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Phenology of *Ceramium tenuicorne* in the SW Gulf of Finland, northern Baltic Sea

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The occurrence of *Ceramium tenuicorne* in the SW Gulf of Finland seems to be determined by physical factors, species competition and adaptation to the seasonal environment of the northern Baltic Sea. Due to the strong competition, in the upper sublittoral *C. tenuicorne* grew mainly epiphytically. Asexual plants were most common around the year. In July–August tiny *C. tenuicorne* was found also in the upper sublittoral. At that time plants with cystocarps, tetrasporangia and propagules were observed. In October, after the decline of *Cladophora glomerata*, a nap-like belt of *C. tenuicorne* grew at depths of less than one metre and a short-lived female generation with cystocarps was observed. In late autumn, most of the filaments close to the shore break down due to wave action, and in winter due to the ice scraping while deeper growing individuals are perennial. *Ceramium tenuicorne* is physiologically adapted to the extreme environment of the Baltic Sea. Photosynthetic pigment content of *C. tenuicorne* exhibit seasonal changes. The higher winter values of pigments can be considered an adaptation to an extreme environment, caused by low light. In summer, pale individuals with red basal parts grew at 1–2 m depth, having grown from old, overwintered basal parts. The pale colour is due to low concentrations of phycoerythrin. The fastest growth occurs in late spring, and in summer months the individuals are tall, the cells are long, and the number of secondary branches is exceptionally high. The cortical cells of many individuals grew upwards in the older parts of the thallus. The form of the cells was often conical, but some individuals with oval cells were observed.

Key words: *Ceramium*, morphology, pigments, production, reproduction

Introduction

The taxonomic status of Baltic *Ceramium* was discussed earlier (Wallentinus 1979). Waern (1952) classified northern Baltic *Ceramium* species as *Ceramium tenuicorne*, which he considered to be widespread in the entire Baltic Sea. This name was used until Waern (1992) himself proposed that there were actually two species in the Baltic Sea, *C. tenuicorne* being confined to the southern Baltic and *C. gobii* occurring in the low-salinity northern Baltic. Nielsen *et al.*

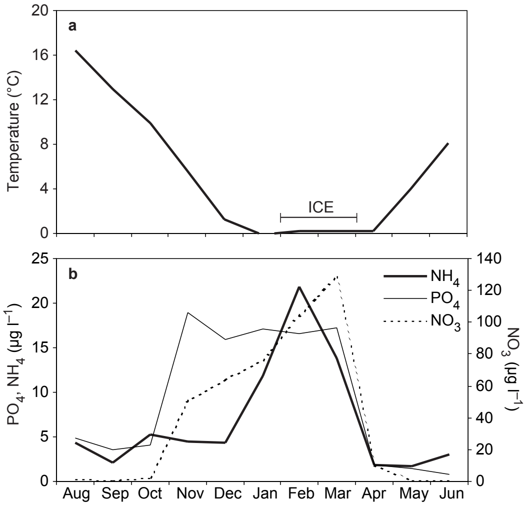

Fig. 1. (**a**) Temperature and (**b**) nutrient concentrations at Furuskär during the study period 1992–1993. Data obtained from Särkelä (1995). PO_4-P concentration of phosphate-phosphorus, NH_4-N concentration of ammonium-nitrogen, NO_3-N concentration of nitrate-nitrogen.

(1995) used the latter name with the remark that "further investigations are necessary to clarify the taxonomic status". However, Gabrielsen *et al*. (2002) showed that the parasporangia that Waern (1992) proposed to be the "*gobii*" type are actually propagules. In her molecular study, she demonstrated that *C. gobii* is a form of *C. tenuicorne*.

The morphological characteristics that were used to segregate *Ceramium tenuicorne* were as follows: the propagules are unilocular, terminal monosporangium-like structures, and the branching is regular and (pseudo)dichotomous, and also secondary branches are produced.

