1993; ANDERSSON & al. 1994) when sediment cover is high and *Pilayella* in October-December when the sediment cover is minimal.

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