In the Baltic Sea, *Ceramium tenuicorne* is reported to be a common and abundant species. Its distribution covers an area with salinity varying between 3‰ and 8‰ (Nielsen *et al*. 1995). *Ceramium tenuicorne* colonises rapidly and withstands wave action. It can occur in lower parts of the hydrolittoral zone (Waern 1952, Leskinen *et al*. 1992). *Ceramium tenuicorne* occurs commonly on other macroalgae, higher plants, and *Mytilus trossulus*. It may extend even down to 9–15 m depth (Waern 1952, Ravanko 1968, Wallentinus 1979). *Ceramium tenuicorne* thrives in the upper sublittoral where it grows on rocky bottoms, stones and pieces of wood (Waern 1952, Ravanko 1968, Kiirikki & Lehvo 1997).

The aim of this work was to evaluate the influence of northern Baltic winter conditions on the survival of *Ceramium tenuicorne* by determining its phenology, e.g. its seasonal occurrence and changes in morphology and photosynthetic pigments.

Material and methods

The study site was at Furuskär, which is located in SW Finland in the archipelago of Tvärminne, off the Hanko peninsula (59°50´0´´N, 23°16´3´´E). The gently sloping rocky shore of Furuskär represents a typical habitat for *Ceramium tenuicorne*. The species was collected monthly from August 1993 until August 1994 from 3-m depth by SCUBA diving. Observations and collections were made simultaneously in the hydrolittoral zone and at 6-m depth. During the study period, the sea water temperature was close to zero in November–March; during the summer months it could rise up to 16.5 °C (Fig. 1a).

The nutrient concentrations of the seawater were measured twice a month during the whole sampling period. All the analytical methods are adopted from Grasshoff (1976). Nutrient measurements were based on a single sample and were carried out in the same week as sampling. From August to October, the inorganic nitrogen and phosphorus concentrations were low (NO_3-N < 1 μg l^{-1}, NH_4-N and PO_4-P < 5 μg l^{-1}; Fig 2b). From October till the beginning of February, the concentrations of ammonium-, and especially nitrate-nitrogen, increased evenly. At the beginning of February, the concentration of NO_3-N was high, about 100 μg l^{-1}. The concentration of phosphate-phosphorus increased in November to 16 μg l^{-1}. After formation of the ice cover in the beginning of February, nitrate and ammonium concentrations continued to increase but they started to decrease already in March 1994 (Fig. 1). Ice melted at the end of March and inorganic nitrogen and phosphorus concentrations decreased rapidly close to the detection limit of 1 μg l^{-1} (Särkelä 1995).

In autumn and winter, sampling of *Ceramium tenuicorne* was carried out once a month and in spring and summer at two-week intervals. A SCUBA diver collected several tufts of *C. tenuicorne* from each depth into a netsack, which was transported back to the laboratory in seawater-filled containers. For the study of the reproductive stage, production and morphological studies, the algal samples were stored at +10 °C in aerated seawater and measurements were carried out 24 hours after sampling.

The material was sorted and thalli were microscopically studied to check their reproductive status. Seasonal changes in the morphology of *Ceramium tenuicorne* were studied by measuring the length of the individuals and the axial cells. Also the main branches of the thalli were counted. The length of the cells was taken as an average of ten cells in the middle part of the thalli and length of the individual was taken as an average of five thalli. The cells were measured with Wild M20 microscope with an ocular at 100× magnification.

Chlorophyll *a* and phycobiliproteins (phycoerythrin and phycocyanin) were determined spectrophotometrically (in triplicates: 0.1–0.5 g algae) from the frozen apical material. Phycoerythrin and phycocyanin were determined according to Beer and Eshel (1985). The concentration of chl *a* was measured with a modification of Kuosa (1991). The samples were homogenised in 5 ml of 98% ethanol and were left in the dark at room temperature for 12–24 h. After extraction, the samples were centrifuged once with a table centrifuge (Heinz Janetzki Type T12) at 3500 rpm for 15–21 min. The absorbance was measured at 0.5 nm intervals at wave lengths of 664–666 nm. The chlorophyll concentrations were calculated as mg chl *a* (g fw)$^{-1}$ according to the formula

$$C = vD_{664\text{–}666}/83.4lm$$

where C = chl *a* (mg g^{-1} fw), v = volume of ethanol (ml), D = max absorbance at wavelengths of 664–666 nm, l = the length of the cuvette (cm), m = fresh weight of the sample (g fw).

Statistical analyses were performed to reveal the differences in plant length, cell length and concentrations of photosynthetic pigments (chl *a*, phycoerythrin and phycocyanin) between the summer and winter months. Winter and summer averages of plant length, cell lenth, phycocyanin and phycoerythrin were compared using a contrast analysis after analysis of variance (error d.f. = 48, 48, 17, 17 respectively). The tests were performed with STATISTIX ver. 2.

Results

In summer *Ceramium tenuicorne* grew between 1- and 6-m depths, mainly being epiphytic on *Fucus vesiculosus* and *Furcellaria lumbricalis*. At 1 m depth, the dominant species was *F. vesiculosus*, and from 3 m downwards *F. lumbricalis*. Some *C. tenuicorne* individuals were also found growing on rocks. At greater depths *C. tenuicorne* also grew on *Phyllophora* sp. and *Mytilus trossulus*. From 9 m downwards, the substratum is sandy. At the beginning of the summer, the population of *C. tenuicorne* was abundant at 1- and 3-m depths. In the middle of the summer, at 1-m depth *Cladophora glomerata* and *Ectocarpus* sp. apparently competed for space with *C. tenuicorne*. *Ceramium tenuicorne* was especially abundant in autumn at 3-m depth.

During the winter, the species was most abundant and grew most strongly at 6 meters. In February and March, ice cover prevented sampling near the shore. Ice was not likely to remove all the algae at a depth of 1 metre, because as early as in April, right after the ice break, there was a vibrant population of *Ceramium tenuicorne* growing at that depth.

Most of the time *Ceramium tenuicorne* was in asexual stage. Even though the sampling was performed twice a month at different depths, not earlier than in July were female gametophytes with cystocarps found to grow only as an epiphyte on *Fucus vesiculosus* receptacle (Fig. 2). A gametophyte generation with cystocarps grew in upper part of the shore also in late September and early October. Propagules and plants with tetrasporangia were observed also in July. Despite intensive sampling, it could be possible that the male gametophyte is so short-lived that it was not found during this study.

The length of the thalli of *Ceramium tenuicorne* varied from 2 to 8 cm (Fig. 3). The significantly longest individuals were sampled in the beginning and the middle of the summer

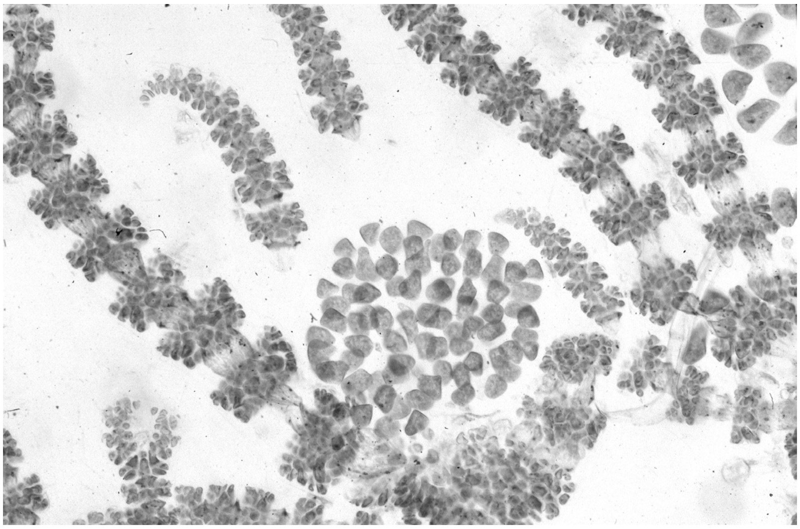

Fig. 2. *Ceramium tenuicorne* with cystocarp. Material collected at Tvärminne in July 1999.

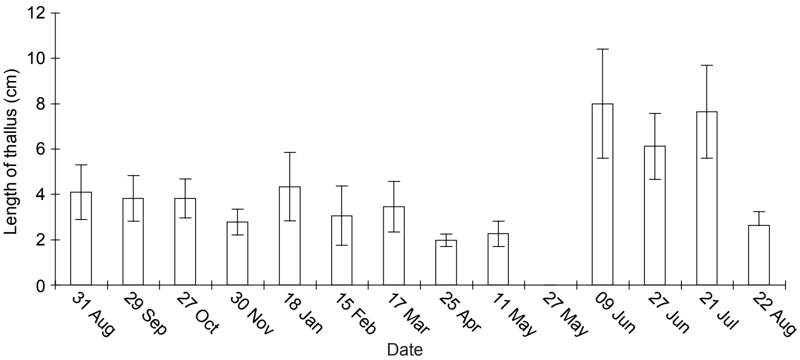

Fig. 3. The length of the thallus of *Ceramium tenuicorne.* The datum of 27 May is missing.

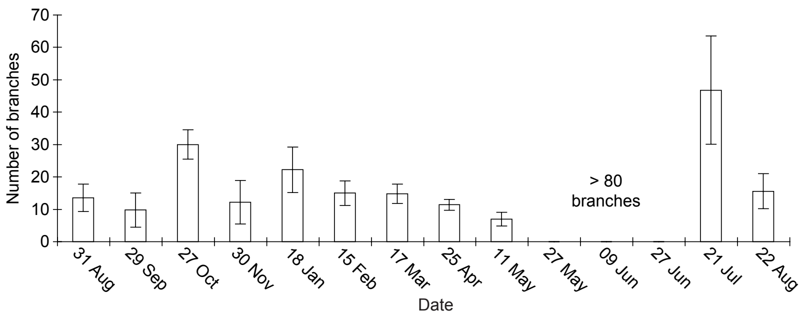

Fig. 4. Change in the number of branches per thallus in *Ceramium tenuicorne*. Between 27 May and 27 June there were numerous secondary branches > 80.

($p < 0.001$). During the other seasons, the length of the thalli varied between 2 and 5 cm. It is difficult to measure the overall length of the individuals, since the thalli were growing in tufts, which are attached to the substrata by rhizoids. Part of the individuals was branched only dichotomously. Most individuals had also secondary branches. These secondary branches were especially abundant in the spring and summer, when the mean number of branches was over 80 (Fig. 4). The axial cells were longer (450 μm) at the end of the summer than in the winter and spring (130–300 μm) ($p < 0.001$) (Fig. 5).

In samples from Furuskär, the cells and cortical bands of many individuals were not clearly distinguishable in winter and early spring. These individuals obviously belong to an old gen-

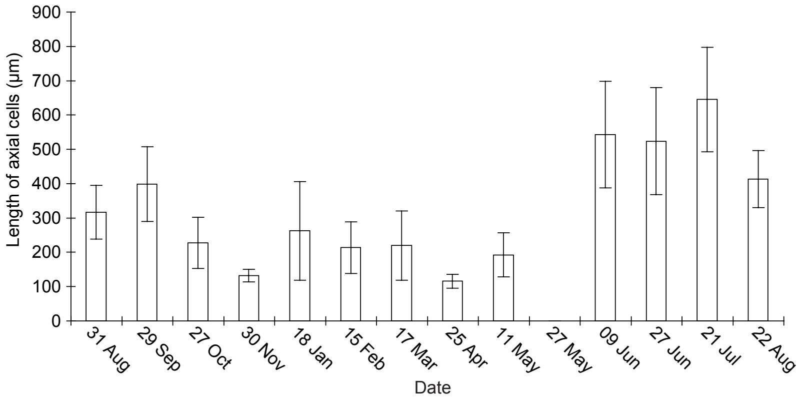

Fig. 5. Length of the axial cells in the middle part of the thallus of *Ceramium tenuicorne*. The datum of 27 May is missing.

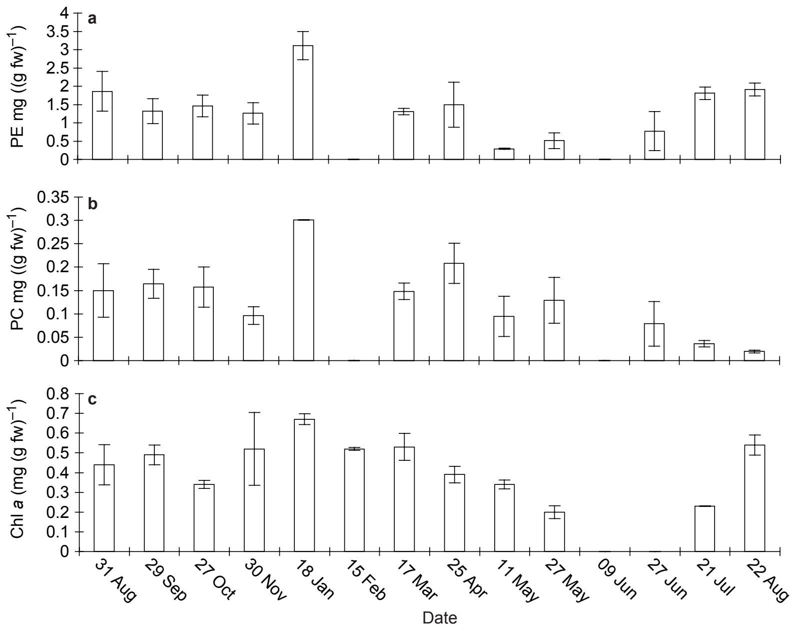

Fig. 6. Concentration of (**a**) phycoerythrin, (**b**) phycocyanin and (**c**) chlorophyll *a* in *Ceramium tenuicorne* in 3 metres depth collected during the study year.

eration. The shape of the cells of *Ceramium tenuicorne* was mainly conical. However, some oval-celled individuals were observed also in Furuskär material. Further, the border of the cortical band was sharp for some individuals and the cortical cells were not growing upwards in the older parts of the thalli, as they typically should in *C. tenuicorne*. In late spring, the individuals of new generation were less heavily covered by epiphytes, and the cells and cortical bands were clearly distinguishable.

The concentrations of phycobilin proteins were higher in autumn and winter than in summer months ($p < 0.001$). The values were highest in January when the concentration of phycoerythrin was about 3.0 mg (g fw)$^{-1}$ (Fig. 6a) and phycocyanin about 0.30 mg (g fw)$^{-1}$ (Fig. 6b). The lowest concentrations of these pigments were measured in spring and the middle of the summer. The phycoerythrin content was then between 0.20 and 1.0 mg (g fw)$^{-1}$, while the concentration of phycocyanin remained below 0.10 mg (g fw)$^{-1}$. In the autumn the concentration of chlorophyll *a* was between 0.33 and 0.50 mg (g fw)$^{-1}$, and increased in January to 0.68 mg (g fw)$^{-1}$ (Fig. 6c). During the spring, the chlorophyll content decreased almost linearly towards the minimum of 0.20 mg (g fw)$^{-1}$ in May. At the end of August, the concentration of chlorophyll increased again to 0.50 mg (g fw)$^{-1}$.

Discussion

In the archipelago of Tvärminne, the zonal occurrence of *Ceramium tenuicorne* (0.5–6 m) is very similar to that reported from other areas (Waern 1952, Ravanko 1968). In Furuskär, a tiny and nap-like cover of *C. tenuicorne* grew as little as 20 cm below the water line in the autumn (Kiirikki & Lehvo 1997). Hence, under favourable conditions, *C. tenuicorne* survives also in the upper part of the hydrolittoral. Waern (1952) observed *C. tenuicorne* to grow mainly as an epiphyte of *Fucus vesiculosus* in low water, and deeper as an epiphyte of *Furcellaria lumbricalis*. Bäck *et al*. (1993) observed *C. tenuicorne* often to be widespread, and usually green in colour close to the water line in the autumn.

In spite of the ice cover that strongly reduces light penetration, *Ceramium tenuicorne* occurred also over winter. During winter 1993–1994, the long-lasting ice cover sheltered *C. tenuicorne* from winter storms (Kiirikki & Lehvo 1997). *Ceramium tenuicorne* may also have overwintered as short basal parts. According to Dixon (1960), many species in the genus *Ceramium* may decline into a fragment consisting of only a few cells. In spring, new individuals develop from these fragments. Kiirikki and Lehvo (1997) reported that epiphytic *C. tenuicorne* was most abundant in July at 6 m as an epiphyte of *Fucus*. Old individuals of *C. tenuicorne* grew on the lower parts of the host, while the young individuals were found on the apical parts.

In Furuskär, the individuals at 3-m depth were as tall in the winter as those in the autumn. The tallest individuals were found in the beginning and middle of the summer. The larger size of the individuals was apparently due to an increase in cell numbers, as well as an increase in cell size. In favourable growth period in summer the temperature of the seawater was 10–15 °C, and the intensity of light was high; the nutrient concentrations, however, were low. The tall individuals in the summer grew epilithic and had many secondary branches. These branches are formed during the time of strong growth.

The observations by Waern (1952) that the asexual plants of *Ceramium* form a bulk of the population in all seasons are confirmed in this study. In Furuskär small and delicate female plants were found only in July and most of the time *C. tenuicorne* was in vegetative stage. Sampling was frequent and there is not any particular reason that male plants were not found, even though they are smaller than female plants (Waern 1952).

In Furuskär (salinity of 5.5–6 PSU) the cell length was only 100–700 μm. These values are lower than those reported in Sjöstedt's (1928) study, in which the length of the cells of *Ceramium tenuicorne* varied between 300 and 1000 μm in late summer in upper sublittoral at the eastern coast of southern Sweden (salinity 7 and 8 PSU). It seems that with decreasing salinity the size of *C. tenuicorne* diminishes, as observed by Waern (1952).

Phycoerythrin is the most abundant (70%) pigment in the northern Baltic *Ceramium tenuicorne*; other pigments are: chlorophyll *a* (about 20%), and phycocyanin (about 10%). The result is very similar to those of Cunningham *et al.* (1990), who found that phycoerythrin accounts for about 60%, and phycocyanin about 10% of the photosynthetic pigments in *Porphyridium cruentum*. Wallentinus (1978) showed that the concentration of chlorophyll *a* is one of the most important factors regulating the production of macroalgae, though she did not mark any relation of the production to the chlorophyll *a* content in *Ceramium tenuicorne*. When comparing the concentration of chlorophyll *a* and production in natural white light, Moon and Dawes (1976) came to the same conclusion with some other red algae.

In the northern Baltic Sea the nutrient content is much higher in winter than in summer months when the nutrients are close to the determination level. Ramus and van der Meer (1983) found that the phycoerythrin concentration of *Grinnellia americana* doubled after nutrient additions. The higher amount of nutrients in the ambient water was likely to have affected the higher concentration of phycoerythrin of *Ceramium tenuicorne*. The phycoerythrin content was highest in January, when the concentrations of ammonium and nitrate were increasing and the concentration of phosphorus had already been at its highest for two months.

The responses of *Ceramium tenuicorne* to the seasonal changes in its habitat in the northern

Baltic Sea are clearly seen in the concentrations of pigments and reproductive biology. *Ceramium tenuicorne* is able to survive even under the ice in nearly complete darkness by increasing the concentrations of pigments. It has both gametophyte and sporophyte generation, which suggests that sexual reproduction takes place. However, it is also able to reproduce vegetatively from the over-wintered old basal parts of the thallus. If the sexual reproduction fails for some reason, those basal parts can be long-lived and act as a stock for new generations.

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